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## ERRATA

- Page 11, line 10 from bottom, for var. *santschii* read var. *santschiellum*.
- “ 11, at end of list of new forms insert *Dorylophila schwabi* (Efulen to Elat, Cameroon), p. 626; and *Ocyplanus kohli* var. *niger* (Mful Aja, Cameroon), p. 627.
- “ 18, first line, for mend read ment.
- “ 21, line 7 from top, for var. *molesta* read var. *molestus*.
- “ 27, twelfth name from top, for *Pseudatta* read *Pseudoatta*.
- “ 39, line 18 from bottom, for *Ecitini* read *Ecitonini*.
- “ 40, line 11 from top, for *Ecitini* read *Ecitonini*.
- “ 52, line 15 from top, for *Cerapachyniæ* read *Cerapachyinzæ*.
- “ 125, lines 15, 16, and 21 from top, insert article “I” before verb “have.”
- “ 125, lines 17 and 19 from top, for *Pheidologetini* read *Pheidologetonini*.
- “ 125, line 22 from top, for *Dacelini* read *Dacetonini*.
- “ 165, line 9 from bottom, p. 167, line 11 from bottom, and p. 168, line 10 from top, for *nossindambo* read *nosindambo*.
- “ 170, line 12 from top, for *Pheidologetini* read *Pheidologetonini*.
- “ 202, line 10 from top, for *okiavoënsis* read *okiavoëense*.
- “ 226, line 8 from top, for *annectans* read *annectens*.
- “ 233, line 3 from top, strike out “*Myrmothrix* (one species, probably introduced).” This species, *C. immigrans* Santschi, is now placed in the subgenus *Dinomyrmex*.
- “ 260, line 20 from top, insert “of” between species and *Myrma*.
- “ 281, line 4 from bottom, for Krober read Kröber.
- “ 316, line 6 from bottom, for extensive read extensile.
- Explanation of Pl. XXII, line 2 from bottom, for emitted read emitted.

BULLETIN  
OF  
THE AMERICAN MUSEUM OF NATURAL HISTORY

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**Article I.—ANTS OF THE AMERICAN MUSEUM CONGO  
EXPEDITION. A CONTRIBUTION TO THE  
MYRMECOLOGY OF AFRICA<sup>1</sup>**

BY WILLIAM MORTON WHEELER

WITH THE COLLABORATION OF J. BEQUAERT, I. W. BAILEY, F. SANTSCHI, AND W. M.  
MANN

PLATES I TO XLV, 47 MAPS, AND 103 TEXT FIGURES

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<sup>1</sup>Scientific Results of the American Museum Congo Expedition. Entomology No. 7.

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## INTRODUCTION

The present volume has grown out of a study of the ants collected by the American Museum Congo Expedition, under the direction of Messrs. Herbert Lang and James P. Chapin, and of a smaller collection made in the same region by Dr. J. Bequaert. The working up of this material has proved to be far from easy, owing to the state of the literature on the African Formicidæ. During the nineteenth century comparatively little work was done on the ants of the dark continent, but during the past two decades, as a result of numerous expeditions and the interest of resident entomologists, Emery, Forel, Santschi, and Arnold, but especially Forel and Santschi, have published a great number of papers dealing with fragments of the Ethiopian fauna. This literature proved to be quite unmanageable until I had carefully catalogued the numerous described species, subspecies, and varieties. After this had been accomplished it seemed best to publish the results as an aid to future students. Getting the catalogue ready for publication, however, was a very annoying task, which I could hardly have undertaken without the assistance of Dr. Bequaert, who patiently verified all the numerous references, added others, and helped in arranging the synonymy and lists of localities. He has also given me the benefit of his expert opinion in regard to many taxonomic details.

Both Mr. Lang and Dr. Bequaert have, in fact, showed such keen and enthusiastic interest in the progress of the work that it seemed advisable to expand it by the addition of other matter of interest not only to the zoologist but to the general public. This, however, required the services of several collaborators. At my request, Dr. F. Santschi kindly undertook to work up the species of *Crematogaster*, a genus to which he has given much attention. A glance at my catalogue of the Ethiopian species will show why I despaired of adequately handling the Congo material of the group. I might have attempted it, if the *Crematogaster* portion of Mr. George Arnold's monograph of the Rhodesian ants had appeared, but the World War had stopped the publication of this important work, so that even in making my catalogue I had nothing to rely on except the confused mess in the existing literature. Mr. Arnold nevertheless sent me some valuable comments on several of the species, together with the following remarks on the genus as a whole: "The genus *Crematogaster* is perhaps the most troublesome of all, and for this there are several reasons. First of all, it is a very large genus, so large that authors get lost in the vast number of described forms and of their collections. Secondly, the species of this genus in Africa are exception-

ally liable to minute variations in all directions even over a very small area (one might almost say 'on a very small number of adjacent trees,' since most of the species are arboricolous), and even within the limits of the same nest. This is a point which can only be properly appreciated by the man on the spot, and is persistently overlooked by the cabinet naturalist. Thirdly, in the separation of species and varieties, too much emphasis has been placed on unreliable characters, such as the length and degree of divergence of the epinotal spines, the strength of the median mesonotal tubercle, and the proportions of the petiole. Lastly, a good deal of confusion is due to sheer carelessness and contempt for exact methods." Other almost equally baffling and disconcerting complexes of forms are presented by *Camponotus (Myrmoturba) maculatus* (Fabricius) and *C. (Myrmotrema) foraminosus* Forel and their numerous subspecies and varieties. My catalogue of these probably has little value except as a record of present taxonomic confusion.

It seemed advisable to include in the work dichotomic tables for the identification of the known genera and subgenera of ants. In constructing these tables I have also been greatly aided by Dr. Bequaert. In drawing up those of the subfamilies Ponerinæ, Cerapachyinae, Dorylinae, and Dolichoderinae, extensive use was made of Emery's fascicles in Wytsman's 'Genera Insectorum.' We have, of course, added brief diagnoses of all the genera and subgenera since published. As the publication of the fascicles on the Myrmicinae and Formicinae was rendered impossible by the German occupation of Belgium, we were compelled to create tables for these two subfamilies from such materials as we could find in the literature and from a study of representative species in my collection. This portion of the tables is, therefore, less satisfactory and may need modification when Emery's account of the Myrmicinae and Formicinae appears.

Among the collections made by Messrs. Lang, Chapin, and Bequaert, there was also considerable material representing portions of the singular plants (myrmecophytes) regularly inhabited by some of the Congolese ants. As Dr. Bequaert, during his sojourn in equatorial Africa, had made many detailed notes and drawings on the relations of ants to plants, he was requested to write an article on myrmecophytism. My colleague, Prof. I. W. Bailey, undertook to study the histology of the plants under discussion and reached such striking and important conclusions, both botanical and zoological, that there could be no doubt about the propriety of including his paper as a portion of the report.

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In addition, the following new names are proposed in this paper:

*Phyracaces santschii* Wm. M. Wheeler, p. 56; for *Phyracaces foreli* Santschi ♀, 1915; not *Phyracaces foreli* Santschi, ♂, 1914.

*Platythyrea cribrinodis* var. *brevidentata* Wm. M. Wheeler, Part VIII; for *Platythyrea cribrinodis* var. *punctata* Arnold, 1915; not *Platythyrea punctata* (F. Smith), 1858.

*Monomorium modestum* var. *smulsi* Wm. M. Wheeler, Part VIII; for *Monomorium modestum* var. *boerorum* Santschi, 1915; not *Monomorium minutum* subsp. *boerorum* Forel, 1910.

*Monomorium salomonis* subsp. *subopacum* var. *santschii* Wm. M. Wheeler, Part VIII; for *Monomorium salomonis* subsp. *subopacum* var. *senegalense* Santschi, 1913; not *Monomorium senegalense* Roger, 1862.

*Æcophylla crassinoda* Wm. M. Wheeler, p. 227; for *Æcophylla brevinodis* Wheeler, 1914; not *Æcophylla brevinodis* Ern. André.

*Polyrhachis militaris* subsp. *cupreopubescens* var. *dido* Wm. M. Wheeler, p. 261; for *Polyrhachis militaris* subsp. *cupreopubescens* var. *argentatus* Stitz, 1910; not *Polyrhachis argentatus* (F. Smith), 1858.

*Protholcomyrmex* Wm. M. Wheeler, p. 162; subgenus of *Monomorium* with *Monomorium rothsteini* Forel as the type.



# I.—ON THE DISTRIBUTION OF THE ANTS OF THE ETHIOPIAN AND MALAGASY REGIONS

BY WM. M. WHEELER

## THE PECULIARITIES OF THE ETHIOPIAN ANT-FAUNA

Owing to the great number of genera and species of ants occurring in Africa south of the Sahara and in Madagascar and the pronounced differences between the two faunas, it will be conducive to clearness if we regard the Ethiopian and Malagasy as representing distinct "Regions," with the limits usually assigned to them by zoögeographers and by the other contributors to the "Scientific Results of the Congo Expedition." For the same reasons, I have listed the Malagasy fauna separately (Part IX). Table I is introduced as a general background for the discussion of the two faunas. It shows the distribution as determined up to date for all the known genera of Formicidæ. A cross is used to indicate the presence; a dot, the absence of a genus; and an S, its occurrence only in the southern portion of a given region. The main data of this table are condensed in numerical form in Tables II and III, the former giving the total number of genera and the number of endemic genera in each region and the number common to the other regions, the latter the total number of genera and number of endemic genera in each of the subfamilies of Formicidæ. A comparison of the figures brings out the following facts.

1.—The total number of Ethiopian genera (90, or 33.5% of the 269 known genera), though but little in excess of the number of Papuan (81) and Australian genera (81), is greater than that of any other region, except the Indomalayan (101) and Neotropical (97).

2.—The number of indigenous, or precinctive, Ethiopian genera (34, or 38%) is decidedly greater than in any other region, except in the Neotropical (48, or 51%).

3.—The Ethiopian fauna has more genera (48) in common with the Indomalayan than with any other region, though it has 34 in common with the Malagasy, 39 with the Papuan, and 34 with the Australian.

4.—The Ethiopian fauna has fewer genera in common with the Neotropical (22) than with any other region, except the Nearctic (19). This is important in connection with the theories of a former land-connection between Africa and South America, and is still further emphasized by the fact that most of the 22 common genera are those of cosmopolitan, or "tramp," species.

Australian and Papuan, and by species of *Stictoponera* in the Indomalayan, and of *Ectatomma* and *Emeryella* in the Neotropical Region.

A fact not brought out in the foregoing tables is the great development of the doryline genera in the Ethiopian Region. All the subgenera of *Dorylus* but one (*Dichthadia*) are represented, some of them by numerous species (*Dorylus*, *sens. str.*; *Anomma*). The genus *Ænictogiton*, known only from male specimens, is peculiar to Africa. The genus *Ænicthus*, however, though well represented in Africa, has more numerous species in the Indomalayan Region and extends to China, Philippines, and northern Queensland. The genus *Dorylus* is represented by very few species in India and Indonesia.

The following 14 genera of Pseudomyrmicæ and Myrmicicæ are peculiar to the Ethiopian Region: *Viticicola*, *Pachysima*, *Cratomyrmex*, *Anergatides*, *Diplomorium*, *Bondroitia*, *Atopomyrmex*, *Atopula*, *Macromischoides*, *Ocymyrmex*, *Tetramyrma*, *Rhoptromyrmex*, *Decamorium*, and *Microdacton*, nearly all of them monotypic or represented by few species. The remarkable peculiarities of the myrmicine fauna come out strongly in the composition of genera common to the Ethiopian and other regions. Thus, *Myrmicaria*, though extending to the Philippines and Indonesia, is represented by the largest and most numerous species in equatorial and South Africa. *Cataulacus* is also represented by more and larger species than in the Malagasy and Indomalayan Region, *Crematogaster* by numerous subgenera, a few of which (*Nematocrema*, *Sphærocrema*) are endemic, and by a much greater number of species, subspecies, and varieties than any other region except, perhaps, tropical America. *Monomorium*, too, comprises more forms in Africa than are met with anywhere else, with the possible exception of Australia, which contains a considerable number of undescribed species. *Pheidole* is represented by many species with a peculiar African habitus and especially by the great development of the *megacephala* group. The hypogæic and termitophilous ants are represented by species of *Diplomorium*, *Bondroitia*, *Solenopsis*, *Æromyrma*, *Oligomyrmex*, *Carebara*, and *Pædalagus*. Africa is, however, very poor in species of *Solenopsis*, compared with South America, and *Meranoplus* has very few African species compared with the number found in Australia. The complex of closely allied genera comprising *Tetramorium*, *Rhoptromyrmex*, *Xiphomyrmex*, *Decamorium*, *Triglyphothrix*, and *Macromischoides* has many African species. This is particularly true of *Tetramorium*, which closely rivals *Crematogaster* and *Monomorium* in the number and variety of forms. In other portions of the globe, notably the Nearctic and Neotropical Regions, there are very few species of *Tetramorium* and *Xiphomyrmex*.

mend of the genera *Acantholepis* and *Plagiolepis*, with the subgenera *Anacantholepis* and *Anoplolepis*, the latter with several large and conspicuous species, and of the genera *Camponotus* and *Polyrhachis*. *Camponotus* is characterized by a few endemic subgenera (*Myrmopsamma*); some striking species of *Myrmopiromis*, *Myrmosericus*, and *Orthonotomyrmex*; an extraordinary development of the species, subspecies, and varieties of the subgenera *Myrmoturba* and *Myrmotrema*, especially of the *maculatus* and *foraminosus* complexes; and a surprisingly feeble development of other subgenera, such as *Colobopsis*, which has so many species in the Indomalayan and Papuan Regions. One species of *Orthonotomyrmex* (*sericeus*) and one of *Myrmosericus* (*rufoglaucus*) have a very wide distribution, ranging not only over the whole Ethiopian but occurring also in the Indomalayan Region. *Polyrhachis*, which is represented by numerous subgenera in the Indomalayan, Papuan, and Australian Regions, has species of only two subgenera, *Myrma* and *Cyrtomyrma*, in Africa. The genus is absent from Madagascar, but a species of the subgenus *Myrmhopla* (*simplex*) occurs as far north as Palestine, so that it would seem that the ancestors of the present Ethiopian species entered the continent by way of the Nile Valley and the Sudan. *Prenolepis* is poorly represented in Africa. The deserticolous genus *Cataglyphis* belongs properly to the Palearctic fauna and such species as are found in the Ethiopian Region must have come from the Sahara or Arabia. *Ecophylla* has a peculiar distribution, ranging clear across tropical Africa and through the Indomalayan and Papuan Regions into northern Queensland but not occurring in Madagascar.

Within the Ethiopian Region the distribution of species evidently depends on the distribution of temperature, moisture, and vegetation. It might be interesting to discuss this matter in detail but the data at present available are hardly sufficient. From the synonymic list, in which all the recorded localities for the various forms are cited, it will be seen that many species, subspecies, and varieties are known only from single stations. Some of the large, common, and conspicuous forms, however, such as *Megaponera fœtens*, *Pallothyreus tarsatus*, *Myrmicaria eumenoides*, etc., are known to occur throughout the Ethiopian Region. Others, e. g. *Pachysima æthiops*, *Viticicola tessmanni*, and several *Crematogasters*, are so intimately associated with certain host-plants as to be restricted to the range of the latter. Still others, such as the species of *Phrymoponera*, *Psalidomyrmex*, *Macromischoides*, and some species of *Polyrhachis* and *Camponotus*, are evidently confined to the rain forests of western equatorial Africa, while a considerable number of species of

about the 1500 m. level-line; between 1500 and 2500 to 3000 m. extends a warm temperate belt, which may conveniently be called the lower mountain region. Its ant-fauna is scanty in species and individuals and includes only a few representatives of the more generally distributed Ethiopian genera. This is shown by the following list of genera of which workers were found by Alluaud and Jeannel on Mt. Kenia, the Aberdare Range, Mt. Kilimanjaro, and Mt. Ruwenzori, between 1500 and 2850 m.<sup>1</sup>: *Bothroponera* (1 sp.); *Dorylus*, *sens. str.* (2 sp.) and subgen. *Anomma* (1 sp.); *Monomorium* (3 sp.); *Messor* (2 sp.); *Pheidole* (5 sp.); *Oligomyrmex* (1 sp.); *Crematogaster* (3 sp.); *Xiphomyrmex* (1 sp.); *Engramma* (1 sp.); *Tapinoma* (1 sp.); *Technomyrmex* (1 sp.); *Plagiolepis* (1 sp.); *Acantholepis* (1 sp.); and *Camponotus* (6 sp.). The number of species represented is very small and most of them also occur at lower altitudes. The absence of certain common Ethiopian genera, such as *Paltothyreus*, *Megaponera*, *Euponera*, *Odontomachus*, *Enictus*, *Tetraoponera*, *Myrmecaria*, *Solenopsis*, *Cataulacus*, *Ecophylla*, and *Polyrhachis*, is very striking; furthermore, it must be noted that most of the montane ants mentioned above have been found below 2000 m. Indeed, on all Central African mountains reaching above 4000 m. there is between 2000 and 3000 m. a belt of very moist and cool forest, which for many hours of the day is often enveloped in clouds; it is well known that such an environment is very unfavorable to ants and accordingly a few species of *Crematogaster* and certain driver ants alone enter these cloud forests. On Mt. Kenia and Mt. Ruwenzori, the alpine region above the cloud forest up to the snowline (about 4500 m. in tropical Africa) is mainly covered with a peculiar swampy heath- and bog-formation, which practically excludes ant-life. Mt. Kilimanjaro, Mt. Meru, and the Aberdare Range, owing to their more eastern location, present, however, very different conditions: the usual cloud forest extends from 1800 to 2600 m. on the eastern and to 3000 m. on the western slopes; then begins a rather dry, alpine, steppe formation, with short grass growing in tussocks, where a few species of ants are found, nesting in the soil [*Melissotarsus emeryi* var. *pilipes* Santschi (Mt. Kilimanjaro, 2740 m.); *Tetramorium squaminode* Santschi (Mt. Kilimanjaro, 2600 to 3800 m.); *T. cæspitum* subsp. *altivagans* Santschi (Mt. Kinangop, 3100 m.); *Engramma ilgi* var. *stygium* Santschi (Mt. Kilimanjaro, 2740 m.); *Camponotus maculatus* subsp. *kersteni* (Gerstæcker), a strictly montane ant, known only from Mt. Kilimanjaro, where it is common between 2500 and 3000 m.]. Most of these ants, with the possible exception of the subspecies of *T.*

<sup>1</sup>Genera which were collected in the winged sexual phases only are not included in this and similar lists because such individuals are apt to be carried to higher altitudes than their nesting sites.



Table I  
General Distribution of the Genera of Ants<sup>1</sup>

	Ethiopian	Malagasy	Indomalayan	Papuan	Australian	Palaearctic	Neartic	Neotropical
<i>Dorylus</i>	+	.	+	+	.	S	.	.
<i>Enicogiton</i>	+	.	.	.	.	.	.	.
<i>Enictus</i>	+	.	+	+	+	S	.	.
<i>Cheliomyrmex</i>	.	.	.	.	.	.	.	+
<i>Ecilon</i>	.	.	.	.	.	.	S	+
<i>Leptanilla</i>	.	.	+	.	.	S	.	.
<i>Eusphinctus</i>	.	.	+	+	+	.	.	.
<i>Sphinctomyrmex</i>	?	.	.	.	.	.	.	+
<i>Cerapachys</i>	+	+	+	+	+	S	S	+
<i>Phyracaces</i>	+	+	+	+	+	.	.	.
<i>Lioponera</i>	?	.	+	.	+	?S	.	.
<i>Acanthostichus</i>	.	.	.	.	.	.	S	+
<i>Cylindromyrmex</i>	.	.	.	.	.	.	.	+
<i>Simopone</i>	+	+	.	.	.	.	.	.
<i>Myrmecia</i>	.	.	.	.	+	.	.	.
<i>Mystrium</i>	+	+	+	.	.	.	.	.
<i>Stigmatomma</i>	.	.	+	+	+	S	+	+
<i>Xymmer</i>	+	.	.	.	.	.	.	.
<i>Amblyopone</i>	.	.	.	+	+	.	.	.
<i>Myopopone</i>	.	.	+	+	+	.	.	.
<i>Paraponera</i>	.	.	.	.	.	.	.	+
<i>Platythyrea</i>	+	+	+	+	+	.	S	+
<i>Paranomopone</i>	.	.	.	.	+	.	.	.
<i>Prionopella</i>	.	.	+	+	.	.	.	+
<i>Typhlomyrmex</i>	.	.	.	.	.	.	.	+
<i>Rhopalopone</i>	.	.	+	+	.	.	.	+
<i>Wheeleripone</i>	.	.	.	+	.	.	.	.
<i>Alfaria</i>	.	.	.	.	.	.	.	+
<i>Stictoponera</i>	.	.	+	+	.	.	.	.
<i>Acanthoponera</i>	.	.	.	.	+	.	.	+
<i>Holcoponera</i>	.	.	.	.	.	.	.	+
<i>Chalcoponera</i>	.	.	+	+	+	.	.	.
<i>Rhytidoponera</i>	.	.	.	+	+	.	.	.
<i>Emeryella</i>	.	.	.	.	.	.	.	+
<i>Ectatomma</i>	.	.	.	.	.	.	S	+
<i>Thaumatomyrmex</i>	.	.	.	.	.	.	.	+

<sup>1</sup> + = present; ? = generic reference doubtful; \* = introduced genera; S = only in the southern part of the region.

Table I (continued)  
General Distribution of the Genera of Ants

	Ethiopian	Malagasy	Indomalayan	Papuan	Australian	Palaearctic	Nearctic	Neotropical
<i>Epirenus</i>	.	.	.	.	.	S	.	.
<i>Trichomyrmex</i>	.	.	+	.	.	.	.	.
<i>Hagiozenus</i>	.	.	.	.	.	S	.	.
<i>Wheeleriella</i>	.	.	.	.	.	S	.	.
<i>Phacota</i>	.	.	.	.	.	S	.	.
<i>Paraphacota</i>	.	.	.	.	.	S	.	.
<i>Xenomyrmex</i>	.	.	.	.	.	.	.	+
<i>Allomerus</i>	.	.	.	.	.	.	.	+
<i>Megalomyrmex</i>	.	.	.	.	.	.	.	+
<i>Liomyrmex</i>	.	.	+	+	.	.	.	.
<i>Epæcus</i>	.	.	.	.	.	.	+	.
<i>Anergates</i>	.	.	.	.	.	+	.	.
<i>Anergatides</i>	+	.	.	.	.	.	.	.
<i>Tranopella</i>	.	.	.	.	.	.	.	+
<i>Carebarella</i>	.	.	.	.	.	.	.	+
<i>Diplomorium</i>	+	.	.	.	.	.	.	.
<i>Bondroüia</i>	+	.	.	.	.	.	.	.
<i>Solenopsis</i>	+	+	+	+	+	+	+	+
<i>Lophomyrmex</i>	.	.	+	.	.	.	.	.
<i>Trigonogaster</i>	.	.	+	.	.	.	.	.
<i>Pheidologeton</i>	?	.	+	+	+	.	.	.
<i>Aneleus</i>	+	.	+	.	.	.	.	.
<i>Aëromyrma</i>	+	+	?	.	.	.	.	.
<i>Oligomyrmex</i>	+	+	+	+	+	S	.	.
<i>Erebomyrma</i>	.	.	.	.	.	.	S	.
<i>Carebara</i>	+	.	+	.	.	.	.	+
<i>Pædalagus</i>	+	.	+	.	.	.	.	.
<i>Podomyrma</i>	.	.	.	+	+	.	.	.
<i>Lordomyrma</i>	.	.	.	+	+	.	.	.
<i>Atopomyrmex</i>	+	.	.	.	.	.	.	.
<i>Dilobocondyla</i>	.	.	+	+	.	.	.	.
<i>Terataner</i>	+	+	.	.	.	.	.	.
<i>Atopula</i>	+	.	.	.	.	.	.	.
<i>Paratopula</i>	.	.	+	.	.	.	.	.
<i>Brunella</i>	.	+	.	.	.	.	.	.
<i>Myrmecina</i>	.	.	+	+	+	+	+	.
<i>Pristomyrmex</i>	.	.	+	+	+	S	.	.
<i>Acanthomyrmex</i>	.	.	+	+	.	.	.	.
<i>Dacryon</i>	.	.	.	+	+	.	.	.

Table I (continued)  
General Distribution of the Genera of Ants

	Ethiopian	Malagasy	Indomalayan	Papuan	Australian	Palaearctic	Neartic	Neotropical
<i>Archæomyrmer</i>	.	.	.	+	.	.	.	.
<i>Mayriella</i>	.	.	.	.	+	.	.	.
<i>Promeranoplus</i>	.	.	.	.	++	.	.	.
<i>Meranoplus</i>	+	+	+	+	++	.	.	.
<i>Prodicroaspis</i>	.	.	.	.	++	.	.	.
<i>Calypomyrmer</i>	+	.	+	+	+	.	.	.
<i>Macromischa</i>	.	.	.	.	.	.	.	+
<i>Macromischoides</i>	+	.	.	.	.	.	.	.
<i>Leptothorax</i>	+	+	+	.	.	+	+	+
<i>Harpagozenus</i>	.	.	.	.	.	++	+	.
<i>Myrmoxenus</i>	.	.	.	.	.	++	.	.
<i>Formicozenus</i>	.	.	.	.	.	++	.	.
<i>Epimyрма</i>	.	.	.	.	.	s	.	.
<i>Symmyrmica</i>	.	.	.	.	.	.	+	.
<i>Rogeria</i>	.	.	.	+	.	.	.	+
<i>Lachnomyrmer</i>	.	.	.	.	.	.	.	++
<i>Apsychoomyrmer</i>	.	.	.	.	.	.	.	+
<i>Adelomyrmer</i>	.	.	.	+	.	.	.	.
<i>Ocymyrmer</i>	+	.	.	.	.	.	.	.
<i>Tetramyrma</i>	+	.	.	.	.	.	.	.
<i>Lundella</i>	.	.	.	.	.	.	.	+
<i>Tetramorium</i>	+	+	+	+	+	+	s	+
<i>Rhopromyrmer</i>	+	.	.	.	.	.	.	.
<i>Acidomyrmer</i>	.	.	+	.	.	.	.	.
<i>Strongylognathus</i>	.	.	.	.	.	+	.	.
<i>Xiphomyrmer</i>	+	+	+	+	+	.	+	.
<i>Decamorium</i>	+	.	.	.	.	.	.	.
<i>Triglyphothrix</i>	+	+	+	+	.	.	.	.
<i>Eudetramorium</i>	.	+	.	.	.	.	.	.
<i>Ochetomyrmer</i>	.	.	.	.	.	.	.	+
<i>Wasmannia</i>	*	.	.	.	.	.	.	+
<i>Cataulacus</i>	+	+	+	+	.	.	.	.
<i>Procryptocerus</i>	.	.	.	.	.	.	.	+
<i>Zacryptocerus</i>	.	.	.	.	.	.	.	+
<i>Cephalotes</i>	.	.	.	.	.	.	.	+
<i>Cryptocerus</i>	.	.	.	.	.	.	s	+
<i>Basiceros</i>	.	.	.	.	.	.	.	+
<i>Daceton</i>	.	.	.	.	.	.	.	+
<i>Acanthognathus</i>	.	.	.	.	.	.	.	+

Table I (continued)  
General Distribution of the Genera of Ants

	Ethiopian	Malagasy	Indomalayan	Papuan	Australian	Palaearctic	Nearectic	Neotropical
<i>Epilritus</i>	+	.	.	+	+	S	.	+
<i>Orectognathus</i>	.	.	.	+	+	.	.	.
<i>Pentastroma</i>	.	.	+	.	.	.	.	.
<i>Rhopalothrix</i>	.	.	+	+	+	.	.	+
<i>Microdactylon</i>	+	.	.	.	.	.	.	.
<i>Epopostruma</i>	.	.	.	+	+	.	.	.
<i>Glamyromyrmex</i>	.	.	.	.	.	.	.	+
<i>Codionomyrmex</i>	.	.	.	.	.	.	.	+
<i>Strumigenys</i>	+	+	+	+	+	+	+	+
<i>Stegomyrmex</i>	.	.	.	.	.	.	.	+
<i>Proatta</i>	.	.	+	.	.	.	.	+
<i>Pseudatta</i>	.	.	.	.	.	.	.	+
<i>Blepharidatta</i>	.	.	.	.	.	.	.	+
<i>Myrmicocrypta</i>	.	.	.	.	.	.	.	+
<i>Apteroxigma</i>	.	.	.	.	.	.	.	+
<i>Mycocarpurus</i>	.	.	.	.	.	.	.	+
<i>Cyphomyrmex</i>	.	.	.	.	.	.	S	+
<i>Sericomyrmex</i>	.	.	.	.	.	.	.	+
<i>Trachomyrmex</i>	.	.	.	.	.	.	+	+
<i>Atta</i>	.	.	.	.	.	.	S	+
<i>Aneuretus</i>	.	.	+	.	.	.	.	+
<i>Dolichoderus</i>	.	.	+	+	+	+	+	+
<i>Linepithema</i>	.	.	.	.	.	.	.	+
<i>Leptomyrme</i>	.	.	.	+	+	.	.	.
<i>Semonius</i>	+	.	+	.	.	.	.	.
<i>Liometopium</i>	.	.	.	.	.	S	+	.
<i>Turneria</i>	.	.	.	+	+	.	.	.
<i>Froggattella</i>	.	.	.	.	+	.	.	.
<i>Dorymyrmex</i>	.	.	.	.	.	.	+	+
<i>Araucomyrmex</i>	.	.	.	.	.	.	.	+
<i>Iridomyrmex</i>	*	.	+	+	+	.	.	+
<i>Bothriomyrmex</i>	.	.	+	+	+	S	+	.
<i>Forelius</i>	.	.	.	.	.	.	S	+
<i>Azteca</i>	.	.	.	.	.	.	.	+
<i>Engramma</i>	+	.	.	.	.	.	.	.
<i>Tapinoma</i>	+	+	+	+	+	+	+	+
<i>Technomyrmex</i>	+	+	+	+	+	.	.	.
<i>Myrmoleas</i>	.	.	+	.	.	.	.	.
<i>Dimorphomyrmex</i>	.	.	+	.	.	.	.	.

Table V

Number of Species, Subspecies, and Varieties of Each Genus Hitherto Recorded from the Ethiopian Region and the Belgian Congo

	ETHIOPIAN REGION			BELGIAN CONGO		
	Species	Subspecies	Varieties	Species	Subspecies	Varieties
<i>Dorylus</i>	41	20	42	26	8	10
<i>Enicogilon</i>	5	..	1	5	..	1
<i>Eniclus</i>	25	6	7	5	1	1
? <i>Sphinctomyrmex</i>	1	1	..	..	..	..
<i>Cerapachys</i>	7	..	3	1	..	..
<i>Phyracaces</i>	6	1	..	3	1	..
? <i>Lioponera</i>	2	..	..	..	..	..
<i>Sinoponc</i>	2	..	..	..	..	..
<i>Mystrium</i>	1	..	..	..	..	..
<i>Xymmer</i>	1	..	..	..	..	..
<i>Platythyrea</i>	14	2	5	4	..	2
<i>Sysphincta</i>	1	..	..	..	..	..
<i>Discothyrea</i>	3	..	1	..	..	..
<i>Probolomyrmex</i>	1	..	..	..	..	..
<i>Escherichia</i>	1	..	..	..	..	..
<i>Pseudosphincta</i>	1	..	..	..	..	..
<i>Centromyrmex</i>	2	..	2	..	..	..
<i>Streblognathus</i>	1	..	..	..	..	..
<i>Paltothyreus</i>	1	1	4	1	..	..
<i>Glyphopone</i>	1	..	..	1	..	..
<i>Leptopone</i>	1	..	..	..	..	..
<i>Megaponera</i>	1	..	1	1	..	..
<i>Ophthalmopone</i>	5	..	..	..	..	..
<i>Bothroponera</i>	18	3	8	5	..	3
<i>Phrynoponera</i>	5	..	5	5	..	5
<i>Ectomyrmex</i>	1	..	..	..	..	..
<i>Euponera</i>	17	2	5	4	..	1
<i>Pseudoponera</i>	2	..	..	..	..	..
<i>Cryptopone</i>	1	..	..	..	..	..
<i>Ponera</i>	17	8	5	3	1	..
<i>Asphinctopone</i>	1	..	..	..	..	..
<i>Plectroclena</i>	4	1	2	3	..	..
<i>Myopias</i>	1	1	..	..	..	..
<i>Psalidomyrmex</i>	5	..	..	3	..	..
<i>Cacopone</i>	1	..	..	..	..	..
<i>Leptogenys</i>	23	6	9	4	1	3
<i>Anochetus</i>	14	1	6	8	..	1
<i>Odontomachus</i>	2	2	5	2	1	3
<i>Tetraponera</i>	21	9	9	5	1	3

Table V (continued)

Number of Species, Subspecies, and Varieties of Each Genus Hitherto Recorded from the Ethiopian Region and the Belgian Congo

	ETHIOPIAN REGION			BELGIAN CONGO		
	Species	Subspecies	Varieties	Species	Subspecies	Varieties
<i>*Iridomyrmex</i>	1	..	..	..	..	..
<i>Engramma</i>	10	2	2	8	1	2
<i>Tapinoma</i>	10	3	4	1	1	..
<i>Technomyrmex</i>	9	2	4	6	..	1
<i>Semonius</i>	1	..	..	..	..	..
<i>Santschiella</i>	1	..	..	1	..	..
<i>Acropyga</i>	1	..	..	..	..	..
<i>Plagiolepis</i>	26	3	8	6	1	1
<i>Acantholepis</i>	20	11	16	5	2	4
<i>Aphomyrmex</i>	2	..	..	..	..	..
<i>Prenolepis</i>	13	..	1	5	..	..
<i>Pseudolasius</i>	4	..	1	3	..	1
<i>Cataglyphis</i>	2	4	2	..	..	..
<i>Ecophylla</i>	2	..	4	1	..	3
<i>Camponotus</i>	94	81	76	37	33	19
<i>Phasmomyrmex</i>	1	..	..	1	..	..
<i>Polyrhachis</i>	37	17	22	23	9	11
TOTAL	920	389	540	318	122	158

#### THE PECULIARITIES OF THE MALAGASY ANT-FAUNA

The Malagasy Region includes Madagascar and a number of small neighboring islands known as the Comoros, Seychelles, and Chagos. The ant-fauna of Madagascar was first studied by Forel in a splendid volume in Grandidier's large work on the physical and political history of the island. More recently, the Swiss myrmecologist has contributed data on the ants of the smaller islands. Turning again to Tables I, II, and III, we note the following facts.

1.—The Malagasy ant-fauna comprises 40 genera, somewhat less than half the number known from the Ethiopian Region, but only four of these (*Champsomyrmex*, *Parapheidole*, *Brunella*, and *Eutetramorium*) are endemic, or precinctive.

2.—Of the 40 genera, 34 are common to the Ethiopian and 32 to the Indomalayan, so that the affinities appear to be about equally divided between these two regions.

3.—The generic affinities with the Papuan and Australian Regions are somewhat less pronounced (29 and 26 respectively), but considerably more than with the Palearctic, Nearctic, and Neotropical (20, 18, and 19 respectively).

4.—The subfamily Dorylinæ is completely absent from the Malagasy Region.

5.—The Dolichoderinæ are poorly represented by two genera.

6.—The Formicinæ are represented by only four genera (*Acantholepis*, *Plagiolepis*, *Prenolepis*, and *Camponotus*).

7.—The Malagasy possesses only two genera (*Aphænogaster* and *Vollenhovia*) which are not known to occur in the Ethiopian Region.

8.—On the other hand, there are 13 genera (*Discothyrea*, *Centromyrmex*, *Ectomyrmex*, *Dorylus*, *Ænictus*, *Myrmecaria*, *Carebara*, *Pædalagus*, *Calyptomyrmex*, *Semonius*, *Pseudolasius*, *Æcophylla*, and *Polyrhachis*) which occur in the Indomalayan and Ethiopian Regions but are not known to occur in the Malagasy.

9.—Three peculiar genera (*Simopone*, *Melissotarsus*, and *Terataner*) are known to occur only in the Ethiopian and Malagasy Regions.

The following remarks on particular genera are of general interest. Of the four endemic, or precinctive, genera, *Champsomyrmex*, *Parapheidole*, and *Brunella* are monotypic and *Eutetramorium* contains only two species. *Champsomyrmex* is very close to *Odontomachus*; *Parapheidole* seems to be very close to and parasitic on *Pheidole*; the species of *Brunella* was originally described as an *Aphænogaster*, and *Eutetramorium*, as the name indicates, is allied to *Tetramorium*. These four genera, therefore, lend nothing very striking to the complexion of the Malagasy ant-fauna. Its distinctive features are due to the peculiar development of species within certain genera which it shares with the faunas of other regions.

Among the Ponerinæ, the very ancient and primitive genera *Simopone* with 3 and *Mystrium* with 5 species show a greater development than elsewhere, though the former occurs also in Africa and the latter both in Africa and the Indomalayan Region. The only known species of *Euponera*, *sensu stricto*, (*E. sikoræ* Forel) is found in Madagascar. *Leptogenys* is beautifully represented by no less than 16 species, including three species of an endemic subgenus, *Machærogenys*. The remaining genera of the subfamily show nothing unusual.

Among the Myrmicinæ, we find *Tetraoponera* represented by 12 species and *Aphænogaster*, which does not occur in the Ethiopian Region, by 2. one of *Aphænogaster*, *sensu stricto*, and one of the subgenus

*Deromyrma*. *Crematogaster* has 21 species, distributed among the following subgenera: *Crematogaster*, *sensu stricto*, 11; *Orthocrema*, 1; *Oxygyne*, 5; *Decacrema*, 4. One of the species of *Vollenhovia* (*lævithorax* Emery) and the single species of *Triglyphothrix*, *T. striatidens* (Emery), are really tropical "tramps" from the Indomalayan Region. *Pheidole* is well represented by 17 species, some of which have a peculiar habitus. The *megacephala* group comprises a number of forms as in the Ethiopian Region. *Teralaner* with 5, *Xiphomyrmex* with 13, and *Cataulacus* with 8 species are unusually well represented, considering the small size of the territory.

The Dolichoderinæ, as previously stated, have a very poor representation, *Tapinoma* by only one species, *melanocephalum* (Fabricius), a common tropicopolitan tramp, and *Technomyrmex* by 4 species, 3 of which are confined to Madagascar, while one, *albipes* (Smith), is widely distributed over the Indomalayan and Papuan Regions.

The greatest representation of Formicinæ is furnished by the genera *Prenolepis* with 11 and *Camponotus* with 47 species. The latter genus is remarkable on account of the great number of subgenera represented (*Camponotus*, *sensu stricto*, with 1; *Myrmoturba* with 4; *Dinomyrmex* with 5; *Myrmosaga* with 7; *Myrmosericus* with 1; *Mayria* with 1; *Myrmotrema* with 2; *Colobopsis* with 1; *Myrmonesites* with 6; *Myrmopytia* with 1; *Myrmorhachis* with 1; *Orthonotomyrmex* with 15; *Myrmosaulus* with 1; and *Myrmopiromis* with 7 species). The subgenera *Mayria*, *Myrmosaga*, *Myrmonesites*, and *Myrmopytia* are confined to Madagascar. The single species of *Brachyomyrmex*, *B. cordemoyi* (Forel), known to occur in the island of Réunion, has been introduced by commerce from South America. In Table VI the Malagasy genera of ants are listed, with the number of known species, subspecies, and varieties. According to Forel,<sup>1</sup> the fauna is made up of groups of species having the following provenience and affinities.

#### A.—Imported Forms

1. Tropicopolitan forms, imported on various occasions by ships . . . . .	8
2. American forms, evidently of recent importation: <i>Brachyomyrmex cordemoyi</i> (Forel), <i>Pheidole flavens</i> Roger . . . . .	2
3. Of recent importation from Indomalaya: <i>Plagiolepis longipes</i> (Jerdon) . . . . .	1
4. Derived from Oceania: <i>Strumigenys godeffroyi</i> Mayr . . . . .	1
5. More or less ancient Indomalayan importations . . . . .	6
6. More or less ancient African importations . . . . .	9
Total . . . . .	27

<sup>1</sup>1907. 'La faune malgache des fourmis et ses rapports avec les faunes de l'Afrique, de l'Inde, de l'Australie, etc.' Rev. Suisse Zool., XV, pp. 1-6.



## B.—Malagasy Forms\*

7. With cosmopolitan affinities (varieties of intercontinental species).....	9
8. With Indomalayan affinities.....	10
9. With Ethiopian affinities.....	9
10. With very distinct Australasiatic (Moluccan and Australian) affinities. To these many might be added from the following group which, on the whole, have Moluccan and Australian affinities.....	9
11. Malagasy forms proper.....	201
Total.....	238

Forel summarizes his views on the Malagasy ant-fauna as follows:

To sum up, the local Malagasy fauna is a fauna of extremely ancient relicts, which have been evolved in certain intercontinental groups (*Camponotus*, *Pheidole*, *Crematogaster*, etc.) to form a very peculiar fauna, the most ancient and primordial affinities of which connect it with the ancient fauna of the Moluccas and Northern Australia. But whereas the Indomalayan genus *Polyrhachis* has invaded Australasia and Australia, it no more exists in Madagascar than does the subfamily Dorylinae. Subsequently, invasions from East Africa and India confused the situation; still analysis is possible, although it is sometimes difficult to distinguish the direction of the invasions, especially that of the Malagasy fauna into Africa and India.

Finally, very recent invasions of cosmopolitan and even of American species, introduced, without doubt, by shipping, have still further complicated the situation, especially in the small Malagasy archipelagos and along the coast. Nevertheless, it is on the whole easy in these cases to detect the invasions and to avoid erroneous interpretations. The genus *Brachymyrmex* admits of no doubt, and an eye-witness, M. Vinson, of St. Denys, was able to give me exact information, through M. de Cordemoy, on the invasion of *Plagiolepis longipes* into Réunion some twenty-five years ago.

Table VI

Number of Species, Subspecies, and Varieties of Each Genus Hitherto  
Recorded from the Malagasy Region

	Number of Species	Number of Subspecies	Number of Varieties
<i>Cerapachys</i>	1	..	..
<i>Phyracaces</i>	2	..	1
<i>Simopone</i>	3	..	..
<i>Mystrium</i>	5	..	1
<i>Platythyrea</i>	4	1	1
<i>Bothroponera</i>	4	1	..
<i>Euponera</i>	4	..	2
<i>Ponera</i>	6	3	2
<i>Leptogenys</i>	16	2	2
<i>Anochetus</i>	2	..	2
<i>Champsomyrmex</i>	1	1	..
<i>Odontomachus</i>	1	..	..
<i>Tetraponera</i>	12	4	4
<i>Aphaenogaster</i>	3	..	3
<i>Parapheidole</i>	1	..	..
<i>Pheidole</i>	17	3	8
<i>Melissotarsus</i>	1	..	..
<i>Cardiocondyla</i>	4	1	2
<i>Crematogaster</i>	21	7	6
<i>Vollenhovia</i>	2	1	..
<i>Monomorium</i>	8	5	..
<i>Solenopsis</i>	1	..	..
<i>Aëromyrma</i>	1	..	..
<i>Oligomyrmex</i>	2	..	..
<i>Terataner</i>	5	..	..
<i>Brunella</i>	1	..	..
<i>Meranoplus</i>	2	..	..
<i>Leptothorax</i>	3	..	..
<i>Tetramorium</i>	5	2	1
<i>Xiphomyrmex</i>	13	2	1
<i>Triglyphothrix</i>	1	..	1
<i>Eutetramorium</i>	2	..	..
<i>Cataulacus</i>	8	..	..
<i>Strumigenys</i>	4	..	..
<i>Tapinoma</i>	2	..	..
<i>Techomyrmex</i>	4	2	1
<i>Acantholepis</i>	1	..	..
<i>Plagiolepis</i>	5	1	..
* <i>Brachomyrmex</i>	1	..	..
<i>Prenolepis</i>	11	4	3
<i>Camponotus</i>	47	16	29
<b>Total</b>	<b>237</b>	<b>56</b>	<b>70</b>



## II.—THE ANTS COLLECTED BY THE AMERICAN MUSEUM CONGO EXPEDITION

BY WM. M. WHEELER

### Dorylinae

**WORKER AND SOLDIER.**—Clypeus as a rule very short and not limited by sutures. Frontal carinae vertical, not covering the insertions of the antennae. Antennae inserted near the mouth and close to each other, often less than 12-jointed. Palpi at most 3-jointed, in *Leptanilla* only one-jointed. Ocelli and eyes often absent (without exception in all African genera). Sutures of the thorax more or less vestigial; mesonotum touching the epinotum on the dorsal face, without interposed metanotum. Spurs of the tibiae pectinate or rudimentary. Postpetiole not always separated by a constriction from the third segment; however, in *Eciton*, *Enictus*, and *Leptanilla*, narrowed into the second joint of a two-jointed pedicel. Sting developed.

**FEMALE.**—Permanently apterous, with the abdomen much enlarged and swollen; very different morphologically from the worker. Clypeus as in the worker. Frontal carinae more or less separated. Antennae 10- to 12-jointed. No ocelli; eyes not more developed than in the worker; female blind when the worker is so. Segmentation of the thorax more or less rudimentary; no traces of wings or a rudiment left at the tegulae (*Dorylus*). Postpetiole never separated from the third segment, the pedicel always composed of one segment. Gaster long and voluminous.

**MALE.**—Clypeus and frontal carinae much as in the female. Mandibles developed, as a rule large; in *Leptanilla* very short. Antennae 13-jointed; scape long, in *Leptanilla* only slightly longer than the second joint. Eyes and ocelli well developed. Thorax with normal segmentation, winged. Postpetiole and pedicel much as in the female. Genitalia completely retractile (*Dorylini* and *Ecitini*) or exerted and not retractile (*Leptanillini*); subgenital lamina split or furcate; cerci absent.

**LARVAE** more or less cylindrical, with short hairs, without hooked setae; mandibles small, slender, falcate.

**NYMPHS** usually naked; enclosed in a cocoon in some species of *Eciton*.

The three castes in this subfamily are so different from one another that their true relations remained for a very long time unsettled. The winged males were the first to be known and were originally placed with the Mutillidae. The workers and females were recognized as ants but at first classified in genera by themselves. Though their relations were more or less suspected by Lepeletier de Saint-Fargeau, Haliday, and Shuckard, the true affinities of the male and worker became only gradually known after 1850, when Savage observed for the first time in West Africa *Dorylus* males walking in an army of *Anomma* workers. The females, leading a permanently subterranean life, are still excessively rare in collections and known only for a few species; their capture in the smaller species is rather fortuitous, whereas in such fierce army ants as *Anomma* it is a very troublesome operation.

G. Arnold<sup>1</sup> gives the following general account of the habits of this subfamily:

The members of this subfamily are commonly known as driver or legionary ants. The males, which are winged and provided with eyes, are frequently taken at lights; on the other hand, the workers are blind, with the exception of some species of *Eciton*, in which there is a pair of single-faceted eyes, and the females (excepting one species of *Eciton*) are both blind and wingless. The members of the genus *Dorylus* are almost entirely subterranean in their mode of life, rarely coming to the surface except in dull, cloudy weather. The species of the subgenus *Anomma*, which live in the more tropical and forested regions of Africa, and to which the term driver ants was originally applied, and the Ecitini of South America, are, however, usually seen above the surface, although, should the rays of the sun prove too powerful, they will construct temporarily tunnels with particles of earth held together by their saliva. The species of *Ecitius* are not so shy of the light and may be seen foraging about even in bright sunlight. It is probable that all, or at least the majority of the species are carnivorous, although *D. orientalis* has been shown by Green to feed also on tubers and the bark of trees.

As far as known the members of this subfamily do not as a rule make permanent nests. This course is determined by their exceedingly predatory habits, which compel the adoption of a migratory form of life together with the formation of temporary nests in localities which are sufficiently productive of animal life to detain them for any length of time. Ranging far and wide in search of prey, which consists of any animal they are strong enough to overpower, these ants must sooner or later exhaust the areas round their nests, and are forced to remove the latter to new and more productive hunting grounds.

But little is known of the habits of the Leptanillini; all species are hypogæic. Santschi found the nest of *Leptanilla nana* Santschi 40 cm. beneath the surface in clay soil; he caught females and workers by inundating the soil so as to force them to come out of their burrows; workers have also been taken by sifting decayed leaves. The males are attracted by lights.

A detailed account of the migrations and habits of some of the African species is given below (see under *Dorylus bequaerti*, *D. opacus*, *D. kohli*, *D. nigricans*, *D. wilverthi*, and *D. fulvus*).

The Dorylinæ are abundantly found in all tropical parts of the world, with the exception of the Antilles and the Malagasy Region; they are absent from the larger part of Australia. A few species reach North Africa, the coasts of Asia Minor, and the central and southern United States.

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<sup>1</sup>1915, Ann. South African Mus., XIV, p. 110.

**DORYLUS** Fabricius

**WORKERS** small or of medium size, without eyes or ocelli, highly polymorphic, constituting a series of forms which may be grouped as *maximæ*, or soldiers, *mediæ* and *minimæ*. In the *maxima* the head is very large and usually broader in front than behind, the mandibles are long and narrow, with a small number of teeth on the inner border, the clypeus is very short and not marked off from the remainder of the head by sutures. Frontal carinæ very short, erect, close together, not concealing the insertions of the antennæ. Antennæ short, inserted very near the mouth, 9- to 12-jointed, according to the species. *Mediæ* smaller, with much smaller and shorter head, but the latter not narrowed in front; anterior border of clypeus more or less projecting in the middle over the mouth. Antennæ as in the *maxima*. *Minima* very small, with the head narrowed anteriorly and the anterior border of the clypeus strongly projecting in the middle. Number of antennal joints reduced, seven being the minimum. Promesonotal suture distinct in all three forms of worker; meso-epinotal suture obsolete. Epinotum always unarmed. Petiole nodiform; postpetiole narrowed anteriorly, not or only indistinctly separated from the first gastric segment. Pygidium with a dorsal impression and terminating in three points. Posterior tibiæ each with a pectinated spur.

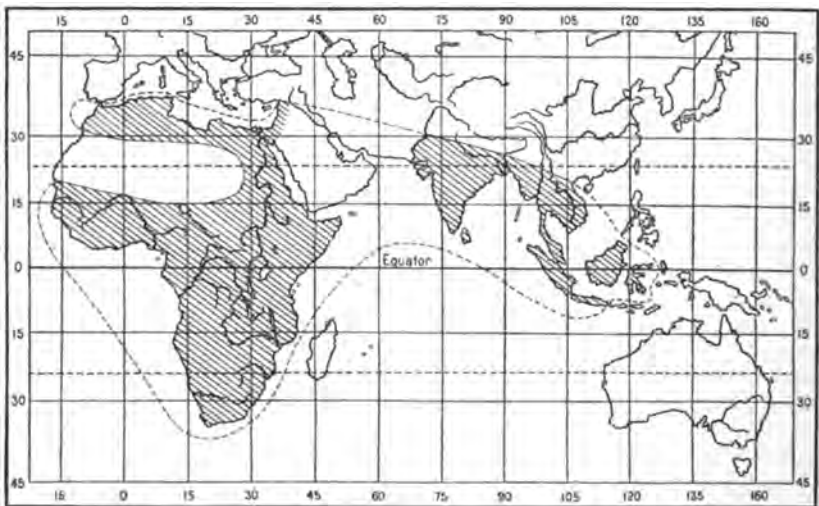
**FEMALE** very much larger than the worker, dichthadiiform, i. e. wingless, with long and voluminous abdomen. The head has the occipital lobes swollen and rounded, separated by a median longitudinal furrow. Eyes and ocelli absent, as in the workers. Clypeus as in the worker *maxima*, or soldier. Mandibles narrow, edentate. Antennæ 11-jointed (12-jointed in the subgenus *Dichthadia*). Thorax segmented, but the mesonotum without differentiated scutum and scutellum; alar insertions vestigial. Petiole large, its posterior corners prolonged as blunt points. Postpetiole shorter than the first gastric segment, but not followed by a constriction. Pygidium and hypopygium gaping or separated so as to expose to view the eighth pair of abdominal spiracles, the anal segment and sting; the pygidium not impressed; the hypopygium surpassing the pygidium considerably and terminating in two lobes or appendages.

**MALE** very large, with very large eyes and ocelli. Clypeus short, prolonged backward between the short, diverging frontal carinæ. Mandibles edentate. Antennæ 13-jointed; scape one-third or one-fourth as long as the funiculus which is filiform. Legs short; femora flattened, tibiæ narrow. Wings with narrow, poorly defined pterostigma, placed near the apical third; radial cell elongate and open; one closed cubital cell, usually one recurrent nervure (two in the subgenus *Rhogmus* and in some anomalies). Petiole nodiform or saucer-shaped, its concavity turned toward the postpetiole, the latter not separated from the gaster by a constriction. Gaster long, cylindrical or club-shaped. Pygidium rounded or split at the posterior border (*Rhogmus fimbriatus*). Genital armature voluminous, completely retractile; annular lamina narrow; stipes and volsella simple; lacinia absent; subgenital plate deeply furcate.

Emery, who has devoted much careful study to the Dorylinæ, divides *Dorylus* into six subgenera (*Dorylus*, *sensu stricto*; *Dichthadia* Gerstæcker; *Anomma* Shuckard; *Typhlopone* Westwood; *Rhogmus* Shuckard; *Alaopone* Emery) mainly on the number of antennal joints and structure of the pygidium in the worker, the number of antennal

joints and shape of the hypopygium in the female, and the shape of the mandibles and petiole in the male. The genus (Map 4) occurs throughout Africa, India, Indochina, the Malayan Region, and Indonesia (Borneo, Java, Sumatra, and Celebes). All but one of the subgenera and most of the species are found in Africa; in Asia there are less than half a dozen species belonging to the subgenera *Dichthadia*, *Typhlopone*, and *Alaopone*.

In the 'Genera Insectorum' (Dorylinæ, 1910, p. 7) Emery makes the following statement on the ethology of the genus *Dorylus*:



Map 4. Distribution of the genus *Dorylus*.

Apart from the subgenus *Anomma* all the species of *Dorylus* lead a subterranean life and come to the surface of the soil only on exceptional occasions, as, e. g., during inundations or in order to accompany the males when they take flight. Their societies are very populous. The soldiers and workers make subterranean expeditions for the purpose of capturing insects and other small animals, and exploit manure piles, cadavers and probably also the nests of termites. The males come to lights at night. Search for the heavy and voluminous apterous females is beset with difficulties so that they are rare in collections. It may be noted that in all the specimens hitherto described, with the exception of the female of *D. fimbriatus* described by Brauns, the terminal tarsal joints are lacking. I infer that the workers tear them off during the underground forays, while they are dragging the colossal queen by all her legs through the narrow galleries.

**Dorylus atratus** F. Smith

A single male from Stanleyville (Lang and Chapin).

**Dorylus brevipennis** Emery variety **marshalli** Emery

A single male from Medje (Lang and Chapin).

**Dorylus bequaerti** Forel

I refer to this species, originally taken by Dr. Bequaert at Sankisia in the Katanga, numerous workers from two colonies, one taken by Mr. Lang at Banana, the other by Dr. Bequaert at Pasaconde near Zambi "in galleries under ground and in a fallen trunk of *Hyphæne*." The largest workers of the former colony are only 4 mm. long and therefore somewhat smaller than those seen by Forel (5 mm.) and the color is paler. They are probably not the largest workers of the colony. The largest individuals taken by Dr. Bequaert are fully 5 mm. long and darker in color. The head is deeply and broadly excavated behind and has straight, subparallel sides; the first funicular joint is distinctly longer than broad, the remaining joints, except the last, broader than long, and the petiole is also slightly broader than long. The whole body is evenly and sharply punctate, the punctures on the gaster somewhat smaller but very distinct. The large workers are rich ferruginous red, with somewhat paler gaster; the smaller workers are decidedly paler, like those taken by Mr. Lang at Banana.

**Dorylus depilis** (Emery)

Faradje, ♂; Medje, ♂; Stanleyville, ♂ (Lang and Chapin). Seven specimens, all belonging to the typical form of this well-known species.

**Dorylus mœstus** (Emery)

A single male from Stanleyville (Lang and Chapin).

**Dorylus staudingeri** Emery

A single male from Medje (Lang and Chapin).

**Dorylus (Anomma) emeryi** Mayr subspecies **opacus** Forel

A fine series of workers of all sizes from a single colony taken at Ngayu (Lang and Chapin). "They appeared during the night, apparently attracted by some bones of large mammals, which they completely covered." The sides of the head of the largest workers are less convex than indicated by Santschi's figure and like that which he gives of *D.*



*emeryi*, though slightly narrower and much more deeply excavated behind. The preapical tooth of the mandibles is lacking in the largest, though present in the mediæ and smallest workers. There are also three workers from Medje, taken from the stomach of a toad (*Bufo funereus*).

***Dorylus (Anomma) funereus* Emery**

Medje, ♂; Stanleyville, ♂; Bolobo to Lukolela, ♂ (Lang and Chapin). Single specimens from each of these localities agree closely with Emery's description of the types from the Gold Coast.

***Dorylus (Anomma) kohli* Wasmann**

Twenty workers from Akenge and Niangara, taken from the stomachs of toads (*Bufo funereus*) and frogs (*Kassina senegalensis* and *Hemisis marmoratum*), and a fine series of workers of all sizes from Avakubi (Lang and Chapin) with the following note: "They usually appear in great masses, coming right out of the ground, underneath a piece of meat. Even palm oil, poured on the floor, will attract them in the same way." This observation shows that the species is hypogæic like the species of *Dorylus, sensu stricto*, and not epigæic like *Dorylus (Anomma) nigricans* and its various subspecies and varieties, and agrees with the observations of Father Kohl, quoted by Wasmann: "This species seems to be intermediate between the subterranean *Dorylus, sensu stricto*, and the driver ants. Its discoverer, Father Kohl, who found it at St. Gabriel near Stanleyville on the Upper Congo, writes as follows: "The ants just mentioned seem always to wander about beneath the surface of the ground; at any rate, I have seen them on the surface only on three occasions and always after a rain.'" Wasmann adds the interesting statement: "The subterranean mode of life of *D. kohli* may also be inferred from its guests, which are much less like those of *Anomma* than of *Dorylus helvolus* L. The development of the eyes of *Pygostenus pusillus* Wasm., which lives with *D. kohli*, is about half way between the small eyes of *P. raffrayi* Wasm., a guest of *D. helvolus* L., and the very large eyes of the *Pygostenus* species which live with *Anomma wilwerthi* Emery. Here, too, there is a hint in regard to the habits of the host." The remarkable wingless phorid *Hexacanthrophora cohabitans*, recently described by H. Schmitz,<sup>1</sup> was also found with *Dorylus kohli* by Father Kohl at St. Gabriel near Stanleyville.

<sup>1</sup>1914. Zool. Jahrb. Abt. Syst., XXXVII, pp. 512-515, Pl. xxix, fig. 1.

***Dorylus (Anomma) kohli* variety *congolensis* Santschi**

Two series of workers, one taken at Leopoldville by Mr. Lang, the other at Thysville by Dr. Bequaert, evidently belong to this variety, in which the head of workers measuring 7 mm. is as broad as long, whereas in the typical *kohli* it is longer than broad in individuals of the same size, with somewhat less pointed posterior angles.

The Leopoldville specimens were found "under a piece of tin on the shore of Stanley Pool," those from Thysville were "marching in a subterranean burrow in a forest gallery."

***Dorylus (Anomma) kohli* variety *langi*, new variety**

A series of more than a hundred workers from Malela (Lang and Chapin), taken beneath the prostrate trunk of a palm, represent a new variety near variety *frenisyi* Forel and variety *minor* Santschi. They range in size from 3 to 8 mm. The largest are very probably the true *maxima* workers as they lack the preapical mandibular tooth. In *frenisyi* the largest workers attain a length of 8.5 mm., in *minor* 8 mm.

The head of *langi* is nearly as broad as long, its sides convex and distinctly converging behind so that the occipital border, which is deeply and rather angularly excised, is about three-fourths as long as the anterior. The dorsal and ventral surfaces of the head are somewhat flattened. The whole body is finely, sharply, and rather uniformly shagreened or minutely and densely punctate and subopaque; the mandibles smooth and shining; the gaster behind its first segment feebly shining. The upper surface of the head, thorax, and gaster are uniformly but sparsely punctate, the punctures nonpiligerous for the most part. The suberect, yellow hairs are very sparse and confined to the gaster and the same is true of the dilute appressed pubescence. Legs and scapes with short stiff and appressed hairs, absent or very sparse on the extensor surfaces of the femora and tibiae. In some specimens a few very fine short hairs can be detected, under a magnification of 20 diameters, arising from the coarse punctures on the vertex or posterior corners of the head. Color rather bright reddish ferruginous, with the legs paler and the mandibles and the upper surface of the head, except the cheeks and occiput, dark brown or blackish. The upper surface of the thorax and gaster, except the posterior borders of the segments of the latter, are darker and more brownish than the pleuræ and venter. The petiole is scarcely longer than broad, its ventral tooth small, compressed and directed backward. The smaller workers have the head of nearly the same shape and proportions as the larger but less deeply excised behind and more shining, as is also the body. The pubescence is also a little more abundant. The color is very similar but paler in the smallest individuals.

***Dorylus (Anomma) kohli* variety *chapini*, new variety**

This is a very distinct form, represented by a series of two dozen workers from Stanleyville (Lang and Chapin), without further data. They measure 1.5 to 6 mm. in length. The largest specimens are probably not the *maxima* forms as they have a preapical mandibular tooth.

The body is only slightly shining and very similar in sculpture to the preceding variety except that the punctures are coarser, sharper and piligerous. They are evenly distributed over the dorsal surface of the head and pronotum, similar but smaller and shallower on the epinotum and gaster, and very indistinct or absent on the petiole. Mandibles and legs smooth and shining. The head, pro- and mesonotum, gaster, scapes, and legs are covered with short, subappressed, yellow hairs arising from the punctures and forming a conspicuous, rather abundant, coarse pubescence. The body is brownish ferruginous, the head slightly darker, and appendages paler, the mandibles blackish. The head is scarcely longer than broad in front, the sides very feebly convex and converging to the posterior border, which is only slightly excised and about four-fifths as long as the anterior border. The petiole is as broad as long. The smaller workers closely resemble the larger, except that the head is a little longer and the color paler.

***Dorylus (Anomma) nigricans* Illiger subspecies *arcens* (Westwood)**

Eleven *maxima* and *media* workers from Medje (Lang and Chapin), taken from the stomach of a toad (*Bufo funereus*), are very dark, almost black, and are evidently referable to this subspecies, though the largest specimens are only about 10.5 mm. long, whereas the largest workers, according to Emery and Santschi, measure 13 mm. The surface of the body is very shining, the head more opaque in front.

***Dorylus (Anomma) nigricans* subspecies *burmeisteri* (Shuckard)**

Seven workers from the stomach of a toad (*Bufo regularis*) taken at Stanleyville; a series of workers of all sizes from Stanleyville and Lukolela to Basoko (Lang and Chapin); also workers from Katala (J. Bequaert).

*Dorylus nigricans* is the famous driver or army ant, which has so greatly impressed all the African explorers. In my ant-book I have quoted some of the accounts of the earlier observers. To the field naturalist the various races of *D. nigricans* and *D. wilverthi* are so similar in appearance and habits that he designates them all as "driver" or "army" ants. It is not surprising therefore that Mr. Lang's notes refer indifferently to both species. The four fine photographs (Pls. II, III, and IV) belong undoubtedly to *D. wilverthi* (*vide infra*) but the following note probably refers to both species: "Wherever they go, even though the file be very small, the army ants clear a road that can be easily seen. But when a large army is passing, they not only build a road but also bridges and frequently even fill in all the depressions between the dried grass with particles of sand or soil until a perfect road has been constructed. Across a pathway used by pedestrians, where they are often disturbed, they build walls and regular tunnels even in

the hardest ground. Particle by particle is carried out by the steady stream of small workers and the soldiers, large and small, watch on both sides of the line, ever ready to attack anything that may approach. They assume a very peculiar attitude, with mandibles wide open and the head and thorax bent up and back till it forms a right angle with the abdomen. When they seize anything, the abdomen can be torn off without their loosening their grip. They are greatly feared by the natives and even the greatest laggard moves rapidly when passing 'the line.'"

In connection with the fact cited by the early explorers, that the drivers are able to kill large animals when confinement prevents their escape, Santschi's quotation of the following observation of Cruchet concerning *D. nigricans* in Benguela is of interest: "Twice during the course of the year we have been compelled to take the cows out of the kraal and drive them elsewhere, because they bellowed so piteously. On looking into the matter we found that the Anommas caused all this disturbance by crawling into the natural orifices of the animals, especially the anus and vulva. A brooding hen had her head half eaten away, but would not abandon her eggs. On three occasions one of my comrades had to quit his chamber during the night and take up his quarters in the work shop."

According to Forel,<sup>1</sup> a very interesting account of the habits of *Dorylus nigricans* in East Africa has been published by Vosseler,<sup>2</sup> but I have not had access to this paper. Forel's paper, however, contains reproductions of three of Vosseler's photographs, one showing the *Anomma* overwhelming a white rabbit and the others showing its army on the march and crossing a stream. Prof. Emery, some years ago, kindly sent me copies of these photographs, which seem to me worthy of being again reproduced for the benefit of my American readers (Pl. V, figs. 1 and 2; Pl. VI, fig. 1).

The singular dichthadigyne, or female of *D. nigricans*, was discovered by H. Schultze in Uganda. It measures 29 to 31 mm. and has been carefully figured and described by Forel in the work cited above (p. 177).

***Dorylus (Anomma) nigricans* subspecies *burmeisteri* variety *rubellus*  
(Savage)**

Several workers from Boma (Lang and Chapin).

<sup>1</sup>1912, Mitt. Naturh. Mus. Hamburg, XXIX, p. 174, footnote.

<sup>2</sup>Pflanser, Nov. 4, 1905, pp. 289-302.

**Dorylus (Anomma) nigricans** subspecies **sjöstedti** Emery

Three large workers from Faradje, Niangara, and Medje, taken from the stomachs of toads (*Bufo regularis* and *B. superciliaris*) and a frog (*Rana occipitalis*); also a large series of workers from Faradje (Lang and Chapin).

This form closely resembles subspecies *burmeisteri* variety *molestus* (Gerstæcker) in having the inferoposterior angles of the petiole prolonged outward as distinct tubercles, but is readily distinguished by having the head of the larger workers (7 to 12.5 mm.) opaque instead of shining and that of the smaller workers elongate.

An interesting account of the habits of *rubellus* and *sjöstedti* has been published by Sjöstedt.<sup>1</sup>

**Dorylus (Anomma) wilverthi** Emery

Plates II, III, and IV

This fine species, the workers of which are easily recognized by the elongated and divergent posterior corners of the head (Fig. 1b), is represented by a large series from Avabuki and a single small worker from

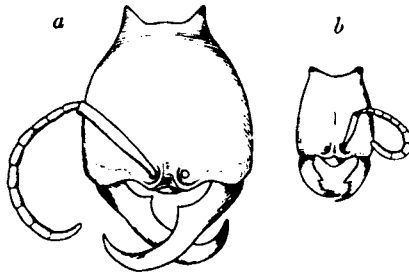


Fig. 1. *Dorylus (Anomma) wilverthi* Emery. a, head of soldier; b, head of worker.

Faradje; also by five workers from Medje and Akenge taken from the stomachs of toads, *Bufo polycercus* and *B. funereus* (Lang and Chapin).

The temporary nest is shown in Plate II, the ants massed on the ground in Plate III. Concerning these ants Mr. Lang says: "We had considerable trouble with them, for they started a nest near our camp at the base of a coffee bush where some pineapple plants were growing. I took two photos before burning the place. One shows the masses of army ants heaped on top of the other. It was impossible to see what they had beneath them, but after the fire, we found that they covered in-

<sup>1</sup>1908, 'Akasiengallen und Ameisen auf den ostafrikanischen Steppen.' In Sjöstedt, Exped. Kili-mandjaro, Meru, etc., II, 8, pt. 4, pp. 111-114.

numerable eggs and larvæ. The other photo shows the mounds or heaps of earth particles carried out by the workers. They come on steadily, each one with a particle of soil in its jaws, and, as soon as they arrive at the summit of the mound, they open their mandibles and the grain of sand rolls into place. After the fire they began to emigrate in enormous numbers, building their roads as they proceeded. There was one main line about an inch wide, excluding the soldiers. I followed this particular line for a distance of about 500 yards into the forest. Sometimes the ants seemed to have disappeared entirely into the ground, since they traveled in tunnels, but by searching I discovered their course some distance beyond. I was unable to ascertain where the huge army deposited its eggs and larvæ. For three days the workers carried larvæ and eggs out of the old nest. The brood was carried under the body so that it could not be seen by the superficial observer." These observations were made at Avakubi.

***Dorylus (Typhlopone) fulvus* (Westwood) subspecies *badius***  
(Gerstæcker) variety *obscurior* Santschi

Vankerckhovenville, ♀, ♂; Faradje, ♀, ♂; Garamba, ♀; Batamā, ♂; Stanleyville, ♂ (Lang and Chapin); Avakubi, ♂ (Lieut. Boyton). Both the worker and male of this form have a characteristic color. Santschi described only the worker from Konakry, French Guinea. The Congo specimens measure 5 to 13 mm. and have the head, thorax, petiole, and legs rich chestnut brown, the gaster brownish yellow, the mandibles and antennæ nearly black. The smallest workers are more uniformly brownish yellow. The differences in form between this and the typical *badius* of South Africa are slight. Santschi describes the head, the base of the epinotum, and the petiole as broader in *obscurior*. In my specimens the head of the soldier (Fig. 2a) closely resembles that of the variety *eurous* from East Africa as figured by Emery.

The males (Fig. 2b-f) taken from the same colony as the workers are also much darker than those of the subspecies *badius* and variety *eurous* or the typical *fulvus* from North Africa. They measure 33 to 36 mm., with the thorax somewhat less than 6 mm. broad, and are chocolate brown, with the head blackish and the gaster a shade paler than the thorax and petiole. The wing membranes are also of a little duller and deeper tint. The hairs and pubescence are less golden and less shining, more grayish. The male genitalia are intermediate in the structure of the stipes between those of the typical *fulvus* and the subspecies *badius*, as will be seen by

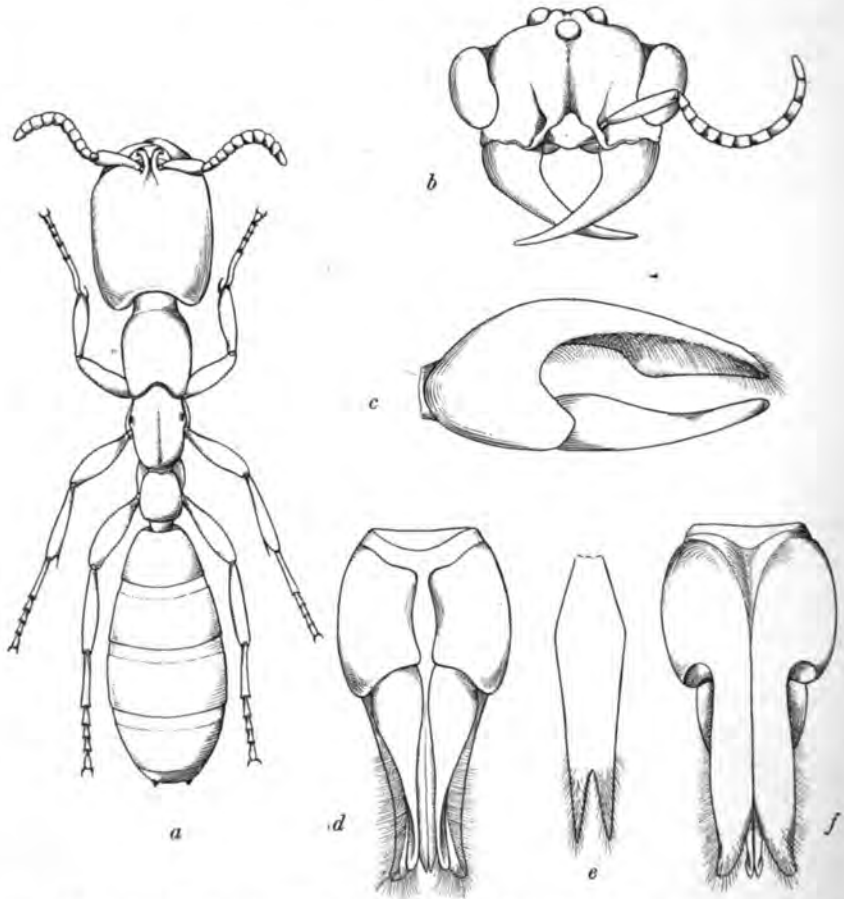


Fig. 2. *Dorylus (Typhlopone) fulvus* subspecies *badius* variety *obscurior* Santschi. a, soldier; b, head of male; c-f, genitalia of male.

comparing my figures with Emery's.<sup>1</sup> The specimens from Batama and Avakubi are distinctly paler than the others in the series but can hardly be regarded as belonging to a different variety.

Concerning the Vankerckhovenville colony from which both workers and males were taken, Mr. Lang writes: "These ants were collected on the floor of an Azande hut. The workers and big males were swarming out of a hole in the ground during the night. These driver ants are not annoying to human beings, but have subterranean habits. They never

<sup>1</sup>1895, Zool. Jahrb. Abt. Syst., VIII, figs. Q and R, pp. 727, 728.

walk in columns on the surface like the others, but whenever a piece of meat or even a jar of oil is deposited on the ground they immediately appear from below, without a tunnel or a gallery being visible from the outside."

***Dorylus (Alaopone) atriceps* Shuckard**

Text Figure 3

Three males from Faradje and two from Stanleyville (Lang and Chapin).

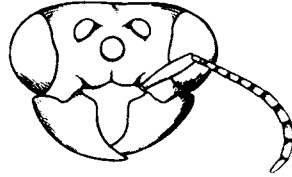


Fig. 3. *Dorylus (Alaopone) atriceps* Shuckard. Head of male.

***Dorylus (Alaopone) conradti* Emery**

Five soldiers and ten smaller workers from Niangara (Lang and Chapin), taken from the stomach of a frog (*Hemisus marmoratum*), agree perfectly with Emery's description and figures of the types from Togo, except that the largest workers measure only 4.5 to 5 mm., whereas Emery's specimens attained a length of 6.5 mm. The soldier is easily recognized by the coarsely punctate thorax and the very elongate head, which, with the closed mandibles, is nearly twice as long as broad.

**Cerapachyinae**

I have recently proposed to regard Forel's tribe "Cerapachysii" as constituting an independent subfamily, the larvæ of these ants being so different from those of the true Ponerinae and much more like the larvæ of the Dorylinae.<sup>1</sup> The limits of this new subfamily agree with those of Emery's section Prodorylinae, and Emery was probably right in contending that the Cerapachyinae are intermediate between the Dorylinae and Ponerinae.

The WORKER caste has a ponerine habitus, but is often long and slender. The postpetiole is separated from the third abdominal segment by a well-marked constriction, and as broad as the third segment. In the Indoaustralian *Eusphinctus* even the gastric segments are marked off from one another. A powerful sting is present.

The characters of the FEMALE in the various genera are peculiarly diverse. In some cases (*Phyracaces*), this caste is winged and not unlike the females of certain Ponerinae; in others (*Parasyscia*, *Eusphinctus*), the female is wingless and ergatomorphic; and, in still others (*Acantho-*

<sup>1</sup>Wheeler, Wm. M., 1920. 'The subfamilies of Formicidæ, and other taxonomic notes.' *Psyche*, XXVII, pp. 46-55.



*stichus*, *Nothosphinctus*), the female is so much like the corresponding caste in the Dorylinæ that it might be regarded as a dichthadiigyne. The MALE, on the other hand, though lacking the cerci, has a decidedly ponerine habitus. The male genitalia are completely retractile; the subgenital lamina deeply and broadly furcate.

The LARVÆ are extremely like those of the Dorylinæ; they are elongate and almost cylindrical, uniformly covered with short hairs, and without piliferous tubercles. The mandibles are small, narrow, pointed, and rather feebly chitinized, and I have failed to find a trophorhinium, or triturating organ in the mouth. Apparently the young are fed only on soft food. Moreover, the foraging habits at least of certain Australian Cerapachyiniæ (*Phyracaces*) resemble those of the Dorylinæ.<sup>1</sup>

Dr. W. M. Mann has recently sent me specimens of his *Cerapachys majusculus* from Fiji, with several worker pupæ which are enclosed in well-developed, brown cocoons. The Cerapachyiniæ seem, therefore, to agree with the Ponerinæ in this character.

#### CERAPACHYS F. Smith

WORKER.—Small ants with peculiar, long, subcylindrical body; the head excavated behind, with prominent, depressed posterior corners and very short clypeus, with which the closely approximated frontal carinæ are fused. The latter are erect, leaving the articulations of the antennæ exposed. The antennal fovea is bounded externally by a distinct carina. Mandibles with distinct, obscurely denticulate apical border. Antennæ stout, 9- to 12-jointed, the scape incrassated distally, the terminal funicular joint large, swollen, oval or glandiform, at least as long as the three preceding joints together, thus forming a one-jointed club. Eyes small, sometimes wanting. Thorax with the promesonotal and mesoëpinal sutures absent or indistinct. Petiole and postpetiole not marginate on the sides, the latter strongly constricted off from the gaster which is largely formed by its first segment.

FEMALE scarcely larger than the worker and very similar, sometimes apterous and ergatoid. Fore wings when present with a discoidal and a single cubital cell.

MALE with the clypeus and frontal carinæ much as in the female. Antennæ filiform, 13-jointed; basal funicular joints short. Mesonotum without Mayrian furrows. Wing venation like that of the female.

The genus has been divided by Emery into four subgenera, distinguished by the number of antennal joints: *Cerapachys, sensu stricto*, having 12; *Parasyscia*, 11; *Ooceræa*, 10; and *Syscia*, 9. The distribution of these subgenera is peculiar. The species of *Cerapachys, sensu stricto*, are known to occur only in the Ethiopian, Malagasy, Indomalayan, and Papuan Regions; those of *Parasyscia* occur in Texas, Guatemala,

<sup>1</sup>Wheeler, Wm. M. 1918. 'The Australian ants of the ponerine tribe Cerapachyini.' Proc. American Ac. Arts Sc., LIII, p. 223.

Syria, Ceylon, India, and Burma; those of *Syscia* have been recorded from Ceylon, Singapore, New Guinea, Queensland, and Hawaii; while *Ooceræa* is known only from Ceylon. As these ants form small colonies and live a subterranean life, they are very rarely seen and this probably accounts for the peculiar discontinuous distribution in the accompanying map (Map 5). It seems hardly possible that species of *Cerapachys*, *sensu lato*, are entirely lacking in South America, but none has been found in any of the many extensive collections that have been made on that continent. Practically all that is known of the habits of the genus is contained in a paper which I published many years ago on the Texan *Parasyscia augustæ* Wheeler.<sup>1</sup>



Map 5. Discontinuous distribution of the genus *Cerapachys*.

#### ***Cerapachys cribrinodis* Emery**

Two workers found in the stomach of a toad (*Bufo funereus*) taken by Lang and Chapin at Medje.

#### **PHYRACACES Emery**

Closely related to *Cerapachys*. The worker and female have 12-jointed antennæ. The terminal funicular joint, however, is not enlarged but tapers from the base to the tip and is not longer or scarcely longer than the two preceding joints together. The eyes of the worker are much larger than in *Cerapachys* and the sides of the petiole and often also of the postpetiole are strongly marginate. The female is winged or apterous and ergatoid; the male is known in certain Australian species.

<sup>1</sup>1902, 'An American *Cerapachys*, with remarks on the affinities of the Cerapachyinae.' Biol. Bull., III, pp. 181-191, 5 figs.

broader than long, tenth joint larger, distinctly longer than broad, terminal joint tapering, not broader than the preceding and not longer than the two preceding joints together. Thorax subrectangular from above, about twice as long as broad, a little broader through the epinotum than more anteriorly, evenly convex above, without traces of dorsal sutures, truncated and sharply marginate anteriorly and posteriorly. The margination separating the base and declivity of the epinotum is enlarged to form a small blunt tooth on each side. The lateral borders of the dorsum are indistinctly marginate, especially in the epinotal region, but the sloping epinotal declivity is sharply marginate laterally. Petiole as broad as the epinotum, rectangular, about one and two-thirds as broad as long, with bluntly dentate posterior corners, marginate in front and on the sides, with truncated, slightly concave anterior, feebly convex dorsal and sloping posterior surface. Ventrally in front it bears a large, triangular, compressed, subtranslucent tooth. Postpetiole as broad as the petiole, as long as broad, very regularly rectangular, flattened above, with only its anterior border marginate. First gastric segment a little larger than the postpetiole, of a similar shape but broader than long, anteroventrally with a blunt tooth or tubercle. Pygidium subcircular, truncate, minutely and indistinctly spinulate on the sides. Legs rather slender, hind coxæ with a large rounded, translucent expansion at the tip on the inner side.

Shining; mandibles coarsely and sparsely punctate. Head with a large, smooth and very shining space on each side between the eye and frontal carinæ; remaining surface with coarse, elongate punctures or foveolæ and posteriorly with a few coarse rugæ. Thorax above and on the sides rather regularly longitudinally rugose, with indications of elongate foveolæ on the humeri and truncated anterior surface; epinotal declivity more finely and regularly longitudinally striated. Sculpture of petiole above similar to that of the thoracic dorsum but with more numerous elongate foveolæ in the interrugal spaces; on the postpetiole the foveolæ are larger and more abundant and the longitudinal rugæ much less distinct; first gastric segment, pygidium and posterior portions of remaining segments coarsely and evenly punctate, the basal portions of these segments more shining and very evenly striolate. Scapes finely, legs more coarsely and much more sparsely punctate.

Hairs grayish, bristly, suberect, moderately long, rather evenly distributed on the body, more abundant on the tip of the gaster, more appressed on the legs; tibiæ and scapes with a few long, suberect hairs. Pubescence short, visible only on the punctate portions of the gaster.

Black; mandibles, antennæ, legs, tip of gaster and sting piceous, coxæ and middle portions of femora and tibiæ darker.

FEMALE.—

Length 5 to 5.5 mm.



Fig. 4. *Phyracaces langi*, new species. Worker.

Very similar to the worker. Pronotum coarsely foveolate; mesonotum small, flat, somewhat pointed anteriorly, with its rugæ converging in front. Postpetiole distinctly broader than the petiole and a little broader than long. Wings whitish hyaline, with very pale yellow veins and large, conspicuous, dark brown pterostigma.

Described from seven workers and eight females taken from a single colony at Lubila, "nesting in a mushroom-shaped termitarium against a tree in the forest" (Lang and Chapin).

Of the four described Ethiopian species of *Phyracaces*, *langi* is most closely related to *P. foreli* Santschi of the Gold Coast. The worker of this species, however, measures only 3.5 mm. and, judging from Santschi's description, has a nearly straight occipital border, shorter antennal scapes, and different sculpture, especially of the head, petiole, and postpetiole. His figure of the petiole shows much longer posterior teeth than in *langi*. The specimen from Samkita, Gaboon, described by Santschi as the female of *foreli* measures 4 mm. and is so different from the worker in the shape of the petiole that I feel sure that it belongs to a distinct species, which may be designated as ***Phyracaces santschli***, new species.

### Ponerinæ

Postpetiole separated from the third abdominal segment by a constriction which is more or less marked (except in the Odontomachini and in certain males of Ponerini), almost always as broad as the third segment (except in *Myrmecia* and a few others). WORKER and FEMALE with a powerful sting. As a rule there is a stridulating organ on the basal surface of the tergite following the postpetiole; it consists of very fine transversal striæ of the articulating surface. Median spur of the tibiæ pectinate, when present, except on the middle tibiæ of a few genera; lateral spur simple. Fore wing as a rule with two closed cubital cells; but there are many exceptions.

The dimorphism of the worker is feebly marked (except in *Megaponera foetens*, where it is very pronounced) and the female as a rule is not very different from the worker; ergatoid females exist in many genera. In a few cases the MALE has no constriction behind the postpetiole; such males can usually be recognized from male Doli-choderinæ by the feeble development of the mandibles. Ergatoid males are known for certain Ponerini.

LARVÆ with the mandibles powerfully developed for ant larvæ; the anterior portion of the body long, slender and neck-like, folded over the swollen abdominal portion; the segments are either densely hairy all over or covered with rows of peculiar tubercles beset with more or less prominent bristles; the larvæ of *Megaponera* and *Bothroponera* are hairless.

NYMPHS enclosed in a resistant cocoon, which may be opened by the adult without intervention of the worker. The West African *Discothyrea oculata* Emery is the only case in which the nymphs are described as having no cocoon.

In the Ponerinæ the larvæ are nearly always fed with pieces of solid food, which is almost invariably animal matter. Arnold says that *Euponera sennaarensis* (Mayr) is possibly an exception to the rule:

This ant preys unceasingly on termites, but its nest very often contains considerable accumulations of grass seeds, which may perhaps be used as food.<sup>1</sup>

The economic value of the Ponerinæ in tropical countries can hardly be overestimated, for it may be safely asserted that at least 80 per cent. of their food consists of termites, and they thereby constitute one of the chief checks to these pests of the tropics. Certain species are exceptional, such as *Plectroctena mandibularis*, which feeds chiefly on millipedes and beetles, and *Platythyrea arnoldi* Forel, whose food consists entirely of small beetles, mostly Tenebrionidæ.

The colonies are usually small in ponerine ants, but may be very numerous in some species, such as *Pallothyreus tarsatus*, *Megaponera fœtens*, *Euponera sennaarensis*, many species of *Leptogenys* and *Odontomachus hæmatoda*.

The habit of foraging in files has been observed in several species of Ponerinæ in different parts of the world. In our region this habit is displayed by *Megaponera fœtens*, and to a slight extent by *Pallothyreus tarsatus*. The former marches in double file, and the striking disparity in size between the two forms composing the colony has a very singular appearance. Their prey consists entirely of termites, and when a suitable hunting-ground containing these animals has been found, the columns break up and pour into every hole and crack which leads to the invaded galleries. The method then adopted is as follows: each ant brings to the surface one or more termites, and then re-enters the galleries to bring up more victims. This is continued until each ant has retrieved about half a dozen termites, which, in a maimed condition, are left struggling feebly at the surface. The whole army reassembles again outside and each marauder picks up as many termites as it can conveniently carry, usually 3 or 4. The columns are then re-formed and march home. Less order is shown by *P. tarsatus*, but I have often seen this ant carrying termites, in short single files composed of about a dozen workers. (G. Arnold, *op. cit.*, pp. 7-8).

### PLATYTHYREA Roger

**WORKER.**—Small or medium-sized, slender, monomorphic, opaque black ants, with pruinose surface and very poorly developed pilosity, with flat clypeus often without a posterior suture, indistinct frontal area and large, thick, expanded and widely separated frontal carinæ. Mandibles large, triangular, with edentate or finely denticulate apical border. Maxillary palpi 6-jointed, labial palpi 4-jointed. Antennæ stout, funiculi without a distinct club. Eyes rather large; ocelli absent. Promesonotal suture distinct, other thoracic sutures feeble or obsolete. Petiole massive, not squamiform, its posterior articulation at the middle of the anterior surface of the petiole. The constriction between the latter and the gaster moderately pronounced. Middle and hind tibiæ with two spurs; claws with a single tooth.

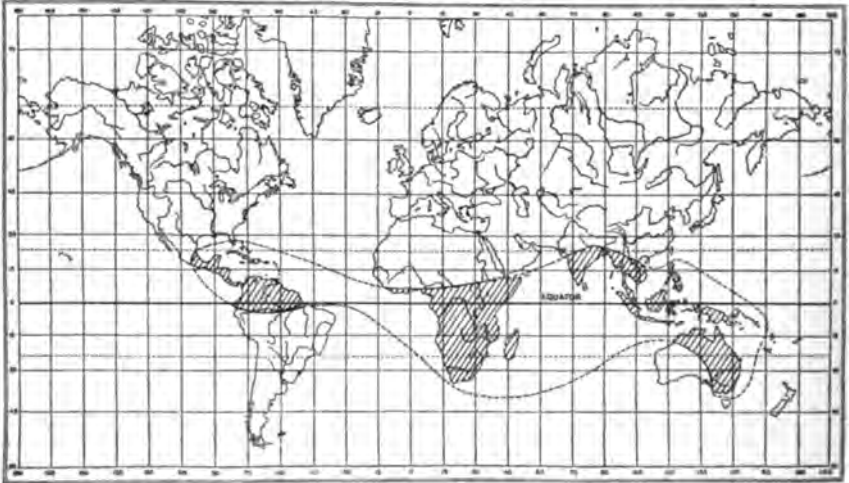
**FEMALE** winged, very similar to the worker and but little larger; eyes larger, but ocelli not always developed. Pronotum large; mesonotum depressed. Wings with two closed cubital cells, a discoidal cell and a closed radial cell as in many other Ponerinæ.

**MALE** more like the female than in most genera of the subfamily; clypeus more convex than in the worker and female; frontal carinæ not dilated anteriorly. Mandibles triangular, with sharp apical border. Antennæ 13-jointed; scape a little shorter

<sup>1</sup>1915, *Ann. South African Mus.*, XIV, p. 7.

than the second funicular joint. Eyes and ocelli very large. Pronotum large, not overarched by the mesonotum, the latter convex, with indistinct Mayrian furrows. Petiole much as in the worker. Pygidium rounded; cerci developed.

This genus, of which more than 35 species are known, ranges over the tropics of both hemispheres (Map 7) and is represented by more species in Africa and Madagascar than in the Indoaustralian or Neotropical Regions. Our American and many of the African species seem to feed largely or exclusively on termites. I have found *P. punctata* (Smith) of the West Indies nesting in termitaria. Arnold gives some notes on the habits of two of the African forms. Of *P. lamellosa* (Roger) subsp. *longinoda* Forel variety *rhodesiana* Forel he says:



Map 7. Distribution of the genus *Platythyrea*.

The nest of this species is so distinctive that it cannot be mistaken for that of any other Ponerinæ. The entrance is surmounted by a dome, from 6 to 8 inches high, by about 12 inches broad at the base. The dome is built up of very even-sized small pebbles, about 5 to 8 mm. in their largest diameter. The entrance is situated in the center above, and this is generally the only entrance, very exceptionally there may be a smaller and less regular opening at the base of the mound.

He gives the following account of *P. arnoldi* Forel:

I have met with this species on only one occasion. The nest, situated on an open piece of ground, was surmounted by a mound with the entrance at the apex, as in *lamellosa* variety *rhodesiana*, but unlike that species the mound of *arnoldi* contains no large pebbles. The surface of the mound was covered with the elytra and carcasses of hundreds of beetles, mostly Tenebrionidæ. Workers were seen carrying live beetles to the nest, the prey being held by its mandibles in a position above and parallel to the body of the ant. Since a careful examination of the rubbish-heap of this nest

failed to show the remains of other insects, it is probable that this species feeds entirely on Coleoptera, differing in this respect from most of the other members of the genus, which in Rhodesia, at any rate, are entirely termitophagous.

***Platythyrea conradti* Emery**

A single worker from Risimu (Lang and Chapin).

***Platythyrea gracillima*, new species**

WORKER (Fig. 5a and b).—

Length 9 mm.

Very slender. Head, excluding the mandibles, fully one and one-half times as long as broad, a little broader in front than behind, with very feebly convex sides and feebly excised posterior border. Mandibles rather long, moderately convex, their apical border with about 10 distinct teeth. Clypeus large, rather flat, more convex

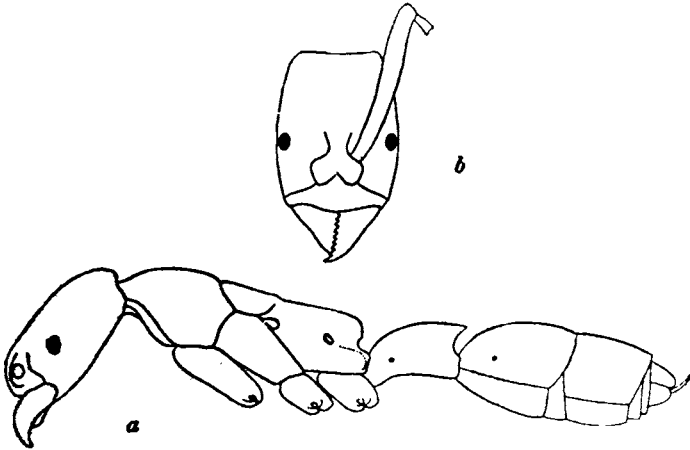


Fig. 5. *Platythyrea gracillima*, new species. Worker. a, lateral view of body; b, head of same from above.

in the middle behind, with broadly rounded, entire anterior border and distinct posterior suture. Frontal carinae very prominent, fused posteriorly. Eyes small, a little in front of the middle of the sides of the head. Antennal scapes long and stout, extending fully one-fourth their length beyond the posterior corners of the head; funiculi lacking, except the first joint, which is three times as long as broad. Thorax long and narrow, laterally compressed, especially in the meso- and epinotal regions; broadest through the pronotum, which is as broad as long and as broad as the head, rounded in front and on the sides. Mesonotum longer than broad. Promesonotal suture very distinct, mesoepinotal suture obsolete. In profile the dorsal outline of the thorax is nearly straight and horizontal; the base of the epinotum nearly twice as long as the declivity. The latter is abrupt, submarginate on the sides, which are obtusely angulate. Petiole laterally compressed; seen from above a little more than twice as long as broad, with straight, parallel sides; in profile evenly rounded in

front, straight above and very sharply and deeply concave behind, the ridge between the dorsal and posterior surface being narrow, transverse and feebly emarginate in the middle. At its posterior end the petiole is fully three-fifths as high as long. Postpetiole distinctly longer than broad, as broad as the gaster behind and not separated from it by a perceptible constriction, narrowed to the breadth of the petiole in front. First gastric segment as long as broad, the remaining segments short, telescoped into it. Legs rather long.

Slightly shining; mandibles more shining, finely and densely punctate; remainder of body even more finely and densely punctate; with a few larger, but very shallow and indistinct, superadded punctures on the head, thorax and petiole.

Hairs absent; pubescence yellowish gray, very short and fine, rather evenly distributed like dust over the whole body and the appendages, longer and more oblique on the mandibles.

Black; mandibles, clypeus, frontal carinæ, antennæ, legs, including the coxæ, posterior corners of the head, dorsal surface of pronotum, epinotum and petiole, and posterior border of postpetiole and first gastric segment, red; remaining gastric segments yellow.

Described from a single rather poorly preserved specimen from Avakubi (Lang and Chapin), taken from the stomach of a toad (*Bufo regularis*).

This species is unlike any of which I have seen specimens or descriptions in the shape of the head and body and especially of the petiole and gaster. In certain respects it approaches *viehmeyeri* Santschi of German East Africa, but is much smaller (*viehmeyeri* measures 13 mm.), and has densely punctate instead of striolate and sparsely punctate mandibles; the latter are denticulate; the head and antennæ are longer; the thorax not submarginate on the sides; the pronotum is not longer than broad; the mesonotum is longer than broad; the color is very different; etc.

#### PALTOHYREUS Mayr

**WORKER.**—Large black ants, with monomorphic workers. Clypeus in the middle with an elevated lobe, which is truncated anteriorly and projecting over the anterior clypeal border, marginate on the sides, excavated in the middle and extending back like a spearhead between the frontal carinæ which are moderately dilated and subtriangularly lobate. Mandibles elongate, triangular, their apical borders finely denticulate. Antennal funiculi slightly thickened distally. Eyes situated in front of the middle of the head. Thorax unarmed, not impressed dorsally; promesonotal suture distinct, mesoepinotal suture obsolete dorsally. Petiole surmounted by an erect scale. Constriction between the postpetiole and the gaster feeble; gaster rather long. Claws with a tooth in the middle.

**FEMALE** very similar to the worker but considerably larger and winged; thorax depressed, pronotum broadly exposed.

**MALE** with triangular clypeus furnished near its anterior border with a small conical tubercle; its posterior portion not prolonged backward between the antennal insertions. Antennæ long, scape much shorter than the second funicular joint.



*superciliaris*, and *polycercus*) captured by Lang and Chapin in the following localities: Niapu, ♀; Niangara, ♀; Ngayu, ♀; Medje, ♀, ♀, ♂; Avakubi, ♀; Akenge, ♀, ♀; Garamba, ♀; Gamangui, ♀; also a single worker from Faradje taken from the stomach of a frog (*Rana occipitalis*).

It is surprising to find that this large ant is represented by a greater number of specimens than any other species in the toad stomachs examined, for the insect is provided with a very formidable sting, is swallowed without mutilation, and can hardly be killed very quickly by the weak gastric fluids of the amphibians.

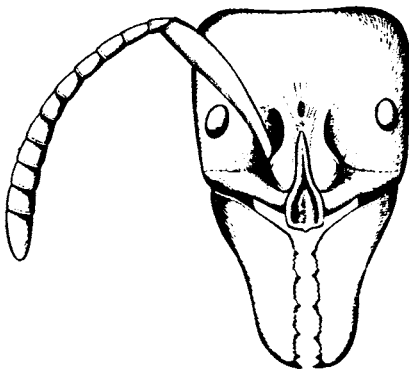


Fig. 6. *Paltothyreus tarsatus* (Fabricius).  
Head of worker.

Concerning the habits of *P. tarsatus*, Arnold writes: "This species is widely but locally distributed. Generally the worker and female go about singly, but occasionally forage in short columns, in single file. The food is varied but consists largely of termites. The nests have several entrances, which are sometimes surrounded by large heaps of finely divided earth. The species has a most powerful and offensive smell, which appears to me to resemble that of the juice in a

foul tobacco pipe." According to Santschi this species "répand une abominable odeur de charogne."

One of the worker specimens from Medje and one from Niangara had a long *Cordyceps* growing out of the side of the thorax. These ants were attached to sticks with their mandibles, a common condition in ants that die from the attacks of these and other fungi. Dr. Bequaert says that "dead specimens of *Paltothyreus tarsatus* thus parasitized are sometimes found, fixed with the mandibles to a leaf or grass-stalk. The fungus has been referred to *Cordyceps myrmecophila* (Cesati), of the family Hypocreaceæ. Its fructification usually grows out between the coxal articulations, on a slender stalk about 2 cm. long and ending in a club-shaped organ which bears the ascocarps" (See part IV).

MALE nearly as large as the worker major, with convex clypeus, not prolonged backward between the frontal carinæ. Mandibles very short, blunt and edentate. Antennal insertions farther from each other than from the sides of the head; scape longer than the second funicular joint. Eyes occupying less than half the sides of the head, their inner orbits slightly emarginate. Posterior border of head strongly marginate, somewhat colliform. Mesonotum prominent, twice as long as the pronotum, without Mayrian furrows. Ventral lamella of petiole with an acute posteriorly directed tooth behind the middle. Pygidium not spined. Claws with three or four minute basal teeth. Wings short, with a discoidal cell, two cubital cells and a closed radial cell.

This genus, like *Pallothyreus*, is monotypic and has much the same distribution, the single species, *M. fœtens* (Fabricius), ranging over a large part of the Ethiopian Region (Map 9).

***Megaponera fœtens* (Fabricius)**

Plate VI, Figure 2

Zambi, ♀; Niangara, ♀, ♀; Rungu, ♀; Avakubi, ♀; Faradje, ♀; Panga to Banalia, ♂; Boyulu, ♀; Niapu, ♀; Garamba, ♀; Akenge, ♀; Gamangui, ♀ (Lang and Chapin); Malela, ♀ (J. Bequaert).

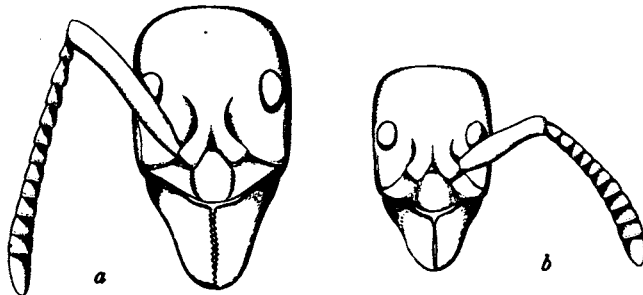


Fig. 7. *Megaponera fœtens* (Fabricius). a, head of large worker; b, head of small worker; both drawn to the same scale.

Seventeen of the specimens from Boyulu, Niapu, Garamba, Akenge, and Gamangui were taken from the stomachs of four species of toads (*Bufo funereus*, *superciliaris*, *regularis*, and *polyergus*) and a male from Faradje was taken from the stomach of a frog (*Rana occipitalis*).

The smaller individuals have the vertex and pronotum very shining, the mandibles toothless, and the funicular joints of the antennæ much shorter and more transverse than in the larger workers (Fig. 7a and b) and were therefore formerly regarded as a distinct species (*M. crassicornis* Gerstæcker). A worker media was also described by Emery as a distinct species, *M. dohrni*. At one time he interpreted the smaller

individuals as the true workers and the larger as ergatomorphic females. Arnold, who found this view improbable for the reason that the large are about four times as numerous as the small individuals in the colony, has recently discovered the true female.<sup>1</sup> It is of the ergatomorphic type, with a slender wingless thorax like the large worker and measures 18.5 mm. The petiole, however, is squamiform and not cuboidal as in the worker and the gaster is much more voluminous. It therefore resembles the females of *Leptogenys* (subgen. *Lobopelta*) and *Onychomyrmex* which I have described in former papers.

Armies of *Megaponera* were frequently observed by Mr. Lang preying on termites or carrying the larvæ and pupæ in files, sometimes of 300 or more individuals. In the literature there are some interesting accounts of the habits of this ant.<sup>2</sup> Wellman observed it in Benguela and informed Forel of its habit of marching in populous columns.<sup>3</sup> In a later paper<sup>4</sup> Forel published some observations of Prell on the same ant in German East Africa. He found it running in single file on the road. Most of the larger individuals were carrying worker and soldier termites in their jaws and Prell was struck both by the sonorous stridulation of the army and by its strong odor, which resembled that of oil of bitter almonds and was imparted to the alcohol of the vial in which the specimens were preserved. Similar observations were made by Bequaert in the Katanga.<sup>5</sup>

A more detailed, though incomplete, account of a raid on termites is given by Alluaud and Jeannel in Santschi's paper on the ants they collected in East Africa:

When they are disturbed and run away the *Megaponera fœtens* stridulate, and the noise made by a troop of them can be heard at a distance of several meters. We noticed this on several occasions, particularly at Fort Hall and New Moschi. At the latter station on the morning of April 10, 1912, in a corner of the forest at the edge of the Rau River, we encountered a troop of several hundred *Megaponera* marching in a column several abreast, apparently moving with decision to a predetermined goal. They descended the bank of the stream, stridulating loudly. We were unfortunately busily occupied at this spot collecting a lot of large *Papilio* which came down to the river to drink, so that we did not think of following the *Megaponera* army. An hour later these ants returned in good order in the reverse direction, each of them carrying

<sup>1</sup>1915, *Ann. South African Mus.*, XIV, p. 48, footnote, fig.

<sup>2</sup>Livingstone in his celebrated 'Missionary travels and researches in South Africa,' 1859, pp. 576-577, has given what is apparently the earliest account of the termite hunting Ponerine of Central Africa. His description of their foraging parties is remarkably accurate; he even mentions that "when disturbed, they utter a distinct hissing or chirping sound."

<sup>3</sup>1909, *Ann. Soc. Ent. Belgique*, LIII, p. 64. In *Entomological News*, XIX, 1908, p. 33, F. C. Wellman gives an account of what is evidently a raiding party of *Megaponera fœtens*, but unfortunately calls the ant "*Polyrhachis militaris cypreopubescens*."

<sup>4</sup>1911, *Bull. Soc. Vaudoise Sc. Nat.*, (5) XLVII, p. 361. See also Prell, H., 1911, 'Biologische Beobachtungen an Termiten und Ameisen,' *Zool. Anzeiger*, XXXVIII, pp. 243-253.

<sup>5</sup>1913, *Rev. Zool. Afr.*, II, p. 422.

in its mandibles a whitish pellet consisting of dead termites glued together with saliva. Some of them carried as many as ten to twelve termite workers thus agglutinated, others only two or three soldiers; one carried a deâlated male, possibly the king of the plundered termitarium. The number of termites in a pellet varied with its size, but not an ant returned without something. While collecting a number of these *Megaponera fatens* with their booty we experienced the effect of their sting, which is lancinating and very painful but very transitory.

In his monograph of the Formicidæ of South Africa (*loco citato*, p. 47) Arnold says:

It is a common ant in Rhodesia and lives almost exclusively on termites, which are carried off by means of carefully arranged raids in which the ants march in double file. This is the species which is popularly called the "Matabele" ant, and like its cousin *Paltothyreus*, it is also endowed with a very offensive odor. They stridulate very loudly when disturbed, and their sting is exceedingly painful. The entrance to the nest consists of one or more simple holes without any mounds of earth around them.

In the Proceedings of the Rhodesian Scientific Association, XIII, 1914, p. 26 et seq., Arnold has recently published a fascinating description of the extraordinary way in which the Matabele ant changes its nesting site and is followed by its numerous guests. I quote the greater part of his account, as the journal in which it appeared may not be accessible to my readers:

This is eminently a termitophagous species, and it is likely that it changes the site of its nest more often than is the case with the majority of our ants. When we bear in mind how continuous their assaults are on the colonies of termites, it seems very probable that the supply of the latter insects may be so diminished within the practical range of the camp of the raiders that the latter may find it advantageous to move their quarters from time to time to new and more fruitful country. The migration of this ant which I am about to describe is of particular interest, apart from the behavior of the guest insects, because it was the occasion of the discovery of the true queen of the species. \* \* \*

My attention was attracted to this migration by seeing a mass of these ants assembled together with their larvæ and pupæ, in the open. On one side, many workers were to be seen bringing along the larvæ in their jaws, on the other side of this mass a few workers were moving in the other direction, in a somewhat hesitating manner. Following the track backwards, I came to the site of the old nest, situated about 15 feet away. Returning to the camp, it was seen that some workers had started to pick up the larvæ again, and were carrying them yet further away from the original nest, only to be laid down again at about another 15 feet further away. Subsequent observations showed that the migration was carried out in three stages, three temporary camps being formed between the old and the new nests, which were about 60 feet apart. The method adopted by the insects was as follows. First of all, the eggs, larvæ, pupæ and males were taken from the old nest and put down at the first camp, from which many workers were to be seen hurrying back to fetch away the rest of their charges. In the meantime, a few workers were to be seen pacing up and down on the other side of the camp. They did not carry any larvæ and it would almost

seem as though they had some idea of the numerical composition of the colony, and of what the volume of the first camp should be, before the old nest could be considered to have been emptied by its inhabitants, and the proper moment to have arrived for another start to be made. However, after about six or seven minutes, the march recommenced; and within a short time the second camp had been made at a distance of about 15 feet from the first. Similarly a third and last camp was formed further on. It was while the first camp was about to break up that I saw an insect then much larger than the largest worker, and which, when captured in the third camp, proved, to my surprise, to be the queen.

The entrance to the old nest was a hole about 1 inch across, which ran down vertically for about 5 inches and then branched off at an angle. Looking down this hole, the various guests and parasites could be seen climbing up the walls in an almost continuous stream, hastening to join their hosts in their new home. These insects comprised a *Lepisma*, two species of staphylinid beetles, a histereid beetle and an onthophagous beetle; there was also a spider. The *Lepismas* as usual were very plentiful; of the larger staphylinid I saw only one specimen, but of the smaller sort and of the other beetles very many examples occurred, and during the half hour or so through which I watched the procession, about two dozen specimens of the spider were counted. Had it been possible to have cinematographed the scene, it would have furnished us with a film of surpassing interest. Here, as in the case of *Myrmecaria*, the myrmecophiles were able to follow the tracks of their hosts without any delay or uncertainty. Occasionally one of the smaller staphylinids would leave the beaten track for a short distance and then return to it again a little further on, but to the majority of these commensals, the odour of their hosts had laid down a path as clearly marked as a macadamized road would be to our eyes, so that with the above exception, it was rare to see any of these insects swerve from the line of march by as much as an inch.

This motley crew of cringers, thieves, murderers and body-snatchers did not appear to attract the slightest attention from their victims the ants, which were too busy with the work in hand to waste any time on the rabble following in their wake. Of all this crowd, the spiders alone were able to keep pace all the time with the ants, but the slowest, the very small histereid, even at its most feverish pace, did not succeed in covering more than 2 inches per minute, so that it would have arrived at the new nest about six hours after leaving the old. Those beetles which managed to reach the different camps, while these were still intact, buried themselves in the heap of larvæ and cocoons, where they remained until the gradual depletion of the mass made it clear that they had not arrived at the site of the real nest and that another wearisome journey had to be made to attain their goal.

The spiders moved about in the camps in a very easy and unconcerned manner, making no attempts to hide under the piles of cocoons. They ran over the backs of the ants, mingling in a friendly way with the crowd; yet even in the hurry and bustle of this march, it was not possible for these animals to conceal entirely their method of earning a living. A worker ant, carrying a larva in its jaws, was seen just about to pass a spider standing on the edge of the camp. The spider ran up to the worker, stroked it with its front pair of legs for a second or two, and then plunged its fangs into the larva. The latter was released by the ant after a little hesitation, and within five minutes had been sucked dry by the spider. We know that there are many ant parasites which live chiefly on the young of their hosts; but usually these insects

regurgitated liquid food, and the strong integument is evidently an adaptation to exposure to the air and light and to the exigencies of frequent and protracted transportation in the powerful denticulate jaws of the workers. The nudity of the integument indicates that even the very young larvæ are carried singly and not in bunches held together by interlocking hairs as in most other species of ants. The cocoons are black and remarkably tough, characters which I have observed in certain Australian Ponerinæ of the genera *Diacamma* and *Rhytidoponera* as adaptations to exposure to sunlight.<sup>1</sup> This interpretation is confirmed by Mr. Lang, who, without knowing of my observations, informed me that he was surprised to find *Megaponera* often exposing its dark cocoons in heaps to the sunlight.

Recently, in a letter to Prof. Poulton,<sup>2</sup> G. D. H. Carpenter records some additional observations which he was able to make on *M. fœtens* southwest of Lake Victoria:

I see a good deal of the ant *Megaponera fœtens* here: one is always coming across their long, solemn, slowly marching, black processions—of any number from 50 to 500 or so. I have never seen them carrying any other booty but the species of termite which abounds here—the one I have alluded to before. It lives underground and makes no hills—coming out of little holes and running about, uncovered, in the open, to get bits of live or dead grass which it carries down the holes. Presumably in correlation with its open-air habits, its color is much darker than the large termite whose hills I used to destroy on the islands, and which devoured my house. This one does not attack wooden posts nor does it make covered runs. Curiously enough, I have never seen any soldiers, which is perhaps why *Megaponera* wages such ceaseless war against it. This ant, when it goes out in column, wanders about looking for the termite holes. Immediately one is found there is great excitement. The little bits of grass which sometimes plug the entrance are dragged out, and the ants scramble down the hole very shortly reappearing with termites, feebly struggling in their jaws. Sometimes there seems evidence of an underground barricade, as ants come up to the surface with bits of dead grass, etc., as if they were breaking down hastily erected barricades! One can almost picture the termites hastily throwing up partitions of grass and earth to keep back the invaders. It would be interesting to know if the reason why *Megaponera* is absent from some parts, is because this particularly defenceless termite is absent also.

#### **BOTROPONERA** Mayr

**WORKER.**—Small, medium-sized or large, opaque or subopaque, usually strongly sculptured black or dark brown ants. Workers monomorphic. Head subrectangular, with the eyes usually well developed, rarely vestigial, placed at or in front of the posterior third of the head. Mandibles subtriangular, with coarsely dentate apical margin. Cheeks without a carina. Clypeus with rounded, obtusely angular or feebly

<sup>1</sup>1915, *Ann. Ent. Soc. America*, VIII, pp. 335-337.

<sup>2</sup>1917, *Trans. Ent. Soc. London*, (1916) *Proc.*, p. cxxix.

and sinuately marginate anterior border, prolonged backward as a narrow point between the frontal carinæ, which are broadly and lobularly expanded, incrassated and covering the insertions of the antennæ. Frontal groove distinct. Antennæ stout, 12-jointed. Thorax with distinct promesonotal suture, but with the mesoëpinotal suture and that between the mesosternum and mesepisternum absent or obsolescent. Pronotum not marginate on the sides; epinotum usually unarmed. Petiole with a thick, more or less transverse node, in a few species somewhat compressed and dentate above or behind. Gaster subcylindrical, with pronounced constriction between the postpetiole and succeeding segment, the postpetiole truncated in front; sting rather short and blunt. Middle and hind tibiæ each with a large pectinated and a simple lateral spur; claws simple.

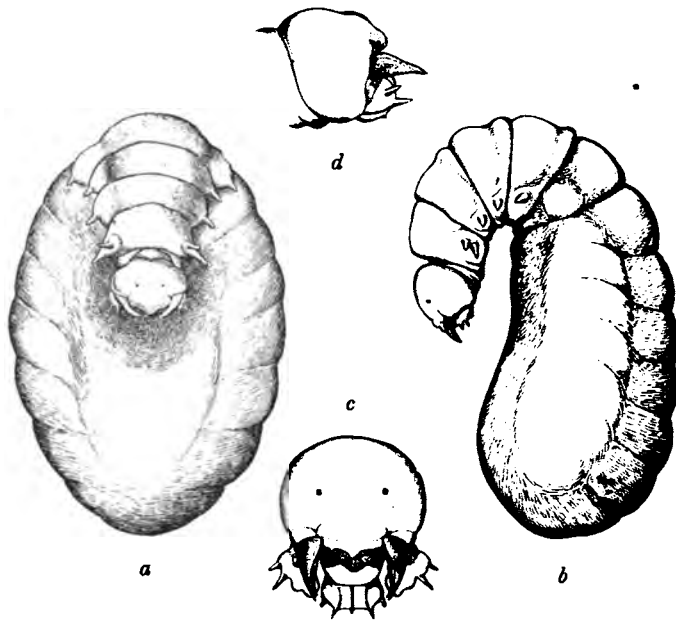


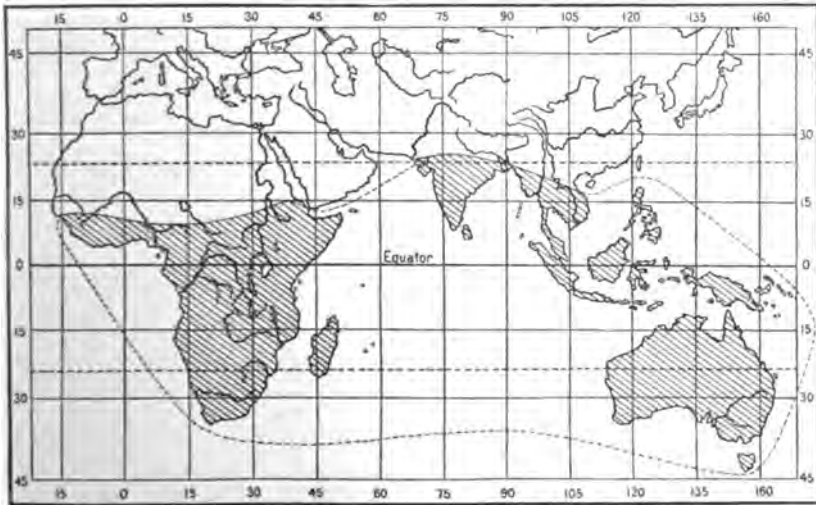
Fig. 9. *Bothroponera sublavisi* Emery. Australia. Adult larva. a, ventral view; b, lateral view; c, head, dorsal view; d, head in profile.

**FEMALE** only slightly larger than the worker; winged; in other respects very similar to the worker; ocelli small; pronotum broad and exposed; mesonotum small, flattened, broader than long. Wings rather broad; with a discoidal cell, two cubital cells and a closed radial cell.

**MALE** nearly the same size as the worker. Head short, rounded behind; eyes and ocelli very large; mandibles small, flat, edentate. Palpi long, the labial pair 3-jointed, the maxillary pair 5-jointed. Frontal carinæ short. Antennæ very long, filiform, 13-jointed; the scape short, scarcely twice as long as broad; the first funicular joint not longer than broad, the remaining joints long and cylindrical. Pronotum transverse, truncated in front; mesonotum without Mayrian furrows; scutellum very

convex. Abdomen strongly constricted behind the postpetiole; nygidium terminating in a downwardly directed spine. In some species the penultimate sternite of the gaster is notched and prolonged on each side as a prominent lobe. Genitalia retracted.

Mayr described *Bothroponera* as a genus; but Emery, Forel, and Santschi have been treating it as a subgenus of *Pachycondyla*. I return to Mayr's conception for the following reasons: First, the larvæ of *Bothroponera* (Fig. 9a-d) are quite different from those of *Pachycondyla*, as I have shown in a former paper.<sup>1</sup> Second, *Bothroponera*, being a strictly paleotropical group may be advantageously separated as a



Map 10. Distribution of the genus *Bothroponera*.

distinct genus from the purely neotropical *Pachycondyla*. *Ectomomyrmex* may be regarded either as a subgenus of *Bothroponera* or as an independent genus. I prefer to adopt the latter course. I also separate out a small group of species of *Bothroponera* (*gabonensis* Ern. André and *sveni* Forel) as a distinct genus *Phrynoponera* (*vide infra*). Third, there are certain peculiarities in the habits of *Bothroponera* which indicate that the species are generically distinct. Like *Pachycondyla*, they form small colonies under stones in rather moist, clayey soil, but are more sluggish and do not sting readily when captured and instead emit from the posterior end of the body a peculiar mass of frothy substance. I have observed this in some of the Australian species, and Bingham and Taylor have seen similar behavior in the Indian *B. rufipes* (Jerdon), according to Wrought-

<sup>1</sup>1918, 'A study of some ant larvæ, etc.' Proc. Amer. Phil. Soc., LVII, p. 299.



on.<sup>1</sup> Bingham says that this ant "blows a whitish, acrid smelling, rather gelatinous froth when seized" and according to Taylor it exudes when seized "a milky substance of a frothy nature which hardens on exposure to the air and resembles fine cotton; it is called 'domona chunti' or 'gendu,' the 'domonas' being the weaver caste in Orissa." *B. tridentata* (F. Smith) of Borneo seems to have the same habit, according to Beccari.<sup>2</sup>

The genus *Bothroponera* is widely distributed over the Ethiopian, Indomalayan, Papuan, and Australian Regions (Map 10). Africa is very rich in species but Australia possesses almost as many.

The following table may be of some assistance in identifying the workers and females of the Ethiopian species of *Bothroponera*.

1. Head, thorax, petiole and postpetiole coarsely punctate, punctate-rugulose or striated.....	2.
These regions finely and densely punctate, sometimes with superimposed, larger but shallow punctures.....	9.
2. Mandibles striate.....	3.
Mandibles smooth, sparsely punctate.....	7.
3. Petiolar node broadly excised posteriorly.....	<i>cariosa</i> Emery.
Petiolar node sharply truncated posteriorly.....	4.
4. Length 8 mm.; testaceous yellow.....	<i>cribrata</i> (Santschi).
Length not less than 9 mm.; black or brownish black.....	5.
5. Antennal scapes reaching to occiput.....	<i>cavernosa</i> (Roger).
Antennal scapes not reaching to occiput; eyes small.....	6.
6. Length 9 mm.; golden pubescence on body, especially on head, abundant; sculpture less pronounced.....	<i>talpa</i> Ern. André.
Length 12 to 15 mm.; golden pubescence less pronounced; sculpture coarser.	<i>pachyderma</i> (Emery).
7. Petiolar node broadly excised posteriorly; body covered with golden pubescence.	<i>granosa</i> (Roger).
Petiolar node truncated behind; body without golden pubescence.....	8.
8. Gaster opaque, finely striated.....	<i>strigulosa</i> Emery.
Gaster more or less shining.....	<i>pumicosa</i> (Roger).
9. Eyes well developed in the workers.....	10.
Eyes vestigial in the workers.....	15.
10. Length 5.5 mm.....	11.
Length at least 7 mm.....	12.
11. Mandibles 7-toothed; petiole as long as broad.....	<i>picardi</i> (Forel).
Mandibles 6-toothed; petiole nearly twice as broad as long.....	<i>silvestrii</i> (Santschi).
12. Mandibles shining, sparsely punctate.....	<i>soror</i> (Emery).
Mandibles finely striate.....	13.
13. Opaque; head ovoid.....	<i>krügeri</i> (Forel).
Subopaque or shining; head subrectangular.....	14.

<sup>1</sup>1891, 'Our Ants.' Journ. Bombay Nat. Hist. Soc., VII, p. 54.

<sup>2</sup>'Nelle foreste di Borneo.' Firenze, 1902, p. 237; teste Emery, 1911, 'Genera Insectorum, Ponerrina', p. 75.

14. Very shining; length 12 mm.; clypeus angularly produced in middle; eyes small. . . . . *lavissima* (Arnold).  
Subopaque; length 7 to 7.5 mm.; clypeus feebly sinuate in middle; eyes larger. . . . . *crassa* Emery.
15. Length only 4.5 to 5.5 mm.; mandibles smooth, sparsely punctate; eyes very small, with less than a dozen facets. . . . . *sjöstedti* (Mayr).  
Length 6.5 to 7 mm.; mandibles striate at the tip; eyes larger, with about 45 facets. . . . . *fugax* (Forel).

***Bothroponera pachyderma* (Emery)**

Manamana, ♂; Bafwasende, ♂; Medje, ♂; Ngayu, ♂; Niapu, ♂, ♀; Niangara, ♂; Akenge, ♂, ♀ (Lang and Chapin). The specimens from Manamana, fourteen in number, are accompanied by the note: "Found under a log. When it was lifted the ants feigned death." The specimen from Bafwasende is very small. The specimens from the other localities, seventy-four in number, were all taken from the stomachs of toads (*Bufo polycercus*, *superciliaris*, *funereus*, and *tuberosus*). One specimen from Akenge was taken from the stomach of a frog (*Rana albolabris*).

I believe I have identified this species correctly. All the specimens, both workers and females, have a blood-red, subtriangular spot at the middle of the posterior border of each gastric segment. I regard Sant-schi's *B. sculpturata*, described from a female, as synonymous with Emery's *pachyderma*.

***Bothroponera pachyderma* variety *funerea*, new variety**

FEMALE (deälated).—

Length more than 13 mm.

Differing from the typical form in its somewhat greater size and in color, being coal black, with only a slight brownish tinge to the legs. Even the frontal carinæ and antennæ are black and there is no red on the gastric segments. The erect hairs on the dorsal surface are also black, at least in certain lights, not fulvous as in the typical form, but the hairs and pubescence on the tibiæ and tarsi are of the latter color. The foveolæ on the gastric segments, especially behind the anterior portion of the first segment, seem to be shallower and both they and the spaces between them to be less distinctly striated than in the typical *pachyderma*.

A single specimen from Medje (Lang and Chapin) taken from the stomach of a toad (*Bufo polycercus*).

***Bothroponera talpa* Ern. André**

Niapu, ♂; Niangara, ♂; Avakubi, ♂; Medje, ♂, ♀ (Lang and Chapin). Eight specimens, all taken from the stomachs of toads (*Bufo funereus*, *polycercus*, and *superciliaris*) and agreeing well with André's description.

**Bothroponera soror** (Emery)

Akenge, ♀, ♀; Medje, ♀, ♀; Ngayu, ♀; Niangara, ♀; Avakubi, ♀; Niapu, ♀; Faradje, ♀ (Lang and Chapin). Forty-one workers and three dealated females. All but three of these specimens were taken from the stomachs of toads (*Bufo superciliaris*, *polycercus*, *funereus*, *tuberosus*, and *regularis*); one from Faradje was taken from the stomach of a frog (*Rana occipitalis*). Arnold records this as a rather rare species in Rhodesia. "It usually nests under stones, and has a very strong smell of cockroaches. The colonies do not usually comprise more than two dozen individuals." Two of the specimens from Medje were taken by Mr. Lang while they were crawling on tree trunks and also on the tents of the expedition. He notes that, "when crushed, they gave off a stench reminding one of a bug."

**Bothroponera soror** variety **ancilla** (Emery)

A single worker from Isangi (Lang and Chapin) differs from the typical *soror* in its smaller size (less than 7 mm.). It differs from Emery's description of the variety *ancilla*, however, and agrees with the typical form in having a trace of the mesoëpinal suture.

**Bothroponera sjöstedti** (Mayr)

Text Figure 10

Eight workers taken by Dr. Bequaert at Malela agree very closely with Mayr's description of the types from Cameroon except in being

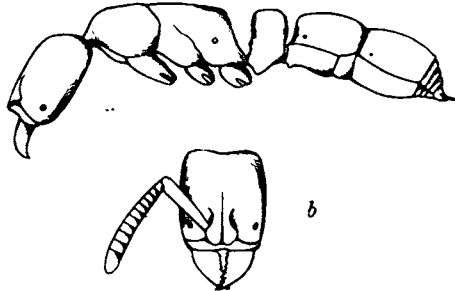


Fig. 10. *Bothroponera sjöstedti* (Mayr). Worker. a, lateral view of body; b, head from above.

smaller. They were nesting "under the fallen trunk of a palm in swampy ground." The type specimens were found by Sjöstedt "in a rotten palm trunk," according to Mayr. The species is peculiar in its very small size, pale coloration and in having the eyes reduced to a few ommatidia.

**PHRYNOPONERA** Wm. M. Wheeler

**WORKER.**—Allied to *Bothroponera* but distinguished by the following characters: body shorter and stouter; mandibles narrower, not triangular, their basal and external borders parallel, the apical border oblique, bluntly dentate, not forming a distinct angle with the basal border. Clypeus short, elevated in the middle, with a median furrow and a ridge on each side, the anterior border broadly rounded and entire or bluntly bidentate, posteriorly extending back between the frontal carinæ as a narrow acute point. Frontal carinæ expanded as lobes but the latter are not thickened as in *Bothroponera*, but depressed except at the edges which are smooth and slightly elevated, concealing the insertions of the antennæ as in *Bothroponera*. Eyes rather large and convex, broadly elliptical, placed just in front of the middle of the head. Antennæ stout, 12-jointed as in most Ponerinæ. Thorax with broad pronotum; promesonotal suture distinct, arcuate; mesoëpinal and mesepisternal sutures obsolete. Epinotum with two stout spines. Petiole surmounted by a flattened scale which curves back over the postpetiole and terminates in a comb consisting of five acute, flattened teeth. Remainder of abdomen very short, oval, the postpetiole which forms nearly half of it, not truncated but rounded in front and not separated by a constriction from the first gastric segment, though the stridulatory surface is well developed as in *Bothroponera*. Sting very long; longer, more slender and more acute than in the latter genus. Legs rather long and stout; middle and hind tibiæ each with a long pectinated and a simple lateral spur; claws simple. Sculpture of body coarse; pilosity short, abundant, coarse and erect.

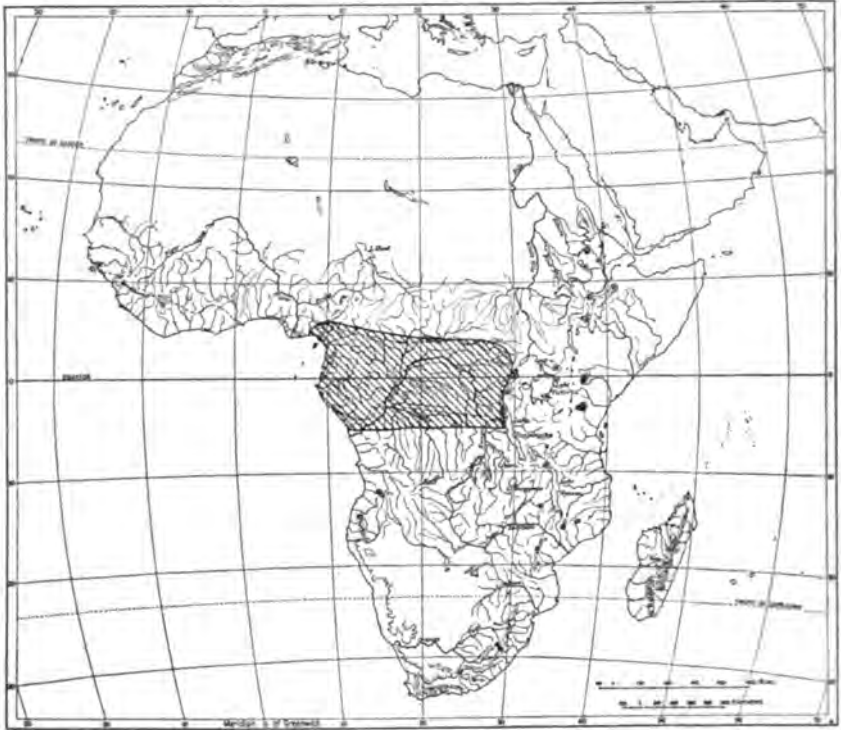
**FEMALE** winged, but wings unknown; in other respects very similar to the worker and scarcely larger. Ocelli small. Pronotum broad and exposed; mesonotum and scutellum flat, together nearly circular, each being broader than long.

**MALE** unknown.

**GENOTYPE:** *Bothroponera gabonensis* Ern. André.

In my opinion this is a very distinct genus and would probably long since have been recognized as such had it not been that only one or two species were known and these very imperfectly, that one species of *Bothroponera* [*B. bispinosa* (Smith) of India] has a spined epinotum, and that another Indian species [*B. rufipes* (Jerdon)] has the petiole antero-posteriorly compressed above and the border denticulate, thus suggesting the conditions in *Phrynoponera*. In reality the latter genus is distinct, not only in the structure of the petiole but also of the mandibles, frontal carinæ, and postpetiole, in the absence of any constriction between the postpetiole and the gaster, and in the abbreviation of the latter. The genus seems to be confined to a narrow region in West-Central Africa (Map 11). The species probably all live in the humus of the rain forest. The workers and females of the forms which I have seen from the Congo may be separated with the aid of the following dichotomy.

1. Clypeus with two large blunt teeth..... 2.  
Clypeus without teeth..... 7.
2. Length 6.5 to 7.5 mm.; mandibles 4-toothed..... 3.  
Length 9 mm.; mandibles 7-toothed..... *heterodus*, new species.



Map 11. Distribution of the genus *Phrynoponera*.

3. Gaster shining, feebly sculptured (*gabonensis*).....4.
4. Gaster opaque or subopaque, strongly sculptured.....5.
4. Mandibles, frontal carinæ, antennæ and legs red... typical *gabonensis* (E. André).
4. Mandibles, frontal carinæ, antennæ and legs blackish.... var. *esta*, new variety.
5. Mandibles smooth, sparsely punctate.....6.
5. Mandibles striated and sparsely punctate. .... var. *striatidens* (Santschi).
6. Mandibles, frontal carinæ, antennæ and legs red... var. *secunda*, new variety.
6. Mandibles, frontal carinæ, antennæ and legs blackish... var. *umbrosa*, new variety.
7. Small species (6 mm.); funicular joints 2 to 10 much broader than long;  
mandibles and appendages black..... *bequaerti*, new species.
7. Large species (8 to 9 mm.); funicular joints 2 to 5 at least as long as broad; 6  
to 10 slightly broader than long; mandibles and appendages red.  
*sveni* (Forel).

#### ***Phrynoponera gabonensis* (Ern. André)**

There are specimens of five different forms of this species in the collection. To *gabonensis*, *sensu stricto*, I refer a single worker from Bafwasende, one from Medje (from the stomach of a toad, *Bufo funereus*),

Described from eight workers and a female from Medje (type locality), two workers from Ngayu, and a female from Gamanguï (Lang and Chapin), all found in the stomachs of toads (*Bufo superciliaris*, *polycercus*, *funereus*, and *tuberosus*).

***Phrynoponera gabonensis* variety *fecunda*, new variety**

WORKER and FEMALE (deâlated).—Having the coloration of the typical form, i. e., with the mandibles, frontal carinæ, antennæ, legs, and posterior borders of the abdominal segments red, but with the postpetiole and gaster opaque, densely and finely punctate, and with superadded coarser longitudinal punctures, or aciculations, having sharp anterior edges. The legs are somewhat more opaque and more coarsely coriaceous than in the typical *gabonensis*. The mandibles are shining and sparsely and coarsely punctate, as in the two preceding forms.

Described from eleven workers and one female from Akenge (type locality), eighteen workers from Medje, two from Ngayu, and one from Avakubi (Lang and Chapin). All the specimens were found in the stomachs of toads (*Bufo superciliaris*, *polycercus*, *funereus*, and *tuberosus*).

***Phrynoponera gabonensis* variety *umbrosa*, new variety**

WORKER.—Coloration like that of the variety *esta*, black throughout, the postpetiole and gastric segments with narrow brown posterior border. The sculpture of the gaster is that of the variety *fecunda*.

Two specimens from Medje (Lang and Chapin) from the stomach of a toad (*Bufo polycercus*).

***Phrynoponera gabonensis* variety *striatidens* (Santschi)**

Medje, ♀; Akenge, ♀; Ngayu, ♀ (Lang and Chapin). Four specimens, all from the stomachs of toads (*Bufo polycercus*, *funereus*, and *tuberosus*). These specimens have the coloration of the typical *gabonensis* and variety *fecunda* and the abdominal sculpture of the latter, but the mandibles are subopaque and finely striated, except at the base, in addition to having the coarse, sparse punctures of the other varieties. The epinotal spines seem to be a little longer and more acute than in any of these forms.

***Phrynoponera heterodus*, new species**

FEMALE (deâlated).—

Length 9 mm.

Very closely related to *gabonensis* but differing in its larger size and in the following particulars: the apical borders of the mandibles are 7-toothed and, in addition to the coarse punctures, are finely striated on their apical halves. The antennæ are somewhat longer, the funicular joints 2 to 7 being as long as broad. The rugæ on the front and vertex are distinctly coarser and more divergent, the eyes somewhat

smaller, the posterior corners of the head more acute, the clypeus bluntly bidentate as in *gabonensis*. The sculpture of the thorax and petiole is also very similar, the postpetiole and gaster sculptured as in the variety *striatidens* but even more sharply, so that the whole surface is opaque. The epinotal spines are broad and flat as in *gabonensis* but the median petiolar tooth is nearly twice as long as the intermediate teeth. The pilosity is, if anything, a little more abundant than in *gabonensis* and its varieties. The color is black, with the mandibles, legs, and posterior borders of the abdominal segments dark castaneous brown.

A single specimen from Stanleyville (Lang and Chapin), without further data. This form might be regarded as a large subspecies of *gabonensis* but its precise status can hardly be determined without worker specimens.

***Phrynoponera bequaerti*, new species**

Text Figure 12

FEMALE (deālated).—

Length 6 mm.

Resembling *gabonensis* and *heterodus* but much smaller. Head, excluding the mandibles, fully as broad as long, the posterior border nearly straight; the sides very feebly and evenly convex; the eyes large, moderately convex, with their posterior orbits at the middle of the sides. Mandibles shaped as in *gabonensis*, with obliquely, bluntly 4-toothed apical borders. Clypeus short, with broadly rounded, entire anterior border, the elevated central portion somewhat concave behind in the middle, with a ridge on each side. Antennæ short and thick, the scapes scarcely extending beyond the posterior border of the head; first funicular joint nearly as long as broad, remaining joints, except the last, decidedly broader than long. Thorax as broad as the head, short, shaped much as in *gabonensis* but the epinotal teeth are proportionally longer, being longer than broad at their bases and as long as the distance between the latter, flattened dorsoventrally, with round lobe-like tips. Petiole with longer spines than in *gabonensis*, the lateral spines being as long as the remainder of the segment and the median spine as long as the lateral.

Mandibles smooth and shining with very coarse, sparse punctures, most numerous near the inner border. Remainder of body subopaque except the borders of the frontal carinæ which are smooth and shining. Head reticulate-rugose, rather coarsely on the sides, on the front and vertex more finely, the rugæ scarcely longitudinal. Thorax covered with coarse umbilicate foveolæ, which are largest on the mesonotum but everywhere so close together that the surface may be described as reticulate-rugose. Anterior surface of petiole with similar sculpture, but the meshes of the

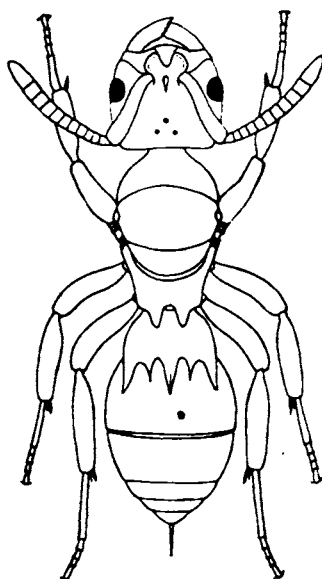


Fig. 12. *Phrynoponera bequaerti*, new species. Deālated female.

reticulum elongate. Postpetiole and gaster appearing longitudinally striate owing to their having a sculpture like that of *P. heterodus* and several of the varieties of *gabonensis*. Legs and antennal scapes nearly opaque, closely coriaceous.

Pilosity and pubescence much as in *gabonensis* and *heterodus* but the former more reclinate on the head, thorax, and abdomen.

Black; mandibles, frontal carinæ, and legs dark brown.

Described from a single specimen taken from the stomach of a toad (*Bufo superciliaris*) from Ngayu (Lang and Chapin) This is a very distinct species, easily characterized by its small size, edentate clypeus, long median petiolar spine and peculiar cephalic and thoracic sculpture.

#### *Phrynoponera sveni* (Forel)

Three workers from Medje (Lang and Chapin), agree perfectly with Forel's description. They all show, however, a beautiful blue opalescence, like that of *Lobopelta iridescens*, on the smooth declivity of the

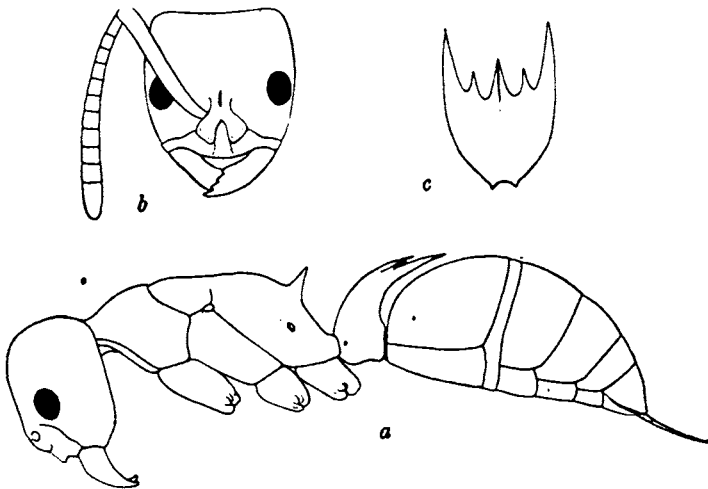


Fig. 13. *Phrynoponera sveni* (Forel). Worker. a, lateral view of body; b, head from above; c, petiole, dorsal view.

epinotum, the sides of the petiole, and the whole surface of the postpetiole. This may have been overlooked by Forel, as the surfaces of these ants are often covered with a layer of dirt. It was only after my specimens had been thoroughly washed in caustic potash that the blue coloration of the parts above mentioned was revealed. *P. sveni* is a strongly marked species, characterized by the long antennæ, toothless clypeus, and slender, pointed and upwardly directed epinotal spines (Fig. 13a-c).



**EUPONERA** Forel

Resembling *Bothroponera* but smaller and much more finely sculptured.

**WORKER** monomorphic, with subtriangular mandibles the apical margins of which are dentate. Cheeks not carinate. Frontal carinæ closely approximated, expanded and lobular in front and concealing the insertions of the antennæ. Eyes placed near or in front of the anterior third of the head, sometimes vestigial or even absent. Clypeus rounded and obtusely pointed in front, usually carinate. Antennæ slender, 12-jointed, the scapes slightly thickened apically but not clavate. Thorax shaped somewhat as in *Bothroponera* but with distinct mesoepinotal suture and usually with distinct mesoepinotal constriction. Petiole surmounted by a thick transverse scale. Middle and hind tibiæ with two spurs; claws simple.

**FEMALE** winged; in some of the subgenera scarcely larger, in one (*Brachyponera*) considerably larger than the worker; in other respects similar.



Map 12. Distribution of the genus *Euponera* (simple crossing) and of *Euponera* (*Brachyponera*) *sensaenensis* (Mayr) (double crossing).

**MALE** much like the males of *Pachycondyla* and *Bothroponera* but differing somewhat in the various subgenera.

Emery has divided this genus into four subgenera: *Euponera*, *sensu stricto*; *Mesoponera*; *Brachyponera*; and *Trachymesopus*. *Euponera*, with a single species, is confined to Madagascar; the other subgenera have a wide distribution over the tropical and subtropical portions of both hemispheres (Map 12). The species live in the ground, either in crater nests or under stones, logs, etc. *Eu.* (*Mesoponera*) *castanea* (Mayr) of New Zealand lives, as a rule, in rotten logs and stumps. The colonies of *Brachyponera* are rather large and populous, those of the other sub-

genera much smaller. In the subgenus *Trachymesopus* there is a pronounced tendency to hypogaëic habits and also, therefore, to a degeneration of the eyes in the worker.

***Euponera (Mesoponera) ingesta*, new species**

Text Figure 14

WORKER.—

Length 5.5 to 6 mm.

Head somewhat longer than broad and about as broad in front as behind, with evenly convex sides and feebly excavated posterior border. Eyes small, flat, broadly elliptical, placed at the anterior fifth of the sides of the head. Clypeus carinate, its anterior border entire, rounded and projecting in the middle, sinuate at the sides.

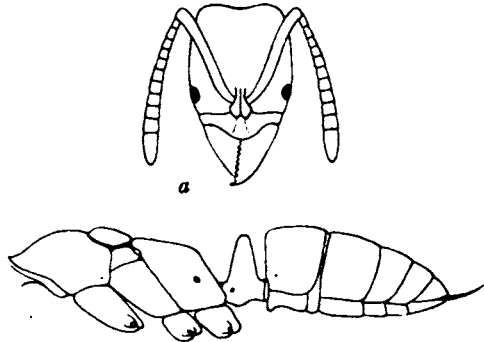


Fig. 14. *Euponera (Mesoponera) ingesta*, new species. Worker. a, head from above; b, thorax and abdomen in profile.

Mandibles moderately long, convex, their apical borders with 8 or 9 subequal teeth. Antennal scapes extending slightly beyond the posterior border of the head; first and second funicular joints subequal, about one and one-half times as long as broad, joints 4 to 6 somewhat shorter, remaining joints, except the last, as broad as long. Pronotum as long as broad, somewhat depressed above and very bluntly submarginate on the sides. Mesonotum convex, transversely elliptical, nearly twice as broad as long, completely surrounded by a strong suture; mesoëpinotal constriction distinct. Epinotum nearly as long as the pro- and mesonotum together, but somewhat lower, the base and declivity straight, subequal, forming an obtuse angle with each other, the former horizontal in profile, the latter flat; marginate on the sides. Petiolar scale in profile high and cuneate, its anterior surface feebly convex from side to side, its posterior surface flat, with a shallow longitudinal impression in the middle; the border evenly rounded, semicircular from behind, slightly narrowed ventrally. Gaster short, postpetiole sharply truncated in front, the constriction between it and the gaster feeble. Legs moderately long.

Mandibles shining, finely and rather indistinctly punctate; remainder of body subopaque; clypeal carina and legs more shining; very finely and densely punctate, especially the head, scapes and thorax.

Hairs almost lacking on the head, thorax, and appendages; on the gaster pale yellow, sparse, erect, slender, and rather uniformly distributed; pubescence very fine, yellowish, moderately abundant, investing the whole body, including the appendages.

Castaneous; legs somewhat paler; mandibles deep red, with black teeth; in some specimens the extensor surfaces of the tibiae are yellowish.

Described from six specimens taken from the stomachs of toads (*Bufo funereus* and *polycercus*) from Akenge (type locality), one from Niapu, also from a toad's stomach (*B. polycercus*), a single specimen from Faradje, and another from Lubila (Lang and Chapin).

***Euponera* (*Mesoponera*) *subiridescens*, new species**

Text Figure 15

WORKER.—

Length 6.5 to 7 mm.

Head longer than broad, as broad in front as behind, with feebly and broadly excised posterior border and feebly convex sides. Eyes rather large, feebly convex, placed with their posterior orbits just in front of the middle of the sides. Mandibles very long, narrow, with feebly concave external borders, the apical border very long, toothless except at the tip where there are four small, blunt, oblique teeth. Clypeus

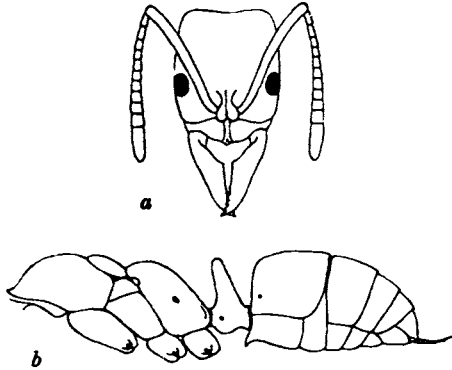


Fig. 15. *Euponera* (*Mesoponera*) *subiridescens*, new species. Worker. a, head from above; b, thorax and abdomen in profile.

carinate, its anterior border broadly projecting, sinuate on each side of the middle and also more deeply at each mandibular insertion. Frontal carinae short, their upper surfaces rather concave. Antennae slender, the scapes extending beyond the posterior border of the head a distance nearly equal to twice their greatest diameter; funicular joints 1 and 2 subequal, almost twice as long as broad; joints 3 to 5 somewhat shorter; remaining joints, except the last, little, if at all longer than broad. Pronotum rather convex and rounded, as long as broad; mesonotum transverse, semicircular, surrounded by an impressed suture. Mesoepinotal constriction distinct. Epinotum as long as the pro- and mesonotum together, the base rounded and convex, somewhat

lower than the mesonotum, passing gradually into the somewhat longer, sloping declivity, which is flat, bluntly marginate on the sides. Petiolar scale shaped as in *ingesta*, but not so thick, with the anterior surface more flattened and the posterior not impressed in the middle. Gaster short and stout, convex above, the postpetiole truncated in front, the constriction between it and the succeeding segment very feeble. Legs moderately long.

Shining; mandibles more so than the remainder of the body, smooth, with only a few large punctures along the apical margin. Remainder of body very finely but not deeply punctate and less densely than in *ingesta*.

Hairs lacking, except on the mandibles, clypeus, pygidium, and hypopygium, where they are pale yellow and rather long; the pubescence, too, is yellowish and rather long and abundant on the body and appendages, longest on the gaster.

Deep castaneous, almost black; the head and thorax with a more or less distinct blue iridescence as in some species of *Lobopelta* (*iridescens*, *chinensis*); inner borders of mandibles, the legs, antennæ, and tip of gaster somewhat paler and more reddish.

Described from six specimens, all from the stomachs of toads; four from Akenge (type locality) from the stomach of *Bufo polycercus*, one from Medje from the stomach of *B. superciliaris*, and one from Ngayu from the stomach of *B. tuberosus* (Lang and Chapin).

Both this and the preceding species seem to be very distinct from any of the previously described African species of *Mesoponera*.

#### ***Euponera* (*Brachyponera*) *sennaarensis* (Mayr)**

Thysville, ♀, ♂, ♀ (Lang and Bequaert); Avakubi, ♀; Leopoldville, ♀, ♂; Faradje, ♀, ♂; Medje, ♀; Zambi, ♂; Stanleyville ♀, ♂; Niapu, ♀ (Lang and Chapin). One of the specimens from Medje was taken from the stomach of a toad (*Bufo funereus*).

This is a well-known ant which seems to be common throughout a large part of the Ethiopian Region and even ranges into Asia (Arabia). Concerning its habits Arnold writes that it is "the commonest ponerine ant around Bulawayo (Rhodesia). A crateriform mound of fine earth surrounds the entrance to the nest, which is as often situated in the open as it is under stones. The economic value of this little species can hardly be overestimated, since it is exceedingly plentiful and preys unceasingly on termites. It is, however, omnivorous, since it will eagerly collect bread-crumbs, insects of all sorts, and seeds of grass. Heaps of the latter are often found in the nests." Escherich, in Abyssinia, and Bequaert, in the Katanga, had previously noted its fondness for collecting grass seeds, a very unusual habit in the Ponerinæ.

The following note by Mr. Lang accompanies the specimens from Avakubi: "I have generally seen this ant, which the natives call 'tussisomee,' singly or two or three together, running swiftly over the sandy

ground, from which they throw up tiny craters about one inch or two-thirds of an inch high. These consist of excavated parti ground loosely put together. From the crater slender channels, three millimeters wide, run laterally or vertically into the har When a knife is stuck into the ground near the crater, one or even ants may be seen hurrying away. I never saw any of the larvæ craters are often quite numerous. Today I counted about 60 o area of 500 square yards. The natives say that these ants bite ( and fear them even more than the 'siafu' (army ants), though never occur in masses. They build their craters in cleared ground, after rainy nights, and are seldom seen during the day time." accounts indicate that the habits of *sennaarensis* are very sim those of the Australian *E. (B.) lutea*, which I have studied in New Wales and Queensland. The latter species, however, prefers t under stones and logs and is, if anything, even more abundant t African cousin.

***Euponera* (*Trachymesopus*) *darwini* (Forel) variety *africana* F.**

A single dealated female from Stanleyville (Lang and Cl This species has an extraordinary range, from Northern Austr the Philippines through India to Nigeria. It is very probably hy in habit as the worker of most of the varieties, including the Afri still unknown.

**PLECTROCTENA F. Smith**

Large or medium-sized black or castaneous ants, with shining surface, punctate.

WORKER monomorphic, with large, rectangular and rather flat head, wit flat, anteriorly situated eyes. Clypeus very short, its anterior border straig middle, emarginate on each side at the mandibular insertion, apparently not ex back between the frontal carinæ, the latter overhanging the clypeus and with the front an elevated lobe, longitudinally sulcate in the middle. M long, linear, feebly curved, with a deep narrow furrow running nearly th length on the dorsal surface, their tips blunt, the inner margin armed with tooth at the basal third and another obtuse tooth, sometimes indistinct, betw latter and the tip. Antennæ 12-jointed, the funiculi somewhat thickened their tips, the first joint shorter than the second. Thorax large and depress mesonotal suture distinct, mesoëpinotal suture obsolete, epinotal declivity me on the sides. Petiole with a laterally compressed node, with the anterior and p surfaces vertical in profile, the dorsal surface horizontal. Constriction betw postpetiole and gaster pronounced, with well-developed stridulatory surface. short, formed largely by the first segment. Median spurs of middle and hir large and pectinated, lateral spurs lacking.

**FEMALE** winged, apterous or ergatomorphic, larger than the worker but otherwise similar. Eyes and ocelli small. Anterior wings with a discoidal cell, two cubital cells and the radial cell closed.

**MALE** about the size of the worker. Frontal carinae short, erect, closely approximated, bringing the insertions of the antennae close together. Antennal funiculi filiform, their first joint very short; scapes stout, shorter than the second funicular joint. Mandibles small, linear, parallel-sided, edentate, with rounded tips. Mesonotum with distinct Mayrian furrows; scutellum longitudinally grooved in the middle. Genitalia retracted; pygidium terminating in a blunt or truncated point. Wings short.



Map 13. Distribution of the genus *Plectroctena*.

This singular genus is confined to the Ethiopian Region (Map 13). Arnold has observed the habits of the type species, *P. mandibularis*, in South Africa. "The entrances to the nest are generally indicated by large heaps of earth. The chambers are placed deep below the surface, seldom less than 2 feet, and the number of individuals seldom exceeds 50. It is a sluggish and timid ant, the workers foraging singly. The food includes termites, but consists chiefly of millipeds and beetles." Another

South African species described by Arnold as *P. subterranea* is castaneous red, measures only 7.5 to 10 mm., and has exceedingly small eyes. It, in all probability, belongs to a different genus. In the generic key it runs down to *Myopias* and is provisionally referred to that genus.

The character of the females in the four described species of *Plectroctena* has not been adequately ascertained. Winged females of *P. minor* and *subterranea* are known, but no winged females of *mandibularis*. According to Arnold, this species has ergatoid females differing "from the worker chiefly in size, but the head and abdomen are proportionally wider and longer. The longitudinal impression on the pronotum is shallower, while that of the dorsum of the epinotum is deeper and wider. In a nest of three dozen or so individuals, not more than two or three of these forms are to be found, and usually only one." It seems that Forel saw one of these ergatoid females and described it as a subspecies (*major*) of *mandibularis*. There is, however, still another type of female, at least in *P. minor*, of which I describe a specimen below, with ocelli and slightly larger eyes than the worker and with the thorax essentially like that of the winged female, but without the slightest indications of ever having borne wings.

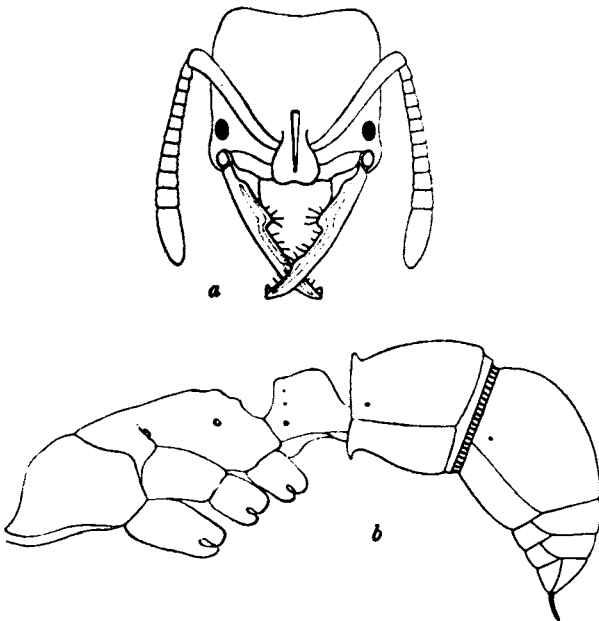


Fig. 16. *Plectroctena cristata* Emery. Worker. a, head from above; b, thorax and abdomen in profile.

**Plectroctena cristata** Emery

Text Figure 16

Medje, ♀; Akenge, ♀ (Lang and Chapin). Eight specimens, all taken from the stomachs of toads (*Bufo superciliaris*, *polycercus*, and *funereus*).

**Plectroctena minor** Emery

A single apterous female from Akenge from the stomach of a toad (*Bufo polycercus*); a single worker from Niapu from the stomach of a frog (*Xenopus tropicalis*); Stanleyville, ♀, ♀, ♂ (Lang and Chapin).

FEMALE (apterous).—

Length about 12 mm.

Smaller than the winged female and with slightly smaller eyes. Ocelli present. The thorax of the same shape as in the winged female but without wing insertions. The tint of the body is a little more reddish than in the winged female.

MALE (hitherto undescribed).—

Head broader than long, broadly rounded behind, the eyes large, moderately convex, about half as long as the sides of the head. Mandibles very small, blunt, edentate. Clypeus rather convex, with feebly and broadly excised anterior border. Antennæ long, filiform; scape about two-thirds as long as the second funicular joint, first funicular joint broader than long. Thorax broader through the wing insertions than the head, narrowed in front; promesonotal suture very deeply impressed. Mesonotum rather flat, with a median pit in front and well-developed Mayrian furrows. Scutellum convex, with a median sulcus so that it appears bituberculate. Base of epinotum somewhat longer than the declivity which is concave and strongly marginate on the sides and above. Petiole narrower, higher than long, the node truncated anteriorly and posteriorly and rounded above and on the sides; its ventral tooth triangular, short and rather acute. Postpetiole broader than long, convex above and sharply constricted off from the gaster, its anterior ventral border projecting as a transverse welt. Gaster of the usual shape, pygidium bluntly pointed at the tip. Legs moderately long and slender. Wings rather short (7.8 mm.).

Shining, finely punctate; thorax more or less rugulose, the pronotum finely, the pleuræ more coarsely, the scutellum and upper portion of the base of the epinotum reticulately rugose, the latter very coarsely. Upper portion of petiolar node very smooth and shining.

Hairs yellowish, present only along the posterior borders of the gastric segments. Pubescence grayish, very fine, covering the gaster, head, and legs.

Black; mouth, mandibles, tibial spurs, and articulations of the legs, ventral portion of petiole, posterior and especially lateral, margins of the gastric segments, red. Wings uniformly brownish, veins and pterostigma dark brown.

The series from Stanleyville consists of a single worker, three females, and two males, all from the same colony. Another male from the same locality and with a different number is considerably larger (13 mm.) and evidently belongs to the same species but probably represents a distinct variety which cannot be named without the worker or female.



The MALE resembles the male of *Plectroctena* but has smaller eyes and the mesonotum is without Mayrian furrows, the scutellum with a deep longitudinal sulcus.

Only four species of this interesting genus have been described. The Lang-Chapin collection contains a fifth, which is described below. They are all rare ants, inhabiting the virgin forest and apparently restricted to Western Equatorial Africa, from French Guinea to the Northeastern Congo (Map 14).

The workers of four species of *Psalidomyrmex*<sup>1</sup> can be readily identified by means of the following table.

1. Mandibles narrow, without distinct basal and apical borders, broadest near the middle, where they are scarcely more than one-eighth as broad as long; scapes not reaching to the posterior corners of the head; petiole longer than broad; dorsal surface of body smooth and shining between the foveolæ.  
*reichenspergeri* Santschi.  
Mandibles much broader, with distinct basal and apical margins meeting at a right angle, broadest at their basal third and about one-third as broad as long; scapes reaching or surpassing the posterior corners of the head; petiole broader than long; interfoveolar surface of head, thorax and gaster, at least, finely striate . . . . . 2.
2. Length 9 to 10 mm. Reddish castaneous; lobes of frontal carinæ smooth and shining; striæ on the postpetiole longitudinal . . . . . *foveolatus* Ern. André.  
Length about 12 mm. Brown-black or black, with brown antennæ, mandibles, clypeus, and legs; striæ on postpetiole arcuate . . . . . 3.
3. Head longer than broad; antennal scapes reaching beyond posterior corners of head; striæ on the head, thorax, and abdomen sharp; pronotum without a median longitudinal groove; mesoëpinal suture obsolete; petiole slightly broader than long . . . . . *procerus* Emery.  
Head as broad as long, antennal scapes shorter; striæ on head and thorax less distinct, foveolæ smaller; pronotum with a median longitudinal groove; mesoëpinal suture distinct; petiole broader . . . . . *obesus*, new species.

*= P. wheeleri Santschi* *Psalidomyrmex procerus* Emery

Text Figure 17

Medje, ♀; Akenge, ♀; Niapu, ♀ (Lang and Chapin). Nine specimens, all taken from the stomachs of toads (*Bufo superciliaris*, *funereus*, and *polycercus*).

*Psalidomyrmex reichenspergeri* Santschi

Text Figure 18

A single worker from the stomach of a toad (*Bufo polycercus*) taken at Akenge (Lang and Chapin).

This species is easily distinguished from *procerus* Emery and *foveolatus* André by its more slender form, smoother surface between the

<sup>1</sup>*P. longicauda* Santschi is only known in the female sex.

foveolæ, the more rectangular head, more elongated and narrower mandibles, longer funiculi, longer petiole, and more distinct mesoëpinal suture.

***Psalidomyrmex obesus*, new species**

Text Figure 19

WORKER.—

Length nearly 12 mm.

Very similar to *procerus* but differing in the following characters: the body is distinctly more robust, the head being rectangular, and without the mandibles as broad as long, the thorax with more rounded surfaces and a swollen appearance. The mandibles are like those of *procerus* but slightly broader at the angle between the basal and apical borders and the tips are less curved. The antennal scapes reach the

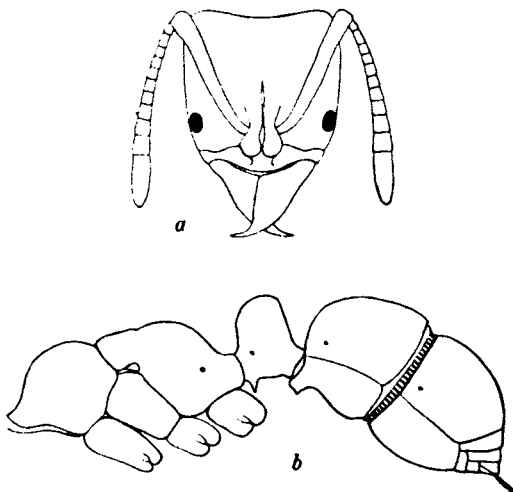


Fig. 19. *Psalidomyrmex obesus*, new species. Worker. a, head from above; b, thorax and abdomen in profile.

posterior corners of the head; funicular joints 3 to 8 as long as broad, 9 and 10 slightly longer than broad. On the thorax the mesoëpinal suture is more distinct than in *procerus* and there is a narrow median longitudinal furrow on the posterior half of the pronotum as well as on the base of the epinotum. The petiole in profile is much shorter and higher and, seen from above, much broader in proportion to its length than in *procerus*, being very distinctly broader than long, flat and truncated posteriorly, more rounded in front, with the anteroventral tooth long and rather acute.

The sculpture differs from that of *procerus* as follows: the longitudinal rugæ covering the mandibles are distinctly coarser, the surface of the head and thorax is more opaque, the foveolæ being somewhat smaller, shallower and less shining, though about as numerous and the striolæ of the interfoveolar surface less sharp. The petiole and postpetiole are smoother and more shining than the head and thorax

and the interfoveolar sculpture is so feeble as to appear more or less coriaceous or alutaceous. The first gastric segment is longitudinally, not arcuately striolate. The femora are transversely, the scapes and tibiæ longitudinally striolate as in *procerus*.

Erect hairs somewhat more numerous on the dorsal surface of the head and pronotum and on the antennal scapes.

Nearly coal black, darker than *procerus*, legs, excluding the coxæ, mandibles, clypeus, frontal carinæ, antennæ, and terminal gastric segments castaneous as in *procerus*.

Described from two specimens from Medje from the stomach of a toad (*Bufo superciliaris*) collected by Lang and Chapin. This form is certainly distinct and is, in my opinion, more than a subspecies of *procerus*.



Map 15. Distribution of the genus *Leptogenys*. This genus also occurs in Georgia.

### LEPTOGENYS Roger

Slender black or reddish ants, of small or medium size, sometimes with bluish iridescence.

The **WORKERS** are monomorphic and vary little in size. Mandibles articulated at the anterior corners of the head, almost or quite toothless and either long and linear or broader and subtriangular, usually with the angle between the basal and apical margin rounded or absent. Clypeus usually carinate and projecting in the middle in the form of a lobe or angle. Antennæ long and slender, the funiculi not enlarged or clubbed apically. Thorax usually with the mesoëpinotal suture distinct. Petiole either laterally or, in a few species, anteroposteriorly compressed. Abdomen small and slender, the constriction between the postpetiole and gaster not very pronounced. Legs slender, claws pectinated.

The FEMALE is wingless and scarcely larger than the worker, either highly ergatomorphic, without ocelli, with the thoracic structure as in the worker but with more voluminous abdomen, or ergatogynous, as in the case of *L. ergatogyna* described below, with ocelli and the thorax more like that of the winged females of other genera, but with the mesonotum and scutellum small and depressed.

The MALE is somewhat smaller than the worker and in some species much paler in color and nocturnal, with very large eyes and ocelli, very long antennæ, small mandibles, and pronounced Mayrian furrows on the mesonotum. The claws are pectinated as in the other phases.

Emery has divided the genus into four subgenera: *Leptogenys sensu stricto*; *Lobopelta*; *Odontopelta*; and *Machærogenys*. The species of *Leptogenys, sensu stricto*, are generally distributed in the tropics of both hemispheres. One *Lobopelta, L. elongata* (Buckley), occurs in the Gulf States from Central Texas eastward to Florida. *Odontopelta* is monotypic and confined to Queensland. Of *Machærogenys*, three species are known, all from Madagascar (Map 15).

Most species of *Leptogenys* form small colonies, each with a single female, and nest in the ground, usually under stones or logs. The workers are timid and extremely quick in their movements. Some species make organized raids on termites; others, like our North American *elongata*, forage singly and apparently only at night.

***Leptogenys stuhlmanni* Mayr subspecies *camerunensis* (Stitz) variety *opalescens*, new variety**

WORKER.—Agreeing with the variety *angusticeps* Forel in all respects, except that the head, thorax, petiole, and to some extent also the gaster, have a peculiar opalescent blue reflection like that seen in *L. iridescens* (F. Smith) and *chinensis* (Mayr).

Thirteen workers taken from the stomachs of toads (*Bufo funereus* and *polycercus*) from Akenge (Lang and Chapin). Forel drew his description of *angusticeps* from a single specimen taken at St. Gabriel, near Stanleyville. He says nothing about the blue reflection, which is very striking, so that I am unable to refer the specimens to his variety.

The habits of the typical *stuhlmanni* have been studied by Arnold.<sup>1</sup> He says:

I have met with this species only in Natal, where it appears to feed exclusively on woodlice; the entrance to the nest can be plainly distinguished by the accumulation of the remains of their prey, bleached a dead white, scattered around it. The nest is not indicated by any mound or other accumulation of earth; but in the neighborhood of Durban at least, it is very frequently found in, or immediately adjacent to, the nests of *Myrmicaria eumenoides* Gerst. I am inclined to think that this *Lepto-*

<sup>1</sup>1915, Ann. South African Mus., XIV, p. 93.

*genys* dispossesses the latter species of a part of their large nest, rather than take the trouble of excavating one for itself. It also has a very noticeable smell, resembling essence of pears.

In 1904<sup>1</sup> I recorded the fact that our North American species feeds very largely on slaters (*Oniscus* and *Armadillidium*) and that "the earth surrounding the entrances to the nests is invariably white with innumerable bleaching limbs and segments of the crustaceans." The use of the same food by two species of *Leptogenys* in such remote regions as Natal and Texas would seem to indicate that the habit must be rather general in the genus.

***Leptogenys (Lobopelta) ergatogyna*, new species**

Text Figure 20

FEMALE.—

Length 7.3 mm.

Head longer than broad, narrower behind than in front, with feebly convex and rather large eyes, placed a little in front of the middle, and three small ocelli, the posterior distinctly smaller than the anterior. Mandibles rather broad, their basal and apical borders subequal, not forming an angle with each other. Clypeus carinate,

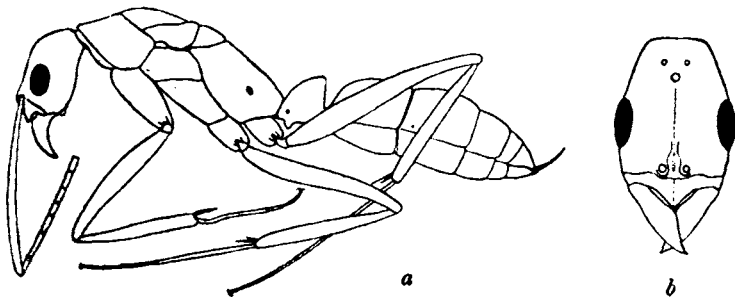


Fig. 20. *Leptogenys (Lobopelta) ergatogyna*, new species. Female. a, insect in profile; b, head from above.

produced as a sharp point or angle in the middle. Frontal carinae erect, closely approximated; frontal groove distinct. Antennae long and slender, scapes extending nearly half their length beyond the posterior border of the head; funicular joints long and slender, the second twice as long as the first, the third and fourth each nearly two-thirds as long as the second. Thorax long and narrow, elongate elliptical, scarcely broader than the head through the eyes, laterally compressed; pronotum large, as long as broad, depressed in profile; mesonotum, tegulae, paraptera, and scutellum developed as distinct but small sclerites, without traces of wings. Mesonotum scarcely longer than the pronotum, somewhat longer than broad, with distinct parapteral furrows. Epinotum long and sloping, without base or declivity. Petiole as high as long, in profile shaped like the quadrant of a circle, its anterior surface evenly arcuate,

<sup>1</sup>A crustacean-eating ant (*Leptogenys elongata* Buckley). Biol. Bull., VI, pp. 251-259.

its posterior surface sharply and vertically truncated, its ventral surface anteriorly with a coarse tooth. Seen from above, the petiole is only one and one-fourth times as long as broad, slightly broader behind than in front, with straight, subparallel sides. Abdomen slender, like that of a normal worker, not enlarged as in the ergatomorphic females of other species. Sting long. Legs long and slender.

Subopaque; mandibles somewhat more shining, finely shagreened and coarsely and sparsely punctate. Clypeus finely longitudinally rugulose; head, pronotum, mesonotum, paraptera, and scutellum densely and finely punctate; postpetiole and gaster more shining, even more finely but a little less densely punctate; pleuræ finely and longitudinally, epinotum transversely and somewhat more coarsely rugulose. Petiole finely and rather irregularly rugulose.

Hairs and pubescence whitish, the former very sparse, erect, delicate, confined to the head, fore coxæ, and tip of gaster, short on the last; the pubescence rather short and abundant on the head, postpetiole, gaster, and appendages.

Black; mandibles, antennæ, and legs, including the coxæ, dark brown; tarsi and funiculi scarcely paler.

Described from a single specimen taken from the stomach of a toad (*Bufo polycercus*) from Medje (Lang and Chapin).

This remarkable insect I regard as the normal female of a species which must be very closely related to *L. havilandi* Forel, known only from the worker. In all the species of *Leptogenys* [*elongata* (Buckley), *diminuta* (Smith), *fallax* (Mayr), *arnoldi* Forel] of which the female is known, this phase is like the worker in the structure of the thorax and in lacking ocelli, but has a more voluminous abdomen. Of the female *arnoldi*, Arnold says that "the mesonotum is also larger and longer than in the worker," and I have found the same to be true of the Australian *fallax*. It would seem, therefore, if I am correct in my interpretation of the specimen above described, that it must be regarded as representing a stage in the degeneration of the formicid female intermediate between the common winged and the extremely ergatomorphic form, the only form of fertile female that has been seen hitherto in the genus *Leptogenys*.

#### ANOCHETUS Mayr

WORKER.—Small ants with monomorphic workers. Head irregularly hexagonal. Mandibles inserted close together at the middle of its anterior border, linear, flattened, with three large terminal teeth bent inward at a right angle and with the inner border toothless or furnished with a row of minute denticles. Eyes usually well developed, rarely vestigial, in front of the middle of the sides of the head. Clypeus small, subtriangular, anteriorly projecting over the insertions of the mandibles and extending backward as a narrow process between the short frontal carinæ, which are lobularly expended in front and more or less convergent posteriorly. Antennal foveæ not confluent behind; head without an oblique welt or swelling on each side starting from the eye and bounding the antennal fovea; sides of head without a marked impression behind the antennal fovea. Antennæ slender, 12-jointed; funiculi long, filiform, not enlarged apically. Thorax long and narrow, with distinct promesonotal and some-

Mandibles shining, smooth; head subopaque, finely and regularly longitudinally rugulose, the rugules spreading fanwise from the frontal carinæ; clypeus, antennal foveæ, sides, and posterior corners of head smooth and shining. Thorax opaque, coarsely rugose, the rugæ irregular but with a feebly longitudinal trend on the pronotum, transverse on the mesonotum, more vermiculate on the epinotum. Petiole rather shining, coarsely coriaceous; gaster subopaque, densely punctate, the posterior margins of the segments more shining.

Hairs delicate, white, rather short and abundant, erect on the body; scapes and legs with dense oblique, short hairs which are also very fine and might be described as long pubescence.

Black; mandibles, clypeus, cheeks, gular surface of head, antennæ, and legs, including the coxæ, dark brown, the middle portions of the femora darker. Posterior margins of gastric segments golden yellow.

Described from three specimens taken from the stomachs of toads (*Bufo funereus* and *polycercus*) from Akenge (Lang and Chapin).

#### **Anochetus bequaerti** Forel

A single specimen taken from the stomach of a toad (*Bufo regularis*) from Garamba (Lang and Chapin).

#### **Anochetus punctaticeps** Mayr

Eighteen workers from Babeyru, forming part of a colony "found under bark on a large tree" (Lang and Chapin).

#### **ODONTOMACHUS** Latreille

Medium-sized or large ants closely resembling *Anochetus*.

In the **WORKER**, however, the antennal foveæ are confluent, being united by a depression of the front behind the frontal carinæ, and there is a welt or swelling which extends out obliquely from the eye and separates the antennal fossa from a depression, equally oblique and very pronounced on the side of the head. Both the apical and subapical teeth of the mandibles acute, the preapical truncated or acute, according to the species; the inner border of the mandibles usually minutely and serrately toothed. Maxillary palpi 4-jointed, labial palpi 3-jointed. Eyes always well developed. Petiole surmounted by a conical node usually terminating in a spine which is inclined backward.

**FEMALE** winged, with large eyes and ocelli, but in other respects like the worker.

**MALE** with the head of the ordinary shape and with very large eyes and ocelli; mandibles very small; maxillary palpi 6-jointed. Antennæ as in *Anochetus*. Petiole ordinarily with a pointed or conical node, but without terminal spine. Postpetiole separated from the succeeding segment by a rather pronounced constriction. Pygidium terminating in a spine. Claws simple.

*Odontomachus* is a tropicopolitan genus with apparently two centers of distribution, one in the Neotropical, the other in the Indonesian and Australian Regions (Map 17). One species, *O. hæmatoda*, represented by

workers and one female (the one described above) taken from the stomachs of toads (*Bufo polycercus*, *funereus*, and *superciliaris*) from Medje, Ngayu, Akenge, Boyulu, and Niangara.

***Odontomachus assiniensis* variety *aterrimus*, new variety**

WORKER.—Length about 10 mm. Differing from the variety *furvior* in being entirely jet black, including the appendages. The sculpture of the head and thorax is distinctly finer than in any of the other forms of the species, so that the surface is more shining. The legs are smoother and also more shining, especially the femora, than in any of the other forms. The unsculptured surfaces of the body, viz., the antennal foveæ, the mesopleuræ, lower portion of epinotum, and the gaster have a distinct blue opalescence. The longitudinal groove on the dorsal surface of the epinotum is continuous.

Described from a single specimen found in the stomach of a frog (*Rana albolabris*) from Niapu (Lang and Chapin).

***Odontomachus hæmatoda* (Linnæus)**

Stanleyville, ♂; Malela, ♂, ♀ (Lang and J. Bequaert); Faradje, ♂; Zambi, ♂, ♀; Avakubi, ♂; Leopoldville, ♂; Vankerckhovenville, ♂; Garamba, ♂; Akenge, ♂ (Lang and Chapin); Matadi, ♂; Katala, ♀ (J. Bequaert). All this material belongs to the typical tropicopolitan form, distributed apparently throughout the Ethiopian Region. The specimen from Akenge was taken from the stomach of a toad (*Bufo funereus*) and a specimen from Faradje was taken from the stomach of a frog (*Rana occipitalis*). In connection with the well-known leaping habit of this ant, Mr. Lang makes the following remark: "This leaping may be of some practical use to the ants when scaly ant-eaters (*Manis*) open their nests. Those jumping out of the immediate range of its glutinous tongue would be fairly safe, since the *Manis* feeds only where the ants and their larvæ are thickest and seldom looks for single individuals."

***Odontomachus hæmatoda* variety *stanleyi*, new variety**

WORKER.—Length 7 to 8 mm. Distinctly smaller than the typical *hæmatoda*, with a distinctly narrower head and the mandibles, antennæ, thorax, legs, and gaster paler and reddish castaneous brown. In many specimens the cheeks, clypeus, antennal foveæ, gula, and borders of the mandibles are yellowish. Petiole with longer and more uniformly slender spine. Sculpture of the head and thorax as in the typical *hæmatoda*, but with the gray pubescence on the gaster distinctly longer and more conspicuous. The sides of the head are much less smooth and shining than in the Neotropical subspecies *insularis* (Guérin), which is of the same size though paler in color.



Described from numerous specimens from two colonies taken at Stanleyville (Lang and Chapin). The cocoons are also distinctly paler than those of the typical *hæmatoda*.

### **Pseudomyrminae**

WORKER monomorphic, very rarely slightly dimorphic. Body elongate, often very slender. Clypeus with rounded posterior margin, not prolonged back between the frontal carinae; in certain species of *Pseudomyrma* there is an apparent posterior prolongation which, however, is the equivalent of the frontal area and is often separated from the clypeus. Antennae 12-jointed, short. Ocelli usually developed. Pedicel usually long, formed by the petiole and the postpetiole. Gaster with well-developed sting. Middle and hind tibiae with pectinate median spurs. The proventriculus or "gizzard" is much more specialized than in the Myrmicinae, being anteriorly developed as an apple- or quince-shaped ball, covered with longitudinal and circular muscles and with four distinct, connate sepals, bluntly rounded and finely hairy at their tips, and posteriorly as a very short, tubular, constricted portion which projects as a button into the cavity of the ventriculus.

FEMALE very similar to the worker, also with 12-jointed antennae; either winged, or ergatoid and wingless, or subapterous. All three forms of females occur together in the same nest of *Vitivicola*. Wings with a discoidal and a closed radial cell; two closed cubital cells, rarely one (*Vitivicola*).

MALE also rather similar to the worker; the antennae 12-jointed. External genitalia well developed, exerted; cerci present.

"The adult LARVAE of all four genera of Pseudomyrminae are much alike. The body is long, straight and cylindrical, not broader posteriorly as in nearly all other ant larvae. The anterior and posterior extremities are blunt and rounded and the segments are all sharply defined. The integument is uniformly thin and perfectly transparent, though tough, only the mandibles, as a rule, being strongly chitinized and the lining of the buccal cavity somewhat pigmented. The prothoracic segment is large and hood-shaped, and in certain species can be drawn down over the head; the meso- and metathoracic segments are narrowed ventrally, the head is large, somewhat flattened, usually subrectangular, about as broad as long and embedded in the ventral portions of the thoracic segments. The antennal rudiments are always distinct as small, rounded papillae, each bearing three sensillae. The mandibles are small, stout and bidentate, sometimes with a vestige of a third tooth, their upper surfaces covered with regular rows of subimbricate papillae. The maxillae are large, swollen and rounded, lobuliform, the labium short and broad, with the transverse, slit-shaped opening of the salivary duct in the middle. The sensory organs which in many other ants have the form of papillae or pegs on the maxillae and labium are in the Pseudomyrminae usually reduced to small areas or feeble eminences, bearing the groups of sensillae. The anterior maxillary organ has five, the posterior two and each labial organ has five of these sensillae. The buccal cavity is broad and transverse, its dorsal and ventral walls being in contact and both furnished with fine, regular transverse ridges (*trophorhinium*). Each thoracic segment bears a rounded papilliform exudatorium ventrally on each side next to the head. The sternal portion of the first abdominal segment is transversely elliptical, swollen, protuberant and furnished with a food-pouch, the *trophothylax*, opening forward, i. e., towards the mouth-parts. The

hairs on the body of the larva are of three kinds: first, short, stiff, very acute hairs, generally and rather evenly distributed over the whole surface (*microchætæ*); second, much longer, stouter, more gradually tapering, lash-like and somewhat curved hairs of unequal length, singly or in a row or loose cluster on each ventrolateral surface of each abdominal segment (*acrochætæ*); and third, long hairs, of uniform length, only slightly tapering, with hooked tips (*oncochætæ*). These are normally present in transverse rows of four to eight on the dorsal surfaces of the three thoracic and first three to eight abdominal segments. On the more posterior segments they are often represented by simple, i. e., pointed hairs."<sup>1</sup>

Nymphs not enclosed in a cocoon.

In 1899 Emery,<sup>2</sup> after a comparative study of the larvæ of several formicid genera, proposed to separate *Tetraponera* and *Pseudomyrma* from the remainder of the Myrmicinae to form the new subfamily of the Pseudomyrminæ. His arguments, however, based on fragmentary material, seemed not convincing at that time; long since Emery himself has reunited these genera with the Myrmicinae and in this he has been followed by all other myrmecologists up to the present. A recent study of numerous larvæ of this group, belonging to the four known genera, has convinced me that we must return to Emery's conception of 1899. I have endeavored to show in a recent paper<sup>3</sup> that neither the larval nor the imaginal Metaponini can be regarded as at all closely related to the Pseudomyrminæ; consequently that tribe should be retained among the Myrmicinae.

Like the Dorylinae and Cerapachyinae, the Pseudomyrminæ are typically inhabitants of the warmer parts of the world; a small number of forms enter the southernmost portions of the Nearctic and Palearctic Regions.

#### TETRAPONERA F. Smith

WORKER.—Small, monomorphic or very rarely (in one South African species, *T. ambigua* Emery, according to Arnold) with the head dimorphic. Body long and slender. Head subrectangular, with large or very large, moderately convex eyes, one-third to two-fifths as long as the head; ocelli vestigial, often absent. Mandibles short and stout, with distinct basal and apical border, the latter with a small number of subequal teeth. Clypeus extremely short, steep, elevated in the middle but not extending back between the frontal carinae, the anterior border emarginate, dentate or crenulate. Frontal carinae small, short, closely approximated, lobular anteriorly, often slightly diverging behind. Maxillary palpi 5-jointed; labial palpi 4-jointed. Antennæ short, 12-jointed, the funiculi somewhat thickened at their tips, without distinct clava. Thorax narrow, with well-developed promesonotal and mesoepinotal

<sup>1</sup>Wheeler, W. M. and Bailey, I. W., 1920. 'The feeding habits of pseudomyrmine and other ants.' *Trans. Amer. Phil. Soc. Philadelphia*, N. S., XXII, pt. 4, pp. 235-279. Pls. 1-v.

<sup>2</sup>1899, 'Intorno alle larve di alcune formiche.' *Mem. Accad. Sc. Bologna*, (5) VIII, pp. 3-10, 2 Pls.

<sup>3</sup>Wheeler, W. M., 1919. 'The ants of the genus *Metapone* Forel.' *Ann. Ent. Soc. America*, XII, pp. 173-191, 7 figs.

sutures and a distinct metanotal sclerite, often constricted in the mesoëpinal region. Epinotum large and rather high, always unarmed. Petiole and often also the post-petiole pedunculate, rather long and slender, both with low, rounded nodes, their ventral portions not swollen or with stout teeth. Gaster narrow and elongate oval, with well-developed, exserted sting. Middle and hind tibiae with pectinated median spurs; claws toothed.

FEMALE very similar to the worker and scarcely larger, winged; the wings short, the anterior pair with a discoidal, two closed cubital cells and a rather narrow, closed radial.

MALE scarcely smaller than the worker and very similar except for the wings. Head shorter. Eyes and ocelli well developed, convex. Mandibles well developed, with dentate apical borders. Antennae 12-jointed, the scape but little longer than the second funicular joint, the first joint much shorter than the second, not swollen. Mesonotum depressed, not overarching the pronotum, without Mayrian furrows and with very feeble parapsidal furrows. There is, at least in some species, a concavity in the pro- and mesosterna, extending dorsally nearly to the mesonotal scutum. External genitalia well developed, exserted. Cerci present. Wings as in the female.

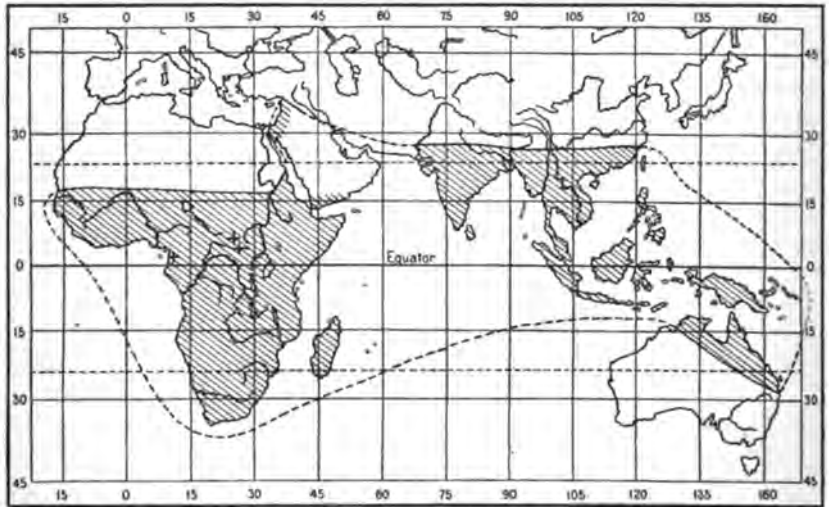
LARVA hypocephalic, with papillary exudatoria on the three thoracic and first abdominal segments. Dorsal surface with long straight hairs, hooked at their tips.

Donisthorpe (1916, Ent. Record, XXVIII, pp. 242-244) has shown that *Sima* Roger, the name used by most authors for this genus, must be sunk as an isonym of *Tetraponera* F. Smith, contrary to Emery's contention (1915, Zool. Anzeiger, XLV, p. 265). The case seems to be very clear, as Smith founded his genus *Tetraponera* (1852) on two species, *atrata* (= *Eciton nigrum* Jerdon) and *testacea*. The latter he afterwards (1855) placed in the genus *Pseudomyrma*. Roger founded his genus *Sima* in 1863 on *S. compressa* Roger (= *Pseudomyrma? allaborans* Walker). Later (1900) Emery separated the genus *Sima* into two subgenera, *Sima, sensu stricto*, and *Tetraponera*, the former with, the latter without ocelli in the worker and selected *Eciton rufonigrum* Jerdon as the type of *Sima, sensu stricto*. This was an improper procedure, since the worker of Roger's type species, *S. allaborans* has no ocelli.

Examination of the males of several of the Indomalayan species of *Tetraponera* shows that they all have 12-jointed antennae. This is also true of the males of *Pachysima*, *Viticicola*, and even of *Pseudomyrma* and, hence, of the whole tribe Pseudomyrmini of Emery. Nevertheless, in his recent classification of the Myrmicinae (1914, Rend. Accad. Sc. Bologna, p. 34) he cites the males of this tribe as having 13-jointed antennae. Bingham and Arnold also give the same number for *Tetraponera*, and Santschi, who was the first to describe the male of *Pachysima aethiops*, failed to notice that it has 12-jointed antennae.

The genus *Tetraponera* is distributed over the Ethiopian, Malagasy, Indomalayan, Papuan, and Australian Regions (Map 18), being best represented in the Ethiopian and Indomalayan. One species, *T. bifoveo-*

*lata* (Mayr), was taken by Dr. W. M. Mann as far north as Palestine. The species all nest in plant cavities (dead wood, twigs, stems of lianas, acacia spines, etc.) and are very quick in their movements. Their habits throughout are very similar to those of the allied Neotropical genus *Pseudomyrma*. The species of the latter, however, are much more numerous and constitute an abundant and conspicuous part of the Neotropical ant-fauna, whereas the species of *Tetraponera* are comparatively rare ants.



Map 18. Distribution of the genus *Tetraponera* (crossed area) and *Vitiicola* (known localities indicated by crosses).

#### ***Tetraponera anthracina* (Santschi)**

Stanleyville, ♂ (Lang and Chapin); Lubutu, ♂; Thysville, ♂ (J. Bequaert). Five specimens which agree perfectly with Santschi's description of the types from the French Congo. Kohl found this species nesting in the hollow twigs of *Barteria fistulosa* and Bequaert's specimens from Thysville bear the note, "running on leaves and twigs of *Barteria fistulosa* whose cavities were apparently not inhabited by ants. Forest gallery in savannah. I have not seen their nest."

#### ***Tetraponera mocquerysi* (Ern. André) variety *lepida*, new variety**

WORKER.—Length 6.5 to 7 mm. Differing from the typical form of the species in color, the thorax, petiole, gaster, and coxæ being very dark brown or black; the head, mandibles, antennæ, legs, anterior and posterior ends and ventral surface of the petiole, brownish yellow. Vertex with a large, transversely elliptical black spot

obsolete. Antennæ short, 12-jointed; the funiculi with distinct 3-jointed club, the first funicular joint very long, joints 2 to 7 very short and transverse. Both maxillary and labial palpi 3-jointed. Thorax much as in *Tetraponera* but more thickset, the pronotum convex and rounded, not marginate or submarginate on the sides, the epinotum very high and convex, hemispherical, with the epinotal gland on each side very long and narrow, extending obliquely upward and forward to the middle of the lateral surface of the segment. Petiole and postpetiole stout, without peduncles, the nodes from above not longer than broad, their ventral portions swollen, without teeth. Gaster and tibial spurs as in *Tetraponera* but the tarsal claws are simple, not toothed.

FEMALE winged, or ergatoid and wingless, exhibiting also subapterous forms. Even the winged form is much like the worker, but has well-developed ocelli, though the eyes are small and flat. Pronotum large and well developed; mesonotum depressed, flat. Petiole and postpetiole even broader and stouter than in the worker; both broader than long.

MALE.—Clypeus longer than in the worker and female; mandibles similar with dentate apical borders. Antennæ short, 12-jointed, the second funicular joint much shorter than the scape, not longer than the first, which is slightly swollen. Eyes and ocelli rather large and convex. Mesonotum flattened or depressed, without Mayrian furrows and with very indistinct parapsidal furrows, not overarching the pronotum. There is a very deep and wide excision, separating the pro- and mesosterna and extending dorsally nearly to the mesonotal scutum. Petiole and postpetiole much as in the worker and female, but with their ventral portions even more swollen and convex. Genitalia extruded, less robust than those of *Pachysima* and *Tetraponera*. Wings with a discoidal cell, a rather broad, closed radial cell and only one cubital cell.

LARVA hypocephalic as in *Pachysima* and *Tetraponera* and like that of the latter genus in the development of the exudatoria and dorsal hairs.

GENOTYPE.—*Sima tessmanni* Stitz.

This monotypic genus seems to me to be sufficiently distinct from *Tetraponera*. The single species is highly specialized in adaptation to life in the stem cavities of a peculiar liana, *Vitex Staudtii* (*vide infra*). The eyes have dwindled and the ocelli have disappeared; the venation of the wings has become more simple and there is a pronounced tendency for the production of wingless and subapterous females—a condition unknown in any species of *Tetraponera*. This peculiarity, the pale color, and the small eyes indicate that the ants never leave the cavities of their host plant, except when the latter is disturbed or during the marriage flight, and the very pale color of the males indicates that this flight must occur at night. The conspicuous development of the epinotum and of its glands suggests conditions like those in some species of *Crematogaster* of the subgenus *Physocrema* (*inflata*, *difformis*, *vacca*, *stethogompha*, etc.) of the Indomalayan Region, the workers of which are supposed to feed on the secretions of one another's epinota (Bingham). As at present known, the distribution of the new genus is restricted to Spanish Guinea and the Ituri Basin of the Belgian Congo (Map 18). It probably also occurs in Cameroon.

**Viticicola tessmanni** (Stitz)

Text Figures 23 and 24

**WORKER.**—

Length 3 to 3.5 mm.

Head longer than broad, a little broader behind than in front, with feebly concave cheeks, rounded posterior corners and nearly straight posterior border, and, on the vertex, with a short longitudinal impression at one end of which the anterior ocellus is sometimes distinctly developed. Posterior ocelli absent. Eyes very small, flat, shorter than half their distance from the mandibular insertions, placed a little in front of the middle of the head. Mandibles short, rather strongly angulate at the base externally, their apical margins oblique, with 5 or 6 denticles, those at the base often indistinct. Clypeus convex and evenly rounded in the middle, its anterior border projecting, entire, strongly emarginate on the sides. Frontal groove absent. Antennæ short, scapes not reaching to the middle of the head, first funicular joint much longer than broad, joints 2 to 8 much broader than long, crowded together, joints 9 to 11 forming a three-jointed club, the last joint being as long as both the others, which are subequal and somewhat broader than long. Thorax narrower than the head, constricted in the mesonotal region. Pronotum from above a little broader than long, evenly rounded and convex; mesonotum transversely subelliptical, feebly convex, surrounded by impressed sutures. Metanotum nearly as long as the mesonotum, concave, with uneven surface. Epinotum very convex and rounded, egg-shaped from above, semiglobose in profile, as high as the pronotum or slightly higher, with the slit-shaped epinotal glands shining through the integument and conspicuously enlarged. Petiole short, scarcely longer than broad, broader behind than in front, convex and rounded above. In profile, its ventral surface is also convex and protuberant, with a small, compressed, blunt, translucent tooth anteriorly. Postpetiole a little broader than the petiole, scarcely broader than long and scarcely broader behind than in front, convex and rounded above and below. Legs and gaster of the usual shape, the latter with well-developed sting.

Very smooth and shining, including the mandibles; impunctate under a magnification of 20 diameters.

Hairs golden yellow, erect, of uneven length, sparse, most numerous on the gaster, especially along its sides. These regions also have more numerous short hairs or suberect pubescence. Antennæ and legs with shorter, more appressed hairs. Cheeks and clypeus densely and conspicuously pubescent, the latter without a fringe of cilia-like bristles.

Clear brownish yellow, with the borders of the mandibles, clypeus and frontal carinæ brown.

**FEMALE** (deālated).—

Length 4.5 to 5 mm.

Very similar to the worker. Thorax elongate elliptical, somewhat flattened above. Mesonotum as long as broad; epinotum subcuboidal, with subequal base and declivity meeting at a rounded right angle in profile, rather sharply marked off by impressed sutures from the more anterior portion of the thorax. Petiole and postpetiole from above subequal and of similar shape, broader than long. Gaster proportionally larger than in the worker.

Sculpture, pilosity and color as in the worker but the hairs and pubescence longer and more abundant. The pubescence is very conspicuous, extending back over the

(Fig. 23g) have the fore wings more developed as a pair of triangular pads with indistinct, contorted veins, and folded back over the anterior corners of the epinotum. The pilosity and pubescence are also intermediate between the worker and female; the color the same.

MALE.—

Length 2.6 to 3 mm.

Head, including the eyes, distinctly longer than broad, rounded behind and impressed in front of the anterior ocellus. Cheeks short. Eyes and ocelli rather large, convex. Mandibles small but with distinct, denticulate borders. Clypeus convex, its anterior border rounded and somewhat projecting. Frontal carinæ very short. Antennal scapes about three times as long as broad, funicular joints all distinctly longer than broad, cylindrical, very gradually increasing in length to the tip. Thorax narrow and long, flattened above, peculiarly and deeply excavated on the ventral side behind the insertions of the fore coxæ; mesosterna swollen. Epinotum resembling that of the female. Petiole and postpetiole much as in the worker, but the former subpedunculate, merging more gradually into the node, without a tooth on its ventral surface. Gaster long and slender. Fore wing with a single cubital cell.

Smooth and shining; hairs and pubescence much as in the worker but less abundant and more delicate.

Color pale yellow of a distinctly lighter tint than in the worker and female. Wings grayish hyaline, with pale brown veins and pterostigma.

Described from numerous specimens of all the phases belonging to a series of several hundred specimens taken at Medje from the hollow stems of *Vitex Staudtii* Guerke. The relations of the ant to the plant are described in Dr. Bequaert's notes in Part IV, and Prof. Bailey has described the woody structure of the plant and its modification by the ants in Part V.

Stitz described and figured only the worker of this species from specimens taken by Tessmann in Spanish Guinea. He gives the native Pangwe name as "odschigeso" and says that the insect stings more severely than *Pachysima æthiops*, which is a much larger and more powerful ant. He also describes one of the ergatoid females but seems to regard it as an unusual worker. In my material about 4 to 5 per cent of the specimens are ergatoid females, so that they must form a normal constituent of the colony. They probably function as egg-laying individuals and thus supplement the reproductive activities of the true females, which, judging from my material, are much less numerous.

The adult specimens of *V. tessmanni* collected by Mr. Lang are accompanied by numerous eggs, larvæ, and pupæ in all stages. I have figured the adult larva (Fig. 24) because it is interesting in connection with the extraordinary larvæ of the two species of *Pachysima* described below. It resembles the larva of *Tetraponera natalensis* figured by Emery,<sup>1</sup> but is longer and more slender and two of the postcephalic

<sup>1</sup>1899, Mem. Accad. Sc. Bologna, (5) VIII, Pl. II, fig. 7.

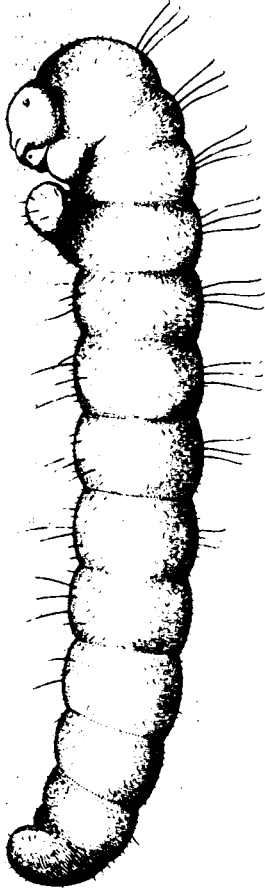


Fig. 24. *Viticicola tessmanni* (Stitz). Adult larva in profile.

segments bear appendages, the significance of which is more fully explained in my remarks on *Pachysima*. The prothoracic segment bears a rounded appendage on each side and applied to the side of the head, which, as in the *Tetraponera* larvæ, is overarched by the protuberant, cowl-like prothoracic segment. The first abdominal segment bears ventrally two large and very protuberant appendages which are fused with each other in the middle line. The anterior segments of the body have on their dorsal surfaces clusters of long hooked hairs, as in *T. natalensis*, and the more posterior segments have simple stiff hairs of very unequal length on their ventral surfaces. There are also numerous short, sparse hairs, scattered over the whole body. The young larvæ are essentially like the oldest in form and pilosity. The mandibles are well chitinized and minutely bidentate at the tip as in *natalensis*, and the head bears minute rudiments of antennæ on its dorsal surface. I find also that the larvæ of certain East Indian *Tetraponera*, e. g., *T. allaborans* (Walker), have a similar structure.

***Viticicola tessmanni* variety *castanea*,  
new variety**

WORKER and FEMALE (deâlated).—In all respects like the typical form except in the color of the body and legs, which are pale chestnut brown, with the antennæ paler and more yellowish.

Of this variety Mr. Lang took numerous workers and females from two colonies at Avakubi. They were nesting in the same species of liana as the typical form.

**PACHYSIMA Emery**

WORKER.—Closely related to *Tetraponera* but larger and more robust, with smaller eyes but distinct ocelli and the frontal carinæ decidedly longer and farther apart. Maxillary palpi 5-jointed; labial palpi 4-jointed. Both the petiole and post-petiole armed beneath with stout teeth. Claws toothed as in *Tetraponera*.

FEMALE.—Much like the worker. Wings very long, with venation like that of *Tetraponera*; radial cell long and narrow.



of the plant *Barteria fistulosa* which it inhabits. According to his observations in the Congo, it is restricted to this plant and an allied species, *B. Deweyrei* De Wildeman and Th. Durand. It inhabits the peculiarly swollen, lateral branches and keeps large coccids in their cavities. The openings to the cavities are not made at definite points predetermined by a peculiar histological structure, as in the case of the Neotropical *Cecropiæ* associated with species of *Azteca*. After the marriage flight the *æthiops* queen gnaws its way into an already hollow twig and while she is establishing her colony the orifice, as in *Cecropia*, closes by growth

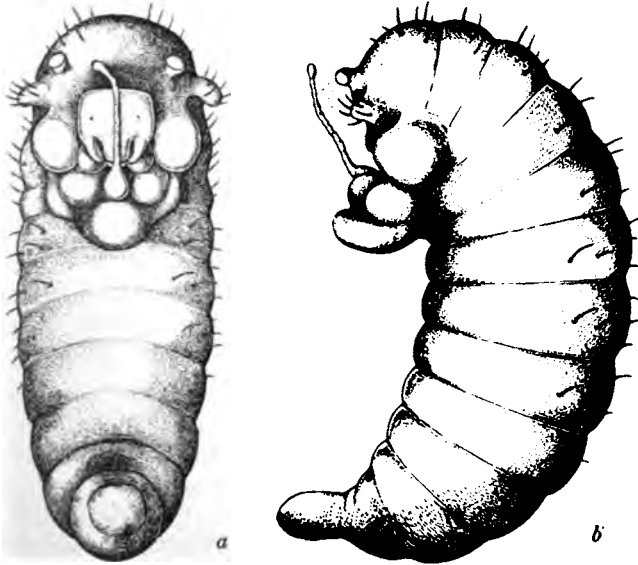


Fig. 26. *Pachysima æthiops* (F. Smith). First stage larva or trophidium. a, ventral; b, lateral view.

of the plant tissue, so that it has to be reopened from within by the workers of the young colony. As several queens enter different internodes of the same plant, their various colonies probably eventually unite to form a single huge colony possessing all the cavities in common, as in the case of *Cecropiæ* tenanted by *Azteca*. Concerning the behavior of *æthiops*, Kohl writes as follow:

The *Simæ* are extremely pugnacious and always ready for a fight as they are equipped with excellent weapons, their stings and mandibles. If a *Barteria* tree is roughly handled or even shaken, innumerable hosts of the ants rush out of all the openings and woe to him who approaches them too closely! I have had many sore experiences with their pointed stings while studying or amputating the branches.

The pain spreads instantly over the whole affected limb and continues for a long time and on the following morning returns with full intensity during one's ablutions. One day my black servant told me that it was customary in his part of the country to punish unfaithful wives by tying them to plants inhabited by the *Sima*.

On examining the series of *æthiops* larvæ, I was struck with their extraordinary appearance. A further study of them and of the larvæ of the only other known species of *Pachysima* (*P. latifrons*) throws considerable light on the *raison d'être* of the peculiar ethological relations of larval ants to their nurses, as I have shown in a recent paper.<sup>1</sup>

Four distinct stages, probably separated by moults or ecdyses, may be recognized in the *æthiops* larva. The first stage larva, just after hatching, is represented in Fig. 26a-b as it appears in ventral and lateral view. The body is curved, convex dorsally and concave ventrally, and terminates behind in a cylindrical projection, with the anus shifted to the ventral surface near its base. The creature is strongly hypocephalic like the larvæ of *Tetraoponera*, *Viticicola*, and *Pseudomyrma*, i. e., with the head on the ventral side. The head is surrounded by a cluster of prominent, tubercle-like appendages. On the prothorax, which is large and forms a hood over the head, there are three pairs of these appendages, an anterior truncate pair, a median pointed pair and a large posterior pair, which are swollen and rounded and embrace the sides of the head. These correspond to the single prothoracic pair figured in the larva of *Viticicola tessmanni*. The mesothoracic segment has a pair of smaller appendages nearer the midventral line. Between them arises a very peculiar organ, with a swollen, pear-shaped base prolonged into a slender, apparently erectile, tentacle-like process which extends up in front of the head and terminates in a small ampulla. The first abdominal segment bears a pair of large swollen appendages, which lie at the lateral bases of the mesothoracic pair and are united with a large and very prominent midventral tubercle. This tubercle and its lateral appendages are represented in the larva of *V. tessmanni* but the others, with the exception of the third thoracic pair, are absent. Sections and stained, cleared preparations of the whole larva show that the various tubercles contain portions of the fat-body, at least in the basal portions of their cavities, and next to the hypodermis a dense, granular substance, evidently a coagulated liquid produced by the adipocytes or trophocytes. The liquid also fills the impaired tentacle, except its pear-shaped base, which contains fat-cells. Around the bases of the tubercles are muscles so arranged that their contraction increases the pressure of the fat and granular

<sup>1</sup>1918. 'A study of some ant larvæ, with a consideration of the origin and meaning of the social habit among insects.' Proc. Amer. Phil. Soc., LVII, pp. 293-243, 12 figs.

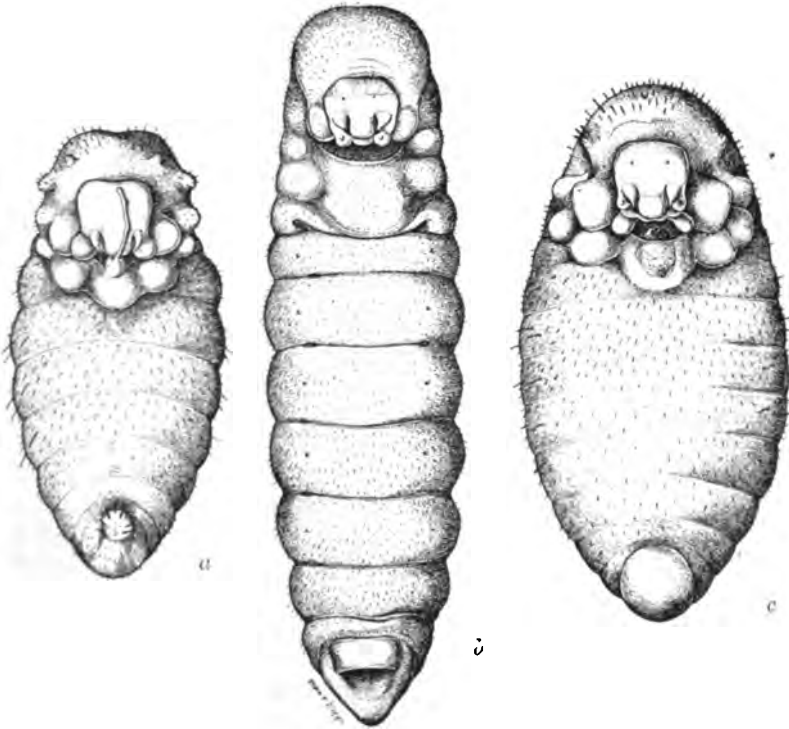


Fig. 27. *Pachysima zhiops* (F. Smith). a, second stage larva; b, third stage larva; c, fourth stage or adult larva.

liquid on the appendages and in all probability causes the liquid to exude through the hypodermis and delicate chitinous cuticle onto the surface. The whole arrangement of the tubercles, in fact, constitutes a system of exudate organs or "exudatoria," as I shall call them, adapted to produce a substance that can be licked up by the ants when they are feeding and caring for the larvæ. In this stage the mandibles are small, soft, and unchitinized, so that the ants must feed the larva by regurgitation on liquid food. The labium of the larva has a peculiar pair of swollen appendages, shown just beneath the mandibles in the figure. The body is naked, except for a few sparse, pointed bristles on the dorsal surface and the median pair of prothoracic appendages. As nothing like this larval stage is known among ants or indeed among the Hymenoptera, I propose to call it the "trophidium."

The second stage larva is shown in Fig. 27a. The various exudatoria are small in proportion to the remainder of the body but are still much

like those of the trophidium. The body is more elliptical, the mandibles are more pointed and distinctly falcate but, even in this stage, they are unchitinized and therefore nonfunctional. The coarse hairs are visible on the dorsal surface but a more uniform investment of small hairs has made its appearance. They are blunt or even clavate, especially on the prothoracic segment. In this and the trophidium stage, I am unable to find any salivary glands in cleared preparations, though rudiments of these organs may, perhaps, be present.

The third stage larva (Fig. 27*b*) is larger and very regularly elliptical. The exudatoria can all be recognized, except the impaired tentacle. It is, however, present in some of the younger individuals but in a greatly reduced and vestigial condition at the bottom of the deep depression which now forms a definite pocket just back of the mouth and under the midventral swelling of the first abdominal segment. In many larvæ I found in this pocket a small rounded, dark-colored pellet which puzzled me at first. In sections it was at once seen to consist of triturated and compacted bodies and parts of small insects. It is, in fact, a food-pellet placed by the worker ants in the pocket just behind the larva's mouth and proves to be merely the pellet which is originally formed in the infrabuccal pocket of the adult ants. In this stage, therefore, the larva is fed on solid food and the strongly chitinized, acute, and bidentate mandibles corroborate this statement. Slender salivary glands may also be detected in this stage indicating that the substance of the food-pellet is subjected to extra-intestinal digestion. The longer hairs on the dorsal integument have almost completely disappeared. The first pair of appendages on the prothorax have disappeared and the second pair is smaller or obsolescent.

In the fourth or adult stage (Fig. 27*c*) the larva is more elongate and cylindrical and much more hypocephalic, the prothorax forming a great protuberance in front of the head. The exudatoria are still recognizable, with the exception of the first and second prothoracic pairs, which have disappeared completely. The labial appendages are reduced. A food-pellet was found in the postcephalic pocket in several of the larvæ of this stage but is not represented in the figure. The coarse hairs have disappeared from the integument, which is now uniformly covered with very short, delicate hairs and the structure of the posterior end of the body is very different from that of the preceding stages.

The conclusions which I draw from the study of these larvæ and from those of *P. latifrons* and *Pædalagus infimus* (*vide infra*) are that the young larvæ are fed by regurgitation, the older larvæ with pellets of

crushed insects, and that, especially during their younger stages, the larvæ are so assiduously fed and cared for because they furnish liquid exudates, small in quantity, to be sure, but of such a quality as to excite the appetite of their nurses and induce regurgitation. I believe that the salivary glands, as soon as they develop, take on the function of supplying exudates and at the same time aid in the extra-intestinal digestion of the food placed in the postcephalic pocket. That the salivary glands may be important as exudate organs throughout life is indicated by certain genera of Myrmicinæ (e. g., *Pædalagus*), the larvæ of which have no exudatoria but greatly developed salivary glands, though the latter are never used for spinning cocoons in the prepupal stage. Thus in ants very much the same "œcotrophobiotic" relations exist between the adults and young as Roubaud<sup>1</sup> has so beautifully described for the wasps of the genera *Belonogaster*, *Ropalidia* (= *Icaria*), and *Polistes*. To these relations, established by a mutual exchange of food-substances and which I have called "trophallactic," the social life of ants in all probability owes its origin, development, and maintenance. Moreover, the exudates of larval ants are strictly comparable with those of various castes of termites among themselves, of the queens of parasitic ants and even of workers (e. g., *Crematogaster inflata* of the East Indies), with the excrement of coccids and aphids, the secretions of lycænid larvæ and the nectar of the extrafloral nectaries of plants. Thus trophallaxis, myrmecophily, termitophily, trophobiosis, and the relations of ants with certain plants (myrmecophytes) are all seen to be merely so many particular manifestations of the same fundamental instinct of ants to foster and defend and, if possible, to feed and transport any small living object which can furnish droplets of agreeable secretion or exudates.

The only account of the *æthiops* larva in the literature is by Emery.<sup>2</sup> He describes the adult larva very briefly and figures its anterior end with some of the exudatoria but erroneously interprets the large prothoracic pair as "ébauches de pattes," or rudiments of the anterior pair of imaginal legs.

In the same paper Emery created the subgenus *Pachysima* for the accommodation of *æthiops* and *latifrons*, because those species have the frontal carinæ of the worker and female much more widely separated than the numerous other species of *Tetraponera* (= *Sima*). I have raised *Pachysima* to generic rank, because the larvæ of the two species are so very different from those of *Tetraponera*.

<sup>1</sup>1916. 'Recherches biologiques sur les guêpes solitaires et sociales d'Afrique.' Ann. Sc. Nat. Zool. (10) I, pp. 1-160.

<sup>2</sup>1912, Ann. Soc. Ent. Belgique, LVI, p. 97.

one cubital cell, the cubitus may be united with the radius by means of a long intercubitus (type of *Solenopsis*) or the intercubitus may disappear, the cubitus and radius being fused in a spot or for some distance (type of *Formica*).

LARVA thick-bodied, orthocephalic, without exudatory papillæ around the mouth. The body is, as a rule, abundantly covered with chitinous hairs of very different kinds; dorsal oncochætæ often present.

NYMPHS never enclosed in a cocoon.

The Myrmicinae is the largest subfamily of ants, containing over 120 genera and many thousands of described species, races, and varieties, nearly as many as the other six subfamilies together. As would be expected, the taxonomic arrangement of this maze is exceedingly difficult and it is no wonder that such keen myrmecologists as Forel and Emery have not yet succeeded in reaching satisfactory results and are obliged to modify their views at every turn of the road. For practical and other reasons, have felt at liberty to change somewhat the classification proposed by Emery,<sup>1</sup> though have followed him in the main. Have united the two tribes Solenopsidini and Pheidologetini, which pass repeatedly into each other and are merely separated by the shape of the radial cell (closed in the Pheidologetini; open in the Solenopsidini), a character the value of which seems to have been overrated by Emery. Have also accepted Forel's tribe Proattini and, furthermore, separated *Stegomyrmex* from the Dacetini as an independent tribe. The very peculiar genus *Archæomyrmex*, recently discovered by Mann in the Fiji Islands, must also constitute a distinct tribe, which I have provisionally placed between the Myrmecini and Meranoplini.

The habits in this subfamily offer no less diversity than the structure. The majority of the species are carnivorous or partly so; but many others are granivorous, the most prominent in this respect being the members of *Messor* and allied genera (*Novomessor*, *Veromessor*, *Oxyopomyrmex*, *Pogonomyrmex*, many species of *Pheidole*, etc.). In these ants the nest often contains spacious granaries full of seeds. Many myrmicine ants are attracted by sugary substances such as are furnished by the nectaries of flowers or various extrafloral plant organs. Often, also, they attend aphids, coccids, psyllids, or leafhoppers for the sake of the honeydew they excrete. The New World "leaf-cutting" or "fungus-growing" ants of the tribe Attini feed exclusively on the food-bodies ("bromatia") produced by fungi cultivated in their nests. There are also many cases of social parasitism which, in its most extreme form, has

<sup>1</sup>Emery, C. 'Intorno alla classificazione dei Myrmicinae,' Rend. Accad. Sc. Bologna, 1914, pp. 29-42.  
 \*Noms de sous-genres et de genres proposés pour la sous-famille des Myrmicinae; modifications à la classification de ce groupe,' Bull. Soc. Ent. France, 1915, pp. 189-192.

lead to the disappearance of the worker caste (*Wheeleriella*, *Epixenus*, *Epipheidole*, *Sympheidole*, *Epæcus*, *Anergates*, *Anergatides*, and probably several other genera of which only males and females are known). Temporary social parasitism is probably the rule in some species of *Aphænogaster* and in the Malagasy and Indomalayan subgenus *Oxygyne* of *Crematogaster*.

#### PHRIDOLE Westwood

Small ants with the worker strongly dimorphic, the two forms being designated as the worker and soldier. In a few species these phases are connected by intermediates (*mediæ*).

**SOLDIER** with very large head, subrectangular or subcordate, more or less deeply notched or excised behind and with a distinct occipital furrow, on each side of which the occipital region is convex. Clypeus short, depressed, carinate or ecarinate but not elevated in the middle, the anterior border entire or notched in the middle, the posterior border extending back between the frontal carinæ, which vary in length, being short in some species and in others greatly prolonged backward and forming the inner borders of more or less distinct scrobes for the antennæ. Frontal area usually distinct, deeply impressed. Mandibles large, convex, usually with two apical and two basal teeth, separated by a toothless diastema. Antennæ 12-jointed; the funiculus with long first joint; joints 2 to 8 small and narrow; the three terminal joints forming a well-developed club. Thorax small, usually with distinct promesonotal and mesoëpinotal sutures and pronounced mesoëpinotal constriction; the pro- and mesonotum raised, more or less convex, the humeri sometimes prominent, the mesonotum often with a transverse welt or torus; the metanotum sometimes represented by a distinct sclerite; the epinotum armed with spines or teeth, in profile with distinct basal and declivous outline. Petiole small and narrow, pedunculate anteriorly, the node posterior, compressed anteroposteriorly, its superior border sometimes emarginate, the ventral surface unarmed. Postpetiole broader than the petiole, convex and rounded above, contracted behind, the sides often produced as angles or conules, more rarely as spines. Gaster rather small, broadly elliptical or subcircular. Femora more or less thickened in the middle; middle and hind tibiæ without spurs; tarsal claws simple.

**WORKER** smaller than the soldier but very similar in the structure of the thorax, pedicel, and gaster; the head, however, much smaller, not grooved nor deeply excised posteriorly; the antennæ longer; the mandibles less convex, with evenly denticulate apical borders. The pro- and mesonotum are proportionally less convex, and the petiole and postpetiole are more slender.

**FEMALE** resembling the soldier but larger; the head proportionally smaller and shorter, usually not longer than broad and not broader than the thorax; the occiput only broadly and feebly excised. Thorax broad and massive; the mesonotum flat, overarching the pronotum in front. Epinotal spines shorter and stouter; petiole and postpetiole more massive; gaster much larger and more elongate than in the soldier. Wings long, with a discoidal cell, two closed cubital cells, and an open radial cell.

**MALE** decidedly smaller and more slender than the female, the head small, with large, convex eyes and ocelli; mandibles small but dentate. Clypeus longer than in

the soldier. Antennæ 13-jointed; the scapes very short, scarcely longer than the second funicular joint, first joint subglobular. Thorax broad; the mesonotum flattened, without Mayrian furrows, anteriorly overarchng the small pronotum; epinotum unarmed. Petiole and postpetiole slender, with low nodes. Gaster slender, elongate. Genital appendages small. Cerci present. Legs long and slender. Wing venation as in the female.

The species of this very large and difficult genus are distributed over the tropics and warmer temperate areas of both hemispheres (Map 20). In the Nearctic Region the northernmost range is southern New England



Map 20. Distribution of the genus *Pheidole*.

and Oregon; in the Palearctic, Japan and northern Italy; in the southern hemisphere it reaches Argentina and Tasmania. Emery has divided the genus into a number of subgenera and has rejected a couple of subgenera, *Allophaidole* and *Cardiophaidole*, described by Forel and myself. The various groups have been characterized by Emery in a recently published portion of the 'Genera Insectorum' on the Myrmicinae.

Nearly all the species of *Pheidole* nest in the ground, either under stones and logs or in crater or small mound nests. Many species feed exclusively on insects and often have a peculiar fecal odor precisely like that of the Dorylinae, which also have an insect diet; but many species are harvesters and store the chambers of their nests with the seeds of small herbaceous plants. This is especially true of the desert species of *Pheidole*. In some species in Australia and the southern United States, the soldiers take on the function of repletes and store in their crops sweet



liquid for the use of the colony during periods of food and water scarcity. One species, *Pheidole megacephala*, has been carried to all parts of the tropics and has become a great pest in and about dwellings and plantations as it assiduously cultivates coccids on many economic plants and ruthlessly destroys and replaces the native ant-faunas. This has been observed in the Madeira Islands, Hawaii, Australia, and the West Indies. In all probability *P. megacephala* is of Ethiopian or Malagasy origin, as it shows a great development of subspecies and varieties in these two regions and nowhere else.

#### ***Pheidole batrachorum*, new species**

SOLDIER.—

Length 4.5 to 5 mm.

Allied to *P. caffra* Emery. Head a little longer than broad, scarcely narrowed in front, with straight sides and deeply excised posterior border, the vertex convex, the occipital region distinctly depressed, the occipital and frontal groove shallow. Eyes small, broadly elliptical, rather flat, at the anterior third of the sides of the head. Mandibles convex with bluntly bidentate tips. Clypeus flat, carinate, its anterior border notched in the middle. Frontal area small, subtriangular, deeply impressed, without median carinula. Frontal carinæ not strongly diverging behind, prolonged backward as a pair of rugæ to the posterior fifth of the head and forming the inner borders of flat, scrobe-like impressions for the antennæ. The latter slender, their scapes distinctly flattened but not dilated at the base, extending to nearly half the distance between the eyes and the posterior corners of the head; club shorter than the remainder of the funiculus; joints 2 to 8 distinctly longer than broad. Pro- and mesonotum not separated by a suture, convex; humeri prominent; mesonotum with strong transverse torus; mesoepinotal constriction very sharp and deep; epinotum broader than long, its base straight and horizontal, as long as the declivity, dorsally with a broad longitudinal groove; the spines acute, stout at the base, as long as the base of the epinotum and as long as their distance apart, directed upward and somewhat backward and distinctly curved downward. Petiole twice as long as broad, scarcely broader behind than in front, with nearly straight sides; in profile with long, feebly concave anterior and short, vertical posterior surface to the node, the superior border transverse, sharp and feebly emarginate. Postpetiole nearly three times as broad as the petiole, broader than long, very convex and rounded above, the sides bluntly angular in the middle. Gaster smaller than the head, subcircular, its anterior border slightly truncated, the dorsal surface somewhat depressed. Legs long, femora thickened in the middle.

Subopaque; mandibles, clypeus, frontal area, and posterior half of gaster smooth and shining. Mandibles coarsely and sparsely punctate; coarsely rugose at the base. Clypeus very finely rugulose, especially on the sides. Head densely and finely, but not deeply punctate, longitudinally rugose, the rugæ being rather widely separated and subsiding on the posterior fifth of the head; the posterior fourth also with a few large, shallow, elongate foveolæ. Thorax, pedicel, and anterior half of gaster more opaque than the head, finely and densely punctate; the pronotum also finely and rather asymmetrically transversely rugulose. Mesoepinotal constriction with sharp

longitudinal carinulae or rugae; declivity of epinotum transversely rugose above. Basal half of gaster with sparse, elongate, piligerous elevations. Legs smooth and shining.

Hairs coarse, pointed, fulvous, long, and erect, lacking on the thorax and sides of head, sparse on the pedicel and gaster and front of head; short and closely appressed on the legs and antennae.

Deep piceous, almost black; mandibles, clypeus, cheeks, and appendages castaneous; the funiculi, tips of scapes, tibiae, tarsi, and articulations of the legs paler and more reddish.

WORKER.—

Length 3 to 3.5 mm.

Head (without the mandibles) nearly circular, the occipital border strongly marginate. Eyes rather small but convex, just in front of the middle of the sides of the head. Mandibles long, deflected, their external borders concave, their tips with two prominent teeth, the remainder of the apical border finely denticulate. Antennae long and slender, the scapes extending fully one-third their length beyond the occipital border of the head. Clypeus rather flat in the middle, ecarinate, its anterior border entire and broadly rounded. Thorax resembling that of the soldier, but the humeri not prominent, the torus of the mesonotum is feebler, the epinotal spines are more slender, and distinctly shorter than the base of the epinotum and more curved than in the soldier. Petiole more slender, the node lower, more conical, its superior border not emarginate, scarcely more than twice as long as broad. Postpetiole campanulate, as long as broad, broader behind than in front. Gaster elongate elliptical, with truncated anterior border, its dorsal surface convex. Legs long and slender.

Shining; mandibles very finely and densely striolate. Clypeus, head, thorax, and pedicel densely punctate or reticulate; the head somewhat smoother and more shining in the middle anteriorly; the sides of the pronotum smooth and polished; cheeks and sides of front with a few longitudinal rugules. Base of first gastric segment sculptured much as in the soldier.

Hairs less coarse than in the soldier, present also on the thorax; hairs on the legs and antennae longer and more abundant, on the scapes abundant and oblique.

Color very much like that of the soldier.

Described from four soldiers and twenty-one workers from Akenge (Lang and Chapin), all taken from the stomachs of toads (*Bufo polycercus* and *funereus*) and frogs (*Arthroleptis variabilis*).

This species is certainly distinct from *caffra* in the greater size and different shape of the head of the soldier, the long acute and curved epinotal spines and different shape of the thorax. It is evidently a Rain Forest insect, whereas *caffra* seems to be confined to dry country.

***Pheidole aurivillii* Mayr variety *attenuata* Santschi**

Medje, ♂, ♀; Bafwabaka, ♂, ♀ (Lang and Chapin); Walikale to Lubutu, ♂, ♀, ♀, "taken from a colony under bark of a fallen tree trunk" (J. Bequaert). I refer numerous specimens from these localities to Santschi's variety, because they are of very small size and dark color, the soldiers measuring only 3.5 to 4 mm., the workers 2 to 2.5 mm.

The type of the species is considerably larger (soldier, 4.6 to 5 mm.; worker, 3 mm.). According to Santschi, the species varies much in stature and color. The females from Walikale measure 7 mm. and are dark brown, like the soldiers and workers, with dull yellowish brown wings. If I am correct in my interpretation, *attenuata* would more properly constitute a distinct subspecies.

***Pheidole caffa*** Emery subspecies ***bayeri*** Forel variety ***thysvillensis***,  
new variety

**SOLDIER.**—Length 4 to 4.5 mm. Smaller than the typical *bayeri*, with the head of the same shape, but subopaque and with only the front and occiput somewhat shining. The occipital depression is less distinct than in the subspecies *abyssinica* Forel, and the rugæ are anteriorly less numerous, coarser, and farther apart, but very fine and distinctly transverse on the occiput. The antennal scapes are shorter than in the typical *bayeri*, reaching only a little beyond the middle of the head. The subrect epinotal spines are not pointed as in *abyssinica* and *bayeri* but somewhat longer, of uniform thickness or even slightly enlarged at the tips, which are blunt. The base of the epinotum is not longer than broad. The postpetiole is somewhat narrower than in *bayeri* and *abyssinica*, with blunter lateral angles. Thorax, petiole, and postpetiole more finely rugulose-punctate than in *abyssinica*; gaster shining, with the base of the first segment subopaque and alutaceous. Color as in *abyssinica*, with the head and thorax ferruginous brown but varying in some specimens to pale ferruginous red, with the gaster black or brown and the base of the first segment and posterior borders of all the segments paler and more reddish or yellowish.

**WORKER.**—Length 2 mm. Smaller than the worker of *bayeri*. Head elliptical, without posterior corners, longer than broad. Antennal scapes extending two-fifths their length beyond the occipital border, which is rather sharply marginate. Shining; head and thorax finely reticulate; mesonotum, epinotum, petiole, and ventral and lateral portions of the postpetiole opaque and densely punctate. Ferruginous brown; head castaneous; mandibles except their teeth, yellowish.

Described from numerous specimens taken both by Lang and Bequaert at Thysville, apparently from the same colony, "nesting in sandy soil in the savannah."

***Pheidole caffa*** subspecies ***senilifrons***, new subspecies

Text Figure 32

**SOLDIER.**—Length 4 mm. Differing from the typical form and the subspecies *bayeri* in the sculpture of the head, the sharp longitudinal rugæ between the prolonged frontal carinae being surrounded by the rugæ from the sides of the head, which run up to the posterior corners, then turn at a right angle and run transversely on the occipital lobes to the occipital furrow. These rugæ are quite as strong as those on the front, but denser. The head is a little longer and a little more depressed posteriorly than in the variety *thysvillensis*, the transverse welt of the mesonotum less pronounced; the blunt epinotal spines distinctly shorter. The sculpture of the thorax and pedicel and the color and pilosity are much as in that variety.

colony taken at Zambé by Lang and Bequaert there are several specimens of an interesting *Microdon* larva, which is figured and described in Part VI. The female specimens from Akenge and Stanleyville, five in number, were taken from the stomach of a toad (*Bufo polycercus*) and a frog (*Rana mascareniensis*).

***Pheidole megacephala* subspecies *ilgi* (Forel)**

A soldier and several workers taken by Dr. Bequaert at Lesse from a colony nesting at the base of a papaya. It was on the head of one of the soldiers in this colony that he found a singular phorid fly, *Plastophora aculeipes* (Collin), subsequently referred to by H. Schmitz.<sup>1</sup>

***Pheidole megacephala* subspecies *melancholica* (Santschi)**

Six soldiers, five workers, and seven females, mostly winged, taken at Garamba (Lang and Chapin) from the stomachs of a toad (*Bufo regularis*) and two frogs (*Rana ornatissima* and *Kassina senegalensis*). The female is a little larger than the female of the typical *megacephala*, with the head and thorax more sharply sculptured and the color of the body, including the clypeus and mandibles, darker, almost black; the legs more yellowish, as in the worker.

This is the host of the singular workerless parasitic ant, *Anergatides kohli*, recently described and figured by Wasmann from the vicinity of Stanleyville.<sup>2</sup>

***Pheidole megacephala* subspecies *punctulata* (Mayr)**

Boma, ♂, ♀, ♀; Ngayu, ♂, ♀; Avakubi, ♂, ♀; Stanleyville, ♂, ♀, ♀, ♂; Bolobo, ♂, ♀; Faradje, ♂, ♀; Zambé, ♂, ♀, ♀; Niapu, ♂, ♀; Garamba, ♂, ♀; Banana ♂, ♀ (Lang and Chapin).

A well-known and widely distributed Ethiopian form, apparently more abundant in the Belgian Congo than the typical *P. megacephala*. The specimens from various colonies show considerable variation in color, some being dark brown, others pale and more yellowish or reddish, especially those from Stanleyville and Banana. Mr. Lang gives the native name of the species as "tuegeke" and his notes give the nesting sites as "under heaps of decomposed, moist grass," "in fallen stems of *Hyphæne*," "in mushroom-shaped termitaria in swamps," and "in the tops of termite mounds."

<sup>1</sup>1916, Zoolog. Meded. Mus. Leiden, II, p. 28.

<sup>2</sup>1915, Ent. Mitt. Deutsch. Ent. Mus. Berlin, IV, p. 281.

***Pheidole minima* Mayr subspecies *malelana*, new subspecies****SOLDIER.—**

Length 2.3 mm.

Head shaped much as in *P. megacephala*, without the mandibles a little longer than broad, distinctly but not broadly depressed in the occipital region. Eyes small, flat, at the anterior third of the head. Clypeus flat, ecarinate. Frontal area small, impressed; frontal carinæ diverging, reaching to the posterior third of the head, bounding distinct scrobes for the antennal scapes, which are half as long as the head. Funicular joints 2 to 8 distinctly broader than long, club longer than the remainder of the funiculus. Mandibles large and convex, coarsely bidentate at the tip. Thorax robust, pronotum very convex, with small but distinct humeral tubercles. Mesonotum falling almost vertically to the pronounced mesoepinotal constriction, with a slight transverse convexity in the middle. Epinotum broader than long, concave and sloping in the middle, its spines rather erect, shorter than the interval between their bases, with pointed tips. Petiole with rather high, anteroposteriorly compressed, distinctly emarginate node. Postpetiole only one and one-half times as broad as the petiole, broader than long, with the sides angularly produced. Gaster much smaller than the head, elliptical, convex, with subtruncate anterior border. Legs stout, femora thickened in the middle.

Shining; mandibles sparsely punctate; clypeus rather smooth in the middle, indistinctly rugulose on the sides; anterior two-thirds of head with sharp, but not coarse, longitudinal rugæ; occipital lobes with small, sparse, piligerous punctures. Pronotum and gaster very smooth and shining; pedicel smooth but less polished; meso- and epinotum opaque, densely punctate.

Hairs yellow, sparse, suberect on the body, short and appressed on the legs and antennal scapes.

Castaneous; pronotum, first gastric segment, borders of clypeus, and mandibles blackish; remainder of mandibles and clypeus, cheeks and anterior portion of front, petiole and postpetiole yellowish red; legs brownish yellow; terminal gastric segments pale brown; posterior borders of all the gastric segments broadly yellowish.

**WORKER.—**

Length 1.5 mm.

Head subrectangular, as broad as long and as broad in front as behind, with very feebly convex sides and nearly straight posterior border. Eyes just in front of the middle. Mandibles with the entire apical border finely denticulate. Clypeus convex, with rounded, entire anterior border. Antennal scapes reaching beyond the posterior corners of the head to a distance equal to twice their diameter. Thorax shaped much as in the soldier, but the pronotum narrower and longer. Epinotal spines reduced to minute slender teeth scarcely longer than broad at their bases. Superior border of petiolar node straight and entire; postpetiole small, a little broader than the petiole, subglobular.

Pilosity, sculpture, and color as in the soldier, but the head smooth and shining, with only the cheeks delicately longitudinally rugulose.

Described from a single soldier and three workers taken by Lang from a colony nesting in a stem of *Hyphæne* at Malela.

This form agrees with the typical *minima* in size and in most of its characters but the color is very different, the postpetiole is much nar-

rower in proportion to the petiole in both soldier and worker, and the antennal scapes of the latter are decidedly longer. Santschi has described a variety, *catella*, from Nigeria and the Gold Coast, which is evidently colored like *malelana* but his description is too brief to enable me to judge of its other characters. He has also described a subspecies, *corticicola*, from the French Congo. The soldier of this form measures 3 mm., the worker 2.3 mm. Both are red or yellow and in the soldier the frontal carinæ extend to the posterior quarter of the head.

### *Pheidole mylognatha*, new species

Text Figure 33

SOLDIER.—

Length 6 mm.

Head large, subrectangular, 2 mm. broad and 2.3 mm. long, as broad in front as behind, with straight, parallel sides, deeply and angularly excised posterior border, with depressed occipital surface and faint depressions on the sides of the front for the antennal scapes. Occipital and frontal groove deep. Eyes small, flat, at the anterior third of the head. Mandibles very convex, probably bluntly bidentate at apex but

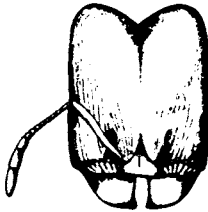


Fig. 33. *Pheidole mylognatha*, new species. Soldier; head from above.

the apical borders are worn away in the specimen. Clypeus very short, concave and indistinctly carinate in the middle, swollen and convex on the sides; the anterior border rather deeply emarginate in the middle and sinuate on each side. Frontal carinæ short, diverging; frontal area indistinct. Antennæ small and slender; scapes when bent outward not reaching to the eyes, terete and slightly curved at the base; joints 2 to 8 only slightly longer than broad; club distinctly shorter than the remainder of the funiculus. Thorax small, much shorter than the head and less than half as wide through the pronotum, which is bluntly tuberculate on the sides both above and below. Mesonotum short, rapidly sloping to the pronounced mesoëpinal constriction, anteriorly with a feeble transverse impression and a small, sharp transverse ridge behind it. Epinotum distinctly broader than long, broadly concave and sloping in the middle, the base shorter than the declivity, marginate on the sides, the marginations continued into the spines which are short, acute, and erect, a little longer than broad at their bases, less than half as long as their interval. Petiole small and short, less than twice as long as broad, broader behind than in front, the node blunt, transverse, and emarginate in the middle. Postpetiole broader than long, its sides produced as short, acute, backwardly directed spines, the distance between the tips of which is about three times the width of the petiole. Gaster smaller than the head, elliptical, flattened dorsoventrally. Femora only moderately thickened in the middle.

Shining; mandibles sparsely punctate in the middle, coarsely striated at the base and along the apical margins. Clypeus rugulose, irregularly in the middle, longitudinally on the sides. Anterior half of head longitudinally rugose, with punctate interrugal spaces, the punctures becoming more numerous on the very feeble scrobe-like depressions; posterior half of head very smooth and shining, with a few

sparse, piligerous punctures. Thorax loosely rugose and somewhat reticulate-punctate on the sides, concavity of epinotum finely transversely striated. Petiole and postpetiole indistinctly punctate-rugulose, the latter smoother and shining above. Gaster and legs smooth and shining, with sparse, piligerous punctures.

Hairs whitish, delicate, sparse, erect or suberect on the body, shorter, more abundant and appressed on the legs; almost absent on the scapes.

Rich castaneous brown; gaster, except the base of the first segment, darker, almost black; legs and funiculi a little more reddish, the femora infuscated in the middle.

WORKER.—

Length 2 mm.

Head a little longer than broad, as broad in front as behind, with feebly convex sides and feebly concave posterior border. Eyes rather convex, just in front of the middle of the sides. Mandibles with the whole apical border very finely denticulate. Clypeus convex, its anterior border entire, broadly rounded. Antennal scapes extending fully one-fourth their length beyond the posterior border of the head. Thorax and petiole very similar to those of the soldier but the mesonotum more sloping and with much feebler transverse convexity. Postpetiole only one and one-half times as broad as the petiole, its sides produced as short angles or conules.

Shining; mandibles finely and indistinctly striate; clypeus and cheeks longitudinally rugulose; area between the frontal carinæ and the eyes reticulate, remainder of head very smooth and shining. Pronotum smooth and shining above, reticulate on the sides; meso- and epinotum subopaque, densely punctate; petiole and postpetiole more finely punctate, the nodes above smooth and shining like the gaster and legs.

Pilosity and color much as in the soldier, but the fine appressed hairs on the scapes as abundant as on the legs.

Described from a single soldier and two workers taken at Banana by Lang and Chapin.

This species is related to *P. schultzei* Forel from the Kalahari Desert, as I find by comparison with cotypes received from Prof. Forel. The head of the *schultzei* soldier, however, has more convex sides, more rounded posterior corners, a less deeply excised posterior margin, less deeply impressed occipital groove, longer antennæ, and a very different color, being yellowish red, with the legs and base of gaster yellow. The worker *schultzei* departs further from that of *mylognatha* in being more slender, with decidedly longer legs and antennæ, in lacking spines on the epinotum and in having a longer postpetiole, which is scarcely angular on the sides. It is sordid or brownish yellow, with the head darker behind and on the sides.

***Pheidole niapuana*, new species**

Text Figure 34

SOLDIER.—

Length 5 to 5.5 mm.

Head, excluding the mandibles, as broad as long (2.3 mm.), cordate, considerably broader behind than in front, and with the occipital border very deeply and arcuately excised. Behind the eyes the sides are convex but in front feebly concave. Eyes small, moderately convex, situated just in front of the anterior third of the head. In profile the head is most convex in the middle both above and below, but depressed in the occipital region. Frontal and occipital groove distinct but rather shallow anteriorly. Mandibles large and convex, with two blunt teeth at the apex. Clypeus flat, carinate, its anterior border emarginate in the middle, bluntly bidentate, sinuate on

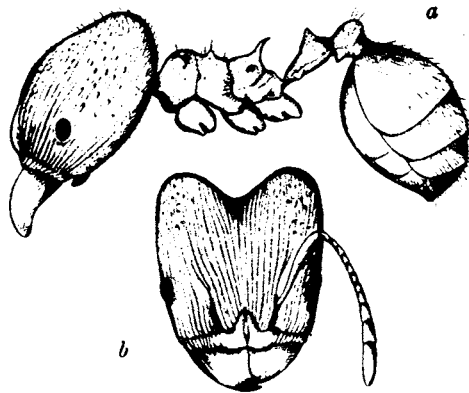


Fig. 34. *Pheidole niapuana*, new species. Soldier. *a*, body in profile; *b*, head from above.

the sides. Frontal area large, subtriangular, without a median carinula; frontal carinae short, diverging, continued back as delicate rugae bordering an indistinct scrobe-like depression for the antennal scapes. Antennae slender; scapes terete, curved at the base, reaching to the middle of the sides of the head; all the funicular joints longer than broad, club somewhat shorter than the remainder of the funiculus. Gula with a pair of very large, blunt teeth at the anterior margin. Thorax short and robust, shorter than the head without the mandibles. Pronotum with very distinct and moderately acute humeral tubercles, mesonotum sloping to a deep mesoepinotal constriction, with a sharp transverse welt or ridge; epinotum broader than long, concave and sloping in the middle; spines acute, somewhat shorter than the base, a little longer than their interval, directed upward and slightly outward and backward, with their tips distinctly curved backward. Petiole very small, narrow, fully twice as long as broad, with subparallel sides, the node short, with acute transverse superior border, distinctly notched in the middle. Postpetiole three times as broad as the petiole, subtriangular, broader than long and broader behind than in front, with prominent, bluntly angular sides, its ventral surface with a distinct tooth, its dorsal surface convex and rounded. Gaster broadly elliptical, smaller than the head. Legs rather slender, femora only moderately thickened in the middle.



***Pheidole saxicola*, new species**

Plate VII; Text Figure 35

**SOLDIER.—**

Length 5.5 to 6 mm.

Head subrectangular, nearly 3 mm. long and very nearly as broad, scarcely broader behind than in front, with straight subparallel sides, rectangular anterior corners, deeply and angularly excised posterior border, and deep occipital and frontal groove. In profile the occipital region is very feebly depressed and the eyes are small, feebly convex, and at the anterior third of the sides. Gula anteriorly with prominent, blunt teeth. Mandibles convex, with two large apical and two basal teeth and a few denticles along the intermediate border. Clypeus convex and carinate in the middle, its anterior border broadly and feebly excised in the middle and sinuate on each side. Frontal carinæ very short, diverging; frontal area distinct, with a median carinula. Antennæ slender, scapes reaching the middle of the head; funicular joints all longer

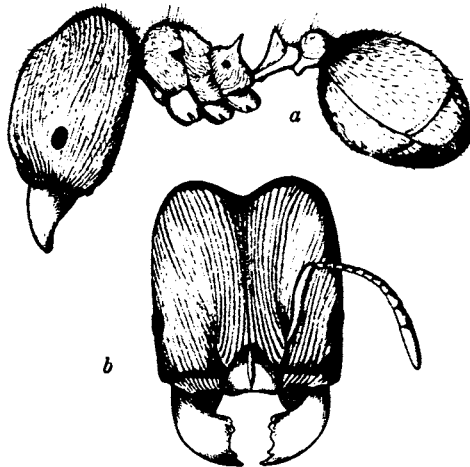


Fig. 35. *Pheidole saxicola*, new species. Soldier. a, body in profile; b, head from above.

than broad; club shorter than the remainder of the funiculus. Thorax shorter than the head, robust, through the pronotum nearly half as broad as the head, with very blunt humeri, convex and rounded in profile. Mesonotum sloping to the deep meso-epinotal constriction with merely a trace of a transverse convexity in the middle. Epinotum broader than long, concave and sloping in the middle, in profile with the base distinctly shorter than the declivity; spines short, suberect, acute, less than half as long as the base and about half as long as their interval. Petiole about one and one-half times as long as broad, broader behind than in front, with concave sides; node transverse, its superior border sharp, feebly excised in the middle. Postpetiole broader than long, about two and one-half times as broad as the petiole, its sides produced as short, acute, slightly backwardly directed spines, its ventral surface with a small, acute tooth. Gaster smaller than the head, subcircular or very broadly elliptical, somewhat flattened above. Legs with moderately thickened femora.

Shining throughout; mandibles coarsely striate, smooth and coarsely punctate in the middle. Clypeus longitudinally rugulose, less distinctly in the middle than on the sides. Head rather finely and sharply longitudinally rugose, the rugæ diverging on the front and continued to the posterior corners, where they meet the also slightly divergent rugæ between the frontal carinæ and the eyes. The interrugal spaces are loosely reticulate. There are no transverse rugæ on the occiput but only a finer continuation of the more anterior sculpture. Thorax, petiole, and postpetiole indistinctly and loosely punctate rugulose, the prothorax transversely; epinotum with fine, dense but shallow punctures, so that the surface is more opaque. Gaster with fine, sparse, piligerous punctures.

Hairs yellowish, partly coarse, sparse, uneven and suberect and partly short, much more abundant, softer and appressed or subappressed like long, coarse pubescence. Legs with numerous short, oblique hairs; scapes with a few longer scattered and coarser hairs.

Dark ferruginous red; mandibles, sides and border of clypeus, and frontal carinæ, blackish; petiole, postpetiole, and gaster, except more or less of the base of the first segment, dark brown or blackish. Legs a little paler than the thorax.

WORKER.—

Length 2.7 to 3 mm.

Head subrectangular, as broad in front as behind, with straight, subparallel sides, rounded posterior corners and nearly straight posterior border. Eyes convex, at the middle of the sides. Mandibles rather large, deflected at the tip, with denticulate apical borders and two larger terminal teeth. Clypeus distinctly carinate, with the anterior border very feebly sinuate in the middle. Antennal scapes extending one-third their length beyond the posterior corners of the head. Thorax similar to that of the soldier, but more slender, especially through the pronotum. Base of epinotum a little longer than the declivity; spines slender, acute, erect, about half as long as their interval. Petiole slender, twice as long as broad, scarcely broader behind than in front, with the sides only very faintly concave; node transverse, its border distinctly notched in the middle. Postpetiole twice as broad as the petiole, as long as broad, subglobose, not toothed on the ventral side. Gaster about as large as the head.

Shining; mandibles subopaque, finely striatopunctate. Sides of head delicately longitudinally rugulose and reticulate. Thorax, petiole, and postpetiole finely and densely punctate, opaque; upper surface of pronotum and postpetiole smooth and shining. Gaster and legs shining, sparsely punctate.

Pilosity like that of the soldier but less abundant. Antennal scapes, like the legs, with numerous oblique hairs.

Brown; head darker above and behind; gaster, except the edges of the segments, middle portions of legs, fore coxæ, and usually also the pronotum and upper surfaces of the petiolar nodes, darker than the posterior portion of the thorax.

Described from numerous specimens taken by Lang, Chapin, and Bequaert at Zambi (type locality) and by the latter at Boma.

This ant is certainly very closely related to *P. sculpturata* Mayr and might be regarded as a subspecies, but it will fit neither Mayr's description of the typical form from South Africa nor Santschi's and Forel's descriptions of the various subspecies from East and West Africa. Mr. Lang's note shows that it is a harvester. "The nests were found on a

gives the length of *cubangensis* as 7 mm. He describes the whole head as opaque, whereas my specimens have a pair of elliptical, very smooth, and shining areas on the vertex in the midst of the opaque and finely punctate sculpture (Fig. 36a and b).

#### MYRMICARIA W. Saunders

Small or medium-sized, coarsely hairy, brown or black ants, with monomorphic WORKERS, which have 7-jointed antennæ, the funiculus enlarged toward the tip but not clavate and all the joints, except the first, considerably longer than wide. Mandibles moderately large, subtriangular, with coarsely dentate apical border. Clypeus broad and convex. Frontal area indistinct behind. Frontal carinæ short, rather far apart, not strongly diverging posteriorly. Eyes not very large, convex, behind the middle of the head; ocelli absent. Thorax with indistinct or obsolete promesonotal suture; mesoëpinotal suture deep, the mesoëpinotal constriction pronounced; the sides of the mesonotum raised and subauriculate behind. Epinotum armed with a pair of long, acute spines, which are often lobate or expanded at the base; inferior corners of pronotum dentate or spined. Petiole with a long peduncle sharply marked off from the abrupt node, which is high and rounded, subconical, sometimes laterally compressed. Postpetiole shaped like the node of the petiole, strongly contracted posteriorly. Gaster subglobose, its basal segment somewhat truncate in front. Legs long; median and hind tibiæ with simple spurs; tarsal claws simple.

FEMALE considerably larger than the worker. Head and antennæ of very similar structure, the latter being 7-jointed. Thorax robust; mesonotum and scutellum very convex, the pronotum vertical in front though well developed, the epinotum with stouter and broader spines than in the worker. Pedicel as in the worker. Gaster much more voluminous, longer than wide, convex above; the basal segment truncate anteriorly. Wings long, with strongly marked veins, the anterior pair with an open radial cell, a single cubital and a discoidal cell.

MALE nearly as large as the female but more slender. Antennæ 13-jointed, filiform, the scape short, about as long as the second funicular joint, the first joint very short, not swollen, the remaining joints all much longer than broad. Eyes large but not very convex; ocelli rather small. Mandibles small and vestigial, sublinear, with rounded edentate tips, which do not meet. Frontal carinæ short. Mesonotum with Mayrian furrows; epinotum without spines. Petiole very long, its node low; that of the postpetiole of a similar shape, decidedly longer than broad. Gaster cordate, scarcely longer than broad, convex above, concave below. External genital appendages long and narrow, blade-like. Cerci present, but minute. Legs slender. Wings rather short, venation as in the female.

This extraordinary genus may be recognized at once by the 7-jointed antennæ of the worker and female and the unique structure of the abdomen in the male. The species are distributed over the Ethiopian, Indomalayan, and Papuan Regions but do not enter Australia (Map 21). The majority of the species and the largest are Ethiopian. The large species form crater nests in the soil; some of the smaller, both in Africa and in the Orient, make small carton nests on the under sides of leaves.

***Myrmecaria eumenoides* (Gerstæcker) subspecies *opaciventris* (Emery)**

Plate VIII, Figures 1 and 2

Malela, ♂; Thysville, ♂; Stanleyville, ♀, ♂; Avakubi, ♂, ♀; Medje, ♂, ♀, ♂; Akenge, ♂; Bafwabaka, ♂; Ngayu, ♂; Faradje, ♂, ♀ (Lang and Chapin); Walikale to Lubutu, ♂, ♀ (J. Bequaert); Yakuluku, ♀ (J. Rodhain). Seventy-five workers and one female from Bafwabaka, Ngayu, Medje, Akenge, and Stanleyville were taken from the stomachs of toads (*Bufo regularis*, *B. funereus*, and *B. superciliaris*); a single worker from Faradje was taken from the stomach of a frog (*Rana occipitalis*).

Neither Forel nor Santschi seems to me to have recognized this form very explicitly. Several years ago I received from the former six workers labelled "Benguela (Buchner)" and, as Emery's ergatotypes bore the same label and were also received from Forel and as my specimens agree perfectly with Emery's description, I feel confident that they are cotypes. Later I received a worker and three dealated females from Gaboon (Staudinger) and, as Emery mentions specimens from the same locality, I believe that I have before me also the female of the true *opaciventris*. The workers measure about 5 to 6 mm. and are pale ferruginous brown, with the antennæ, legs, and gaster more fuscous. The mandibles have oblique 5-toothed blades; the clypeus is carinate. The epinotal spines are rather slender and very slightly bent downward, the base of the epinotum is less concave than in the typical *eumenoides*, the peduncle of the petiole is distinctly shorter and not longer than the node. The petiolar and postpetiolar nodes are laterally compressed and of the same height, the ventral surface of the postpetiole, unlike that of *eumenoides*, is swollen, and projecting and angular in front. The surface of the head and thorax is somewhat less shining than in *eumenoides*, the rugæ on the front, pleuræ, pro-, meso- and base of epinotum more sharply and regularly longitudinal and not reticulate. The gaster has the basal half or, in some specimens, the whole surface opaque and densely punctate, whereas it is smooth and shining in typical *eumenoides*. The nodes of the petiole and postpetiole have shining summits and in some specimens the sides of the petiole are also smooth and shining, in others like those of the postpetiole, finely punctate and even feebly longitudinally rugulose. In the female, which measures 13 mm., the petiole and postpetiole are sharply longitudinally rugose, the summit of the former concentrically rugose, the scutellum vermiculately rugose. Emery's description of the male, which I have not seen, includes no mention of characters that would distinguish it from the male of the typical *eumenoides*.

Numerous specimens from the various Congo localities cited above seem to me to be referable to Emery's subspecies, though they differ more or less in the sculpture of the petiole, postpetiole, and gaster and in being mostly of a darker color. They average larger than the specimens of variety *congolensis* and variety *crucheti*, the workers being 5 to 6.5 mm. The petiole and postpetiole, especially the latter, are nearly always more or less longitudinally rugulose on the sides, though sometimes merely punctate, as Emery remarks in the original description. The specimens from Walikale have the entire gaster opaque and punctate, whereas in others it is punctate usually only on the anterior half of the first segment. This character, however, varies in individuals from the same colony. Santschi says that the gaster of the worker is "entièrement sculpté, mat, brun clair," but Emery describes the gaster as fuscous, with the anterior half of the first segment opaque.

Trägårdh<sup>1</sup> and Arnold<sup>2</sup> have described the nests of the typical *eumenoides* of East and South Africa. The latter's account runs as follows.

The colonies of this species are usually very large, often comprising 1000 or more workers. The latter bite and sting fiercely, but the sting is rather blunt, and does not easily pierce the human skin. Although their gait is slow, they are nevertheless active insects, travelling over large areas in search of food, which seems to consist chiefly of other insects. They do not appear to be aphidicolous, nor to attend membracid or lepidopterous larvæ for their secretions, yet they are known to harbour in their nests many myrmecophilous insects. A nest examined by me contained the following species of beetles: *Allodinarda myrmicarix* Brauns; *Ogmocerus raffrayanus* Brauns and *Batrissus myrmecariophilus* Brauns. The Botanical Gardens in Durban are infested with this species, but the examination of a large number of nests revealed only one species of myrmecophile, *Allodinarda kohli* Wasm.; which, however, was plentiful, as many as three dozen being taken in one nest. The nest has numerous entrances, and is surrounded by large heaps of excavated material, often covering an area of several square feet.

Arnold<sup>3</sup> has also described and figured the puparium of a fly (possibly a form allied to *Microdon?*), with a peculiar tray covered with trichomes at the posterior end of the body, as occurring in the nest of *M. eumenoides* with the myrmecophilous beetles cited in the foregoing quotation. The following is his account of the migration of the colony and its guests to a new nest.

I left this nest without filling up the hole, so that in about a week's time it was filled with rain after a heavy shower. The water must have filtered through the soil and almost saturated the nest, for it took nearly half an hour for all the water to dis-

<sup>1</sup>1914, Med. Göteborgs Mus. Zool. Afd., III, p. 45.

<sup>2</sup>1916, Ann. South African Mus., XIV, p. 266.

<sup>3</sup>1914, Proc. Rhodesia Sc. Assoc., XIII, p. 25.

appear from the hole. This state of affairs had evidently made the nest so uncomfortable that the ants decided to move to new quarters about 9 feet away. They began to do this about seven o'clock that evening, or perhaps a little earlier, for the migration was in full swing when I came on the scene again at that hour. Remembering the reputation which this ant has for harboring guests, and also the observations made by various entomologists on some European ants which, when moving to a new nest, are in the habit of carrying their guests with them, I decided to watch this migration carefully. At first I could see no guests at all; the workers were carrying in their mandibles only their own larvæ, pupæ or males. In fact I was looking at the workers so attentively that I failed to notice their smaller companions on the road, to which my attention was directed by suddenly catching sight of a Lepismid running by. Going back then to the old nest, I saw at intervals various myrmecophiles crawling out of the pit made by my former excavation, and following the tracks of their hosts, to which they were guided, of course, by the sense of smell. These parasites included three different species of beetles, viz. a staphylinid, and two species of pselaphids, together with the common lepismid found in the nests of nearly all our ants. No time was wasted by any of these insects, for once over the brow of the pit, they continued straight along the narrow path leading to the new quarters. While on their march they were utterly ignored by their hosts, but on arriving at the entrance of the new nest, it was noticed that some of the pselaphids were seized by the ants dawdling around, and taken down into the nest. This change of dwelling took some hours to complete, for at midnight it was still in progress.

Mr. Lang contributes the following note on the habits of the subspecies *opaciventris* at Avakubi: "These ants, called 'dufluguntu' by the natives, are very common and noticeable because they tend to congregate in great numbers about any piece of meat or a dead insect. On one occasion I saw them tear up and carry off a butterfly two inches in diameter in exactly two minutes and a half. They are harmless and therefore not feared by the natives. A young *Manis*, which I kept in captivity, enjoyed making a meal of them. The nests, as a rule built at the bases of trees or bushes, can be easily recognized by the mound of loose earth thrown up while the chambers are being excavated. The walls of the chambers are not hardened or smoothed as in the nests of some other ants. One nest which I examined extended seventeen inches below the surface. It had many ramifications, though most of the brood was found around the roots of the tree. The whole nest, when exposed, covered an area less than two feet in diameter. These ants build long tunnels open above or with small openings (one-eighth inch), surrounded by a heap of loose particles. One of these, more than an inch wide, crossed a certain road in several places. I have seen a number of these tunnels superimposed one above another so that I could drop a stick down thirteen inches. In these tunnels the ants travel back and forth in great numbers."

***Myrmecaria eumenoides* subspecies *opaciventris* variety *congolensis*  
(Forel)**

This form is not represented among the material collected by Lang, Chapin, and Bequaert. Santschi regards it as an independent subspecies, but it seems to me to be merely a variety of *opaciventris*. Three cotypes of *congolensis* were given me by Forel. Comparison of these specimens, which were taken from the stomach of a scaly ant-eater (*Manis temmincki*) captured by Solon in the Lower Congo, with *opaciventris* show relatively slight differences. They are somewhat smaller, of a more sordid yellowish brown color (possibly due to the action of the gastric juices of the *Manis*), and with much the same sculpture and lower portion of the postpetiole. The epinotal spines, however, are decidedly more slender and more strongly deflected, a character not mentioned in Forel's original description, though noted by Santschi; the head is proportionally smaller and narrower, with straight cheeks, and the gaster is opaque only at the base of the first segment, the remainder being rather shining.

***Myrmecaria eumenoides* subspecies *opaciventris* variety *crucheti*  
(Santschi)**

Stanleyville, ♀; Leopoldville, ♀; Ngayu, ♀; Avakubi, ♀ (Lang and Chapin). The workers from Avakubi, 22 in number, were taken from the stomachs of toads (*Bufo regularis* and *B. funereus*). I refer numerous specimens from these localities to the variety *crucheti* since they agree with Santschi's very brief description in size (5 to 5.5 mm.) and in having slender but straight epinotal spines. The petiolar node in my specimens is distinctly broader and less compressed laterally than in the typical *eumenoides* and not shorter than the peduncle. The surface of the petiole is not so smooth, though it is not longitudinally rugulose. I have received this same form in all three phases from Rev. Geo. Schwab, who took it at Metit, Cameroon. The female is very similar to that of the typical *eumenoides*, but the head is somewhat smaller, with slightly more prominent posterior corners and the gaster is entirely opaque and punctate, except the bases of the second and following segments. I am unable to detect any differences between the males of the two forms. Arnold describes the wings of the male *eumenoides* as paler than those of the female. This is certainly not the case in *crucheti*.

***Myrmicaria salambo*, new species**

Plate IX, Figures 1 and 2; Text Figure 37

**WORKER.—**

Length 6 to 7 mm.

Of rather uniform stature and closely resembling *eumenoides* but a little more elongate. Head relatively smaller, as broad as long, excavated behind, convex above, flattened below. Mandibles 5-toothed. Clypeus ecarinate, with entire anterior border. Eyes somewhat larger and more convex than in *eumenoides*. Thorax very similar but promesonotal suture very distinct, impressed, the mesonotal lobes less compressed, their posterior outline in profile less abrupt, more sloping so that the mesoepinotal impression, though deep, is shallower and less acute than in *eumenoides* and appears longer. Epinotal spines longer, slightly sinuous, with very feebly up-turned points, directed backward and slightly outward. Base of epinotum longitudi-

Fig. 37. *Myrmicaria salambo*, new species. Worker in profile.

nally concave. Peduncle of the petiole longer than the node, which is thick and evenly rounded, not compressed laterally above. The ventral surface of the petiole armed below with two long, delicate hyaline spines, which curve towards each other and enclose an elliptical space. Postpetiolar node of the same size and shape as that of the petiole, its ventral surface straight in profile, not bulging nor angulate in front. Gaster and legs of the usual shape, the former with a straight, anterior border.

Shining; mandibles coarsely longitudinally striated; clypeus smooth in the middle, with a few rugules on the sides. Rugosity of head, thorax, and pedicel much as in *eumenoides*, but the rugæ on the dorsal surface of the head and thorax less numerous and less pronounced, without distinct anastomoses; sides of the head with finer and less distinct rugules, so that the surface is more shining. Gaster opaque and very finely punctate only at the extreme base above, otherwise shining. Legs and scapes shining, finely striate.

Hairs dark brown, in length and arrangement much like those of *eumenoides*.

Reddish brown; gaster brownish yellow; legs, including the coxæ and lower pleuræ, darker than the thorax. Mandibular teeth and antennæ blackish.

Described from numerous specimens taken at Garamba (Lang and Chapin) attending scale insects on the buds of a *Protea* which is shown in Plate IX.



This form is so closely related to *eumenoïdes* that it might, perhaps, be regarded as a subspecies. It is easily recognized by the unique ventral appendages of the petiole. These are so brittle that they are easily broken off, but their basal insertions on the low hyaline lamella in the midventral line of the petiole are usually discernible. Evidently *salambo* is also related to *M. striata* Stitz, specimens of which I have not seen.

***Myrmicaria exigua* Ern. André subspecies *ksaugani*, new subspecies**

WORKER.—

Length 3 to 3.5 mm.

Head through the eyes scarcely longer than broad, evenly rounded behind. Mandibles 4-toothed. Clypeus ecarinate, convex, with entire, rounded anterior border. Frontal carinæ subparallel. Eyes convex, just behind the middle of the head. Antennal scapes extending about two-fifths their length beyond the posterior border of the head; apical funicular joint fusiform, enlarged as in the typical *exigua*. Pronotum more flattened above, though bluntly angular on the sides and without inferior teeth. Promesonotal suture distinct. Mesonotum with a small but distinct tooth on each side in front and the posterior lobes larger, erect, and rather acute. Mesoëpinotal impression very distinct and rather long. Epinotum not longer than broad, scarcely narrowed in front, its base longitudinally grooved in the middle, marginate on each side and not longer than the declivity, which is also marginate laterally; spines not longer than their distance apart at the base, straight, directed backward, upward, and outward, their tips not bent inward as in the typical *exigua*. Petiolar peduncle as long as the node, swollen at the spiracles; node longer than broad, as high as long, laterally compressed, constricted behind. Postpetiole longer than broad, broader and higher behind than in front, its node distinctly lower than that of the petiole. Anterior border of gaster straight or even slightly concave, with prominent anterior corners.

Shining; mandibles subopaque, longitudinally striate. Clypeus smooth in the middle, delicately rugulose on the sides. Head smooth in the middle of the front, delicately and irregularly longitudinally rugulose on the sides, posteriorly reticulate-rugose, but much less sharply than in the typical *exigua*. Pronotum with a few longitudinal rugæ, sometimes absent in the middle line; in some specimens reticulately-rugose over the whole surface, with very large meshes as in *exigua*. Sides of pronotum smooth and shining; meso- and metapleuræ subopaque, longitudinally rugulose. Base of epinotum transversely rugulose, declivity smooth and shining. Pedicel, gaster, and legs smooth and shining, with very sparse and minute, piligerous punctures.

Pilosity like that of the typical *exigua*, gray or whitish.

Piceous, nearly black; tips of mandibles, peduncle of petiole, declivity of epinotum, base of postpetiole and in some specimens the whole gaster or only the base of the first segment brown.

Described from numerous specimens taken at Stanleyville (Lang and Chapin) "crawling about the base of an orange tree."

I have compared this form with two cotypes from Sierra Leone (Mocquerys), received many years ago from André, and a worker from

Gaboon (Staudinger). The new subspecies differs in its much darker color, feebler sculpture, laterally more compressed petiolar node and in the shape of the mesonotum, which in the typical form of the species lacks the anterior tooth on each side and has only feeble indications of the posterior lobes. Forel has described a variety, *rufiventris*, from carton nests 3 to 4 cm. in diameter on leaves at St. Gabriel, Lumaliza, and Bati-amponde (Kohl), all localities near Stanleyville. This form is larger (3.8 to 4.6 mm.) and, according to Forel, "differs from the type of André only in its paler, reddish abdomen and in having the head more elongate and narrower behind." What Stitz has described as a distinct species, *gracilis*, is evidently nothing more than a subspecies of *exigua*, as is shown by a comparison of his and Forel's descriptions with the cotypes. André failed to mention the enlarged apical antennal joint, but it is very conspicuous in his specimens. Stitz says of the petiole: "Hinten schnürt sich von seiner Basis ein kleines, sekundäres Knötchen ab." This seems to refer to the swelling of the peduncle at the spiracles, a swelling which is visible, though less accentuated in other species of the genus, when the peduncle is viewed directly from above. Forel, however, interprets Stitz's "secondary node" to mean the constricted portion of the segment behind the node. As neither Stitz nor Forel compared their specimens with André's cotypes, they were led to regard *gracilis* as a species.

#### CARDIOCONDYLA Emery

**WORKER** minute, smooth, almost hairless. Clypeus projecting over the bases of the mandibles, steep in front, with rounded anterior border. Frontal area strongly impressed. Frontal carinae short and straight. Eyes well developed; ocelli lacking. Mandibles broad, triangular, dentate. Antennae 12-jointed, with long first funicular joint and 3-jointed club, the last joint very large. Promesonotal suture indistinct; mesoepinotal constriction well developed. Epinotum armed with spines or teeth. Petiole with long peduncle and small, rounded node. Postpetiole conspicuously large, cordate or transversely elliptical. Gaster formed in large part by the first segment.

**FEMALE** winged (except in *C. emeryi* Forel), somewhat larger than the worker; head of the same shape but with ocelli. Pronotum not covered by the mesoscutum in front. Petiole and postpetiole usually broader than in the worker. Wings with reduced venation; pterostigma near the middle of the costal border; one closed cubital cell; distal portions of radius and cubitus obsolete; brachius not developed beyond the nervulus but bending up into the submedius. According to Emery, the female of *C. emeryi* is wingless and has the posterior ocelli vestigial.

**MALE** usually ergatomorphic but winged in *C. emeryi*. In this form the antennae are 13-jointed but in ergatomorphic males they are 10- to 12-jointed; with long scape and more indistinct club. Petiole and postpetiole resembling the corresponding segments of the female, in the male of *emeryi* much as in the worker.

### **Cardiocondyla emeryi** Forel

A single worker taken at Thysville by Bequaert. This minute ant is very widely distributed through the tropics of both hemispheres. It was originally described from the island of St. Thomas in the West Indies, but was later recorded from Syria, Madeira, Madagascar, and the East Indies. Arnold records it from South Africa and my collection contains specimens from the Bahamas, Cuba, Porto Rico, Jamaica, Bermuda, Tepic in Western Mexico, and Miami, Florida. According to Arnold it "is usually found nesting in grassy soil; the entrance to the nest is a minute hole, not surrounded by earth or other substances."

### **CREMATOGASTER** Lund

*Crematogaster* is one of the largest and most sharply defined genera in the family Formicidæ. The species are all small, with monomorphic worker, decidedly larger female, and the male usually as small as the worker. The worker and female have 10- or 11-jointed antennæ, those of the male are usually 12-jointed. All the phases can be readily recognized by the peculiar structure and articulation of the petiole and postpetiole. The former does not bear a node but is more or less flattened above, the latter is short and articulated to the anterodorsal surface of the gaster, instead of to its anterior end as in other ants. The gaster, moreover, is in the worker and male subtriangular or subcordate, with pointed tip, and its upper surface is concave or more or less flattened, its ventral surface more convex and protuberant. These peculiarities in the structure of the abdomen enable the workers of many species to turn the gaster forward over the thorax and head, so that they are sometimes called "acrobat ants." As a rule, the sting is feebly developed. The anterior wings of the male and female have a discoidal and a single closed cubital cell.

The species of *Crematogaster* all form populous colonies which nest in the ground, under stones, in logs, the cavities of living plants, or in peculiar carton nests attached to the branches or trunks of trees. This habit of making carton nests is best seen in the tropical species, but traces of it survive even in the species inhabiting temperate regions, such as the North American *C. lineolata* (Say). Many of the species have rank and disagreeable odors.

The genus is cosmopolitan (Map 22), though the species scarcely enter the colder portions of the north and south temperate zones. Our common *C. lineolata* (Say) of North America occurs, however, as far north as Nova Scotia. The vast majority of species are confined to the tropics, being particularly numerous in the Neotropical and Ethiopian Regions. The African forms are so numerous and so variable that they constitute a veritable welter of subspecies and varieties. Mayr, Forel, Arnold, and Santschi have all dispaired of reducing this chaos to order. Unfortunately the portion of Arnold's work dealing with the South

difficult to get rid of them, as they work themselves upward on the body, attacking by preference the softer parts of the skin."<sup>1</sup>

***Crematogaster (Sphaerocrema) bequaerti* (Forel) variety *atraplex*  
Santschi, new variety**

"**WORKER.**—Length 4 mm. Rather dull yellow; gaster, postpetiole and femora yellowish brown; tips of the epinotal spines brownish black. In other respects like the type of the species and the var. *mutabilis* (Santschi), but the median impression of the pronotum is feebler. The dark tips of the spines contrast with the pale color of the thorax." (Santschi)

A dozen workers from Yakuluku (Lang and Chapin).

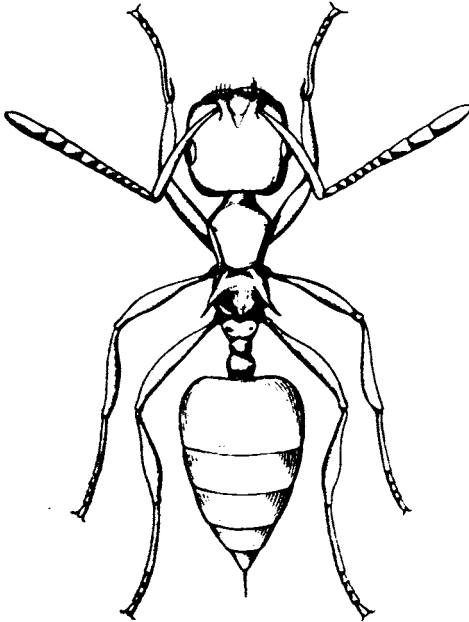


Fig. 38. *Crematogaster (Sphaerocrema) concava* Emery. Worker from above.

***Crematogaster (Sphaerocrema) concava* Emery**

Text Figure 38

Akenge, ♀; Stanleyville, ♀; Lukolela to Basoko, ♀ (Lang and Chapin). The specimens from Stanleyville were taken in twigs of *Barteria fistulosa* (Part IV); those from Lukolela were found running

<sup>1</sup>Santschi has recently described a variety *pluton* of this race, collected by Dr. Bequaert from similar carton nests in the crowns of *Papyrus*, at Zambi.

over fire-wood. Three specimens from Akenge were taken from the stomach of a toad (*Bufo polycercus*).

***Crematogaster* (*Sphaerocrema*) *pronotalis* Santschi variety *liebkechti* (Forel)**

Text Figure 39

Numerous workers from Yakuluku and Garamba (Lang and Chapin). According to a note accompanying the specimens from the

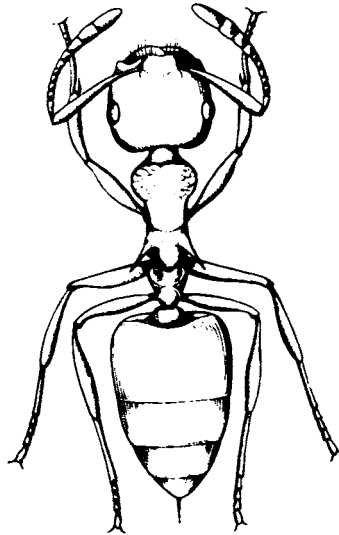


Fig. 39. *Crematogaster* (*Sphaerocrema*) *pronotalis* variety *liebkechti* (Forel). Worker from above.

latter locality, this ant "builds small carton nests on the blades of grass. It is common in swamps, from three to five feet above water level."

***Crematogaster* (*Sphaerocrema*) *rugosior* (Santschi)**

"FEMALE (undescribed).—Length 8 mm. Thorax smooth and shining like the posterior half of the head and that of the worker, except its upper surface and the sides of the epinotum which have rugæ as in the worker. Head rectangular, a little longer than broad, scarcely arcuate laterally. The eyes occupy nearly the middle third of the sides and the scapes barely extend beyond its posterior fourth. Clypeus with a strong median impression near its anterior border. Thorax as broad as the head. Epinotum nearly vertical, but the insertion of the spines is marked by an angular ridge which occupies nearly the upper half of the sides of the segment. Petiole

as in the worker, with a tooth beneath. Wings 7 mm. long, hyaline, with brownish veins. Otherwise like the worker." (Santschi)

Numerous workers and a few females from Stanleyville (Lang, Chapin, and J. Bequaert), without further data.

***Crematogaster* (*Sphærocrema*) *striatula* Emery variety *obstinata*  
(Santschi)**

Numerous workers taken by Dr. Bequaert at Leopoldville in the peculiarly inflated stipules of a species of *Uragoga*, a rubiaceous plant (Part IV). The spaces inhabited by the ants are not true nests but merely kraals or stables for Coccidæ, as no larvæ or pupæ were found in the structures.

***Crematogaster* (*Atopogyne*) *africana* (Mayr) variety *schumanni* (Mayr)**

A number of workers taken by Dr. Bequaert at Leopoldville in the hollow stems of a *Barteria Dewevrei* (Part IV).

***Crematogaster* (*Atopogyne*) *africana* subspecies *laurenti* (Forel)**

Numerous workers taken by Dr. Bequaert in the Rain Forest on the Tshopo River, near Stanleyville, in the hollow stems of *Plectronia Laurentii* (Part IV).

***Crematogaster* (*Atopogyne*) *africana* subspecies *laurenti* variety *zeta*  
(Forel)**

Many workers and a few females taken by Dr. Bequaert at Pale (Niembo, between Walikale and Lubutu) from the myrmecodomatia of *Plectronia Laurentii* (Part IV) and at Leopoldville in the rudimentary leaf pouches of *Randia physophylla* (Part IV); also by Lang and Chapin at Stanleyville in the stem cavities of *Cuviera angolensis* (Part IV.)

The female of this form is black and striated as in the typical *C. africana*.

***Crematogaster* (*Atopogyne*) *africana* subspecies *tibialis* Santschi, new  
subspecies**

"WORKER.—

"Length 3.5 mm.

"Pale castaneous. Epinotum, postpetiole, and posterior half of gaster of a deeper castaneous tint, passing to reddish brown. A spot on the vertex and the appendages dark brown, the tibiæ and metatarsi blackish, the tarsi and the ex-

tremity of the thorax reticulate, the epinotum more finely, with some fine longitudinal rugæ on the whole basal surface. Sides of the mesonotum regularly reticulate-punctate. Sides of the pronotum more shining and of the epinotum longitudinally striate. Petiole finely reticulate; gaster finely shagreened, almost smooth. The pubescence is rather well developed on the head, the gaster, and the appendages, sparse on the thorax. The hairs are very sparse, except around the mouth and at the tip of the gaster. Head square, with rather convex sides and straight posterior border. Eyes at the middle of the sides. Frontal area short, feebly impressed behind. Frontal carinæ developed. Clypeus slightly convex, with rather arched anterior border. Mandibles striate-punctate, with four blackish teeth. The pronotum forms with the basal surface of the mesonotum a plane surface with a contour like that of *C. castanea* Smith. Sides of the basal surface of the mesonotum blunt, not marginate, with the anterior eminence scarcely indicated. Promesonotal suture little or not at all impressed. Sides of the pronotum marginate. Declivity of mesonotum oblique, feebly concave from right to left, above with marginate sides. Mesoepinotal furrow moderately deep. Basal surface of epinotum trapezoidal, its length equal to its width anteriorly in the small worker. It is convex in front, more feebly behind. The spines are as short as a fifth of the interval between their bases, which is concave. They are directed backward and slightly outward. Declivity as long as two-thirds of the basal surface and forming with it an angle of about  $145^\circ$ . Petiole trapezoidal, as broad as long, and as broad as the epinotum. Last antennal joint reddish. A fine and dense striation disposed as in *africana* (Mayr) but more or less effaced on the front, vertex and occiput, where the reflection is more shining than silky. Epinotum transversely striate-rugose. Petiole smooth, postpetiole and gaster very finely shagreened, almost shining. The head is, moreover, punctate as in *africana* and much less smooth in the individuals with large head.

"The head, which varies in size independently of the rest of the body, which is almost invariable, is sometimes longer than broad and scarcely emarginate behind, sometimes broader than long, strongly concave behind and with convex sides. Eyes more posterior than in *africana*. Frontal area narrow, strongly impressed and shining. Mandibles punctate, feebly striate. Mesoepinotal impression stronger than in *africana*, the pronotum less marginate anteriorly. Mesonotum carinate, more elongate and with the declivous surface much less abrupt than in *africana*, with longer epinotal spines, even longer than in the variety *variegata* (Mayr) and a little farther apart. Petiole and postpetiole as in *africana*." (Santschi)

Numerous workers taken at the village of Mosekowa between Walikale and Lubutu by Dr. Bequaert from the peculiar pouches of *Macaranga saccifera* (Part IV) growing in the Rain Forest. As only adult ants and no brood were found in the pouches, Dr. Bequaert does not regard them as true nests. The openings of the pouches were not closed with fibrous carton.

**Crematogaster (Atopogyne) africana** subspecies **winkleri** (Forel) variety **fickendeyi** (Forel)

Numerous workers taken by Dr. Bequaert at Masongo, between Walikale and Lubutu, in the cavities of the branches of a species of *Sarcocephalus* related to *S. sambucinus* (Part IV).

***Crematogaster (Atopogyne) depressa* (Latreille) variety *fuscipennis*  
Emery**

Plate X

Stanleyville, ♀; Medje, ♂, ♀; Niapu, ♂; Ambelokudi, ♂, ♀; Niangara, ♂ (Lang and Chapin); Leopoldville, ♂ (J. Bequaert).

The beautiful carton nest of this ant is shown in Plate X, from a fine photograph taken by Mr. Lang at Ambelokudi. "It was built along the trunk of a tree near the ground. The ants, especially when squeezed, gave off a stench like certain bugs. They came out of the nest in great numbers and let themselves drop to the ground."

The female *C. depressa* is very aberrant in the form of the head, which is large, flat, and rectangular, with peculiar mandibles. It has long been known and has been repeatedly renamed, but only recently has it been correlated with the conspecific worker.

***Crematogaster (Atopogyne) theta* (Forel)**

Plate XI, Figures 1 and 2; Plate XII, Figures 1 and 2; Plate XIII, Figure 1

Medje, ♂; Avakubi, ♂; Stanleyville, ♂, ♀, ♂ (Lang and Chapin).

According to Santschi (*in litt.*), "this form represents the extreme limit of the subgenus *Atopogyne*. The worker has a feeble groove on the postpetiole, and the promesonotal impression is feeble. Moreover, the female is brown, smooth, and shining, with spined epinotum, very different from the female of *C. africana* (Mayr) and the variety *zeta* (Forel)."

The specimens from Avakubi were collected by the natives, who call this ant "lona." The carton nests are shown in Plate XI and XII. Concerning the specimens from Stanleyville, Mr. Lang writes: "These small black ants are very common. They build carton nests in trees, on the trunks of which they travel up and down in uninterrupted columns. At the slightest disturbance the nest is covered with workers. They appear and move so rapidly that it is very difficult to study them, especially as they sting disagreeably. Large numbers of nests may be found in the same tree, sometimes as low as ten feet from the ground, or even in bushes as well as in the tops of the tallest trees, living or dead. They have almost any shape, depending on their position, whether in forks of the branches or about twigs. In the latter situations they resemble mere lumps. The more regular nests, however, are somewhat conical, like the tops of termite hills and are placed upright on the boughs. In color, the carton is grayish or dark brown. In size, the structures are rarely more than two feet in height and about a foot in diameter. Their cells are irregular,



the walls of the chambers being from 1 to 3 mm. thick, and there are many entrances and exits. Though very light, the nests are so tough that slices can be chopped off with a hatchet without breaking the remainder. The carton seems to be made from the fibres of rotten leaves worked up with secretions from the oral glands of the workers. The chambers are often full of brood, which is not confined to any particular part of the nest. The rufous females were present in such numbers that twenty or more could be lifted at a time clinging to one another on the points of the tweezers."

***Crematogaster (Atopogyne) transiens* (Forel)**

A few workers from Avakubi and a female from Stanleyville (Lang and Chapin).

***Crematogaster (Nematocrema) stadelmanni* (Mayr)**

A single female from Stanleyville (Lang and Chapin), apparently taken at light, seems to be referable to this, the typical form of the species.

***Crematogaster (Nematocrema) stadelmanni* variety *dolichocephala*  
(Santschi)**

Plate XIII, Figure 2 and Plate XIV

Bengamisa, ♂, ♀; Manamana, ♂, ♀; Kwamouth, ♂; Ngayu, ♂, ♀ (Lang and Chapin). Numerous specimens from all these localities. The specimens from Bengamisa were accompanied by the photograph of the nest shown in Plate XIV, and the following note: "Ants from a pendent nest in very hard, woody carton. These nests are very common in the Rain Forest. They often fall to the ground but, in spite of the great moisture, resist disintegration fairly well. The ants leave as soon as the nest has dropped. The nests are precisely like those of some termites in shape and material, so that it is often impossible to decide from their external appearance which insect inhabits them. The internal cellular structure is very irregular and seems to follow no particular plan. The larvæ and pupæ are found in any of the cavities. The nest represented in the photograph was fixed to several creepers and was practically swaying in the wind about twenty-five feet above the ground. Size and shape vary much according to the situation of the structure." The following note accompanies the specimens from Kwamouth, together with the photograph shown in Plate XIII, fig. 2: "Black ants taken from a

These subgenera (see the key, Part VII) may be arranged more or less according to their natural affinities in the following sequence:

- |   |   |
|---|---|
| 1. <i>Anillomyrma</i> Emery                           | 7. <i>Monomorium</i> , <i>sensu stricto</i> |
| 2. <i>Martia</i> Forel                                | 8. <i>Notomyrmex</i> Emery                  |
| 3. <i>Lampromyrme</i> Mayr (= <i>Mitara</i><br>Emery) | 9. <i>Xeromyrmex</i> Emery                  |
| 4. <i>Chelaner</i> Emery                              | 10. <i>Parholcomyrme</i> Emery              |
| 5. <i>Adlerzia</i> Emery                              | 11. <i>Isolcomyrme</i> Santschi             |
| 6. <i>Syllophopsis</i> Santschi                       | 12. <i>Holcomyrme</i> Mayr                  |
|   | 13. <i>Corynomyrme</i> Viehmeyer            |

The genus *Monomorium*, though cosmopolitan and of even wider distribution than *Crematogaster* since it occurs even in New Zealand and Patagonia, is represented by the great majority of species in the Old World. The Neotropical Region possesses only a few species of the typical subgenus *Monomorium* and the species of *Martia*, which are not known to occur elsewhere. The subgenera *Notomyrmex*, *Adlerzia*, and *Chelaner* are exclusively Australian. *Anillomyrma* is monotypic and known only from Ceylon. *Isolcomyrme* and *Syllophopsis* are exclusively Ethiopian. *Xeromyrmex* is properly African but spreads into the Palearctic and Indian Regions. *Holcomyrme*, *Parholcomyrme*, and especially *Monomorium*, *sensu stricto*, are more widely distributed. Several of the species of *Monomorium*, *sensu stricto*, (*minutum*, *floricola*, *pharaonis*), *Xeromyrmex* (*salomonis*), and *Parholcomyrme* (*gracillimum*, *destructor*) have been widely disseminated by commerce. The species of *Holcomyrme* are harvesting ants of dry regions and this is true of certain Australian species which are allied to *Parholcomyrme*, though I assign them to a new subgenus **Protholcomyrme** (with the type *Monomorium rothsteini* Forel) to be described in a later paper.

#### ***Monomorium pharaonis* (Linnaeus)**

Numerous workers and females from Stanleyville and Thysville (Lang and Chapin). This is the well-known, little, red house ant, spread by commerce throughout the world.

#### ***Monomorium* (*Xeromyrmex*) *bicolor* Emery**

Several workers from Leopoldville (Lang and Chapin), found "living beneath a log," and two from Garamba, taken from the stomach of a toad (*Bufo regularis*). This species is apparently widely distributed in the Ethiopian Region.

**Monomorium (Xeromyrmex) afrum** Ern. André variety **fultor** Forel

Many workers from Niapu and Garamba (Lang and Chapin). Those from Niapu "came in thousands to the body of a dead bird. They had their nest in a cleared place about thirty yards away. The following day they had moved their nest to the base of a decomposed root but towards evening had returned to their original nest. This extended about two feet below the surface of the soil." At Garamba the species was found "making crater nests about three inches high about the stalks of grasses in a dry plain (savannah) with few trees." Thirteen specimens from this locality were taken from the stomach of a toad (*Bufo regularis*).

**Monomorium (Parholcomyrmex) gracillimum** (F. Smith) subspecies **robustius** Forel

Several workers from Yakuluku (Lang and Chapin); found living in small mushroom-shaped termitaria. The typical form of the species is widely distributed in Asia Minor, Arabia, Central Asia, India, etc., and is evidently spreading to other parts of the Old World tropics (Africa, Java, Laysan, etc.). According to Emery, it occurs in the desert of Algiers, nesting under stones. The subspecies *robustius* was originally described from Somaliland. Yakuluku is in the dry portion of the Belgian Congo towards the type locality.

**SOLENOPEIS** Westwood

A large and difficult genus of mostly hypogæic ants; usually with very small, pale workers and much larger and dark-colored females and males.

The WORKERS are usually monomorphic but in a few species, such as *puncticeps* Mayr, *ævisissima* (Smith) and *geminata* (Fabricius), distinctly polymorphic. Antennæ 10-jointed, first funicular joint large, club large, distinctly 2-jointed, the last joint very long. Mandibles narrow, with few (usually 4) teeth. Clypeus raised in the middle and projecting anteriorly, with two diverging ridges, or carinæ, each in all but a few species terminating anteriorly in a strong tooth flanked by a smaller tooth on the side. Frontal carinæ short, somewhat diverging behind. Eyes small, often minute or vestigial; ocelli very rarely present. Promesonotal suture indistinct, mesoepinotal suture well developed. Thorax more or less impressed at the latter. Epinotum always unarmed. Petiole with short peduncle and high, rounded node; postpetiole rounded, much lower than the petiolar node.

The FEMALE has 11-jointed (rarely 10-jointed) antennæ and moderately large eyes and ocelli. Fore wings with one cubital and one discoidal cell; radial cell open.

The MALE is somewhat smaller than the female, with 12-jointed antennæ. Scape very short, first funicular joint globular. Eyes and ocelli very large and prominent. Mesonotum without Mayrian furrows. Postpetiole campanulate; first gastric segment large; legs slender.

The genus *Solenopsis* is cosmopolitan, but represented by the greatest number of species in the Neotropical Region. There are a few forms even in Australia. The species with small, nearly blind, yellow workers, like *S. fugax* (Latreille) of Eurasia and *S. molesta* (Say) of North America, are hypogæic and usually live in the nests of other ants and termites, feeding on their brood (cleptobiosis). Some species, however, (*punctaticeps*, *sævissima*, *geminata*, *gayi*, etc.) live in large independent colonies. *S. sævissima* and *geminata*, the well-known "fire-ants" of the tropics, sting very severely. They have well-developed eyes and lead an epigæic life, not only feeding on insects and other animal food but also harvesting seeds or destroying the tender shoots or fruits of plants.

***Solenopsis punctaticeps* Mayr subspecies *kibaliensis*, new subspecies**

WORKER.—

Length 2 to 2.8 mm.

Apparently less polymorphic than the typical *punctaticeps* and the subspecies *caffra* Forel and therefore more like the subspecies *erythræa* Emery. Head in all the individuals rectangular, with straight sides, as broad in front as behind, not longer than broad in the largest, distinctly longer in the smallest individuals. Median teeth of the clypeus long and slender, lateral teeth obsolete or indicated only by feeble projections. Petiolar node broader than the petiole, its upper border straight and transverse.

Sculpture much as in typical *punctaticeps* and the hairs almost as abundant as in that form, but much shorter and less erect, especially on the head. Color yellowish brown, legs and antennæ yellow; mandibular teeth dark brown. Small workers scarcely paler.

MALE.—

Length 4.3 mm.

Head with very large eyes and ocelli, the latter extremely prominent; without the mandibles broader than long. Mandibles with 3 denticles. Antennal scapes nearly as long as the first two funicular joints together. Thorax broadly elliptical, slightly flattened above, only slightly longer than broad, much broader than the head. Epinotum bluntly subangular in profile, the base distinctly longer than the declivity. Nodes of petiole very low, rounded. Wings rather long; legs very slender.

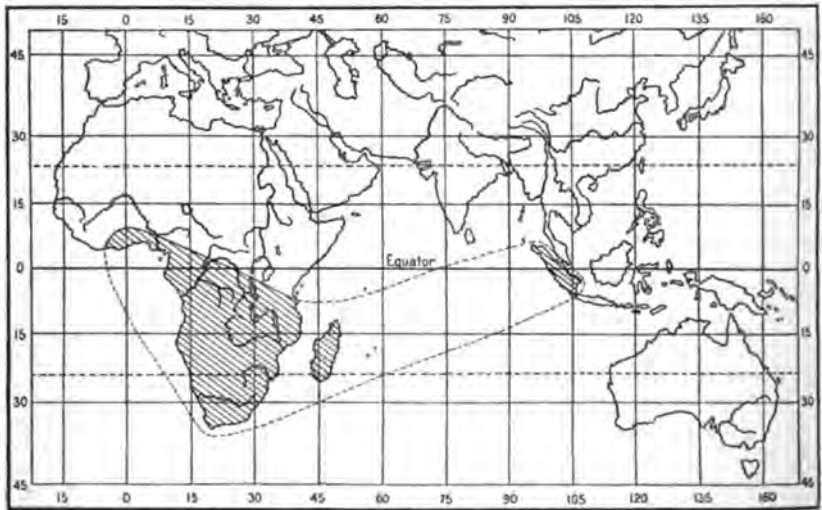
Smooth and shining; head subopaque and finely longitudinally striate behind.

Hairs sparser and more reclinate than in the worker.

Brown; head black around the ocelli; mandibles, antennæ and legs yellowish. Wings rather opaque brownish hyaline, with very distinct brown veins and pterostigma.

Described from twenty workers and a single male from Vankerckhovenille (Lang and Chapin), on the Kibali River or Upper Uele. The specimens were living in small craters in the soil and were seen feeding on dead insects.

For many years the genus was supposed to be monotypic and peculiar to Madagascar, but within recent years eight species and a variety have been described from the Ethiopian Region; Forel has also described a species from Sumatra (Map 23). A single soldier in the collection made by Lang and Chapin is certainly different from any of the species known in that phase. I describe it as new, although it may prove to be the soldier of one of the species based on workers.



Map 23. Distribution of the genus *Aëromyrma*.

### ***Aëromyrma petulca*, new species**

Text Figure 40

**SOLDIER.**—

Length 2.5 mm.

Head suboblong, nearly one and one-half times as long as broad, with feebly convex sides and rather deeply and angularly excised posterior border. Anterior ocellus well developed; eyes very small, consisting of about six ommatidia, situated at the anterior third of the head. Posterior corners of the latter with a low but distinct ridge produced on each side into a minute tooth. Mandibles convex, with 4 small, subequal, rather acute apical teeth, and a large blunt and flattened basal tooth. Clypeus flat, ecarinate, its anterior border feebly and sinuately excised in the middle, its posterior portion narrow, rectangular, extending back between the diverging frontal carinæ. Frontal groove distinct. Antennæ 10-jointed; scapes rather slender and curved at the base, reaching to the middle of the sides of the head; joints 2 to 7 of the funiculus minute, subequal, nearly as broad as long (somewhat too long in the figure); club a little shorter than the remainder of the funiculus, with the basal joint longer than broad and about one-third as long as the terminal joint. Thorax decidedly

Emery<sup>1</sup> believes that *Aëromyrma* should be reduced to the rank of a subgenus under *Oligomyrmex* "because in *O. debilis* Santschi the worker has 9-jointed, whereas the soldier (and probably also the female) has 10-jointed antennæ, so that if one wished to distinguish the groups as heretofore, the worker of *O. debilis* would be classified in the genus *Oligomyrmex*, the soldier in the genus *Aëromyrma*." While admitting that the two genera are very closely related, I prefer to retain *Aëromyrma* as an independent genus until the species are better known. Probably there are important differences in habit between the species of the two groups. At any rate, *A. nossindambo* and *petulca* are cleptobiotic with termites, whereas two or three species of *Oligomyrmex* which I collected in Australia were always found nesting in small cavities in rotten logs quite apart from termites.

#### **Aëromyrma** species

A single winged female from Akenge, taken from the stomach of a frog (*Arthroleptis variabilis*), cannot at the present time be referred to any of the described species, mostly known from soldiers and workers.

#### **CAREBARA** F. Smith

**WORKER** minute, monomorphic, yellow, without eyes or ocelli; antennæ 9-jointed, joints 2 to 6 very small, the two terminal joints forming a large and distinct club, with very long last joint. Mandibles with oblique 3- or 4-toothed apical margins. Frontal carinæ short; frontal groove and frontal area absent. Clypeus simple, unarmed, without carinæ. Epinotum unarmed. Petiole with a short peduncle, its node higher and larger than that of the postpetiole; both nodes from above transverse, subelliptical.

**FEMALE** enormously larger than the worker, dark-colored, with well-developed eyes and ocelli. Antennæ short, 10-jointed, the funiculi without a distinct club, their joints 2 to 5 not much narrower than the remaining joints. Thorax large and robust, convex above, higher than the head, the mesonotum anteriorly more or less over-arching the small pronotum, with well-developed parapsidal furrows. Epinotum unarmed, or with low flattened lobes or protuberances on the sides. Tarsi densely clothed with short, stiff bristles. Wings large, the anterior pair rather pointed, with one cubital, a discoidal, and a closed radial cell and a well-developed pterostigma.

**MALE** somewhat smaller than the female, but similarly colored, with long, 13-jointed antennæ, scapes short, first funicular joint not swollen nor globular, remaining joints long and cylindrical. Mesonotum large, without Mayrian furrows. Nodes of petiole and postpetiole only feebly developed.

The genus *Carebara* (Map 24) is represented by seven species in the Ethiopian and two in the Indochinese Region (*C. lignata* Westwood and *C. castanea* F. Smith). Santschi described some females and males

<sup>1</sup>1915, Rond. Accad. Sc. Bologna, N. S., XIX, p. 59, footnote.

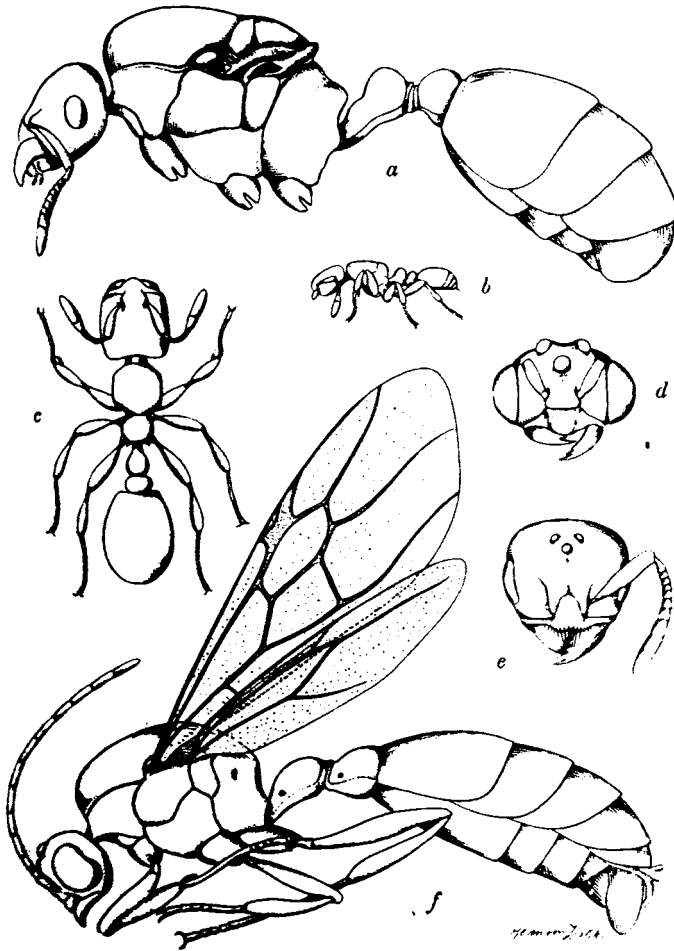


Fig. 41. *Carebara osborni*, new species. *a*, deellated female; *b*, worker in profile; *c*, same more enlarged; *d*, head of male; *e*, head of female; *f*, male in profile.

irregularly and indistinctly rugulose, somewhat transversely in the middle. Head coarsely and umbilicately punctate, finely striate in the spaces between the punctures. Mesonotum, scutellum, mesopleuræ, gaster, and nodes of petiole and postpetiole covered with umbilicate punctures of the same size as those on the head but sparser and with the shining interspaces very minutely and sparsely punctate. Opaque portions of epinotum and pedicel very finely striate. Legs with larger and minute punctures like the gaster, but the larger punctures are smaller and denser. Antennal scapes finely and densely punctate.

Hairs yellow, short, bristly, suberect, rather uniformly distributed over the body, arising from the large umbilicate punctures, longer on the gula and tip of the gaster, more abundant on the latter; very short, delicate and appressed on the legs and scapes.

Reddish brown; gaster and legs somewhat paler; mesonotum with indistinct traces of castaneous stripes, especially posteriorly. Mandibular teeth blackish.

MALE.—

Length 7 to 7.5 mm.

Head through the eyes much broader than long, broadest at the median transverse diameter, short and rounded behind. Eyes very large; ocelli large and prominent. Mandibles narrow, 3-toothed. Clypeus very convex and rounded in the middle with projecting, entire anterior border. Antennæ 13-jointed, long, filiform, of uniform thickness; scapes about three times as long as the first funicular joint, which is as broad as long but not swollen; remaining joints cylindrical, fully three times as long as broad, the terminal joint longer. Thorax robust, nearly as broad as long, through the wing insertions slightly broader than the head, convex above, in front somewhat overarching the pronotum. Epinotum short, shaped like that of the female, but without the marginate projections on the sides. Petiole resembling that of the female but with node scarcely developed; postpetiole much less convex, longer in proportion to its length. Gaster rather slender, scarcely flattened above; external genitalia voluminous, more or less exerted, the outer valves large, rounded at their tips. Legs slender.

Subopaque; scutellum, gaster, and upper surfaces of petiolar and postpetiolar nodes shining. Mandibles, head, thorax, and pedicel very finely and densely punctate; gaster also with fine but sparser punctures, those on the scutellum coarser but not so dense as on the remainder of the thorax.

Hairs finer, much shorter, and denser and more appressed on all parts of the body than in the female.

Brown; ocellar region black. Wings brownish, rather opaque, with the veins and pterostigma of the same color as the body.

Described from four workers, one female, and numerous males taken from a single colony at Niangara (Lang and Chapin) in the mound of a termite (*Termes natalensis* Haviland). According to Mr. Lang, the specimens were found "south of Niangara in one of the grass-covered termite hills which give the treeless landscape of the savannah its characteristic appearance (Plate XV). These hills extend as far as the eye can reach. They are never very high—rarely more than twelve feet—though they may attain a diameter of fifty feet at the base. Usually they appear as mere undulations of the ground, covered with grass which may be as much as ten feet high. The *Carebara* queen, males and workers were living in a flattened chamber about three feet above the general level of the soil near the center of a medium-sized termitarium."

*C. osborni*, though a true *Carebara*, is entirely unlike any of the known species in the small size of all the phases. In this respect and in the color of the male and female it approaches the species of the genus *Oligomyrmex*.



**Carebara vidua** F. Smith

Niangara, ♀; Faradje, ♀ (Lang and Chapin); Yakuluku, ♂ (J. Rodhain). The specimens from Niangara have the gaster black and therefore belong to the variety *dux* of Forel; one specimen from Faradje has the gaster castaneous and is therefore transitional to Santschi's variety *abdominalis*. Arnold has shown that these color differences are merely nest variations, so that they may be relegated to the synonymy of *vidua*.

**PÆDALGUS** Forel

The WORKER of this peculiar genus which is closely related to *Carebara* and *Oligomyrmez*, is monomorphic, minute, brownish yellow, with the eyes reduced to one or two ommatidia placed near the anterior third of the sides of the head. Ocelli absent. Maxillary and labial palpi each 2-jointed. Mandibles rather narrow, with oblique 4-toothed apical borders. Clypeus convex and projecting in the middle, extending back between the frontal carinæ, with a pair of longitudinal carinæ, which converge somewhat behind but do not terminate in teeth anteriorly. Antennæ rather stout, resembling those of *Carebara*, 9-jointed, with joints 2 to 6 of the funiculus small and transverse, the club large and distinct, 2-jointed. Thorax short and broad; the pronotum with rather angular humeri. Promesonotal suture lacking and, in the African species, with the mesoëpinotal suture scarcely indicated. Epinotum sloping, the declivity on each side with a low vesiculate lamina resembling in structure the epinotal laminæ of certain species of *Strumigenys*.

The FEMALE is considerably larger than the worker, with well-developed eyes and ocelli and 10-jointed antennæ, the club of the latter being 3-jointed and longer than the remainder of the funiculus. Mandibles 5-toothed. Clypeus convex, ecarinate. Thorax short, high, and arched, much broader than the head. Wings unknown.

The MALE has not been seen.

Forel founded this genus on *P. escherichi*, a species discovered by Escherich in a small cavity in a mound of *Termes obscuriceps* at Peradenya, Ceylon. The minute workers were "running about on the back of their huge queen, like lice." Santschi in 1913 described as *Oligomyrmez infimus* from French Guinea the worker of a second species, which he later (1914) recognized as a *Pædalgus*. The following species is very similar.

**Pædalgus termitolestes**, new species

Plate XVI; Text Figures 42 and 43

**WORKER.**—

Length 1 mm.

Head subrectangular, a little longer than broad, nearly as broad in front as behind, with feebly rounded sides and feebly excavated posterior border. Eyes very small, situated at the anterior third of the head. Mandibles rather narrow, with four subequal teeth. Clypeus convex in the middle, bicarinate, with the anterior border

projecting and truncated in the middle, narrow on the sides. Antennæ robust, scapes reaching to the second third of the sides of the head; funicular joints 2 to 6 subequal, much broader than long, together but little longer than the first joint; basal joint of club slightly longer than broad, less than one-third as long as the apical, which is nearly as long as the remainder of the funiculus. Thorax narrower and somewhat shorter than the head, broad in front, narrowed in the epinotal region, with subangular humeri; its dorsal surface in profile straight and horizontal to the base of the sloping, very bluntly angular epinotum, without promesonotal and mesoepinotal sutures; the epinotal declivity on each side with a low, subtriangular, vesiculate lamina. Petiole with a short, stout peduncle, its node high, rounded, about one and one-half times as broad as long, transversely elliptical from above. Postpetiole smaller than the petiole, its node much lower, only a little broader, a little less than twice as broad as long. Gaster elliptical, its anterior border concave in the middle. Legs rather short.

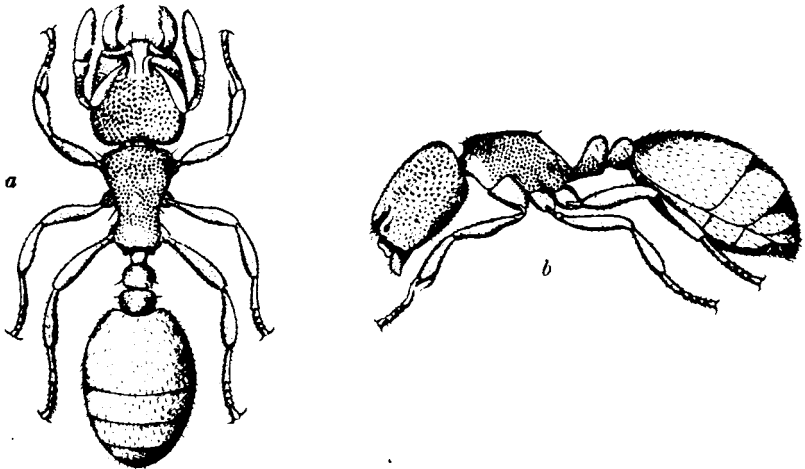


Fig. 42. *Pseudaligus termitolestes*, new species. Worker. a, from above; b, in profile.

Head, thorax, petiole, and postpetiole opaque, covered with shallow, saucer-shaped punctures, arranged in regular rows on the head and each bearing in its center a short hair. Upper surfaces of petiolar and postpetiolar nodes smoother and somewhat shining. Gaster and legs very smooth and shining, with minute, sparse, piligerous punctures. Mandibles and antennæ subopaque, the former sparsely and coarsely punctate.

Hairs yellow, short, bristly, suberect, longer on the clypeus and gaster. There is a long bristle at each humeral angle, one on each side of the mesonotum near the base of the epinotum and one on each side of the petiolar and postpetiolar nodes.

Brownish yellow; legs and antennæ a little paler; mandibles and clypeus a little darker.

Described from numerous specimens taken from a single colony at Malela by Lang, Chapin, and Bequaert in a mound-shaped termitarium

to possess unusually voluminous salivary glands. The youngest individuals, scarcely 0.2 mm. long, have the receptacle full of clear secretion (Fig. 43a). In older larvæ (Fig. 43b), the secretion after dehydration forms great masses in the receptacles and lumen of the glands. As these organs are not used in spinning a cocoon, it is very probable that the secretion, like the exudate of *Viticicola* and *Pachysima* larvæ described above, is elaborated and used as a food for the workers (trophallaxis).

The observations of Lang, Chapin, and Bequaert show that the African species of *Pædalagus* have the same habits as the Ceylonese *P. escherichi* and as the species of *Carebara*. Since, however, the majority of African termites cultivate fungus-gardens, the interesting question as to whether the minute workers of *Pædalagus* feed on the termites, on the fungus mycelium, or on both can be answered only by future observations on artificial compound nests of the ants and their hosts.

#### ATOPOMYRMEX Ern. André

WORKER variable in size, but only feebly polymorphic, with 12-jointed antennæ and 3-jointed antennal club. Clypeus subtriangular; moderately and evenly convex, its anterior border feebly notched in the middle and on the sides. Frontal area and groove distinct. Frontal carinæ far apart, in the large workers continued back some distance as diverging ridges bordering scrobe-like impressions for the antennal scapes. Mandibles triangular, convex, with toothed apical margins. Eyes small, flat, nearly circular, placed near the middle of the sides of the head. Ocelli absent. Pronotum flattened above with rectangular humeri. Promesonotal suture indistinct. Mesonotum bituberculate; separated from the epinotum by a wide and deep constriction. Epinotum armed with two long diverging spines; its base bituberculate anteriorly. Petiole and postpetiole very small, the node of the former bispinose above; postpetiole transverse with distinct anterior angles. Legs long and stout, femora incrassated in the middle; middle and hind tibiæ without spurs. Gaster broadly elliptical, somewhat compressed dorsoventrally. Body without erect hairs; pubescence extremely short and sparse, appressed.

FEMALE considerably larger than the worker. Scrobe-like impressions of the head more distinct. Antennæ 12-jointed. Eyes small, but larger than in the worker; ocelli very small, close together. Thorax short, through the wing insertions slightly narrower than the head. Pronotum visible from above as the mesonotum is rather small and flat. Epinotum abrupt, without distinct base and without spines. Petiolar spines reduced to two blunt tubercles. Gaster large, elongate, convex above and below, nearly as long as the remainder of the body. Anterior wings with a discoidal, a single cubital and a closed radial cell, with a distinct intercubitus (*Solenopsis*-type).

MALE with short, stout, denticulate mandibles. Head broad and long, much broader than the thorax and with marginate occipital border. Clypeus carinate. Frontal carinæ strongly diverging. Eyes rather small, occupying only about one-fifth of the sides of the head. Antennæ 13-jointed; scapes very short, scarcely two and one-half times as long as broad; first funicular joint as broad as long, not swollen; remaining joints cylindrical. Epinotum and petiole unarmed. External genital valves long, triangular, pointed at the tip. Wings as in the female.

in the strength of the cephalic and thoracic sculpture. The latter is noticeably strong in the specimens from Akenge, so that the head is scarcely shining in the occipital region.

The specimens taken by Lang and Chapin were nesting in cavities in dead wood. Those taken by Dr. Bequaert were "sucking nectar from the flowers of a tree (Anacardiaceæ) in the rocky savannah." Arnold says of the variety *curvispina* that "it is a slow ant, living in trees and mainly carnivorous in its diet. The nest is usually situated in a hollow stem, some distance above the ground. Like *Crematogaster*, these ants, when disturbed, exude a whitish and rather sticky secretion from the anal glands. It has not been found by me except in districts containing large trees." Bequaert found the nest of the typical *mocquerysi* "in a cavity in the wood at the base of a fig-tree (River Lovoi, near Kikondja, October 18, 1911)." He writes further: "I captured the male and female of this species in copula, flying in bright daylight (at noon) at the beginning of October (beginning of the rainy season)." The male and female of the species was first described by Forel from these specimens taken by Bequaert in the Katanga.

***Atopomyrmex mocquerysi* subspecies *cryptoceroideus* (Emery)**

Thirteen specimens from Malela (J. Bequaert) are referable to this form, which, I believe with Forel, is to be regarded merely as a subspecies of *mocquerysi* and not as an independent species. It is easily distinguished by its more shining head, coarser thoracic sculpture, and longer, stouter and, in the large workers, basally more flattened epinotal spines. The small workers have the spines slender, more curved, and more backwardly directed, just as in the small individuals of the true *mocquerysi*.

The habits of *cryptoceroideus* are evidently the same as those of the typical form, as it had been previously taken by Bequaert at Elisabethville in the Katanga "nesting in the rotten wood of a felled tree."

***Atopomyrmex mocquerysi* subspecies *cryptoceroideus* variety *melanoticus*,  
new variety**

Text Figure 44

**WORKER.**—Length 4.2 to 8 mm. Differing from the typical form of the subspecies in color. The small workers are entirely black instead of brown; the large ones black, with the head blood red, darkened on the vertex, the antennal scapes black, the funiculi dark brown, especially towards their tips, and the thorax in some apparently less mature individuals, deep castaneous. The medium and large workers have the flattened bases of the epinotal spines distinctly and often sharply angulate externally.

Numerous specimens collected between Lukolela and Basoko "on fire-wood" by Lang and Chapin.

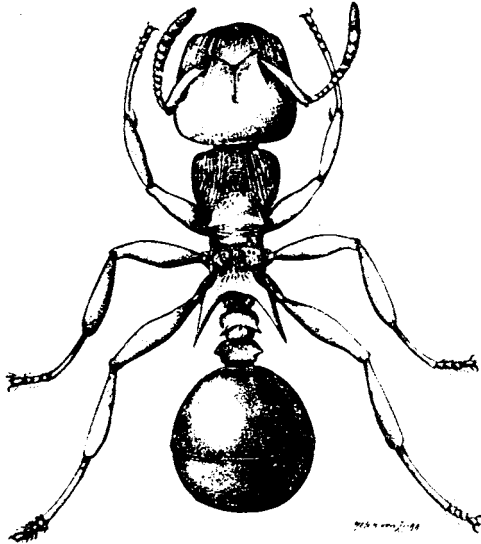


FIG. 44. *Atopomyrmer mocquerysi* subspecies *cryptoceroidea* variety *melanoticus*, new variety. Worker from above.

#### MERANOPLUS F. Smith

**WORKER.**—Body short and stout, somewhat flattened. Head broader behind than in front, convex above with frontal carinae far apart, diverging behind and prolonged backwards as the upper margins of deep scrobes above the eyes for the accommodation of the whole folded antennae. Eyes prominent, placed near the posterior corners of the head; ocelli absent. Clypeus short and steep. Mandibles small and stout, with a few subequal teeth. Antennae 9-jointed, with a large 3-jointed club; the scapes thickened distally. Thorax short and broad, flattened above, the pro- and mesonotum marginate or lamellately expanded on the sides and behind, forming a disc with spined or toothed anterior corners and with the posterior margin lobed or toothed and overhanging the epinotum, which is very steep or vertical and usually armed with spines. Petiole squamiform, cuneate in profile. Postpetiole with a cuboidal, globose or squamiform node. Gaster large, oval or cordate, emarginate anteriorly at the articulation of the postpetiole. Body usually more or less opaque or subopaque and sculptured, covered with long, abundant and soft or flexuous hairs.

**FEMALE** decidedly larger than the worker, with 9-jointed antennae. Thorax stout; pronotum large and exposed above; mesonotum large and convex, rounded on the sides; epinotum unarmed. Fore wings with large pterostigma, a cubital, a discoidal and a closed radial cell.

**MALE** only slightly larger than the worker, rather slender, with 13-jointed antennae; the scape very short; the first funicular joint globose, the second not much longer than the scape. Head produced behind, with very prominent eyes and ocelli. Antennal scrobes absent. Mesonotum with Mayrian furrows, rounded and unarmed on the sides or behind. Epinotum abrupt, unarmed. Nodes of petiole low. Legs slender. Wings as in the female.

sides of thorax and epinotum nearly smooth, as are also the petiole and postpetiole. First gastric segment evenly covered with shallow punctures interspersed with extremely minute punctures.

Hairs white, delicate, soft, and abundant, forming a uniform erect fleece on the upper surface of the body, more oblique on the appendages, on the legs interspersed with a few exceptionally long hairs.

Brown; upper surface of head and first gastric segment, except at the base, dark brown; mandibles, except the teeth, legs, and antennæ brownish yellow.

FEMALE.—

Length 4.5 to 4.8 mm.

Head like that of the worker. Thorax broader than the head, about one and three-fourths times as long as broad; broadest through the pronotum, the sides of which are somewhat swollen, but have blunt, though distinct, teeth. Mesonotum somewhat broader than long. Petiole and postpetiole much as in the worker, but the postpetiolar node is thicker above in profile.

Sculpture like that of the worker, but the mandibles coarsely striate and the sides of the thorax coarsely and irregularly reticulate rugose.

Hairs yellow, coarser, and shorter, especially on the gaster, than in the worker.

Color like that of the worker, but the mesonotum with three large, poorly defined, dark brown patches. Wings yellowish hyaline, with pale yellow veins and pterostigma.

MALE.—

Length 2.5 mm.

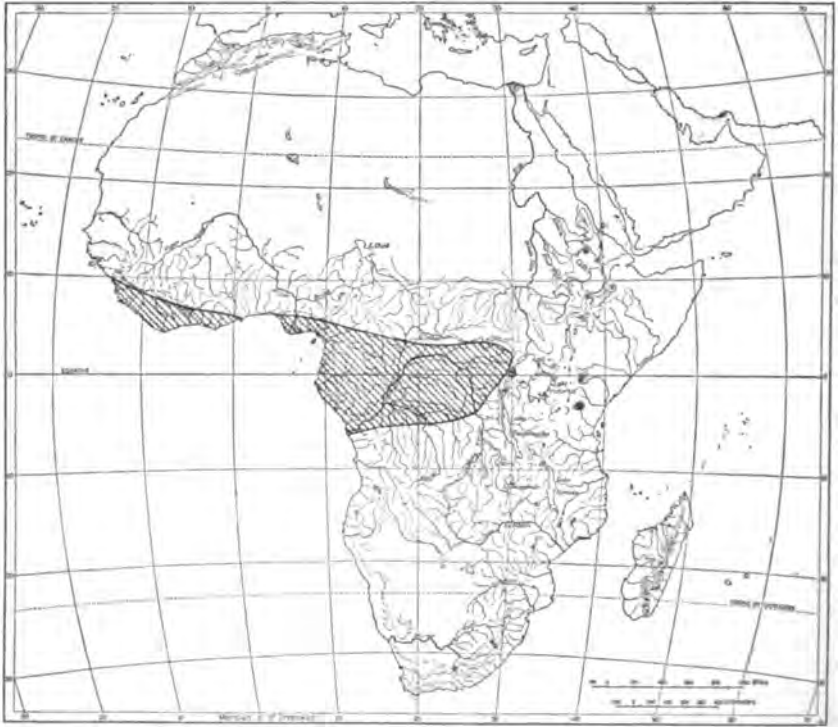
Head, including the eyes, as broad as long, very convex behind. Eyes and ocelli large and convex; cheeks very short. Clypeus convex in the middle. Antennal scapes scarcely more than twice as long as broad; first funicular joint globose, second somewhat longer than the scape but distinctly more slender than the third joint. Thorax short, broader than the head including the eyes. Mesonotum convex, with distinct Mayrian furrows. Epinotum like that of the worker, but more sloping. Petiole longer than high or broad, the node low, angular in profile, with subequal anterior and posterior slopes, the former straight, the latter slightly concave. Postpetiole as long as high, somewhat depressed above, transverse, broader than the petiole.

Clypeus smooth and shining in the middle. Head subopaque, reticulate-rugulose. Pronotum and epinotum indistinctly punctate-rugulose, subopaque; mesopleuræ smooth and shining; mesonotum and scutellum less smooth but shining, indistinctly punctate. Petiole longitudinally rugulose-punctate; postpetiole smoother. Gaster as in the worker but the large punctures are less distinct.

Pilosity much as in the female, but the hairs on the body are even less even and on the legs are shorter and more appressed.

Colored like the worker, but the antennæ and legs are yellow. The veins and pterostigma of the wings are distinctly paler than in the female.

Described from numerous workers, five females, and six males taken at Avakubi (type locality) and a number of workers from Medje (Lang and Chapin). According to Mr. Lang, these ants "build small crater nests in the plantations. One crater was one and one-half inches high and four inches in diameter. The whole nest, three inches wide, extended beneath the surface to a depth of only six inches. The workers



Map 27. Distribution of the genus *Macromischoides*.

I include in this genus also Mayr's *M. africana*, which is hardly more than a subspecies of *aculeata*. Emery placed both of these forms in *Tetramorium*. Their habitus is certainly that of certain forms of *Macromischa*, as Mayr observed, but Emery was right in excluding them from that Neotropical genus. Both species are confined to the rain forests of West Africa (Map 27) and do not nest in the ground like the species of *Tetramorium* but build loose carton nests between leaves or on their under surfaces. Mayr claimed that the male *aculeata* has 11-jointed antennæ, but Emery, after examination of six specimens, maintained that these appendages are 10-jointed and that Mayr's specimens must have been abnormal. There are four males in the Congo collection from two different localities and all of them have 11-jointed antennæ. Emery probably overlooked the third funicular joint, which is rather rigidly articulated with the second joint so that the suture can be distinctly seen only in a favorable light. The number of joints in the male antennæ, the shape of the clypeus in the worker and female, the absence of spurs

on the middle and hind tibiæ, the long slender legs and antennæ, the absence of the Mayrian furrows in the male, and the reduced number of palpal joints are all characters which seem to me to justify a new generic name. The peculiar habits, too, are important in this connection, although alone they would hardly justify a change in Emery's allocation of the species, since in a well-marked genus like *Myrmicaria* we have seen that some of the smaller species build carton nests on leaves whereas the larger species nest in the ground. The genus *Tetramorium* certainly becomes more homogeneous by the removal of the two Mayrian species.

***Macromischoides aculeatus* (Mayr)**

Plate XVII, Figure 1

Stanleyville, ♂; Avakubi, ♀, ♀; Bafuka, ♂; Medje, ♂, ♀, ♂; Isangi, ♀; Leopoldville, ♂ (Lang and Chapin); Bumba, ♂ (J. Bequaert) Many workers and females and four males.

The following note by Mr. Lang accompanies the specimens from Medje: "These ants build their nests by filling out interstices between neighboring leaves with a rough-looking, light mass of decomposed vegetable matter. They prefer densely leaved trees and there are sometimes several hundred nests on the same plant. If one touches the tree, the ants at once rush out of their nests in great numbers and hurry along the branches to reach the intruder. They cling to the human skin and double themselves up while biting and stinging. The result is rather painful and very annoying. There is no swelling but the pain endures for several minutes. All of the ants climb towards the head. The nests are often empty and contain only a few workers, but sometimes they are filled with brood and winged individuals. These ants have a strong odor, especially when rubbed between the fingers." In the plate (Pl. XVII, fig. 1) two of the nests are shown, one *in situ*, the other with one of the two thick leaves between which it was built removed.

*M. aculeatus* is so common in the Congo that its nests have been seen by several previous observers. Santschi<sup>1</sup> says of these structures: "Their nest consists of the leaf of a tree or shrub rolled up and lined with a felt-work of very fine vegetable débris and of a mycelium bearing fructifications. It would be interesting to study this fungus where it grows and to ascertain whether or not it is used habitually by the ants as food and is cultivated for this purpose." Commenting on the variety *rubroflava*, Forel<sup>2</sup> remarks that it was "found in nests woven of silk, fixed to

<sup>1</sup>1909, Ann. Soc. Ent. France, LXXVIII, p. 385.

<sup>2</sup>1916, Rev. Suisse Zool., XXIV, p. 421.



leaves, and, according to Mr. Kohl, similar to those of *Ecophylla* and *Polyrhachis*. From this fact I conclude that the nest of *T. aculeatus* is probably only superposed on a woven tissue, i. e., it is a combination of carton and tissue, as I have proved to be the case in many species of *Polyrhachis*."

Examination of a nest of *aculeatus* preserved in alcohol by Mr. Lang and conversation with Dr. Bequaert, who is well acquainted with the habits of the ant in the Congo, have convinced me that both Santschi and Forel labor under a misapprehension in regard to the structure of the nest. It consists of particles of the most diverse vegetable substances, bits of bark, dead leaves, trichomes, etc., loosely felted together and invaded by fungus mycelium, but the latter bears nothing resembling fructifications or ambrosial bodies such as are found in the gardens of fungus-eating ants. Dr. Bequaert informs me that *aculeatus* often nests in forests that are inundated during the rainy season and, as fungus hyphæ in such situations in the tropics grow readily on any dead vegetable matter, it is not surprising that we should find them invading the loose carton of the *aculeatus* nests. These hyphæ were interpreted as silk by Forel and suggested to Santschi the possibility of the ant being mycetophagous.

#### **Macromischoides aculeatus** variety **wasmanni** Forel

Numerous workers from Zambi (Lang and Chapin); one female from Stanleyville. This variety is smaller than the typical *aculeatus*, with somewhat shorter epinotal spines, less regularly sculptured and somewhat paler.

#### **TETRAMORIUM** Mayr

WORKER small, monomorphic. Antennæ 12-jointed, with a 3-jointed club. Clypeus narrowed on the sides where its posterior margin is raised in the form of a short trenchant ridge or carina as the anterior border of the antennal socket. Frontal carinæ rather far apart, usually continued back some distance and often the full length of the head as subparallel ridges forming the inner borders of scrobes or demiscrobes for the accommodation of the antennal scapes. Maxillary palpi 4-jointed; labial palpi 3-jointed. Eyes well developed; ocelli absent. Mandibles rather large, triangular, their apical border with a few large and several small teeth. Promesonotal suture indistinct, mesoepinotal suture more or less distinct; mesoepinotal constriction usually feeble; epinotum with two spines or teeth and episterna usually spined or dentate. Petiole with a short but distinct peduncle and the node large, subcuboidal, rounded above, rarely squamiform; the postpetiole usually broader than the petiole. Legs rather short, middle and hind tibiæ with small, simple spurs. Head, thorax, and petiole sculptured, usually rugose or reticulate rugose.

***Tetramorium pusillum* Emery variety *hemisi*, new variety**

WORKER.—Length 2.5 to 2.8 mm. Agreeing closely with Emery's description of the typical *pusillum* in size, sculpture, and coloration, but with the basal third or fourth of the first gastric segment densely punctate and nearly opaque, and with the epinotal teeth acute. The latter are distinctly larger than the metasternal teeth.

Described from fourteen workers taken from the stomach of a frog (*Hemisus marmoratum*) from Niangara (Lang and Chapin). The Abyssinian subspecies *ghindanum* Forel is slightly larger than this variety (at least this is true of several cotypes sent me by Prof. K. Escherich many years ago) and the opaque basal portion of the gaster is more extensive and finely striolate-punctate.

***Tetramorium setigerum* Mayr subspecies *quærens* Forel**

Plate XVIII, Figures 1 and 2

Numerous workers from Niapu (Lang and Chapin). The note accompanying the specimens states that they "form a ring of loose particles of soil about the entrance of their nests during the rainy season, each ant carrying the particle to a certain distance and then letting it drop and returning at once to the entrance. During the dry season they carry out the particles and food-remnants without attempting to construct a crater. The photographs (Pl. XVIII) show the difference in the appearance of the nest during the wet and dry seasons. These ants are very common, as about a dozen colonies were observed about the village of Niapu. They were usually situated along the paths or in clearings and seem to prefer dry soil."

***Tetramorium simillimum* (F. Smith)**

A single worker from Stanleyville (Lang and Chapin). This is a common tropicopolitan ant, now widely distributed by commerce.

***Tetramorium simillimum* subspecies *ispingense* Forel variety *dumezi* Forel**

A single worker taken by Dr. Bequaert at Thysville.

**XIPHOMYRMEX Forel**

This genus is very closely related to *Tetramorium*, differing only in having the antennæ of the worker and female 11- instead of 12-jointed. The scrobes of the antennæ are well developed in all the species known to me.

The genus is widely distributed, being represented by a number of species in tropical Africa, Madagascar, the Indomalayan and Australian Regions and by one species, *X. spinosus* (Pergande), with several subspecies, in the Sonoran Province of North America. The various species nest in the ground, like *Tetramorium*, often in very populous colonies.

**Xiphomyrmex angulinodis Santschi**

Medje, ♂, ♀, ♂; Irumu, ♀ (Lang and Chapin).

Santschi has described all three phases of this species from the French Congo and has figured the worker and male. The specimens before me agree perfectly with his account. They bear no data beyond the localities.

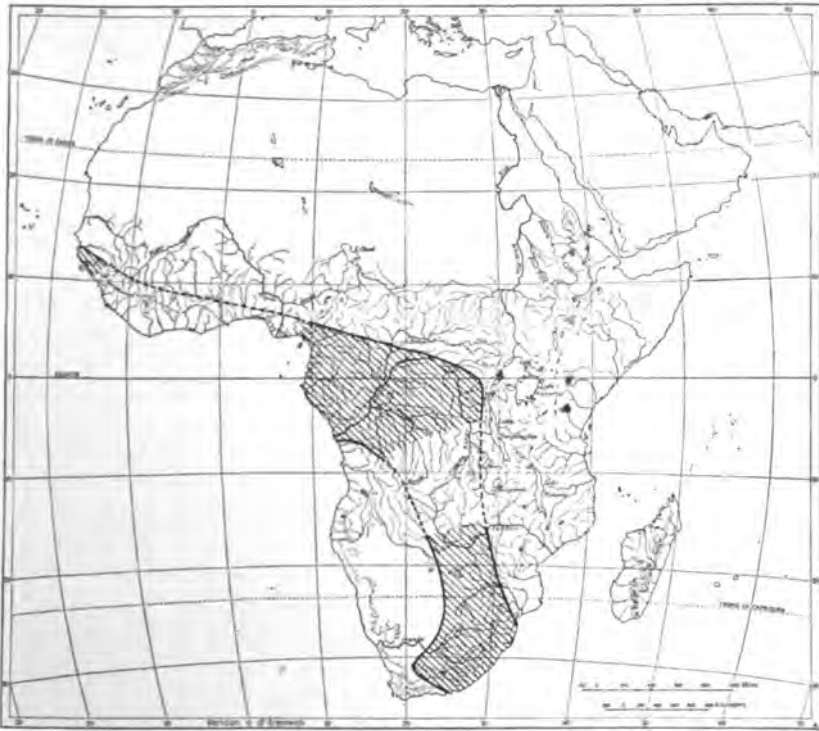
**Xiphomyrmex occidentalis Santschi subspecies akengensis, new subspecies**

**WORKER.**—Length 1.8 to 2 mm. Smaller than the typical form, which measures 3.5 mm., with the mandibles red, the tarsi, middle and hind coxæ and tips of fore coxæ brownish yellow, and the remainder of the legs and the antennæ reddish brown. The seventh funicular joint is as long as broad; the eyes smaller and more flattened than in the type, scarcely more than one-sixth as long as the side of the head, with the anterior orbits somewhat narrowed and bluntly pointed. The postpetiole is twice as broad as long, its node somewhat transverse and compressed anteroposteriorly, the petiolar node also somewhat broader and more squamiform than in the type. In other respects agreeing very closely with Santschi's figure and description.

Described from numerous specimens taken at Akenge (Lang and Chapin) from a single colony in "a dark brown paper nest." There is nothing to show that these specimens were not inhabiting the abandoned nest of some other ant. A single dealated female from Liberia in my collection belongs, in all probability, to this subspecies. It measures nearly 2.5 mm. and is very much like the worker. The larger eyes are not bluntly pointed in front, though rather flat. The thorax is small, with small mesonotum, bluntly pointed in front and not covering the pronotum, the epinotal spines are much stouter and further apart than in the worker, the petiolar node is broader, more squamiform and more transverse above, more sharply separated from the peduncle, and with its anterior surface decidedly concave. The color is the same as that of the worker, the body being brownish black with the appendages paler.

**RHOPTROMYRMEX Mayr**

**WORKER** small, allied to *Tetramorium*. Antennæ 12-jointed, with 3-jointed club, as long as or slightly longer than the remainder of the funiculus. Maxillary palpi 3-jointed; labial palpi 2-jointed. Head broader behind than in front, with convex sides and small, moderately convex eyes at the middle of its transverse diameter. Ocelli absent. Clypeus flattened or moderately convex, cearinate, its anterior border entire, a little produced, narrowed on the sides and bluntly ridged in front of the small antennal foveæ. Frontal carinæ short and more or less diverging; frontal area large but not impressed. Scrobes absent. Thorax short and stout, convex and rounded above, with feeble or obsolete promesonotal suture, somewhat constricted or impressed at the mesoepinotal suture, the epinotum unarmed. Petiole pedunculate, the node



Map 28. Distribution of the genus *Rhoptromyrmex*.

rounded, narrower than the postpetiole, which is transversely elliptical and rounded above. Gaster oval, formed very largely by the first segment. Legs moderately long, femora not incrassate in the middle, the middle and hind tibiae with or without short simple spurs.

FEMALE somewhat larger than the worker, with 12-jointed antennæ, but differing considerably in structural details in the various species. Fore wings with a cubital, a discoidal and an open radial cell.

MALE with 10-jointed antennæ and elongate second funicular joint, as in *Tetramorium*, and closely resembling the males of this genus also in other respects. Wings as in the female.

The species of this genus are confined to the Ethiopian Region (Map 28). A few Indian forms formerly referred to the genus have been recently placed by Emery in a new genus, *Acidomyrmex*, characterized by having very long, straight and diverging epinotal spines.

#### ***Rhoptromyrmex opacus* Forel**

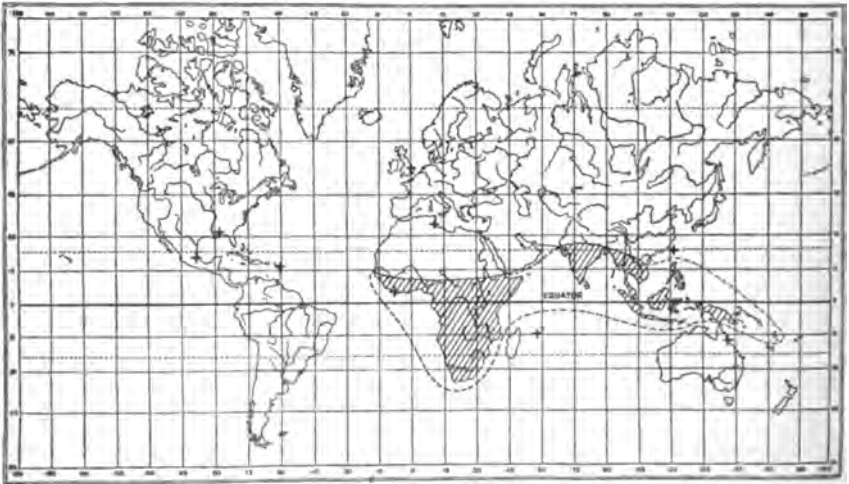
Numerous workers taken at Thysville by Bequaert. These were found nesting in sandy soil in the savannah.

**TRIGLYPHOTHRIX** Forel

Small ants closely allied to *Tetramorium*.

The WORKER has 12-jointed antennæ, the funiculus terminating in a 3-jointed club. Mandibles and clypeus as in *Tetramorium*. Head with distinct scrobes, often divided by a longitudinal carina for the reception of the folded scape and funiculus. Thorax short and stout, the promesonotal and mesoepinotal sutures nearly or quite obsolete. Epinotum and episterna armed with spines much as in *Tetramorium*. Petiole pedunculate, its node and especially that of the postpetiole decidedly broader than long. Hairs on the body abundant, soft, erect, trifid or many-branched, covering the surface like a delicate white mould.

FEMALE similar to the worker but larger; anterior wings with one closed cubital cell and an open radial cell.



Map 29. Distribution of the genus *Triglyphothrix*. The crosses indicate the localities where *T. striatidens* (Emery) has been found outside of its range.

MALE with 10-jointed antenna, the second funicular joint very long, the third shorter than the first. Mesonotum with Mayrian furrows. Petiolar and postpetiolar nodes narrower than in the worker and female, the petiole subpedunculate.

This genus is paleotropical, ranging over the Ethiopian, Indomalayan, and Papuan Regions (Map 29). One Indian species, *T. striatidens* (Emery), is rapidly spreading to other parts of the world and has been taken in such widely separated localities as Queensland, Formosa, Tunis, Sierra Leone, Seychelles, Barbados, Mexico, Louisiana, and England. In the locality last mentioned it occurs in the hothouses of Kew Gardens.

The species of *Triglyphothrix* are all very timid, usually curling up and feigning death when touched. They live in the ground. One South African species, *T. arnoldi* Forel,<sup>1</sup> according to Arnold, "is most fre-

<sup>1</sup>According to Emery, this species is a typical *Tetramorium*, in which genus I have placed it in the catalogue of Ethiopian ants.

protuberant. Pedicel formed by the petiole alone, the postpetiole forming the basal segment of the gaster; the following segment without stridulating surface. Sting vestigial, except in *Aneuretus*, where it is well developed and can be protruded. Usually there is one pectinate spur on the middle and hind tibiæ, homologous with the median spur of the Ponerinæ; sometimes with a second, lateral spur which is much smaller and simple. FEMALE always winged; similar to the worker. Some genera still retain a more generalized wing venation with two closed cubital cells and one discoidal cell; but frequently the venation is more or less reduced, often considerably so in the MALE. Antennæ of the male 13-jointed, even in *Semonius*.

The Dolichoderinæ males with two closed cubital cells can usually be separated by the well-developed mandibles from such Ponerinæ as have no constriction behind the postpetiole. The clypeus protruding between the frontal carinæ is a good character by which to separate them from the male Formicinæ with a similar venation.

NYMPHS never enclosed in a cocoon.

The anatomy of the gizzard or proventriculus is very important for the taxonomy of this subfamily; for a description of this organ the student is referred to the writings of Forel<sup>1</sup> and Emery.<sup>2</sup>

The larvæ are fed with liquid food, almost always of vegetable origin, regurgitated by the workers; the *Aztecæ* are mostly insectivorous. All the workers possess anal glands, the secretion of which hardens on exposure to the air, becomes sticky, and has a peculiar, often unpleasant odor like that of rotten cocoanuts or rancid butter; it is used as a means of protection against other insects. The habits are rather varied; many species are inconspicuous, shy, and live in small colonies under bark of trees or in dead wood. In the Australian *Leptomyrmex* the worker can store vegetable liquids in its much inflated crop (honey ants). Several species of *Iridomyrmex*, *Azteca*, and *Engramma* inhabit the cavities of various myrmecophytic plants, and are undoubtedly adapted to this peculiar form of symbiosis. Other species of *Aztecæ* build carton nests, often of large size, which may be free, attached to branches or trunks of trees, or may be placed inside cavities; certain species are associated with epiphytes which cover their carton nests; according to Ule, these "gardening ants" carry soil and seeds of these epiphytes in the branches of the trees.

The Argentine ant, *Iridomyrmex humilis* (Mayr), is one of the most troublesome pests of tropical and subtropical countries. Its original home was South America, whence it has recently spread through a large part of the globe. It is sometimes found in hothouses of temperate regions. In the Ethiopian Region it has thus far been recorded from

<sup>1</sup>Forel, 1878, 'Anatomie du gésier des fourmis,' Bull. Soc. Vaudoise Sc. Nat., XV, pp. 339-362, Pl. XXIII.

<sup>2</sup>Emery, 1888, 'Ueber den sogenannten Kaumagen einiger Ameisen,' Zeitschr. Wiss. Zool., XLVI, pp. 378-412, Pls. XXVII-XXIX; 1912, 'Genera Insectorum, Dolichoderinæ,' pp. 4-5. See also Wm. M. Wheeler, 1910, 'Ants,' pp. 33-35.

South Africa only, where its appearance is said to date from the time of the last Boer War, when it was probably introduced with forage (Arnold). It is now a great pest in houses near Cape Town; it is also very injurious to fruit-trees.<sup>1</sup>



Map 31. Distribution of the genus *Engramma*.

### **ENGRAMMA** Forel

Closely related to *Tapinoma*.

**WORKER** small, monomorphic, with the head more or less excised behind and the anterior border of the clypeus semicircularly notched in the middle and posteriorly extending back between the short but widely separated frontal carinae. Maxillary palpi 4-jointed; labial palpi 3-jointed. Antennae 12-jointed, with long first and last funicular joints. Gizzard with narrow, separated, anchor-like sepals. Gaster large, its first segment overlying the petiole; anus terminal or subterminal.

**FEMALE** larger than the worker; its fore wings with a discoidal, one cubital and a closed radial cell.

<sup>1</sup>See the references given under this species in the catalogue of Ethiopian ants.

MALE as small as the worker, with 4-jointed labial and 5-jointed maxillary palpi. Antennæ long, filiform, 13-jointed, the scape as long as the first and second funicular joints together. Mandibles large, denticulate, decussating. Mesonotum not over-arching the pronotum. Wings as in the female.

This genus has been known only since 1910 and comprises six described species. It has a very narrow range, being confined to equatorial Africa and in all probability to the forest regions (Map 31). Most of the species evidently live in the cavities of myrmecophytes. At least one, however, lives in the ground (*wolffi*) and another, *zimmeri* subspecies *okiavoënsis* of the Congo, is said to inhabit "a large pale gray nest, soft, woven and mixed with fine vegetable matter and applied to the trunk of a tree."

The workers of the previously known and of three new species described below may be separated by means of the following table.

1. Mesoëpinotal constriction very deep and long, so that the thorax is halteriform; epinotum with a pair of denticles above. . . . . *denticulatum*, new species.  
Mesoëpinotal constriction only moderately deep, acute; epinotum without denticles. . . . . 2.
2. Body long and slender; head and thorax opaque; antennal scapes extending at least one-fifth their length beyond the occipital border. . . . . 3.  
Body more thickset; head and thorax shining; antennal scapes shorter. . . . . 4.
3. Scapes surpassing the occiput by one-fifth their length; clypeal notch very large and deep and the median border behind it with a small triangular impression; all the funicular joints twice as long as broad; color black, with brown appendages. . . . . *wolffi* Forel.  
Scapes surpassing the occiput by about one-fourth their length; clypeal notch broad and shallow, the median border without an impression; funicular joints shorter; color yellowish red, gaster black, its segments narrowly bordered with yellow. . . . . *zimmeri* Forel.
4. Eyes very large, nearly one-third as long as the sides of the head. . . *ilgi* Forel.  
Eyes much smaller. . . . . 5.
5. Head, without the mandibles, as broad as long, deeply excavated behind. . . . 6.  
Head longer than broad, feebly excavated behind. . . . . 8.
6. Antennal scapes slightly surpassing the occipital border; funicular joints 2 to 7 slightly longer than broad; base of epinotum nearly as long as the declivity, horizontal; pilosity well developed. . . . . *lujæ* Forel.  
Antennal scapes not reaching the occipital border; funicular joints 2 to 7 broader than long; base of epinotum much shorter than the declivity, sloping forward; pilosity less abundant. . . . . 7.
7. Brown; length 2.25 to 3 mm. . . . . *laurenti* Emery.  
Dull yellow, with brown gaster; smaller, length 1.8 to 2.2 mm. . . . *kohli* Forel.
8. Antennal scapes reaching the occipital border; funicular joints 2 to 7 broader than long; epinotum evenly rounded, without distinct base and declivity.  
*griseopubens*, new species.



convex like the promesonotum, with two blunt denticles and prominent spiracles. Petiole stout, through the distinct node-like thickening at its anterior end nearly half as high as long. Gaster shaped as in the other species of the genus, with the first segment overlying the petiole; anus terminal.

Shining; head and clypeus finely but distinctly longitudinally aciculate; mandibles smooth, with coarse, scattered punctures; pronotum finely and indistinctly punctate; meso- and epinotum opaque, densely and rather coarsely punctate; gaster finely reticulate.

Pilosity and pubescence very sparse, the latter distinct only on the appendages.

Deep castaneous, nearly black; apical portions of mandibles, bases of scapes, terminal tarsal joints and petiole yellowish.

Described from two specimens taken by Lang and Chapin between Lukolela and Basoko on fire-wood. Two imperfectly preserved specimens were taken by Bequaert at Masaki, between Masisi and Walikale, from the caulinary swellings of a *Cuviera* (probably *C. angolensis*; Part IV).

This is a very strongly marked species on account of the peculiar shape of the thorax, the two denticles of the epinotum, and the peculiar sculpture of the head and thorax.

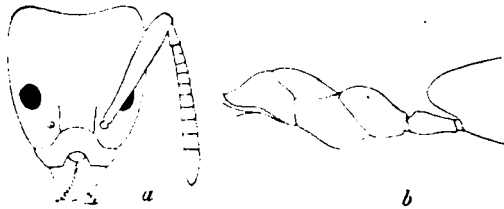


Fig. 52. *Engramma griseopubens*, new species. Worker. a, head from above; b, thorax and petiole in profile.

### ***Engramma griseopubens*, new species**

Text Figure 52

#### WORKER.—

Length 2.7 mm.

Head without the mandibles slightly longer than broad, much broader behind than in front, with somewhat angularly excised posterior border and feebly convex sides. Eyes small and flat, in front of the middle of the head. Mandibles rather large, convex, their long apical margins with numerous crowded denticles. Clypeal notch semicircular, about one-fifth as broad as the anterior margin. Frontal carinæ somewhat closer together than to the lateral margins of the head. Frontal area and groove obsolete. Antennæ rather slender, scapes not reaching to the posterior corners of the head; first funicular joint twice as long as broad, remaining joints except the last, as broad as long. Thorax with sharply marked promesonotal and mesoepinotal sutures, the pro- and mesonotum forming a hemispherical mass, the latter circular, the humeri rounded; the mesoepinotal constriction moderately deep, acute; the epinotum lower than the promesonotum, only a little longer than the mesonotum, broader than long, in profile rather convex, sloping, without distinct base and declivity.

Petiole of the usual shape, elliptical, with its anterior border thickened above as the vestige of the node. First gastric segment overlying the petiole as in the other species of the genus; anus nearly terminal. Legs rather slender.

Shining; whole body very finely and uniformly punctate.

Hairs absent, except on the mandibles and tip of the gaster, where they are very short. Pubescence gray, short and fine, rather abundant, uniformly covering the whole body, but not concealing the surface.

Black; mandibles, sides of clypeus, cheeks and gula brown.

Described from a single specimen taken by Lang and Chapin on fire-wood between Lukolela and Basoko. This species is quite distinct in the shape of the thorax, in sculpture, and in pilosity.

The following species, though not from the Congo, may be most conveniently described in this place.

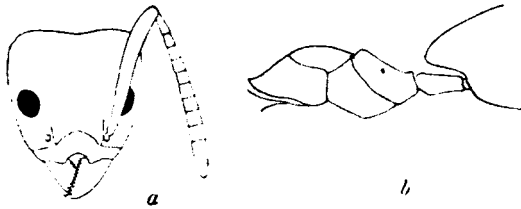


Fig. 53. *Engramma gowdeyi*, new species. Worker. *a*, head from above; *b*, thorax and petiole in profile.

### ***Engramma gowdeyi*, new species**

Text Figure 53

#### WORKER.—

Length 2.4 to 2.7 mm.

Head without the mandibles distinctly longer than broad, broader behind than in front, with feebly concave posterior border and feebly convex sides. Eyes flat, in front of the middle of the head, about one-fifth as long as its sides. Mandibles convex, with about a dozen even, crowded teeth. Clypeal notch about one-fourth the length of the anterior border, broader than deep, with sharp, slightly produced corners. Posterior clypeal border distinct; frontal area and groove obsolete; frontal carinae nearer to the sides of the head than to each other. Antennal scapes extending about one-sixth their length beyond the occipital border; funicular joints 2 to 10 perceptibly longer than broad. Thorax short, seen from above with distinctly angular humeri; promesonotal and mesoepinotal sutures distinct; pro- and mesonotum moderately convex, the latter broadly elliptical, slightly broader than long; mesoepinotal constriction rather deep, acute; epinotum as long as broad, broader behind than in front, in profile with a short base, rising rather steeply from the mesoepinotal suture, one-fourth as long as the flat, backwardly sloping declivity. Petiole elliptical, flat, its node obsolete. Gaster rather voluminous, its first segment overlying the petiole; anus terminal. Legs rather slender.

Shining: very finely and uniformly punctate.

the recurrent vein, there being no discoidal cell (*Camponotus*, *Ecophylla*). An intercubitus is only rarely present and then very short (*Myrmoteras*, which has the most primitive venation of this subfamily).

**NYMPHS** usually enclosed in cocoons; but there are some exceptions (*Ecophylla*, *Prenolepis*).

The members of this subfamily are morphologically the most highly developed of all ants; this is also true for their ethological peculiarities. Not only are their habits very diverse, but they show the most specialized form of mental and social behavior. The diet is in large part vegetarian and these ants show great predilection for sugary substances, which are sometimes stored in a special, replete form of worker (honey ants: *Melophorus*, *Myrmecocystus*, certain *Plagiolepis*, etc.). The species of *Ecophylla* and certain *Polyrhachis* and *Camponotus* build silk nests in leaves, using their larvæ as silk-producing shuttles. Moreover, the nesting habits in this subfamily are very varied. Certain species of *Formica* and *Polyergus* are slave-makers; the species of *Polyergus* are true social parasites of *Formica*, entirely dependent upon their slaves, but the worker caste is still present.

#### PLAGIOLEPIS Mayr

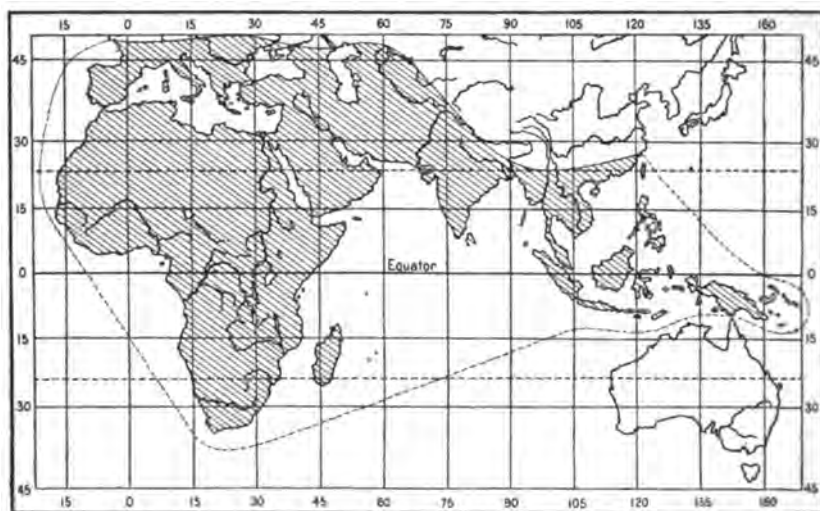
**WORKER** medium-sized to very small, monomorphic or feebly polymorphic. Mandibles rather narrow, with oblique, usually 5-toothed, apical borders. Clypeus large, convex, carinate or subcarinate, lozenge-shaped, its anterior border arched and projecting somewhat over the bases of the mandibles. Maxillary palpi 6-jointed, labial palpi 4-jointed. Frontal carinæ short, subparallel, rather far apart. Frontal area poorly defined. Antennæ 11-jointed, inserted very near the clypeal suture, the funiculi slender, gradually thickened towards their tips, the first joint long, the remaining joints gradually lengthening distally, the terminal joint elongate. Eyes moderately large and flat, placed in front of the middle of the head. Ocelli usually absent. Thorax short, more or less constricted in the mesonotal region, the epinotum simple and unarmed. Petiole with its scale anteriorly inclined, its superior border entire. Gaster rather voluminous, elliptical. Legs slender. Gizzard with the calyx strongly reflexed, parasol-shaped.

**FEMALE** much larger than the worker. Head small, thorax and gaster massive, the mesonotum somewhat flattened above, the gaster elliptical. Antennæ 11-jointed. Wings long, with one cubital cell and usually without a discoidal cell.

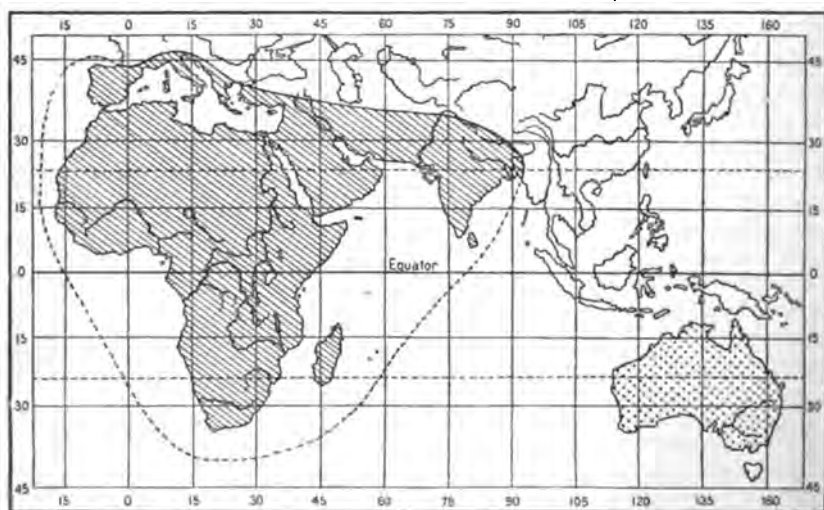
**MALE** somewhat smaller than the female. Mandibles acutely toothed. Frontal area large. Antennæ 12-jointed, with long scapes; funiculi with elongate first joint. Thorax voluminous, mesonotum large, flattened above, covering the small pronotum. Petiole as in the female. External genital valves large, rounded. Wings as in the female.

**PUPÆ** enclosed in cocoons.

This genus is peculiar to the warmer parts of the Old World (Maps 34 and 35) and is represented by the largest and most numerous species in the Ethiopian Region. Two of the latter, *P. custodiens* and *stein-*



Map 34. Distribution of the genus *Plagiolepis*.



Map 35. Distribution of the subgenus *Anacantholepis* (crossed area) of *Plagiolepis* and of the allied genus *Stigmacros* (dotted area).

It is the host of *P. nuptialis* Santschi, which was discovered by Dr. Brauns at Willowmore, Cape Province. Up to the present time only males of this ant have been taken. Dr. Brauns, who sent me a series of them, writes me March 24, 1920, as follows: "I am well aware of the interest attaching to the parasitic habits of *P. nuptialis*. Hitherto I have been unable to discover the female, but hope to unearth it eventually. The males always come out of the nests of *P. custodiens* and most years are not uncommon at Willowmore. I also found the male flying in numerous swarms over the Keurbooms River on the coast, near Plettenberg Bay, during a rain-storm, but could nowhere find them *in copula* with females. Perhaps the female is unable to fly! The males often remain for months at a time in the *custodiens* nests before swarming, which occurs only during a shower. The nests of *P. custodiens* and *steingröveri* are frequently close together, but the latter does not harbor *nuptialis*, though both species usually have the same myrmecophiles. At Willowmore *steingröveri* is showing a tendency to displace *custodiens*." It would seem from Dr. Brauns' observations that *nuptialis*, like the North American species of *Epæcus*, *Sympheidole*, and *Epipheidole*, must be a workerless parasite.

***Plagiolepis (Anoplolepis) tenella* Santschi**

Niapu, ♀; Bafwasende, ♀; Garamba, ♀, ♂; Akenge, ♀; Medje, ♀ (Lang and Chapin). The specimens from Akenge and Medje were taken from the stomachs of toads (*Bufo funereus* and *polycercus*) and two males from Garamba from the stomach of a *Bufo regularis*. The Niapu specimens were found running about on the ground in the clearing of a native village.

The female of this species was mentioned by Forel from specimens found in the stomach of a pangolin (*Manis temmincki*) from the Lower Congo, but was not described. The hitherto undescribed male measures about 5 mm. The wings are long (6 mm.). The head is only about half as broad as the thorax, broader through the eyes than long, with small, acutely 5-toothed mandibles. Color, sculpture and pilosity as in the worker, but the head is dark brown behind and the thorax is more shining, with three obscure, brownish, longitudinal blotches on the mesonotum.

**ACANTHOLEPIS Mayr**

WORKER small, monomorphic. Head subquadrate, rounded laterally and posteriorly. Mandibles with oblique, dentate apical borders. Clypeus broad and high, carinate or subcarinate. Clypeal and antennary foveæ confluent. Frontal area small but distinct, triangular. Frontal carinæ subparallel, short, rather far apart. Maxillary palpi 6-jointed, labial palpi 4-jointed. Antennæ 11-jointed, inserted close

to the clypeal suture; scapes long, funiculi slender, not thickened distally. Eyes moderately large, ocelli distinct, rather far apart. Thorax constricted at the mesonotum, the pronotum broad and usually convex anteriorly, somewhat compressed posteriorly; promesonotal and mesoepinotal sutures distinct; epinotum more or less swollen and obtusely dentate on each side. Petiolar scale bidentate or more or less excised above. Gaster broadly oval, with rather pointed tip. Legs slender. Gizzard much like that of *Plagiolepis*.

**FEMALE** larger than the worker. Head resembling that of the worker but broadened behind. Thorax robust, mesonotum large, gibbous in front where it overhangs the pronotum, obscurely longitudinally carinate in the middle as is also the scutellum. Epinotum unarmed or bluntly dentate. Wings with a single cubital cell and usually without a discoidal cell.

**MALE** scarcely larger than the worker and resembling that caste in the shape of the head. Eyes large, cheeks very short. Antennæ 12-jointed; scapes long and slender; funiculi filiform, all the joints elongate, the first shorter than the two following together. Thorax massive, about as broad as high; epinotum oblique, unarmed; mesonotum slightly convex but not subcarinate. Petiolar scale inclined forward, its upper border entire. External genital valves small, elongate, triangular. Wings long and broad.

**PUPÆ** enclosed in cocoons.

Like *Plagiolepis*, the genus *Acantholepis* is confined to the warm parts of the Old World, one species, *A. frauenfeldi* (Mayr), occurring as far north as southern Europe, Syria, and Persia. In Australia the genus is represented by a peculiar group of species, *Stigmatoceros*, which Forel regards as a subgenus but which, I am inclined to believe, should be raised to generic rank. The colonies of *Acantholepis* are moderately populous and usually nest in the ground, under stones, or in the fissures of rocks, rarely in the cavities of plants.

***Acantholepis capensis* Mayr variety *anceps* Forel**

Stanleyville, ♂; Medje, ♀ (Lang and Chapin). Numerous specimens. This variety is close to the subspecies *depilis*, having sparse, short, whitish pilosity. In shape the epinotum and scale, as Forel remarks, approach those of the subspecies *simplex* Forel. The variety was originally described from specimens taken by Kohl in the Belgian Congo, probably near Stanleyville. According to a note by Mr. Lang, this ant makes tiny craters in the soil after the rain. The colonies seem to be rather small, judging from the few workers seen outside the nests.

***Acantholepis capensis* variety *guineensis* Mayr**

A single worker from Thysville (Lang and Chapin) appears to belong to this variety, which is not black, like the other forms of the species, but reddish brown. The hairs are yellowish. It was originally described from the Gold Coast.

**Acantholepis capensis** variety **validiuscula** Emery

Thysville, ♀ (J. Bequaert, Lang and Chapin). Five specimens. This variety is decidedly larger and more robust than the typical *capensis*, with abundant, erect, dark brown pilosity. It seems to have a wide distribution, since it is known from Abyssinia, the Congo, Rhodesia, and Cape Province.

**Acantholepis capensis** subspecies **canescens** (Emery)

Thysville, ♀ (J. Bequaert); Avakubi, ♀ (Lang and Chapin). A form with long, white pilosity and abundant pubescence, distributed throughout the Ethiopian Region. A note by Mr. Lang states that "these small ants had their nest in the dirt which had accumulated at the bases of the cut leaves on the stem of an oil palm. They were numerous and travelled continually up and down, one by one, without forming a regular file. There were numerous nests along the trunk of the palm, but all of them were situated in the higher portion of the hollowed, partly decomposed stumps of the leaf-stalks, which had been cut off for some time. These hollows had evidently been made by the ants themselves."

**Acantholepis capensis** subspecies **canescens** variety **cacozela** Santschi

Faradje, ♀ (Lang and Chapin). Four workers taken from the hollow stems of an unidentified plant belonging to the family Melastomaceæ (*Dissotis*). This variety has longer hairs than the typical *canescens* and the petiolar scale is thickened at the summit, with scarcely excised border.

**Acantholepis carbonaria** Emery

Two workers from Banana (Lang and Chapin), without further data. This opaque species, originally described from Somaliland, has also been previously taken in the Belgian Congo.

**PRENOLEPIS** Mayr

WORKER small to very small, monomorphic, the body, legs, and scapes usually beset with sparse, coarse, erect, blunt hairs. Head rounded subrectangular or subelliptical, with rather narrow, dentate mandibles, their apical borders oblique. Clypeus large, convex, its anterior border entire or sinuately emarginate in the middle, not or scarcely produced over the bases of the mandibles. Frontal carinæ very short and straight; frontal area poorly defined. Antennary and clypeal fossæ not confluent. Maxillary palpi 6-jointed; labial palpi 4-jointed. Antennæ 12-jointed, inserted near the posterior angles of the clypeus; scapes elongate, funiculi filiform or slightly thickened distally. Eyes moderately large; ocelli absent. Thorax short, more or less constricted in the mesonotal region. In some species the mesonotum is elongate and subcylindrical. Promesonotal and mesoepinotal sutures distinct. Epinotum more or

***Pseudolasius bufonum*, new species**

Text Figure 55

WORKER MAJOR.—

Length 2.8 to 3 mm.

Head scarcely longer than broad, subrectangular, with nearly straight, subparallel sides and sinuately excised posterior border. Mandibles 5-toothed, the median tooth small, the apical long and pointed, the others shorter and subequal. Clypeus convex, subcarinate in the middle, its anterior border entire, only slightly projecting over the bases of the mandibles. Eyes very small, consisting of only three or four ommatidia, situated a little in front of the median transverse diameter of the head. Antennal scapes not reaching to the posterior corners of the head; first funicular joint longer

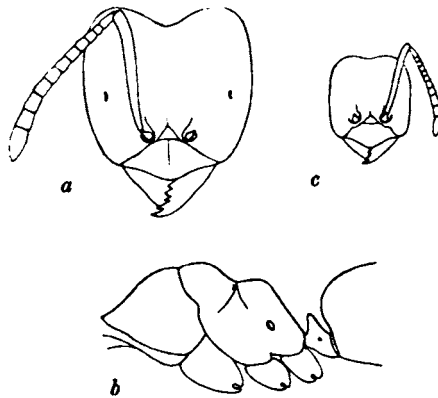


Fig. 54. *Pseudolasius weissi* variety *sordidus* Santachi.  
a, head of worker major; b, thorax and petiole of same in profile; c, head of worker minor.

than the two succeeding joints together; second joint as broad as long, joints 3 to 7 slightly longer than broad. Thorax short, stout; pronotum large and broad, longer than the mesonotum, which is as long as broad; epinotum broader than long. In profile the pro- and mesonotum form a large convexity with rather uneven outline, interrupted by the strong promesonotal suture. Mesoëpinotal impression short and not very deep, the stigmata prominent. Epinotum decidedly lower than the mesonotum, in profile rounded and sloping, with very short base and long sloping declivity. Petiole small, rather strongly compressed antero-posteriorly, with entire superior border. Gaster elongate elliptical. Legs rather stout.

Mandibles opaque, very finely and longitudinally striated. Remainder of body shining, very finely and rather densely punctate, but not more coarsely on the head and thorax than on the gaster. Clypeus smoother and more shining than the remainder of the head.

Hairs and pubescence yellowish, abundant; the former erect, longest on the thoracic dorsum, sparser and shorter on the scapes and legs; pubescence rather long and dense over the whole body but only slightly obscuring the shining surface.

Yellowish brown; gaster and appendages paler and more yellow; mandibles castaneous, their teeth and a blotch on the vertex blackish.



Sculpture and pilosity much as in the worker. Color yellowish brown above, with brownish yellow appendages, genitalia, venter, and anterior portion of head. Ocellar triangle dark brown. Wings paler than in the female.

Described from four major and eleven minor workers, three females, and eight males, all taken from the stomachs of toads (*Bufo superciliaris* and *polycercus*) captured at Medje (Lang and Chapin).

This species differs from *weissi* in the shape of the head of the major worker, the slightly larger eyes, more strongly striated and more opaque mandibles, shorter antennæ, and much more abundant pilosity and pubescence, and especially in having erect hairs on the scapes and legs. The female is smaller than that of *weissi*, with a differently shaped head, less excised behind, larger and more nearly circular eyes and longer antennæ.

***Pseudolasius bucculentus*, new species**

Text Figure 56

**WORKER MAJOR.—**

Length 3.2 mm.

Head large, as broad as long, broader behind than in front, with convexly inflated sides and front and deeply and angularly excised posterior border, the posterior corners being somewhat conical. Mandibles apparently 5-toothed, folded under the clypeus, which is short and in the middle convex and obtusely carinate; its anterior border in the middle with a shallow excision. Eyes very small and indistinct, situated a little in front of the median transverse diameter of the head. Frontal groove rather distinct; frontal carinæ very short; frontal area transverse, triangular, not impressed. Antennæ rather slender, the scapes not reaching to the posterior corners of the head; first funicular joint as long as the two succeeding joints together; joints 2 to 7 of subequal length, all slightly longer than broad. Thorax robust, pronotum broad, in profile only feebly convex above, the mesonotum rising higher than the pronotum to its middle and then sloping and concave to the mesoëpinotal suture. Epinotum with distinct base and declivity, the former short, sloping upward but not reaching the height of the mesonotum, the declivity flat and gradually sloping backward, more than twice as long as the base. Petiole small, with sharp, compressed, very distinctly notched superior border. Gaster voluminous, subelliptical, its anterior segment flattened in front and overlying the petiole. Legs long and stout.

Whole body, including the mandibles, shining and very finely and uniformly punctate, except the mandibles, which are longitudinally striate.

Pilosity and pubescence yellow, the former short, very sparse, absent except about the mouth and on the thoracic dorsum and as a single row of hairs along the posterior border of each gastric segment. Pubescence short and delicate but very dense, more conspicuous on the head and gaster than on the thorax, very fine and short on the appendages, the latter without erect hairs as in *bufonum*.

Uniformly brownish yellow; mandibular teeth and eyes blackish.

**WORKER MINOR.—**

Length 2.2 to 2.5 mm.

Differing from the major in the shape of the head, which is distinctly longer than broad, as broad in front as behind, with less convex, subparallel sides and less deeply

the pro- and mesonotum forming together an evenly rounded convexity; mesopleuræ somewhat compressed; epinotum short, nearly horizontal, lower than the mesonotum, passing through a curve into the sloping, flat declivity. Petiolar scale narrowed above, its sides curved, its superior border rather blunt, truncated, entire. Gaster elliptical. Legs rather short.

Whole body smooth and shining, except the mandibles, which are opaque and very finely and densely striated. Integument of the body and appendages apparently microscopically but not densely punctate.

Hairs and pubescence white, the former sparse, conspicuous only on the clypeus, thorax, and gaster, the appendages being without erect hairs. Pubescence short, rather dense on the head and gaster, longer on the latter, slightly oblique on the scapes and legs.

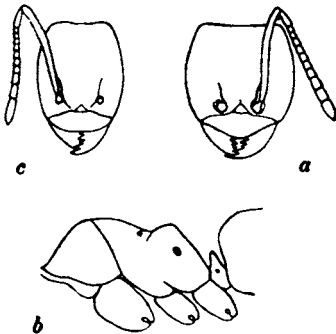


Fig. 57. *Pseudolasius gowdeyi*, new species. a, head of worker major; b, thorax and petiole of same in profile; c, head of worker minor.

Pale yellow, the head and thorax a little darker, mandibular teeth dark brown.

**WORKER MINOR.**—

Length 1.8 to 2 mm.

Differing from the major worker in its smaller head, which is elongate and with very feeble occipital excision. Antennal scapes reaching nearly one-fourth their length beyond the posterior corners of the head; joints 2 to 6 of the funiculus as broad as long.

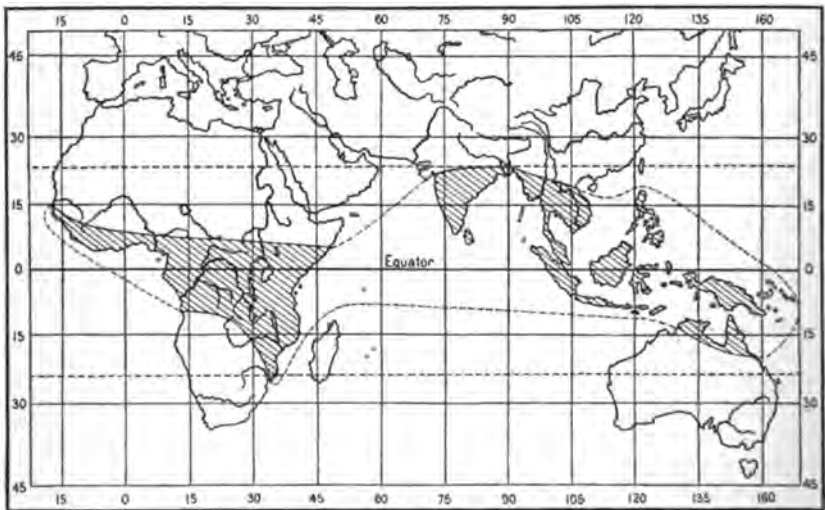
Described from two major and sixteen minor workers taken by Mr. C. C. Gowdey at Entebbe, Uganda. They were found attending subterranean coccids (*Pseudococcus citri* Risso) about the roots of coffee.

This is readily distinguished from all the preceding species by its smaller size, paler color, the complete absence of eyes even in the major workers, the shape of the head and thorax, and the pilosity.

**ŒCOPHYLLA** F. Smith

**WORKER** medium-sized, slender, slightly polymorphic. Head rather large, broader behind than in front, with rounded sides and posterior corners and semi-circularly excised occipital border, very convex above. Eyes large, convex, broadly elliptical, situated in front of the middle of the head. Ocelli absent. Palpi very short, maxillary pair 5-jointed, labial pair 4-jointed. Mandibles long and large, triangular, with nearly straight lateral borders, a very long curved apical tooth and numerous short denticles along the straight apical border. Clypeus very large and convex, but not distinctly carinate, its anterior border entire or very feebly sinuate in the middle, depressed and projecting over the bases of the mandibles. Frontal area rather large, subtriangular; frontal carinae moderately long, subparallel. Antennae very long, 12-jointed, the scapes inserted some distance from the posterior corners of the clypeus, rather abruptly incrassated at their tips; the first funicular joint very long and slender, longer than the second and third together, joints 2 to 5 much shorter, subequal,

accumulating in my collection for the past twenty years, together with the fine series of specimens taken by Lang and Chapin in the Congo, has convinced me that there are really two distinct species: *Æ. smaragdina* (Fabricius) of the Indomalayan and Papuan Regions, with the varieties *selebensis* Emery, *gracilior* Forel, and *gracillima* Emery and the subspecies *subnitida* Emery and *virescens* (Fabricius); and *Æ. longinoda* (Latreille) of the Ethiopian Region, with the varieties *textor* Santschi, *rubriceps* Forel, *annectans*, new variety, and *fusca* Emery. Ern. André described a form *brevinodis*, from Sierra Leone, as a distinct species, and Stitz has recently cited it from Spanish Guinea, remarking that *longinoda*



Map 37. Distribution of the genus *Æcophylla*.

occurs on the coast, *brevinodis* in the hinterland, and that there are no transitions between the two. He implies also that *brevinodis* does not make silken nests like *longinoda*. The abundant Congo series from various nests shows, however, without the slightest doubt, that *brevinodis* is nothing but the worker minima of *longinoda* (see Fig. 58c), as Emery maintained as long ago as 1886, and the localities of the material before me show that this species is not confined to the west coastal region. It occurs also in East Africa, Santschi's variety *textor* being from Zanzibar. Several authors have cited the true *smaragdina* from East Africa. Unfortunately I have little material from that region and what I have is certainly *longinoda*, presumably belonging to *textor*, though this variety seems to me to be poorly characterized and possibly not distinct from

the typical form of the species. I am unable to say, therefore, whether *Æ. smaragdina* actually occurs on the African continent.

According to Emery, *longinoda* is the most primitive of the existing forms of *Æcophylla*, because most closely allied to *Æ. sicula*, which he described from the Miocene amber of Sicily. In the Baltic amber I have recognized two species of the genus, *Æ. brischkei* Mayr and *brevinodis* Wheeler. As the latter name is preoccupied by *brevinodis* André, which was based, as I have shown, on the minima worker of *longinoda*, I suggest that the fossil species be called **crassinoda** (new name). In the shape of the petiole both of the Baltic amber forms, being of Lower Oligocene age and therefore older than *sicula*, are also more like *longinoda*, and especially its smaller workers, than the Oriental *smaragdina*.

***Æcophylla longinoda* (Latreille)**

Plate XX, Figures 1 and 2; Text Figures 58 and 59

Faradje, ♀, ♀, ♂; Malela, ♀; San Antonio, ♀ (Lang and Chapin); Katala, ♀; Leopoldville, ♀ (J. Bequaert).

The following differences between this species and *smaragdina* may be noted. In the worker the polymorphism is greater, for not only do the individuals of the same colony show a greater range in size (from 3 to 9 mm.) but the minima differ more from the media and maxima in the shape of the thorax and petiole. The head of the worker *longinoda* is distinctly more triangular than that of *smaragdina*, being broader behind, with less convex sides; the eyes are distinctly larger, the mandibles shorter, the clypeus more nearly subcarinate behind, its anterior border sometimes feebly and sinuately emarginate in the middle, the pronotum less convex, the petiole decidedly stouter, more thickened behind, with the stigmata much less prominent when the segment is viewed from above and its ventral surface much more convex anteriorly on the ventral side, when viewed in profile. The sculpture, pilosity, and color are very similar in the two species, but in *longinoda* the integument is more decidedly opaque, the mandibles are somewhat more coarsely striated, always darker, being concolorous with the posterior portion of the head, at least in the large workers and especially in the dark varieties. The transverse furrow on the second and succeeding gastric segments just behind the anterior border is more pronounced in *longinoda*.

The female of this species measures 12 to 14 mm. (wings 16 mm.) and is, therefore, distinctly smaller than the corresponding sex of *smaragdina*, which measures 15 to 17 mm. (wings 18 to 19 mm.). The body of the African species is much more opaque throughout, the wing-veins more

heavily bordered with dark brown, and the transverse bands at the bases of the second and following gastric segments are broader, darker, and more sharply marked off from the remainder of the segments. The green portions of the typical *longinoda* female are slightly more olivaceous and less pea-green, and the basal bands of the gaster are more exposed and brownish; the appendages are more brownish.

The male *longinoda* is scarcely smaller than that of *smaragdina* and measures 6 to 6.5 mm., but the head, thorax, and petiole are darker and

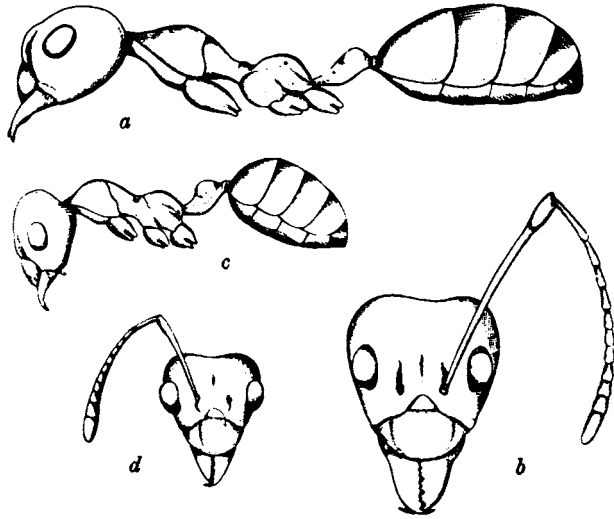


Fig. 58. *Ecophylla longinoda* (Latreille). a, body of worker major in profile; b, head of same; c, body of worker minima in profile; d, head of same.

more blackish; the head is decidedly broader, especially behind, the mandibles, petiole, antennal scapes, and wings are decidedly shorter and the integument is less shining.

The workers of the various subspecies and varieties of the two species may be separated by means of the following key.

1. Petiole very slender, its stigmata seen from above very prominent, its ventral surface nearly straight or very feebly convex in profile (*smaragdina*) . . . . . 2.
- Petiole stouter and higher, its stigmata seen from above not prominent, its ventral surface strongly convex in profile (*longinoda*) . . . . . 7.
2. Body ferruginous or testaceous . . . . . 3.
- Gaster and sometimes the head pea-green, head more rounded and less truncated behind; size smaller, petiole somewhat shorter (Queensland, New Guinea, Islands Aru and Key) . . . . . subspecies *virescens* (Fabricius).

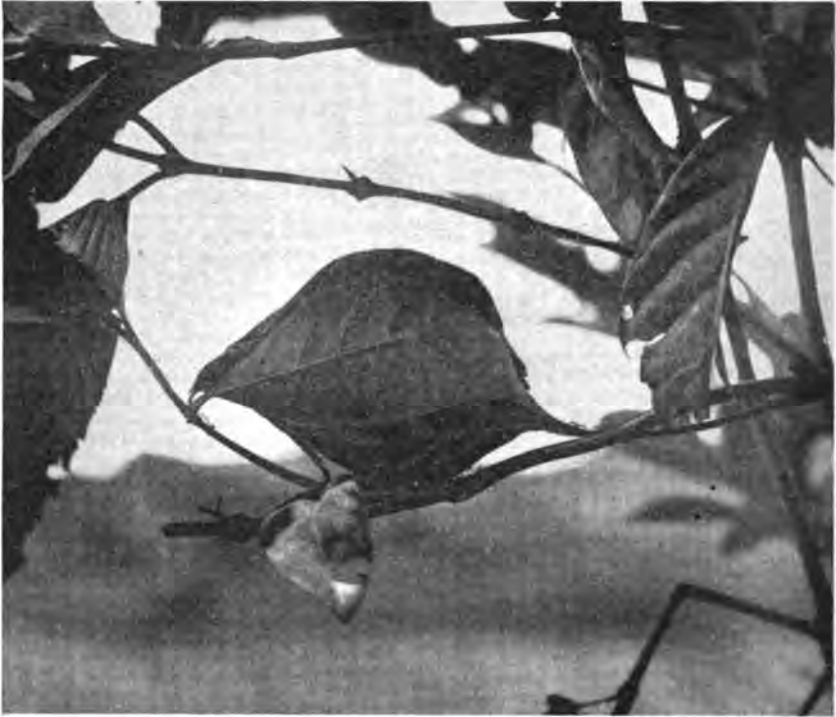


Fig. 59. Nest of *Ecophylla longinoda* (Latreille) at Avakubi, October 27, 1909. This nest, 16 cm. long, was placed about four feet from the ground in one of the coffee trees of a deserted plantation. Photograph by H. Lang.

from the ground. Text Fig. 59 shows a nest of this ant placed in a coffee tree at Avakubi. The habits seem to be the same in all essential particulars as those of *smaragdina*.

***Ecophylla longinoda* variety *annectens*, new variety**

WORKER very similar to the typical form but brown instead of ferruginous, the gaster sometimes slightly darker than the remainder of the body. Mandibles, except in the small workers, darker brown than the front, cheeks, and clypeus. Incrassated tips of antennal scapes with a dark brown spot; funiculi, knees, tarsi, and tips of tibiae pale yellow; pulvilli black.

FEMALE brown, instead of green and brown like the typical *longinoda*, with darker brown markings on the thorax. Second and following gastric segments with the basal bands velvety black, so that the gaster is distinctly fasciate. Funiculi, tips of scapes, tibiae, tarsi, and vertex paler, more reddish brown. Wings slightly darker than in the typical form, with deeper brown margins to the veins.

MALE darker brown than the worker. Mandibles, antennæ, tarsi, and articulations of legs brownish yellow; last tarsal joint black. Wings distinctly paler than in the female.

Described from long series of specimens from the following places: Avakubi (type locality), ♂, ♀, ♂; Stanleyville, ♂; Niangara, ♂ (Lang and Chapin); Malela, ♂ (J. Bequaert).

#### ***Ecophylla longinoda* variety *rubriceps* (Forel)**

WORKER black or dark brown, the head dull, blood red, often darker laterally and posteriorly, tips of antennal funiculi and second to fourth tarsal joints pale brownish yellow. Gaster in specimens from some colonies brown, the posterior margins of the segments paler.

FEMALE dark brown, almost black, the gaster very little paler, the bands at the bases of the segments velvety black; tarsi and tips of funiculi pale brown. Wings even darker than in the variety *annectens*.

MALE black; mandibles, legs, and funiculi piceous; wings paler than in the female but darker than in the male *annectens*.

Described from many specimens from two colonies taken at Stanleyville (Lang and Chapin). The workers of one colony agree closely with Forel's description of the types from the Belgian Congo in having the gaster nearly or quite concolorous with the thorax, and some of the larger specimens are scarcely distinguishable from the variety *fusca*; the workers of the other colony have the gaster rather pale brown and, therefore, connect the variety with *annectens*, which seems to be a more stable form than *rubriceps*.

#### ***Ecophylla longinoda* variety *fusca* (Emery)**

WORKER differing from *rubriceps* only in having the head entirely black or dark brown, though sometimes with a reddish tinge above. Mandibles black, with dark brown teeth. Large workers have the clypeal border very feebly sinuate in the middle and the surface just behind it with a faint longitudinal impression. The smallest workers are a little paler, with paler mandibles, but in the structure of the thorax and petiole precisely like the corresponding phase of the other forms of the species.

FEMALE like that of *rubriceps*, but perhaps a shade darker.

MALE indistinguishable from the male of *rubriceps*, except that the erect white hairs on the dorsal surface of the head, thorax, and gaster are distinctly longer and more abundant.

Redescribed from specimens taken at Stanleyville and Garamba (Lang and Chapin). There is also a worker of this variety from Monrovia, Liberia, (J. Morris) in my collection.

**CAMPONOTUS** Mayr

**WORKER** medium-sized to very large, polymorphic, rarely dimorphic, the worker maxima having a large, broad head, the minima a much smaller head and more slender body, the media being intermediate in structure. Head differing considerably in form in different species, usually broad and more or less excised behind, narrower in front, very convex above and flattened beneath. Mandibles powerful, short, triangular, with coarse teeth on their broad apical borders; external border and upper surface convex in large individuals. Palpi moderately long, the maxillary pair 6-, the labial pair 4-jointed. Clypeus large, trapezoidal or subrectangular, usually carinate or subcarinate, often divided into a large, median, subhexagonal and two small, triangular, lateral divisions, which do not reach the lateral border of the cheeks, the anterior border entire or emarginate, often excised on each side, with a broad, more or less projecting median lobe. Frontal area small, triangular or lozenge-shaped; frontal groove distinct; frontal carinae long, prominent, marginate, and sinuate or S-shaped, rising from the posterior border of the clypeus. Eyes moderately large, broadly elliptical, not very prominent, situated behind the middle of the head; ocelli absent, the anterior ocellus sometimes indicated. Antennae 12-jointed; scapes sometimes thickened distally, inserted some distance behind the posterior border of the clypeus; funiculi long, filiform, not enlarged at their tips, all the joints longer than broad. Thorax differing greatly in shape in the various species, typically broadly and more or less evenly arcuate in profile, broad in front, laterally compressed behind, the epinotum usually simple and unarmed. Rarely the mesonotum is impressed or sellate. Petiole surmounted by an erect scale, the upper border of which may be blunt or anteroposteriorly compressed, entire, subacuminate or more or less emarginate. Gaster rather large, broadly elliptical, its first segment forming less than half its surface. Legs long and well developed. Gizzard with a long slender calyx, the sepals of which are not reflected at their anterior ends.

**FEMALE** larger than the worker maxima but usually with smaller head. The latter and the petiole much as in the worker. Ocelli present. Thorax elongate elliptical; pronotum short, its posterior margin arched, its posterior angles reaching back to the insertions of the wings, mesonotum and scutellum long, convex; metanotum depressed below the scutellum. Gaster elongate elliptical, massive. Wings long and ample, the anterior pair with a radial, one cubital, and no discoidal cell.

**MALE** small and slender; head small, with very prominent eyes and ocelli. Mandibles small and narrow. Antennae 13-jointed, slender, scapes long. Petiolar node thick and blunt; gaster elongate, with small slender genital appendages. Legs very slender. Wing venation as in the female.

**PUPÆ** nearly always enclosed in cocoons.

This huge cosmopolitan genus, comprising more than 1000 described forms, has become so unmanageable that Forel and Emery have recently split it up into some thirty-six subgenera. The frequent occurrence of species of *Camponotus* in all countries, except Great Britain and New Zealand, and the extraordinary variability of many of the species in response to slight differences of environment make the genus one of considerable interest to the student of geographical distribution. In the Ethiopian Region, it is represented by numerous species assignable to no



occur in all the continents; *rufoglaucus*, with many varieties, ranges from southern China across India and equatorial and South Africa to the Gulf of Guinea; and *sericeus* occupies a similar range, though showing little tendency to produce subspecies and varieties.

The species of *Camponotus* often form very populous colonies and exhibit a great diversity of nesting habits. Many live in the ground, either under stones or in crater nests, others under bark, in dead wood, hollow twigs, and galls, and a few construct carton nests or employ their larvæ, after the manner of *Æcophylla*, in spinning together particles of vegetable detritus with silk (*C. senex* and *formiciformis*). The food of the various species consists of miscellaneous insects, the excreta of aphids (honeydew), and nectar. Many of the smaller forms are stolid, apathetic, or timid, but the maxima workers of the large species belonging to the subgenera *Dinomyrmex*, *Myrmoturba*, *Myrmothrix*, and *Myrmo-piromis* are very pugnacious and capable of inflicting painful wounds with their powerful mandibles.

***Camponotus (Myrmoturba) maculatus* (Fabricius)**

Medje, ♂, ♀, ♀; Yakuluku, ♂, ♀; Garamba, ♂, ♀; Vankerckhovenille, ♀; Faradje, ♂ (Lang and Chapin). Six of the workers from Garamba, all minors, were taken from the stomach of a toad (*Bufo regularis*). The major workers agree perfectly with Donisthorpe's description<sup>1</sup> of the Fabrician type of this ant in the Banks Collection, presumably from Sierra Leone, except that they have a few short, erect hairs on the gular surface of the head.

The distribution of *C. maculatus* and its various forms is shown on Map 39.

***Camponotus (Myrmoturba) maculatus* subspecies *guttatus* Emery**

I refer fourteen minor workers from Zambi (Lang, Chapin, and J. Bequaert) to this pale subspecies. The specimens were taken "only at night-fall, visiting the tables in the camp. They are shy and fast runners."

***Camponotus (Myrmoturba) maculatus* subspecies *melanocnemis* (Santschi)**

Faradje, ♂, ♀; Yakuluku, ♀ (Lang and Chapin). Numerous specimens from several colonies.

<sup>1</sup>1915, Ent. Record, XXVII, p. 221.

**Camponotus (Myrmoturba) maculatus** subspecies **solon** variety **jugurtha**,  
new variety

WORKER MAXIMA.—Differing from the typical *solon* in its much paler color, the antennæ, head, and thorax being red; the mandibles, front, and a streak down the middle of the clypeus castaneous; the posterior corners of the head, the legs including the coxæ, the petiole, and the three basal gastric segments brownish yellow; the tip of the gaster more brownish. The mandibles are very finely striated and the petiolar scale is much compressed and prolonged above as in the typical *solon* and not blunt as in *brutus*. In the feebler punctuation of the head this variety is also like the typical *solon*.

A single specimen from Batama (Lang and Chapin), without further data.

**Camponotus (Myrmoturba) maculatus** subspecies **brutus** (Forel)

Avakubi, ♂, ♀; Medje, ♂, ♀; Faradje, ♂, ♀, ♀; Bafwasende, ♂, ♀; Stanleyville, ♂, ♀, ♀; Batama, ♀; Lukolela, ♀; Malela, ♂, ♀; Isangi, ♂, ♀; Nouvelle Anvers, ♂, ♀; Zambi, ♀; Poko, ♂; Akenge, ♂, ♀; Niangara, ♂, ♀ (Lang and Chapin); Malela, ♂, ♀ (J. Bequaert). The workers from Akenge and Niangara, ten in number, are from the stomachs of toads (*Bufo funereus*, *polycercus*, and *regularis*). To judge from the many series of specimens, this large red ant must be very common in the Congo. Its native name, according to Mr. Lang, is "maola." It nests in rotten wood. The specimens from Nouvelle Anvers were found nesting in an old oil palm trunk.

**Camponotus (Myrmoturba) maculatus** subspecies **brutus** variety  
**lycurgus** Emery

Two major and four minor workers, taken at Leopoldville (Lang and Chapin), may be referred to this variety, which has the dark head and thorax of the typical subspecies *solon*.

**Camponotus (Myrmoturba) acvapimensis** Mayr

Faradje, ♂, ♀; Garamba, ♂, ♀; Bolengi, near Coquilhatville, ♂, ♀; Stanleyville, ♀; Thysville, ♀; Vankerckhovenville, ♂, ♀; Niangara, ♂, ♀; Akenge, ♂, ♀ (Lang and Chapin); Zambi, ♂, ♀; Thysville, ♀ (J. Bequaert). Of the numerous specimens of this small black species, thirty from Garamba and Niangara are from the stomachs of toads (*Bufo regularis* and *funereus*). A single major worker from Faradje is from the stomach of a frog (*Rana occipitalis*). The specimens from Bolengi were found nesting in the trunk of an oil-palm; some of those from Faradje were captured while attending plant lice on the young leaves of orange trees. The distribution of this species is shown on Map 40.

Body subopaque, the petiole, gaster and legs more shining. Mandibles coarsely and sparsely punctate, their tips striated, their bases sharply shagreened. Head very densely, evenly and finely punctate, so that it appears granular; the clypeus, cheeks, front, and vertex also with large, scattered, irregular, piligerous punctures. Sculpture of the thorax like that of the head but finer, especially on the pleuræ; the dorsal surface with coarse, sparse, piligerous punctures. Gaster finely, sharply and transversely shagreened, with coarse, sparse, transverse piligerous punctures. These have minutely papillate anterior borders so that the coarse hairs seem to rise from small projections. Legs finely shagreened or coriaceous.

Hairs fulvous red, coarse, erect, rather abundant, long on the dorsal surface of the head, thorax, and gaster, somewhat shorter on the gula and petiolar border, still shorter but suberect on the cheeks, scapes and legs. Pleuræ, anterior and posterior surfaces of petiole hairless. Pubescence rather coarse, very sparse, visible on the cheeks and gaster.

Brownish black; funiculi, tips of scapes, legs, including the coxæ, petiole, and gaster rich castaneous, the legs and funiculi slightly paler.

WORKER MINOR.—

Length 5 to 7.5 mm.

Differing from the major worker in the shape of the head, which is longer than broad, with straight, parallel sides and broadly convex posterior border. The eyes are more convex, the antennal scapes longer, extending somewhat more than half their length beyond the posterior corners of the head. The clypeal lobe has more rounded corners.

Described from numerous specimens from two colonies taken at Avakubi (Lang and Chapin). According to a note accompanying one lot, "these ants are said to be common in the forest in the decayed wood of large trees. Native name 'maguassa.'"

This species bears a striking resemblance to *C. festai* Emery from Asia Minor. The single worker major cotype of this insect in my collection lacks the head, so that in making comparisons of this part of the body I have to rely entirely on Emery's description. The head of the worker major of *festai* is evidently larger (3.5×3.5 mm.), more narrowed in front, with the posterior border slightly concave; the mandibles are 7-toothed, the scape is somewhat flattened, the declivity of the epinotum much shorter than the base, the petiole much broader above, with sharper border; the hind tibiæ are prismatic, with dorsal groove and their flexor border has a row of bristles; the hairs and pubescence are yellow, the latter much longer and more conspicuous on the gaster than in *maguassa*, and the hairs on the legs are distinctly longer; the head and gaster are black, the thorax, legs, and petiole deep brownish red.

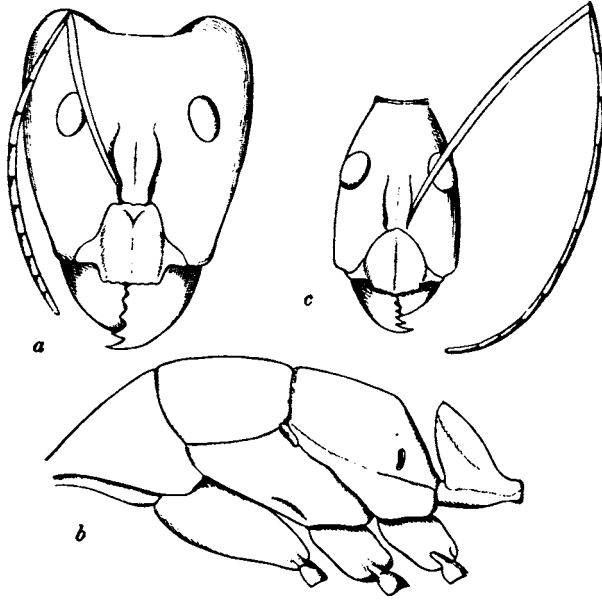


Fig. 60. *Camponotus (Dinomyrmex) pompeius* subspecies *caseius*, new subspecies. a, head of worker maxima; b, thorax and petiole of same in profile; c, head of worker minima.

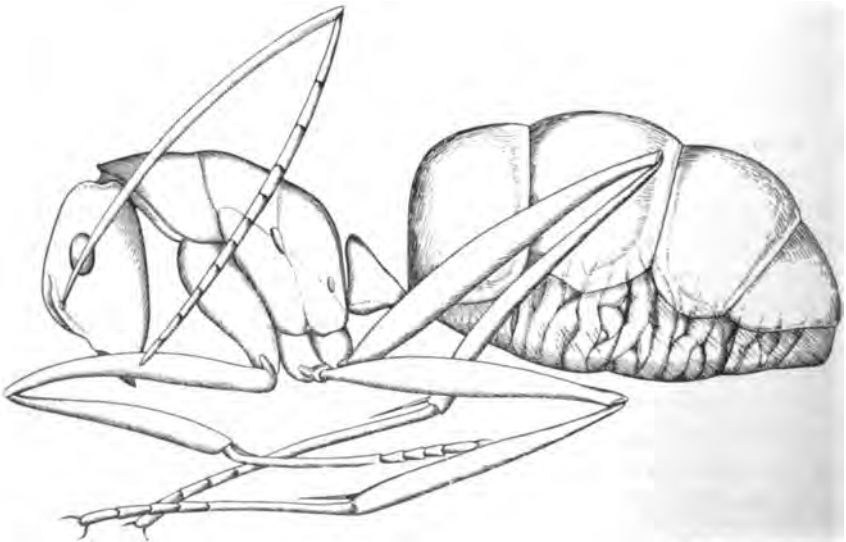


Fig. 61. *Camponotus (Dinomyrmex) pompeius* subspecies *caseius*, new subspecies. **Mermithergate** from Medje.

**Camponotus (Dinomyrmex) langi**, new species

Text Figure 62

**WORKER MAXIMA.**—

Length 12.5 to 14 mm.

Head unusually small, decidedly longer than broad ( $4.1 \times 3$  mm., without the mandibles), slightly narrower in front than behind, with broadly and not deeply excised posterior border and evenly, feebly convex sides. Eyes rather small and elongate, situated twice their length from the posterior border of the head. Mandibles rather small, convex, with 7 short teeth. Clypeus carinate, its anterior border emarginate on each side, the median lobe very short, its border coarsely crenulate, its corners obtuse. Frontal area small, subtriangular; frontal carinae closely approximated, especially in front. Antennae long (4.5 mm.) and slender, not enlarged distally, their bases distinctly flattened but not dilated, reaching nearly half their length beyond the posterior border of the head; funiculi long, filiform. Thorax low and narrow; metanotum distinct; epinotum long, its base nearly four times the length of the declivity, with a distinct, transverse impression in the middle. Petiole very low, subquadrate, and as broad as long when seen from above, in profile scarcely higher than long, obliquely truncated anteriorly and posteriorly, with very blunt superior border. Gaster long and narrow. Legs very long and thin; tibiae triangular in cross-section, deeply channelled on all three surfaces, their flexor borders without row of bristles.

Mandibles, clypeus, legs, sides of thorax, and sides and venter of gaster somewhat shining, remainder of the body opaque. Mandibles more opaque at the base, where they are densely shagreened, smooth and coarsely punctate in the middle, coarsely striated towards the tip. Clypeus, head, and thorax very densely shagreened, the head more distinctly; clypeus, cheeks, and sides of head with small, scattered shallow, piligerous punctures. Gaster very finely and transversely shagreened, with very sparse piligerous punctures.

Hairs and pubescence golden yellow, very sparse and short, more abundant on the gula and top of the head, very short, sparse, and appressed on the appendages. Sides of head with short, sparse, stiff hairs. Pubescence very dilute, distinct on the gaster and all parts of the head, longest on the gula.

Head and gaster deep castaneous; mandibles dark red, with black borders; clypeus and adjacent portions of cheeks often reddish; tips and insertions of antennal scapes, palpi, thorax, petiole, trochanters, and femora dull brownish yellow; upper surface of pronotum, mesonotum, and base of epinotum dark brown with paler sutures; tibiae, femora, and tarsi dark brown, the latter somewhat paler at their tips; posterior borders of gastric segments rather broadly yellowish and shining.

**WORKER MINIMA.**—

Length 11 to 12 mm.

Head very long (3.4 mm., without the mandibles) compared with its width (1.9 mm.), the portion in front of the eyes nearly as broad as long, a little broader in front, with straight sides; behind the eyes it narrows rapidly into a neck with concave sides, the occipital border being somewhat less than one-third of the anterior border. Eyes prominent, situated more than twice their length from the occipital border. Clypeus resembling that of the maxima. Antennae longer, the scapes not flattened, straight, reaching fully three-fifths of their length beyond the occipital border. Thorax and petiole as in the maxima but lower, and the transverse impression on the base of the epinotum scarcely indicated.

Sculpture much finer, pilosity and pubescence even sparser than in the maxima. Color paler; clypeus, cheeks, funiculi, petiole, ventral portions of thorax, coxæ, and femora yellow; mandibles, scapes, posterior portion of head, tibiæ, and dorsal surface of thorax and gaster brown.

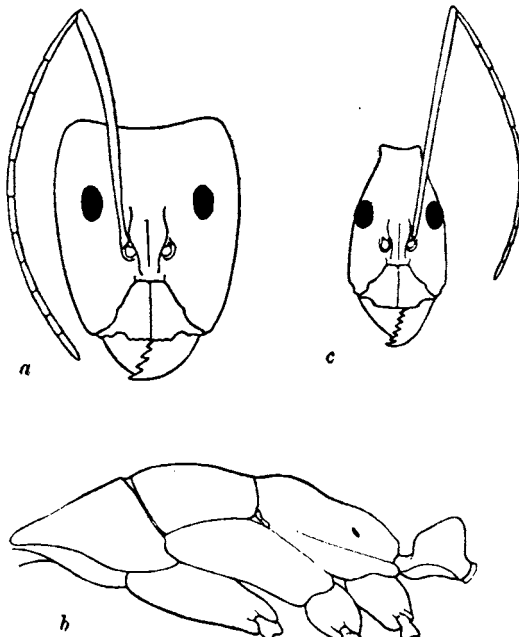


Fig. 62. *Camponotus (Dinomyrmex) langi*, new species. a, head of worker maxima; b, thorax and petiole of same in profile; c, head of worker minima.

**FEMALE (deâlated).—**

Length 21 mm.

Head large, slightly longer than broad, broader behind than in front, with straight sides and feebly and broadly excised posterior border. Mandibles more convex than in the maxima, clypeus very similar. Antennal scapes very slightly flattened at the base, extending nearly one-third their length beyond the posterior corners of the head. Thorax through the wing-insertions not broader than the head; mesonotum as long as broad. Petiole much higher than in the worker, nearly twice as high as long, elliptical from behind, its anterior and posterior surfaces convex, its border narrowed above and slightly notched in the middle, in profile rather acute.

Mandibles shining, coarsely punctate, their bases opaque. Head and body more shining than in the maxima, but similarly sculptured.

Pilosity like that of the maxima but the pubescence very long and abundant on the prosterna, fore coxæ, and lower portions of the metapleuræ; as long but sparser on the gula and posterior surfaces of the head; short on the scapes, but longer and oblique towards their tips. Tibiæ and tarsi with short, stiff, oblique hairs.

Head black; mandibles, sutures of thorax, upper portions of mesopleuræ, and pro- and mesonotum, scutellum, and gaster castaneous; remainder of thorax, petiole, middle and hind coxæ, and trochanters yellowish red. Legs castaneous, tips of tarsi paler.

MALE.—

Length 13 mm.

Head twice as long as broad, the portion in front of the eyes long, with subparallel, slightly concave cheeks, the posterior portion rapidly narrowed to the occiput, the sides and occipital border nearly straight. Eyes convex, at the middle of the sides of the head. Mandibles spatulate, bluntly pointed, edentate but with overlapping tips. Clypeus carinate, without an anterior lobe, its border broadly rounded. Antennæ very long and slender. Thorax and gaster long and narrow; epinotum elongate, evenly convex, sloping, without distinct base and declivity. Petiole much as in the worker minima. Legs very long.

Mandibles, head, thorax, and legs rather opaque; epinotum, petiole, and gaster shining, punctuation feeble and inconspicuous.

Hairs yellow, short, and sparse as in the worker minima.

Brownish yellow; head, mesonotum, scutellum, tibiæ, and tarsi brown; mandibles darker. Wings distinctly yellow, with yellowish brown veins and dark brown pterostigma.

Described from forty-one workers from Faradje (type locality), a female and worker minima from Garamba, and two males from Faradje (Lang and Chapin). The following note accompanies the specimens from Faradje: "These long-legged ants are very fond of sugar or anything sweet, such as fruits, etc. They are seldom seen during the daytime. The colony had made its nest between boxes that were piled up on the verandah of a house, and the ants were assembled in a hollow space about half an inch wide. A few fibrous particles of detritus were used in the construction of the nest." There are no data accompanying the two specimens from Garamba, so that I am not certain that the female is conspecific with the worker.

*C. langi* is very peculiar in the small, narrow head of the maxima and the long neck-like occipital region of the minima. There can be no doubt that what I have described as the maxima is really the largest worker form. Fifteen specimens of the series all agree in the shape and size of the head as represented in the figure; the remaining specimens are all minimæ. Mediæ, apparently, do not exist.

#### ***Camponotus (Dinomyrmex) cæsar* Forel**

A single imperfect worker minima from the stomach of a frog (*Rana occipitalis*) taken at Faradje (Lang and Chapin) seems to belong to this light-colored species.

**Camponotus (Myrmosericus) rufoglaucus (Jerdon) subspecies cinctellus**  
(Gerstæcker)

Five workers from Zambé (J. Bequaert).

The distribution of *C. rufoglaucus* and its various forms is shown on Map 42.

**Camponotus (Myrmosericus) rufoglaucus subspecies cinctellus variety**  
**rufigenis** Forel

Faradje, ♂; Niangara, ♀; Garamba, ♂; Stanleyville, ♂; Medje, ♂; Poko, ♂; Akenge, ♂ (Lang and Chapin). Six of the workers from Garamba are from the stomach of a *Bufo regularis* and a single worker from Akenge is from the stomach of a *B. funereus*. The specimens from Faradje were taken while they were attending plant-lice on young orange trees.

**Camponotus (Myrmosericus) rufoglaucus subspecies sypfax, new**  
subspecies

Plate XXII, Figure 1

WORKER very similar to the subspecies *zulu* Emery from Natal and quite as large, the largest specimens measuring fully 9 mm., but not more slender than other forms of the species. The scapes and tibiae are distinctly compressed, the former as in *C. eugeniae* Forel, but not so broad. Epinotum evenly arcuate in profile, without distinct base and declivity. Pubescence dull yellowish, not very long, slightly golden on the gaster of large individuals, only feebly converging at the mid-dorsal line on the posterior portions of the second and third segments. Color brownish black, the legs a little paler, the funiculi, cheeks, clypeus, mandibles, and tarsi castaneous. Gastric segments with very narrow, dull-yellowish posterior margins.

Numerous specimens from Zambé (type locality) and Boma (Lang, Chapin, and J. Bequaert).

The Zambé specimens are from three colonies, two of which bear the following notes. "Ants forming numerous small craters in the white sand (Pl. XXII, fig. 1). Only a few individuals were seen outside the nest before noon. The nest extended to a depth of 50 cm. below the surface." "Nest in the rotten base of a *Hyphæne*. No larvæ nor pupæ could be seen, though there were certainly as many as 1000 workers in the colony. The nest was loosely arranged in the soft, decomposing mass." Bequaert says of the specimens from Boma that they "run very swiftly and were nesting in the road."

Workers of this ant were sent to Prof. Emery, who compared them with his cotypes of the subspecies *zulu*. He pronounced them to belong to a new subspecies "with the pubescence on the gaster much more parallel and less sinuous."



**Camponotus (Orthonotomyrmex) vividus variety semidepillis,**  
new variety

**WORKER.**—Exactly like the typical form, except that the erect hairs on the dorsal surface of the head and body are distinctly paler and only about half as numerous. The pubescence, too, is more dilute and shorter, especially on the gaster.

Described from numerous workers from Medje (type locality) and Leopoldville (Lang and Chapin). The following note relates to the specimens from the former locality: "These ants were taken out of their nest in the rather rotten portions of a tree. Their galleries were often large enough to admit one's finger. The workers, when disturbed, ran out and bit viciously. The specimens were taken about five miles south of the Nepoko while we were collecting accessories for the Museum group of Okapis."

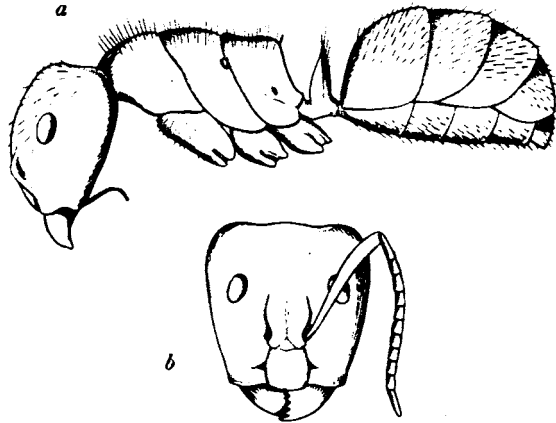


Fig. 64. *Camponotus (Orthonotomyrmex) vividus* subspecies *cato* (Forel). Worker major. a, body in profile; b, head, dorsal view.

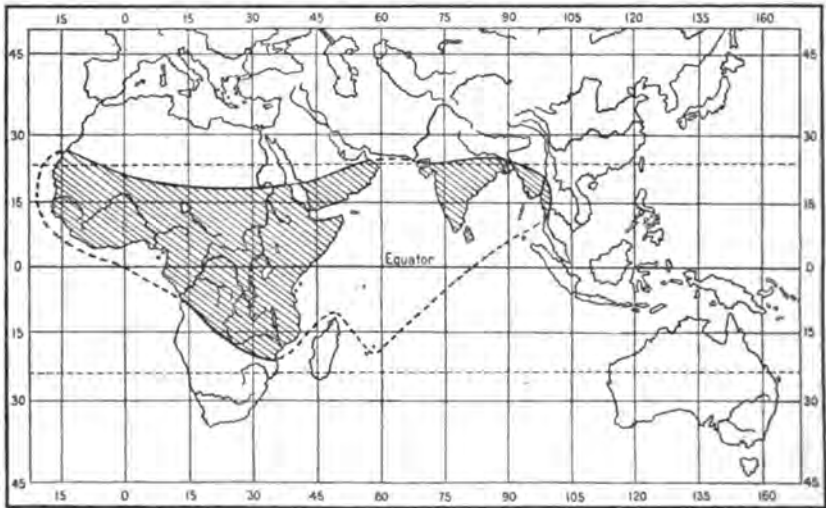
**Camponotus (Orthonotomyrmex) vividus subspecies cato (Forel)**

Text Figure 64

Stanleyville, ♂, ♀, ♀; Garamba, ♂, ♀; Medje, ♂, ♀, ♀; Avakubi, ♂, ♀; Akenge, ♀; Thysville, ♀; Bengamisa, ♀, ♂; Niangara, ♀, ♂ (Lang and Chapin). The workers from Akenge, two in number, were taken from the stomach of a *Bufo polycercus*, a female from Medje was from the stomach of a *B. funereus*, and one from Stanleyville from the stomach of a frog (*Rana mascareniensis*).

Under separate numbers two different native names, "suma" and "likulu," are given for this ant. The specimens from Stanleyville were

dently not molested by the ants. The snails were so tightly attached to the surface that they were often broken when an attempt was made to remove them. About this time (the latter half of December and beginning of February) the grass is burned all over the country. The flames leap high and the heat is incredible, many of the branches of the trees being killed by the fire. This may be a reason for the snails' seeking refuge in the cavities made by the ants." The snails belonged to *Pachnodus herbigradus* Pilsbry.<sup>1</sup> (See p. 154).



Map 43. Distribution of *Camponotus (Orthonotomyrmex) sericeus* (Fabricius).

***Camponotus (Myrmotrema) foraminosus* subspecies *hæreticus* Santschi**

A single worker major from Lukolela (Lang and Chapin) seems to be referable to this subspecies.

***Camponotus (Myrmotrema) foraminosus* subspecies *europubens* Forel' variety**

A single minor worker from Stanleyville (Lang and Chapin), which I am unable to assign with certainty to any of the described forms of this subspecies.

<sup>1</sup>Pilsbry, 1919, Bull. American Mus. Nat. Hist., XL, p. 308.

**Camponotus (Myrmotrema) perrisi** Forel subspecies **jucundus** Santschi

Text Figure 66

Kwamouth, ♂, ♀, ♂, ♀; Niangara, ♂, ♀; Faradje, ♂, ♀, ♀; Garamba, ♂, ♀ (Lang and Chapin). Many specimens, some of which were identified by Prof. Emery as belonging to this subspecies. Those from Kwamouth were found with their pupæ nesting in the galleries of a large, conical termitarium; those from Faradje were taken in small mushroom-shaped termitaria. Those from Niangara, however were nesting "in the hollow of a tree."

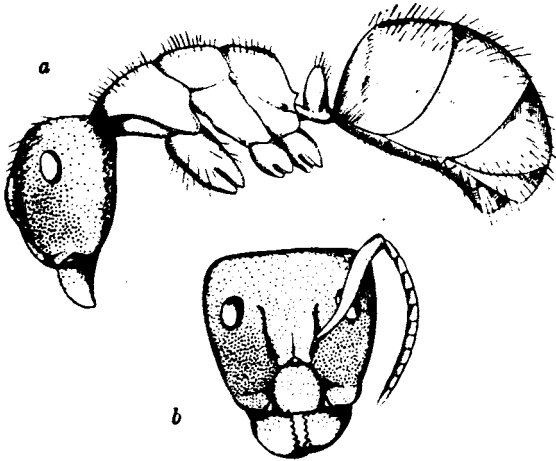


Fig. 66. *Camponotus (Myrmotrema) perrisi* subspecies *jucundus* Santschi. Worker major. a, body in profile; b, head, dorsal view.

The female of this subspecies measures 11 to 11.5 mm. (wings 12.5 mm.) and resembles the major worker very closely in sculpture, pilosity, and color, except that the erect whitish hairs are shorter and less numerous on the upper surface of the head and thorax. The antennal scapes are not so pale at their base. The wings are suffused with brown and have dark brown veins and pterostigma. The male measures 7 to 8 mm., is black throughout, with wings colored like those of the female, but paler. The scapes and hind tibiæ are distinctly flattened, though much less so than in the worker and female, and the upper border of the petiole is straight and transverse, with a small elevation or tooth on each corner. The body is rather shining; the thorax without erect hairs above.

**Camponotus (Myrmotrema) perrisi** subspecies **jucundus**  
variety **grandior** (Forel)

Yakuluku, ♂, ♀; Garamba, ♂, ♀ (Lang and Chapin). Numerous specimens. Those from Yakuluku were found "nesting in small mushroom-shaped termitaria, which were only about five yards apart."

**Camponotus (Myrmotrema) olivieri** (Forel) variety **sorptus** (Forel)

Seven minor workers taken at Kwamouth, Leopoldville, Lukolela, and Stanleyville (Lang and Chapin). The types were taken by Forel from the stomach of a pangolin (*Manis temmincki*).

**Camponotus (Myrmotrema) bayeri** Forel

Thirteen workers from Faradje (Lang and Chapin), without further data.

**Camponotus (Myrmotrema) micipsa**, new species

Text Figure 67

WORKER MAJOR.—

Length 9 to 10 mm.

Head large, longer than broad (without the mandibles,  $3.8 \times 3$  mm.), broader behind than in front, with excised posterior border and evenly and very feebly convex sides. Mandibles very convex, with 6 short, subequal teeth. Clypeus rather flat, longer than broad, ecarinate and feebly longitudinally grooved in the middle, subhexagonal, narrower in front than behind, its anterior border somewhat truncated, straight. Frontal area impressed, lozenge-shaped; frontal carinæ widely separated, as far apart as their distance from the sides of the head. Antennal scapes distinctly flattened but not dilated, somewhat narrower at their tips than in *perrisi*, extending a little beyond the posterior corners of the head. Eyes rather small and flat. Promesonotal and mesoepinotal sutures more impressed than in *perrisi*; the epinotum somewhat cuboidal, as long as broad, the base and declivity subequal, nearly rectangular in profile, the former flattened, the latter very feebly concave, both slightly submarginate on the sides. Petiole similar to that of *perrisi* but broader above, the upper margin feebly notched in the middle. Hind tibiæ somewhat flattened but neither prismatic nor channelled, their flexor borders without a row of bristles.

Mandibles, clypeus, upper surface of head, thorax, and gaster opaque; mandibular teeth, frontal area, antennal scapes, gula, sides of thorax, posterior surface of petiole, legs, and venter shining. Mandibles finely punctate on a very finely and evenly shagreened ground. Head very finely, densely and evenly punctate; the clypeus and cheeks with coarse, shallow, rather sparse, piligerous foveolæ, which are elongate and oblique, with their posterior edges more pronounced. Front and sides of head with similar but more scattered and less pronounced foveolæ. Antennal scapes covered with round punctures of very unequal size. Thorax and gaster very finely and densely punctate like the head, with small, rather sparse, piligerous punctures.

Hairs pale, yellow, coarse, erect, rather long and abundant on the upper surface of the head, thorax, and gaster and on the venter, absent on sides of thorax, petiole and gaster. On the cheeks and clypeus each foveole bears a short, stiff, blunt, sub-erect hair. Pubescence dull yellow, very short, dilute and inconspicuous on the head and thorax, but very long and dense on the dorsal surface of the gaster, where it forms a shining golden pelage nearly concealing the surface.

Coal black throughout, only the apical portions of the funiculi and the ends of the tarsi dark brown.

**WORKER MEDIA.—**

Length 7.5 mm.

Differing from the worker major only in the smaller and shorter head, which is not longer than wide behind. The foveolæ of the cheeks and clypeus are less distinct, but the stubby, erect golden hairs arising from them are as striking as in the major.

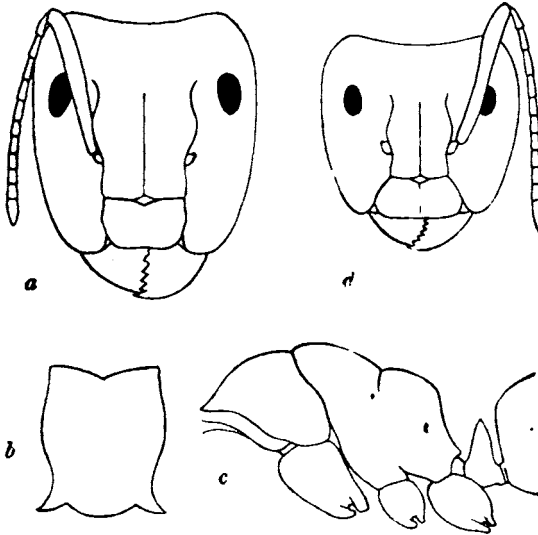


Fig. 67. *Camponotus (Myrmotrema) micipsa*, new species. a, head of worker maxima; b, clypeus of same; c, thorax and petiole of same in profile; d, head of worker media.

Described from three major workers and a single media "collected on the fire-wood taken aboard the boat between Leopoldville and Yumbi" (Lang and Chapin). This species is evidently allied to *perrisii*, *olivieri*, *bayeri*, and *maynei* Forel, but distinct from all of them in the structure of the head, sculpture, pilosity, etc., though apparently most closely related to *maynei*.

**Camponotus (Myrmorhachis) polyrhachioides Emery**

Lukolela, ♂, ♀; Lie, ♂ (Lang and Chapin). The workers from the latter locality, two in number, were taken from the stomach of a toad (*Bufo regularis*); the specimens from Lukolela, comprising two workers and three winged females, were found running on fire-wood.

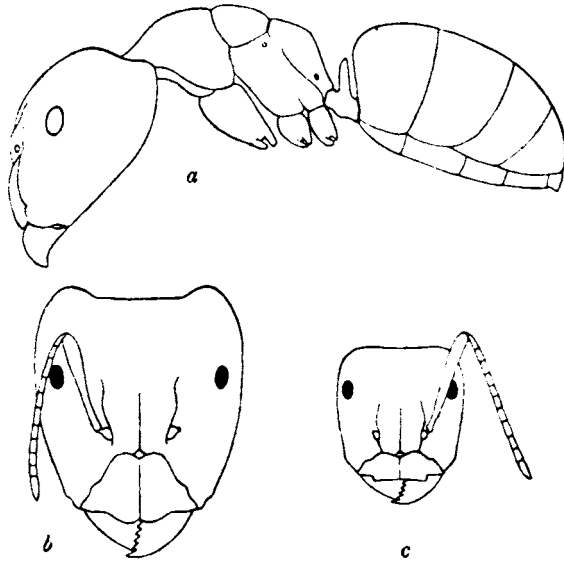


Fig. 68. *Camponotus (Myrmamblys) chapini*, new species. a, worker major, body in profile; b, head of same, dorsal view; c, head of worker minor.

**Camponotus (Myrmamblys) chapini, new species**

Text Figure 68

**WORKER MAJOR.—**

Length 5.5 to 6.5 mm.

Head very large in proportion to the remainder of the body, longer than broad (without the mandibles,  $2.4 \times 2.2$  mm.), broader behind than in front, with deeply excised posterior, rather convex lateral borders and prominent, rounded posterior corners. Mandibles stout, convex, coarsely 6-toothed. Clypeus flattened, strongly carinate, its anterior border notched on each side, with a short median lobe, angularly emarginate in the middle and rounded at the corners. Frontal area obsolete; frontal groove distinct; frontal carinae approximated in front, subparallel and widely separated behind, nearly as far apart as their distance from the lateral borders of the head. Eyes small and flat. Antennae short, scapes (1.2 mm.) curved, somewhat flattened basally and thickened at their tips, which extend only about three times their greatest diameter beyond the eyes. Thorax small, short, and robust, not longer than the head, very broad through the pronotum, which is as broad as long, very rapidly narrowed

to the laterally compressed epinotum; the meso- and epinotum together not longer than the pronotum. Promesonotal suture strongly impressed, metanotum very small and short, but distinct. In profile the general dorsal outline of the thorax is arcuate, but the mesonotum is somewhat raised in front at the suture above the pronotum; the epinotum sloping, rounded, with indistinct, subequal base and declivity. Petiole small, its scale elliptical from behind, evenly rounded above, with a slight angular projection in the middle of the superior border; in profile scarcely thicker below than above, much compressed anteroposteriorly, about three times as high as thick, with blunt superior border. Gaster much smaller than the head, the first segment anteriorly truncated, the dorsal surface convex. Legs rather stout, tibiae slightly flattened, tarsal claws rather long.

Shining throughout; mandibles coarsely punctate, at their bases shagreened and subopaque. Clypeus and head sharply shagreened and covered with coarse, sparse punctures, which are very uniform on the clypeus and cheeks, somewhat shallower and more scattered on the front and vertex. Posterior corners of head with a few elongate foveolæ. Thorax and gaster more finely shagreened than the head, the gaster transversely, and both with scattered piligerous punctures.

Hairs yellow, sparse, coarse, erect, and rather short. Petiolar border with four setæ; gula with only a few short hairs; cheeks hairless. Scapes naked; tibiae with numerous, very short subappressed hairs. Pubescence sparse, appressed, distinct, short on the mandibles, clypeus, and cheeks, longer on the gaster.

Head deep castaneous, almost black; mandibles and anterior portion of clypeus deep red; antennæ, pronotum, coxæ, and legs brownish yellow or testaceous; remainder of thorax, petiole, gaster, and an inverted V-shaped spot on the dorsal surface of the pronotum, pale castaneous.

WORKER MINOR.—

Length 3 to 4.5 mm.

Differing from the major in its much smaller size and the shape of the head, which is as broad as long, a little broader behind than in front, with straight sides and feebly convex posterior border. Clypeus strongly carinate as in the major, but its anterior lobe with straight entire anterior border and subdentate angles. Mandibles smoother than in the major, much less distinctly punctate. Antennal scapes extending about one-fifth their length beyond the posterior corners of the head.

Sculpture, pilosity, and color much as in the major worker, but the thorax uniformly brown throughout, and the head paler, though darker than the thorax and gaster.

Described from five major and eleven minor workers from Garamba (type locality), a major from Medje, and a minor from Faradje (Lang and Chapin). The specimen from the locality last mentioned is from the stomach of a frog (*Rana occipitalis*) and three of the workers from Garamba are from the stomach of a toad (*Bufo regularis*). According to a note accompanying the Garamba specimens, "these ants nest in small conical termitaria." And the further remark is added: "There are few of these termitaria without ants, which sometimes run about in the same galleries as the termites but seem more often to have no dealings with these insects."

**PHASMOMYRMEX** Stitz

**WORKER.**—Rather large, elongate, monomorphic, varying little in size. Head rectangular, with rounded posterior corners. Clypeus rather flat, indistinctly carinate, without an anterior lobe, its anterior border broadly and angularly excised. Thorax long, flattened above, obtusely marginate on the sides; anterior corners of pronotum angular; metanotum distinct, bounded by well-defined sutures anteriorly and posteriorly, its stigmata situated below its lateral marginations; mesometanotal suture impressed; epinotum subcuboidal, truncated behind. Petiolar node thick, with a distinct angle at the sides of its dorsal margin. Gaster small. Legs long, hind tibiae three-sided.

**FEMALE.**—Head as in the worker. Thorax depressed, pronotum seen from above nearly as long as the mesonotum and overarched by the latter only very slightly. Scutellum not projecting over the postscutellum or epinotum. Wings as in *Camponotus*.

**MALE** unknown.

A single species, originally described by Forel as *Camponotus buchneri* and known only from the West African region, from Cameroon to Angola (Malange) and eastward to the Ituri forest.

**Phasmomyrmex buchneri** (Forel)

Lukolela, ♀; Avakubi, ♀; Medje, ♀ (Lang and Chapin); Lubutu, ♀ (J. Bequaert). Single specimens. Those from Avakubi and Lukolela were taken on fire-wood brought in from the forest.

**POLYRHACHIS** F. Smith

Large or medium-sized ants closely allied to *Camponotus*.

**WORKER** monomorphic. Head orbicular, oval or rounded subrectangular, very convex above, with very prominent, long and sinuate frontal carinæ. Palpi long, the maxillary pair 6-jointed, with the basal about half as long as the second joint, the labial pair 4-jointed. Clypeus well developed, usually convex or more or less carinate. Antennæ long, 12-jointed, the scapes inserted some distance behind the posterior border of the clypeus, as in *Camponotus*; funicular joints considerably longer than broad. Thorax more or less arcuate above, often more or less carinate on the sides, and more or less dentate or spinose, but exhibiting great differences in conformation in different species. Usually either the pronotum or the epinotum or both are armed with teeth or spines, rarely the mesonotum. The petiole has a large scale, the superior border of which is nearly always armed with pairs of spines or teeth, more rarely also with a median, unpaired spine or tooth. Gaster large, broadly elliptical or subglobular, very convex above, the first segment forming more than half of its surface and often more or less truncated or concave in front. Legs long and well developed, the tibiae often constricted at the base. Gizzard much as in *Camponotus*.

**FEMALE** decidedly larger than the worker, with massive thorax. Spines and teeth on the thorax and petiole smaller. Wings long, the anterior pair with a radial and a single cubital cell; discoidal cell lacking and cubital vein usually reaching the outer margin of the wing. Gaster massive, its first segment often proportionally shorter than in the worker.



tion of *Myrma*, would seem to indicate that it is the most archaic of all the subgenera of *Polyrhachis*.

The species of *Polyrhachis* form only moderately large colonies and none of them is sufficiently common to be of economic importance. Many of them are, in fact, rare and sporadic. They are very timid or pacific insects and are most frequently found singly walking up or down tree-trunks or on the foliage of trees or bushes. Their nesting habits are very diverse. According to my observations in Australia, the species of *Campomyrma* nest in the ground, under stones, or more rarely in crater nests. The same is true of the species of *Hagiomyrma* and *Chariomyrma*, though I have always found *P. (Hagiomyrma) semiaurata* Mayr in large logs and certain species of *Chariomyrma* in earthen termitaria. So far as known, none of the species of these three subgenera employs silk in the construction of the nest. The species of *Hedomyrma*, as Mann and I have observed, live in high trees, but we have been unable to find the nests. Several of the larger species of *Myrma* nest in the ground or in logs and some of them line their nests with silk spun by the larvæ. Many of the smaller species of this subgenus make carton and silken nests on or between the living leaves of trees, and this is the general habit also of many species of the subgenera *Myrmhopla*, *Myrmothrinax*, *Myrmatopa*, and *Cyrtomyrma*. A few species of *Myrma* and *Myrmhopla* live in hollow stems or in old galls. Jacobson and Mann have described the beautiful carton and silk nests built by various *Myrmatopa* species on the under sides of leaves in Java and the Solomon Islands. *P. (Myrmhopla) armata* of the Indomalayan Region sometimes builds its nest in houses. *P. (M.) dives* and some of the allied species construct small globular nests of nearly pure silk, somewhat like those of tent-caterpillars, on low bushes. The nest of one of the few species of the subgenus *Polyrhachis*, *sensu stricto*, the East Indian *P. bihamata*, was found by Bingham. "It was of silky, yellowish brown material, placed close to the ground in the center of a clump of bamboos, and measured about a foot in diameter." Some species of *Polyrhachis*, when irritated, emit a strong, pleasant smell. According to Bingham, the odor of *P. (Myrmhopla) venus* Forel is like that of the tuberose.

***Polyrhachis (Myrma) laboriosa* F. Smith**

Plate XXII, Figure 2; Text Figure 69

Six workers from Stanleyville and Bafwasende, without further data and a number of workers, larvæ, and cocoons from a nest at Niagara (Lang and Chapin).

This species is easily distinguished from all the other African members of the genus by the peculiar petiole, which bears a single pair of long, hook-shaped spines. The nest (Pl. XXII, fig. 2) seen by Mr. Lang is described as follows. "It was found on a small tree about three meters from the ground and was 16 centimeters wide, built in a fork between a cluster of finer twigs and consisted of old vegetable fibres and leaves fastened together. It was naturally extremely light, as no soil had been used in its construction. The general color outside was dark gray. Its walls were very thin, scarcely one millimeter in thickness. As far as I could see, there were many entrances, though they were somewhat

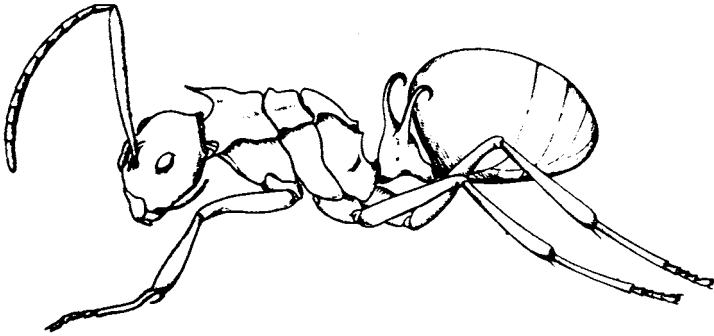


Fig. 69. *Polyrhachis (Myrma) laboriosa* F. Smith. Worker.

damaged. Still, a great many intact openings were visible. The fine hairs on the abdomen of this ant are conspicuously bronzy. When disturbed, the workers make a rattling noise by striking the nest with their abdomens. They bend the abdomen forward between their legs and discharge from its tip a copious spray of formic acid, which is quickly diffused through the air."

A nest of this ant, described and figured many years ago by Mayr and Aurivillius,<sup>1</sup> was 17 cm. long, 7.7 cm. broad, and 5 cm. thick. It was rather triangular in outline, with a large opening at one end and several small openings scattered over the surface. It was attached to some thin, leafy twigs and consisted of brown, fibrous vegetable detritus resembling decomposing cowdung, agglutinated "by means of a glue-like substance." The interior contained partitions of a similar structure.

Examination of the nest fragments contained in the vial with the workers from Niangara shows that the coarse vegetable particles are bound together by a small quantity of silk. This was also noticed by

<sup>1</sup>1896, Ent. Tidokr., XVII, p. 255, Pl. IV, fig. 3.

Santschi in two nests which he examined.<sup>1</sup> Concerning one of them, containing only the mother queen and her first brood of larvæ and still in process of construction, he remarks: "The walls of the nest already contain silk, which seems to show that the female is able to use the larvæ as shuttles, or perhaps the young larvæ spin the silk spontaneously around themselves on vegetable detritus placed at their disposal." That the latter supposition is probably erroneous is evident from what is known concerning the behavior of the female *Æcophylla* when founding her nest.

***Polyrhachis (Myrma) militaris* (Fabricius)**

Stanleyville, ♀; Panga, ♀; Lukolela, ♀; Avakubi, ♀; Leopoldville, ♀; Medje, ♀; Lubila, ♀; Ngayu, ♀; Boyulu, ♀; Lie, ♀ (Lang and Chapin). Numerous specimens. Those from Ngayu, Boyulu, and Lie, four in number, were taken from the stomachs of toads (*Bufo funereus* and *regularis*). The only specimen from Lubila is "from a nest in a mushroom-shaped termitarium." Many of the specimens from the other localities were captured on fire-wood. Some of the workers have the pubescence on the gaster rather golden and therefore approach the subspecies *cupreopubescens* Forel.

The large Ethiopian species *Myrma*, comprising *militaris*, *schistacea*, *gagates*, *schlüteri*, and *nigriseta*, are so variable and exhibit so many annectant subspecies and varieties that one is tempted to regard the whole complex as a single, extraordinarily unstable species. Santschi, however, believes that there are several species with a pronounced tendency to hybridize. The materials in collections at the present time are quite insufficient to substantiate either of these views, and the matter must be left to some future myrmecologist, resident in equatorial Africa, who can study these ants intensively both in the field and in the laboratory.

***Polyrhachis (Myrma) militaris* subspecies *cupreopubescens* Forel**

A fine series of workers and females taken at Avakubi from "a nest built in an upright rotten stump, about four feet from the ground" and a single female from Medje (Lang and Chapin).

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<sup>1</sup>1909, Ann. Soc. Ent. France, LXXVIII, p. 393.

***Polyrhachis (Myrma) militaris* subspecies *cupreopubescens* variety *nkomoensis* Forel**

A single worker from Akenge, taken from the stomach of a toad (*Bufo polycercus*). As Forel states, the epinotal teeth of this variety are very long, erect, and strongly recurved. The middle pair of petiolar spines are more erect and less inclined backward than in the typical *cupreopubescens*, and the lateral spines are much longer, more slender, and farther from the median pair. The pubescence seems to be dimmer and less golden, but this may be due to the action of the toad's gastric juices.

***Polyrhachis (Myrma) militaris* subspecies *cupreopubescens* variety *dido*, new name**

This name is suggested to replace *argentatus* Stitz, which is preoccupied by *P. argentatus* F. Smith [= *Formica argentata* Fabricius = *P. serspinosa* (Latreille)].

I possess two workers of this beautiful variety from Mt. Coffee, Liberia, collected by R. P. Currie. The thorax, petiole, coxæ, and ventral portions of the gaster are covered with dense, brilliant, silver pubescence, the upper surface of the gaster with brilliant golden pubescence as in *cupreopubescens*. The lateral spines of the petiole are very short.

***Polyrhachis (Myrma) schistacea* (Gerstæcker) variety *divina* Forel**

Thysville, ♀; Poko, ♀; Boma, ♀; Zambi, ♀ (Lang and Chapin); Zambi, ♀, ♀ (J. Bequaert). The specimens from Zambi were found climbing on grass-stalks in the savannah; the others bear no data except the localities. The nesting habits of this ant are very probably the same as those of the closely allied *gagates* (*vide infra*), also taken in the savannah and in the same locality.

***Polyrhachis (Myrma) schistacea* subspecies *rugulosa* (Mayr) variety *divinoides* Forel**

A single worker from Banana (Lang and Chapin) seems to be referable to this variety.

***Polyrhachis (Myrma) schistacea* subspecies *atrociliata* Santschi variety *benguelensis* Santschi**

Six workers from Yakuluku and one from Garamba (Lang and Chapin) run to this variety in Santschi's table.<sup>1</sup> The hairs on the body are black, short and sparse, whereas in the typical *atrociliata* they are long and abundant.

<sup>1</sup>1914, 'Voy Alluaud et Jeannel Afr. Orient., Formicide,' p. 142.

diverge from the middle of the anterior border and there is also a similar, though less pronounced, tendency in the mesonotal rugæ; those on the epinotum are strongly arcuate on the sides. Sides of the thorax punctate-rugulose; anterior and posterior surfaces of the petiole transversely and rather vermiculately rugulose, except the tips of the spines, which are smooth and shining, as is also the declivity of the epinotum. Gaster very finely and densely punctate; the anterior two-thirds of the first segment longitudinally rugulose, the rugules being sharp and occasionally anastomosing. Scapes and tibiæ coarsely rugulose, with large, elongate piligerous punctures.

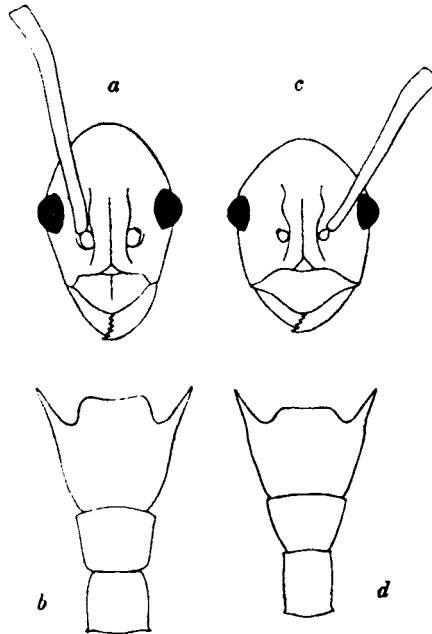


Fig. 72. *a*, *Polyrhachis (Myrma) concava* Ern. André, head of worker; *b*, thorax of same, dorsal view; *c*, *Polyrhachis (Myrma) atrope*, new species, head of worker; *d*, thorax of same, dorsal view.

Hairs silvery white, long, erect, abundant, covering the whole body, except the apical half of the funiculi; as conspicuous on the scapes, cheeks, and legs as on the thorax and gaster. Pubescence grayish, very fine, short, and appressed, distinct only on the gaster, where it is sufficiently abundant to dim the surface but not to conceal the sculpture.

Black; palpi, tibial spurs, and terminal joint of tarsi testaceous; tips of funiculi and wings brownish, the latter with pale brown veins and dark brown pterostigma.

A single specimen from Stanleyville (Lang and Chapin), without further data. This species is evidently very closely related to Ern. André's *P. sulcata*, which is also known only from the female. This form,

however, according to the description, is slightly larger (9 mm.), has the mandibles very superficially and almost indistinctly rugose, the eyes are more than hemispherical; the rugæ on the epinotum are described as "transversalement arquées"; the petiole is higher than broad and the pilosity is duller. *P. atalanta* may eventually prove to be merely a subspecies of *sulcata*.

***Polyrhachis (Myrma) concava* Ern. André**

Text Figure 72a and b

A single worker from Akenge, taken from the stomach of a toad (*Bufo funereus*), and a dealated female from Stanleyville (Lang and Chapin). Forel took several workers of this species from the stomach of a pangolin (*Manis temminckii*). Two of these specimens are in my collection.

***Polyrhachis (Myrma) aërope*, new species**

Text Figure 72c and d

**WORKER.—**

Length somewhat less than 6 mm.

Head longer than broad, subelliptical, not broader behind than in front, narrowed behind the eyes to the occipital border, which is indistinctly marginate, very convex in the middle above through the frontal carinæ, the cheeks rather straight, the gular margin bluntly submarginate. Eyes at the middle of the sides of the head, large, prominent, broadly elliptical, their external orbits slightly sinuate. Mandibles narrow, their apical borders rather oblique, with five subequal teeth. Clypeus convex, bluntly carinate in the middle, its anterior border broadly rounded, entire. Frontal area broadly triangular, indistinct; frontal carinæ high, rather closely approximated, moderately sinuate, somewhat farther apart and subparallel behind. Antennæ long, scapes slightly enlarged and deflected at their tips, extending fully one-half their length beyond the posterior border of the head. Thorax much like that of *P. concava* Ern. André, long and narrow, the dorsal surface concave with strong, upturned lateral carinæ, notched at the pronounced, transverse promesonotal and mesoepinotal sutures. Pronotum as long as broad, narrowed behind, its anterior spines straight, acute, slightly divergent, flattened, more than twice as long as their width at the base. Mesonotum trapezoidal like the pronotum, but smaller and broader than long; base of epinotum regularly rectangular, one and one-third times as long as broad, its posterior corners with two small, erect, slightly recurved teeth, which are as long as broad at their bases, its posterior border not marginate but, as in *concava*, passing over into the sloping declivity, which is slightly longer than the base and feebly convex in profile. Petiole and gaster shaped as in *concava*, but with the median pair of spines of the former straight, when seen from the front, and not slightly curved inward. Tibiæ distinctly constricted at their bases.

Shining; gaster smooth and polished. Mandibles finely striated and sparsely and finely punctate; head, thorax, and petiole finely coriaceous or shagreened; the clypeus somewhat smoother. Gaster very minutely and superficially punctate.

Hairs and pubescence whitish, the former erect, very sparse, present only on the tip of the gaster and posterior portion of venter; the pubescence very short and dilute, delicate, and appressed, visible only on the sides of the thorax and on the clypeus and appendages.

Black; only the palpi and insertions of the antennæ reddish.

Described from a single specimen from the stomach of a frog (*Xenopus mülleri*) taken at Niangara (Lang and Chapin).

This form is so close to *concava* André that it might be regarded as a subspecies. It differs, however, very decidedly in the proportions of the head and thorax, as shown in the accompanying figures, and is also smaller (*concava* measures nearly 7 mm); the pubescence on the body is much less developed and the legs are darker.

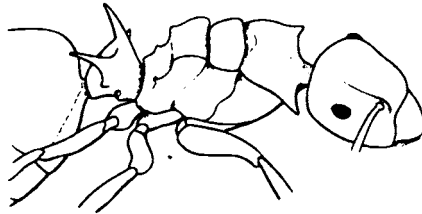


Fig. 73. *Polyrhachis (Myrma) alluaudi* Emery. Head, thorax, and petiole of worker; after Emery (1891).

***Polyrhachis (Myrma) alluaudi* Emery variety *anteplana* Forel**

Text Figures 73 and 74

A single worker taken from the stomach of a frog (*Phrynobatrachus perpalmatus*) captured at Stanleyville (Lang and Chapin).

This variety, originally described from the same locality, differs from the typical *alluaudi* by "the epinotum and its teeth being longer, the pronotum flatter. The transverse mesoepinotal fissure is vertical, very narrow and deep. The teeth of the epinotum are triangular, slightly curved forward; the spines of the pronotum are less than twice as long as their width at the base."

The worker and nest of the typical form were described and figured by Emery in 1892 from specimens taken by Alluaud in Assinie. I reproduce the figures (Figs. 73 and 74) because of the peculiar and interesting structure of the nest, which Emery describes in the following words: "The nest was found on a bush, 1.70 m. from the ground, attached to the lower surface of a leaf. It consists of a single low-vaulted chamber, with the entrance prolonged as a kind of chimney. Its walls are made of rather coarse vegetable particles loosely glued together."

elliptical, their anterior orbits at the median transverse diameter of the head. Mandibles feebly convex, with five acute, subequal teeth. Clypeus convex, carinate, especially behind, the anterior border evenly rounded, entire. Frontal area very indistinct; frontal carinæ very long and rather far apart, feebly sinuate, subparallel behind. Antennæ stout, the scapes only slightly enlarged and scarcely deflected at their tips, extending about one third their length beyond the posterior border of the head. Thorax short, as high as long, the dorsal surface strongly carinate laterally, the border deeply notched at the pronounced promesonotal and mesoepinotal sutures, especially at the latter. Pronotum very broad, without the neck nearly twice as broad as long, decidedly broader in front than behind, at the anterior angles with rather large, acute, triangular spines, which are flattened, diverging, and fully as long as broad at their bases. The surface of the pronotum is feebly convex. Mesonotum short and rather flat, more than twice as broad as long, narrower behind than in front, where it is almost as broad as the posterior border of the pronotum; its sides straight, but rounded at the corners. Epinotum extremely short, abruptly sloping, the base and declivity being in the same plane, the former strongly convex in

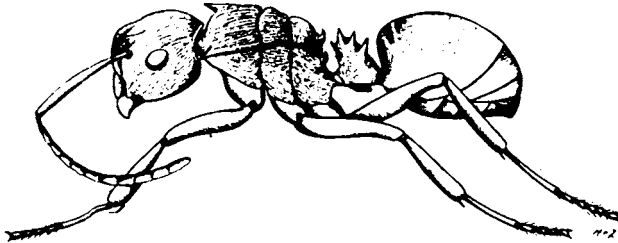


Fig. 75. *Polyrhachis (Myrma) decemdentata* Ern. André. Worker.

front just behind the mesoepinotal suture, or fissure, which is much more deeply impressed than the promesonotal suture. The posterior corners of the base bear acute, slender, erect, recurved spines, which are fully twice as long as the diameter of their insertions. The surface of the base is bluntly and longitudinally carinate in the middle, the declivity feebly concave. Seen from behind, the base is distinctly broader than long, a little broader behind than in front, with convex, arcuate sides; the declivity, however, has concave and more feebly marginate lateral borders. Petiole thick, very convex anteriorly and posteriorly, especially anteriorly, as broad as high, its blunt upper border with four long, slender, acute, equidistant spines, the outer pair distinctly longer than the inner and all directed upward and somewhat backward, with their tips somewhat more strongly curved than their bases. Gaster subglobular, very slightly broader than long, very convex above, the first segment concave anteriorly for the accommodation of the convex posterior surface of the petiole. Legs rather stout, tibiae distinctly constricted at the base.

Shining; mandibles smooth, with rather coarse scattered punctures; clypeus, cheeks, and anterior portion of front very smooth and shining; remainder of head regularly and rather finely longitudinally rugose, with punctate interrugal spaces. Pronotum and mesonotum above sharply and regularly longitudinally rugose, the rugæ on the former coarser than on the head, on the latter radiating backward from a point in the middle of the anterior border. Base of epinotum with very regular trans-



PLATE II

Temporary nest of the driver ant *Dorylus (Anomma) wilverthi* Emery. at Akenge, October 17, 1913. This nest extended over 3.50 m. and could not be shown entirely in the picture.



PLATE III

Army of driver ants, *Dorylus (Anomma) wilverthi* Emery, on the march near Avakubi, October 22, 1909.





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#### PLATE VI

Fig. 1. *Dorylus (Anomma) nigricans* Illiger, at Amani, Usambara, East Africa. Army crossing a path. The workers carrying the brood pass between solid walls of soldiers which, with their mandibles lifted and wide open, protect the main body of the army.

Photograph by Dr. J. Vosseler

Fig. 2. *Megaponera jätens* (Fabricius), at Avakubi, October 22, 1909. Entrance to a nest, surrounded by a small mound of excavated earth, situated in a deserted plantation. When dug up, five galleries were found to open into the single aperture. On two occasions Mr. Lang observed from 30 to 40 pupa cases lying outside in the sun, near the entrance, with a few ants in steady attendance. There are no true chambers in the nest, but the galleries for the pupæ and larvæ are rather wide. When touched, these insects sting before using the mandibles, which can even pierce the thick skin of the hand. The columns of these ants contain relatively few individuals and, when closely approached, break up at once, the members scurrying nervously in all directions and making a stridulating noise. After a minute or so they reform the ranks and continue their march. They are great termite robbers, and Mr. Lang counted as many as eight such insects held between the mandibles of a single ant. They never opened the jaws to drop their prey, even when taken up with the forceps.



1



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**PLATE VII**

*Pheidole saricola* Wheeler, at Zambi, June 1915. This seed-storing ant works chiefly during the night and early morning, forming columns in various directions to forage. Near the entrances to the nests heaps of refuse are shown, consisting of seeds and chaff, and often also of dead ants and other insects.



### PLATE VIII

*Myrmecaria eumenoides* subspecies *opaciventris* (Emery).

Fig. 1. Crescent-shaped craters of excavated earth at the entrances to nests in level, hardened soil at Rungu, July 7, 1913. The ants usually burrow their galleries after a heavy rain, either by day or night. The workers then busily carry out particles of soil which they drop near the edge of the crater. Often the moist earth does not roll down but sticks to the upper margin which thus becomes an overhanging crest. The mounds in the photograph are of typical form, but some of the best are often twice as high (5 to 6 cm.). It is said that these craters suggested the shape of the famous hairdresses of the Mangbetu tribe.

Fig. 2. Crescent-shaped crater at the entrance to a nest at Avakubi, October 22, 1909. In this case it was not as true to form as those shown in Fig. 1 because the entrances were placed near the base of a bush. The galleries showed many ramifications and extended 17 inches below the surface; but the whole nest, when exposed, did not cover an area more than two feet in diameter. Most of the pupæ were found about the roots of the bush. These harmless and common ants also build subterranean tunnels in various directions from their nest and make themselves noticeable by their immediate appearance in great numbers around a piece of meat or dead insect.



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PLATE IX

*Myrmicaria salambo* Wheeler. Low tree of the genus *Protea* from the Savannah at Garamba, September 1912, on the buds of which this ant attends scale insects.

Fig. 1. A flowering branch of the tree.

Fig. 2. The entire tree in its typical surroundings. This plant is a characteristic element of the extreme northeastern Congo Savannah, on the divide between the Congo and the Nile. It does not extend southwest of Faradje.



1



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PLATE X

*Crematogaster (Atopogyne) depressa* variety *fuscipennis* Emery, at Ambelokudi, October 20, 1910. Nest built of rather solid, brownish carton against the trunk of a tree in the forest, a short distance above the ground.



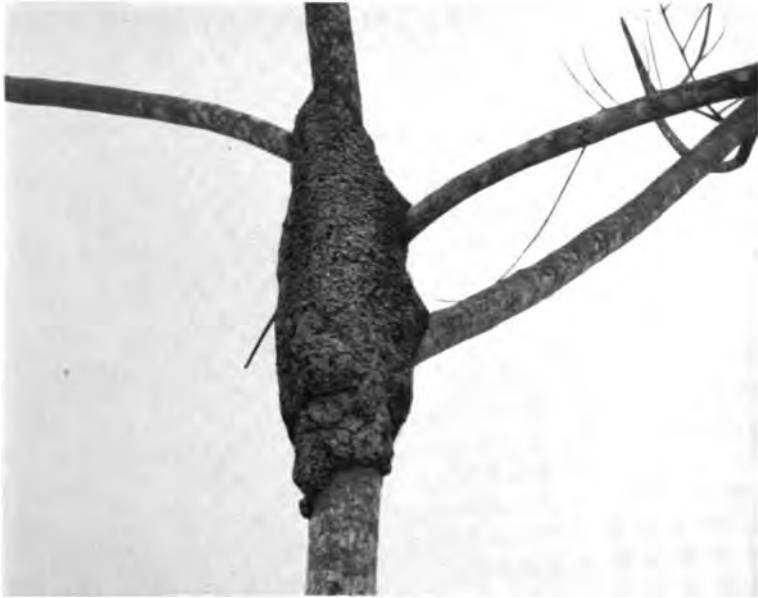


PLATE XI

*Crematogaster (Atopogyne) theta* (Forel).

Fig. 1. Carton nest at Stanleyville, August 10, 1909, built on the trunk of a tree, about 5 feet from the ground.

Fig. 2. Another nest of this species in the same locality, but of different shape.



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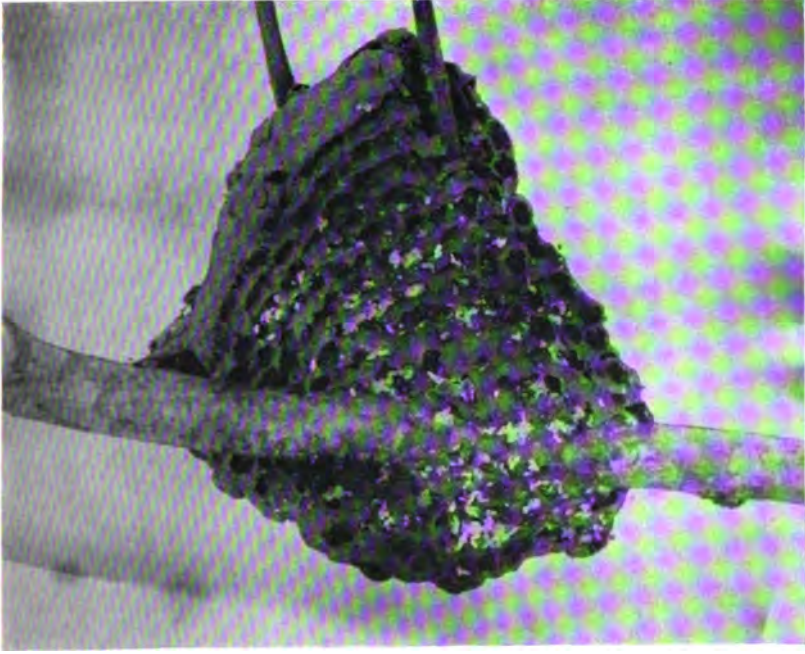
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PLATE XII

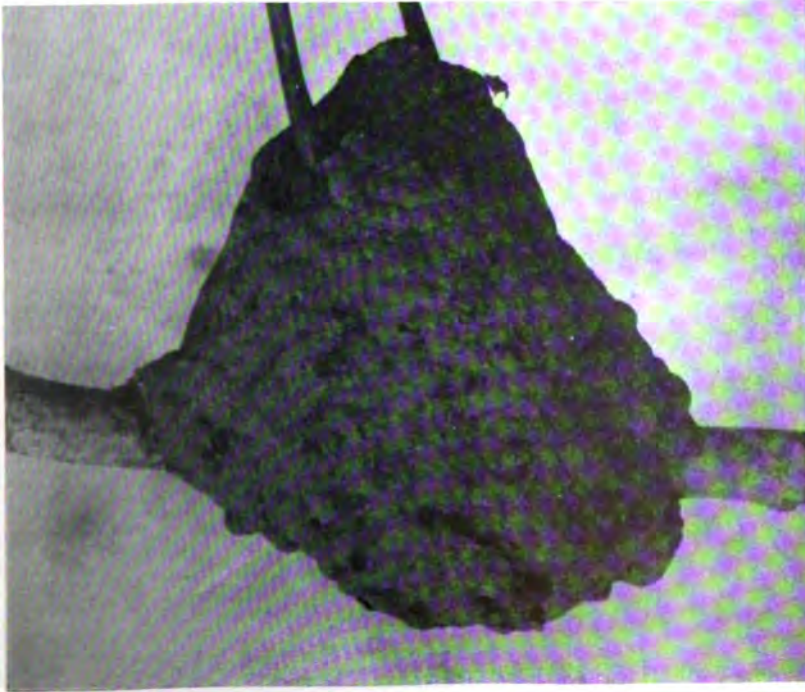
*Crematogaster (Atopogyne) theta* (Forel), at Medje, June 15, 1914.

Fig. 1. Outside view of a carton nest made of vegetable matter of very light gray or brownish color. The caterpillar shown on Plate XIII, fig. 1 was crawling over the surface of this nest.

Fig. 2. Inside, cross-section view of the same nest. The white masses are the brood (eggs, larvæ, and pupæ). The structure was 10.4 cm. broad and 9.8 cm. long and attached to a small tree in the forest, about 8 feet from the ground. When disturbed, the ants stream outside and let themselves drop upon the intruder. Their sting is painful and can be felt for many minutes afterwards.



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### PLATE XIII

Fig. 1. Portion of the outer surface of the nest of *Crematogaster (Atopogyne) theta* (Forel) shown on Plate XII. In the upper right corner is seen a caterpillar that was found crawling over the surface, its segmentation being visible at the time; but when the creature stops and tightly adheres to the nest, its body becomes quite unnoticeable as it then resembles one of the numerous protuberances of the formicary.

Fig. 2. Nest of *Crematogaster (Nematocrema) stadelmanni* variety *dolichocephala* (Santschi), at Kwamouth, July 14, 1914. This cone-shaped carton nest was hanging in a tree, about nine feet from the ground. It was fastened to several small branches in such a way that it moved about when the boughs were tapped with a stick. The outside surface was quite rough and simulated crumpled up leaves that cover one another like the shingles of a roof. The cellular structure inside was irregular, with very thin walls, and a great many exits; larvæ were especially abundant in the lower portion. It measured about 18 inches in length and 11 inches in width at the top.



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PLATE XIV

*Crematogaster (Nematocrema) stadelmanni* variety *dolichocephala* (Santschii), at Bengamisa, September 27, 1914. Pensile nest of very hard, woody carton, resembling that of certain termites in shape as well as in material, a fact usually making it impossible to tell from the outside appearance which insect inhabits it. The example photographed was so fixed to several creepers that it swayed in the wind about twenty-five feet from the ground. It was approximately two feet long. The shape and size of these carton nests vary greatly according to the location. Their inner structure is irregular, the galleries and cells seemingly arranged without plan: larvæ and pupæ may be found anywhere throughout the fornicary.





PLATE XV

Landscape in the Savannah near Niangara, May 10, 1913, showing numerous hillocks of *Termes natalensis* Haviland scattered over an almost treeless grass plain. The ant *Carebara osborni* Wheeler lives in cleptobiosis with these termites.



PLATE XVI

Mushroom garden of *Acanthotermes militaris* (Hagen) from a nest at Malela, July 6, 1915. The minute ant, *Pædalqus termilolestes* Wheeler, had established its nest close to the surface in the upper part of the termitarium (upper right hand corner).



PLATE XVII

Fig. 1. *Macromischoides aculeatus* (Mayr), at Medje, May 1914. Two nests of these small ants, built with loosely connected vegetable fibres between leaves.

Fig. 2. *Tetramorium sericeiventris* subspecies *continentis* (Forel), at Zambi, June 30, 1915. Craters of white sand at the entrances to the nest of these ants.



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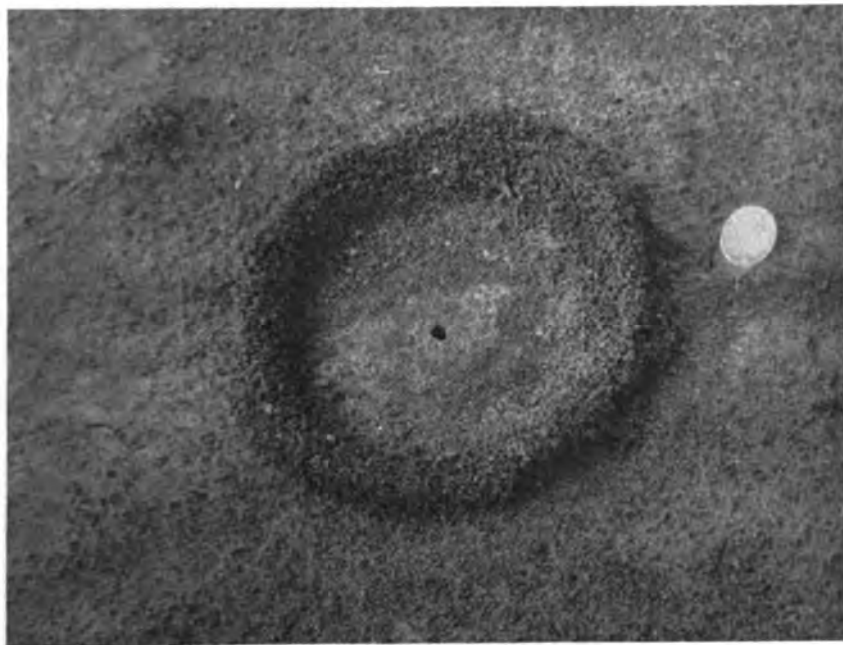
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PLATE XVIII

*Tetramorium setigerum* subspecies *quarens* Forel, at Niapu.

Fig. 1. Regular ring-shaped craters of loose particles of soil constructed about the entrance of the nest during the rainy season. These ants are very common in open places.

Fig. 2. Aspect of the entrance to the nest of the same ant during the dry season. At that time the insects merely carry out débris and particles of soil without attempting to construct a crater.



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PLATE XIX

*Plagiolepis (Anoplolepis) custodiens* (F. Smith).

Fig. 1. Shore of the Atlantic Ocean a short distance north of Banana, showing the narrow beach of white sand in the upper part of which the nests of *P. custodiens* are excavated.

Photograph by J. Bequaert

Fig. 2. Nest of *P. custodiens* in the sandy beach of the Atlantic near Banana, August 1915.



PLATE XXI

Fig. 1. Carton nest of a termite about five feet from the ground; deserted by its builder and now occupied by a colony of *Camponotus (Orthonotomyrmex) vividus* (F. Smith); near Malela, July 7, 1915. The structure was established around the stem of a sapling in swampy woods.

Fig. 2. Interior of the same nest, showing the chambers excavated by the ants in the termitarium.



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PLATE XXII

Fig. 1. Craters of white sand at the entrances to the subterranean nest of *Camponotus (Myrmosericus) rufoglaucus* subspecies *syphax* Wheeler, at Zambi, June 30, 1915.

Fig. 2. Nest of *Polyrhachis (Myrma) laboriosa* F. Smith, at Niangara, November 1910. It was built in a fork of a bush in a cluster of fine twigs, and consisted of old vegetable fibres and leaves fastened together. It was extremely light since no soil entered into its construction; dark gray outside, brown inside. Though the nest was somewhat damaged there were apparently many exits. When disturbed, the ants made a rattling noise by striking the nest with their gaster; at the same time they emitted considerable quantities of formic acid, bending their gaster forward between the legs.

PLATE XXIII

Nests of *Polyrhachis (Myrma) gagates* F. Smith, excavated in sandy soil at Zambi.  
June 30, 1915.

Fig. 1. Craters of white sand surrounding the entrances from which the grass-stalks have been cut away.

Fig. 2. As the nest appeared before the vegetation was removed.



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### III.—THE PREDACEOUS ENEMIES OF ANTS

By J. BEQUAERT

The various means by which Nature prevents an excessive increase of the species not only forms in itself an interesting chapter of ecology, but its study is also of great importance in an understanding of the true meaning of Natural Selection. In the case of ants it has been contended that they are better defended than other insects against the attacks of predatory animals. Poulton<sup>1</sup> evidently takes this for granted when he considers that ants, together with wasps, are among the favorite models for "mimicking" insects and other arthropods. These ant-like arthropods, having acquired by Natural Selection their resemblance "to the aggressive, abundant, and well-defended ants," would according to this theory escape many of the attacks of their deceived and disgusted predaceous enemies. Though the evidence presented in the following pages is still very fragmentary, I trust the reader may easily conclude for himself to what extent such resemblances, which, in some cases at least, can hardly be doubted, have a real protective value. There is certainly little or no evidence to show that, as the theory is often expressed, ants are unpalatable to most insectivorous animals and are merely eaten accidentally or "during the time in which young birds or other animals are learning what to eat with impunity and what to reject."<sup>2</sup>

Another consideration of interest is the relative efficacy of parasitism and predatism in acting as a check on the reproductive power of the species. This point has been profusely discussed, and the argument has frequently been made that parasitism is in this respect of foremost importance. It must, however, be kept in mind, that, while we have been very completely and steadily informed of the activities of parasites, predatism has been much less investigated. It is not my intention to go further into this question; but I think a rather conservative view will be to consider that ecto- and endoparasites, while working all the time, though affecting only a small number of individuals at once, constitute a more regular check to the increase of the species. On the other hand, predatory enemies as a rule destroy large numbers of individuals at a

<sup>1</sup>Poulton, E. B., 1908, 'Essays on evolution,' (Oxford), pp. 252-261. See also Jacobi, A., 1913, 'Mimikry und verwandte Erscheinungen,' (Braunschweig), pp. 95-114; Marshall, G. A. K., 1902, 'Five years' observations and experiments (1896-1901) on the bionomics of South African insects, chiefly directed to the investigation of mimicry and warning colors,' *Trans. Ent. Soc. London*, pp. 287-584, Pls. ix-xxiii; McAtee, W. J., 1912, 'The experimental method of testing the efficiency of warning and cryptic coloration in protecting animals from their enemies,' *Proc. Acad. Nat. Sci. Philadelphia*, pp. 281-364; Pocock, E. I., 1911, 'On the palatability of some British insects, with notes on the significance of mimetic resemblances,' *Proc. Zool. Soc. London*, II, pp. 809-868.

<sup>2</sup>H. C. McCook (1890, 'American spiders and their spinningwork,' II, pp. 357-365) has fully discussed the possibility of ant-mimicking spiders having arisen by means of Natural Selection, either to enable them to more readily obtain their food or to protect them from natural enemies.

time, but only at intervals. They are also apt to make their influence more felt when their prey for some reason or other suddenly multiplies on an exceptional scale. Professor Forel's aphorismic statement that "the most dangerous enemies of ants are always other ants, just as the worst enemies of man are other men," may be true in a general way for temperate regions, where ants are not superabundant and lead a rather inconspicuous life, but it can hardly be applied to the tropics. Ants, it is true, attract comparatively few of the predaceous arthropods, against which they are very effectively armed. They form, however, a considerable portion of the diet of many reptiles, amphibians, birds, and certain insect-eating mammals, some of these vertebrates being almost exclusively myrmecophagous. It may be further mentioned that many of these predaceous animals by no means confine their attacks to the smaller, more timid species of ants, but rather prefer the large-sized, powerfully defended members of the ponerine and doryline groups.

The information contained in the following pages is based to a considerable extent upon examination of stomachs and pellets of predaceous animals in the wild state. I fully agree with Swynnerton that these sources of information are most valuable with regard to the general preferences of a predaceous animal, the insects it usually feeds upon and on which it for the most part "fills up." But I also believe with the same author that a knowledge of its detailed preferences must come in the main from continuous observation of individual wild animals and from special experiments both in nature and in captivity. The experimental method has been used with much skill and care by Swynnerton<sup>1</sup> to test the palatability of butterflies and its bearing on the efficiency of cryptic form and coloration. Miss A. H. Pritchett<sup>2</sup> has also published the results of a number of experiments with lizards and various insects, including ants, that possess protective, mimetic, and warning colors or that have some disagreeable characteristics which in a measure are supposed to prevent their being devoured by insect-eating animals. Such investigations with ants and their natural enemies should be extended and could not fail to add considerably to a better understanding of predatory habits.

<sup>1</sup>Swynnerton, C. F. M., 1919, 'Experiments and observations bearing on the explanation of form and colouring, 1908-1913,' Journ. Linn. Soc. London, Zool., XXXIII, No. 224, pp. 203-385. See also Poulton, E. B., 'The experimental proof of the protective value of colour and markings in insects in reference to their vertebrate enemies,' Proc. Zool. Soc. London, 1887, pp. 191-274; Dahl, F., 1913, 'Vergleichende Physiologie und Morphologie der Spinnentiere unter besonderer Berücksichtigung der Lebensweise,' (Jena), I, vi+113 pp.; Heikertinger, F., 1919, 'Die metöke Myrmekoidie. Tauschenmaterial zur Lösung des Mimikryproblems,' Biol. Zentrabl., XXXIX, pp. 65-102; Dahl, F., 1921, 'Täuschende Ähnlichkeit mit Bienen, Wespen und Ameisen,' Naturw. Wochenschr., N. F., XX, pp. 70-75.

<sup>2</sup>Pritchett, A. H., 1903, 'Some experiments in feeding lizards with protectively colored insects,' Biol. Bull., V, pp. 271-287.

## ARTHROPODS

In the following account I shall consider only the arthropods which prey on ants without entering their nests; the nidal synechthrans, or carnivorous inmates of ant nests, are better studied in connection with true ant guests, though they may in some cases have been derived from outside marauders. Neither have the predaceous activities of ants towards other ants of the same or of different species been considered here.

Ants are comparatively immune from the attacks of predaceous arthropods, being themselves usually well provided against such enemies with offensive, defensive, or repulsive weapons. They nourish, however, a host of parasites and commensals belonging to almost every group of arachnids and insects, but these fall outside the scope of the present account. It must be admitted that, with the exception of certain of the most striking cases, such as ant-lions, but little attention has been paid to ant-hunting arthropods.

## Arachnida

Ants do not often fall a prey to spiders and their relatives, except in the winged phases during the short period of the nuptial flight when large numbers of them perish in spider webs. The cautious ways of most worker ants make them a difficult game for terrestrial arachnids and in the larger forms the sting is an effective weapon against the attack of the soft-bodied spider. At one of the meetings of the Entomological Society of London, Poulton exhibited a spider and its prey taken at Itigi (former German East Africa) by Carpenter, the specimens being accompanied by the note: "Spider seen coming out of a nest of *Megaponera* bearing one feebly struggling, upside down in its fangs. Caught in a box the spider settled down to feed on the ant."<sup>1</sup> Poulton comments upon the remarkably small size of the spider as compared with its victim, which is one of the largest of African ponerine ants.

Certain terrestrial spiders of the Old World genus *Zodarion* Walckenaer (= *Enyo* Audouin) are true ant hunters. "The *Zodarion*," says E. Simon,<sup>2</sup> "which I have observed in southern Europe, live at the expense of the ants and settle in their vicinity. They make neither snare nor web to stop their prey, but during their hunting hours they roam about the formicaries and mix with the long rows of ants, going from one

<sup>1</sup>1918, Trans. Ent. Soc. London, (1917), Proc. p. lx.

<sup>2</sup>1893, 'Histoire naturelle des araignées', (Paris), I, pt. 2, pp. 434-435. See also Simon, E., 1874, 'Les Arachnides de France', (Paris), I, p. 242; van Hasselt, A., 1891, Tijdschr. v. Ent., XXXIV, pp. xxxiv-xxxvi; Krausse, A., 1913, 'Eine Spinne (*Zodarion nigriceps* Sim.) an den Abfallplätzen der Ernteameisen auf Sardinien,' Arch. f. Naturg., LXXIX, A, Heft 9, pp. 66-67.

to another and unexpectedly seizing feeble individuals, or such as are hurt or hampered by too heavy a burden. When the spider has caught its prey, it drags it aside, near its own abode; this is always surrounded by remains which leave no doubt as to the nature of its diet. These observations relate to *Z. elegans* and *nigriceps* E. Simon which, in southern France, Sardinia, and Corsica, live at the expense of the ants of the genus *Atta*" (= *Messor* Forel).

Many other terrestrial spiders are probably to some extent myrmecophags. Such is the case, for instance, with *Cælotes atropos* Walckenaer, which was observed in the act of capturing ants by Wasmann<sup>1</sup> in southern Germany. According to H. Lebert,<sup>2</sup> *Dysdera erythrina* Latreille, in Switzerland, constructs its tubular silk tent near ant hills, or sometimes even in the middle of ant nests, and plays great havoc with these insects.

E. Wasmann<sup>3</sup> and H. Schmitz<sup>4</sup> describe the skill with which the "gallows-spider" (*Theridion triste* Hahn) of western Europe preys upon the blood-red ant (*Formica sanguinea* Latreille) and related species. This spider spins no web, but lies in wait on a low plant for foraging worker ants: suddenly it drops from its lurking place on to an unsuspecting victim passing below. Then, quickly rendering the ant helpless by a few threads entwined around the body, the spider hoists its prey up to the plant as to a gallows and fastens it there. The sucked bodies of the ants are left hanging from the plant, either singly or in groups of two or three. Here again, there is a strange disproportion between the large and fierce worker ant and the small, soft-bodied, feebly armed spider.

Another European species, *Theridion riparium* (Blackwall), was observed by Henking<sup>5</sup> feeding chiefly on the workers of *Myrmica lævinodis* Nylander. This spider spins an irregular web between leaves and branches a short distance from the ground; in the middle of the web is woven a conical tent of silk, closed above, open below, and densely covered on the outside with bits of earth and remains of insects. A number of oblique or vertical sticky threads connect the whole structure with the ground and serve to entrap the ants. If a worker *Myrmica* happens to touch one of these snares with the antennæ or legs, its frantic efforts to get loose attract the attention of the spider hidden in her tent;

<sup>1</sup>Quoted by van Hasselt, A., 1892, Tijdschr. v. Ent., XXXV, p. xxii. In the same periodical (1890, XXXIII, pp. 212-214), van Hasselt gives an account of European spiders associated with ants, including those that have been found inside formicaries.

<sup>2</sup>1877, Neue Denkschr. Schweiz. Naturf. Ges., XXVII, Abth. 2, p. 33.

<sup>3</sup>1898, 'Ameisenfang von *Theridion triste* Hahn,' Zool. Anzeiger, XXI, pp. 230-232.

<sup>4</sup>1916, 'De Nederlandsche mieren en haar gasten,' Jaarb. 1915 Natuurb. Genootsch. Limburg, Maastricht, pp. 110-111 (of separate).

<sup>5</sup>Henking, H., 1886, 'Nahrungserwerb und Nestbau von *Theridion riparium* (Blackw.) Thor., Kosmos, XVIII, pp. 1-11.

she at once rushes to the thread pulled by the ant and tries to drag her intended victim into the air; if the ant succeeds in holding fast to the soil, the spider runs down the thread, throws some additional silk on her prey, which sooner or later loses its grip and is then quickly dragged up and entangled in the irregular maze above.

In his account of the agricultural ant of Texas, H. C. McCook<sup>1</sup> writes:

The only other natural enemies of [*Pogonomyrmex*] *barbatus*, so far as observation has yet determined, are the spiders. There is a large theridioid (*Theridion lineamentum* McCook = *T. lineatum* Hentz) who is especially destructive of these ants. I found her nest established upon the grass-grown disks in the following manner: several stalks of the *Aristida* were bent over near the top, or midway of the spire, and firmly bound together by silken cords. Within this tent and just below the apex, the strong snare of right lines (retitelarian) was fixed, in the midst of which the spider hung in the usual inverted position. The ants are constantly climbing the grass-stalks for purposes which I could not divine. . . . They thus become entangled in the snare and fall victims to the watchful aranean. It is not impossible that the spider, whose snare sometimes hung quite near the ground, swings down and seizes the ants as they pass through the tent. Their dry shells might be seen clinging to the threads, or the yet warm bodies trussed up and swathed for food. Under one of these tents I picked up a small ball of six or eight ant skeletons rolled up and tied together just as they had been cast out of the snare.

### Coleoptera

One might expect that certain of the predaceous members of this order, both larval and adult, occasionally capture ants, though this kind of prey is often carefully avoided. Adult tiger-beetles (Cicindelidæ) have been seen catching ants. Wasmann<sup>2</sup> mentions the fact that in the vicinity of Pará, Brazil, the columns of the leaf-cutting saúba-ant (*Atta sexdens*) are often attacked by *Megacephala* (*Tetracha*) *rutilans* J. Thomson. Chitty, in England, observed *Cicindela campestris* holding a *Myrmica rubra* in its jaws:

I thought the ant was struggling, for it was alternately right inside the mouth of the beetle and then nearly out, but I think this was really the mode adopted by the beetle in devouring its food. Finally the mesothorax and spiny metathorax were ejected from the mouth and also the shell of the abdomen, which had been sucked empty. The rest of the ant was apparently consumed, but possibly it was only the contents of the abdomen that were really eaten.

The larvæ of the tiger-beetles are very voracious and fierce. They live in deep, tube-like holes which they burrow more or less vertically

<sup>1</sup>1879, 'The natural history of the agricultural ant of Texas,' (Philadelphia), p. 203.

<sup>2</sup>Quoted by Horn, W., 1908, 'Genera Insectorum, Fam. Carabidæ, Subfamily Cicindelinae,' p. 10.

<sup>3</sup>Chitty, A. J., 1904, '*Cicindela campestris* feeding on *Myrmica rubra*,' Ent. Record, XVI, p. 206.

firmly held by the loop around the thorax or behind the head, the loop thus taking the place of the ant-lion's jaws. Many years ago a similar funnel-burrowing fly larva was discovered by Prof. J. H. Comstock in the Sierra Nevada, California, but could not be reared to the adult stage. Prof. W. M. Wheeler has recently been more successful in obtaining the flies of these larvæ, thus adding a second, North American species to the genus *Vermileo*.<sup>1</sup> He states that the larva is in behavior and structure very similar to that of *V. vermileo*, and that it also traps in its pitfalls small insects, especially ants.

The adults of the allied genus *Lampromyia* are very distinct in their greatly lengthened, slender, stiff proboscis, but the larvæ differ only in minor details from those of *Vermileo*. P. Marchal<sup>2</sup> has written an interesting paper on the habits of *Lampromyia pallida* Macquart (= *L. miki* Marchal), of which he discovered the funnel-burrowing larvæ near Tunis. Three other species have been described in this genus: *L. cylindrica* (Fabricius) from Northern Africa and Spain, *L. canariensis* Macquart from the Canary Islands, and *L. sericea* Westwood from Damaraaland. During my stay at Algiers in June 1910, I had the good fortune to observe rather closely the larvæ of a species of this genus, probably *L. pallida*. They were found in numbers on the outskirts of Mustapha Supérieur, along the highway to Blidah, in the suburb of Colonne Voirol. Wherever the soft sandstones of the road banks happened to be excavated or weathered into miniature caves, one was sure to find the dry, powdery dust beneath the shelter of the overhanging rock fairly dotted with the funneled pits of *Lampromyia*. At that season adult flies were frequently seen resting on the rocky ceilings of the excavations. I found that the most common victims of these larvæ were workers of the little *Tapinoma erraticum* (Latreille).

Robber-flies (Asilidæ) are occasionally observed sucking the juices of winged ants, but I am not aware that they ever attack the workers.

Certain tropical muscid flies of the genus *Bengalia* have developed predaceous habits quite unique among the calyprate Muscoidea; they are frequently found on roads and in clearings hunting for soft-bodied insects after the well-known manner of robber-flies. Attention was first called to these peculiar habits by Nangle<sup>3</sup> in India and E. E. Green<sup>4</sup> in Ceylon; in both cases the flies, *Bengalia obscurepennis* (Bigot), were

<sup>1</sup>Wheeler, W. M., 1918, '*Vermileo comstocki*, new species, an interesting lepid fly from California.' Proc. New England Zool. Club, VI, pp. 83-84.

<sup>2</sup>Marchal, P., 1897, 'Notes d'entomologie biologique sur une excursion en Algérie et en Tunisie. *Lampromyia Miki*, nov. species: Cécidies.' Mém. Soc. Zool. France, X, pp. 5-25, Pl. 1.

<sup>3</sup>1905, Journ. Bombay Nat. Hist. Soc., XVI, No. 4, p. 747.

<sup>4</sup>1906, Spolia Zeylanica, III, p. 220; 1907, *ibid.*, IV, pp. 183-184 (the fly is here called *Ochromyia jejana* F.). Poulton, Trans. Ent. Soc. London, 1906, p. 394.

hunting winged termites flying at night. J. W. Yerbury saw the same species "trying to take her burden from a large ant (*Lobopelta* species)." F. W. Thomson made the following observation with regard to the Indian *B. jejuna* (Fabricius): "I always noticed specimens of this species on the ground, or on a stone or leaf near an ant's nest. On watching, I saw them swoop down on any ant carrying an 'egg' or larva, take it from the ant, carry it away a short distance and proceed to suck it."<sup>1</sup> *Bengalia latro* de Meijere, in Java, lurks in the neighborhood of the columns of *Pheidologeton diversus* (Jerdon); when a worker ant comes along carrying its prey, the fly dashes into the moving ant column, quickly steals the prey from the carrier, and returns to its perch where it devours its catch at leisure.<sup>2</sup> Lastly, G. R. Dutt, in his entertaining 'Life Histories of Indian Insects,'<sup>3</sup> writes of *Monomorium indicum* Forel as follows: "One morning I observed the inmates of a nest marching out with young ones. Close to the nest was sitting a muscid fly (*Ochromyia* species) which attacked from time to time the larvæ and pupæ that were being carried by the workers. The fly never snatched the victim from the grasp of the ant, but simply 'licked' it from its place with the proboscis, which when withdrawn left the larva or pupa quite shrivelled up."

The African *Bengaliæ* evidently have much the same habits as their Indian congeners. According to W. A. Lamborn,<sup>4</sup> *Bengalia depressa* (Walker), in Southern Nigeria, regularly follows the marauding armies of *Dorylus nigricans*, to rob them of their prey. On one occasion the whole performance was closely watched and described as follows:

I soon saw three or four of the muscids flying about the moving column and occasionally settling near it, sometimes on the ground quite close to the ants, sometimes on a blade of grass, stone or other raised object. Such as settled on the ground were extremely alert, and being able to run rapidly, never allowed any ants to approach any nearer to them than about a quarter of an inch. When, as frequently happened, any ant made a little circuit away from the main body, a fly would generally pursue it at a distance of about half an inch, but backing away directly the ant turned towards it. Other flies, having rested motionless a few minutes, flew up and poised themselves on the wing over the ants, but, immediately the drivers realized their presence and stretched out towards them with widely opened mandibles, flew again to a place of rest. Eventually I saw a muscid stalking a minor ant which had strayed from the main body carrying a pupa in its jaws. Suddenly the fly rushed forward, and it must have driven its proboscis, which seems to me armed with strong bristles, into the pupa, for the ant was brought to a standstill with a sharp jerk. Then ensued

<sup>1</sup>Observations recorded by Poulton, 1914. Trans. Ent. Soc. London, (1913), Proc., pp. cxxviii-cxxix.

<sup>2</sup>Jacobson, E., 1910, 'Pheidologeton diversus Jerdon und eine myrmecophile Fliegenart,' Tijdschr. v. Ent., LIII, pp. 328-335. Meijere, J. C. H. de, 1910, 'Ueber drei von Jacobson auf Java bei Pheidologeton diversus Jerdon beobachtete Fliegen,' ibid., LIII, pp. 336-340.

<sup>3</sup>1912, Mem. Dept. Agric. India, Ent. Ser., IV, No. 4, p. 251.

<sup>4</sup>1914, Trans. Ent. Soc. London, (1913), Proc., pp. cxxv-cxxviii.

a tug-of-war between ant and fly fastened on at opposite ends of the pupa, but neither had the advantage till, as it seemed to me, the ant must have got annoyed and loosening its hold rushed towards the fly, which of course instantly flew off with the pupa, and this it proceeded to suck on the ground about a foot away from the ants. It allowed me to get quite close before taking to the wing with its prey, and it settled again two or three feet further off and became so preoccupied with its meal that it fell an easy victim to my net. I then carefully watched a fly hovering over the ant column. It suddenly swooped down and rose instantly with an ant pupa, with the driver that had been carrying it still hanging on, fixed to its proboscis. The fly carried this burden for about a foot, then dropped it and alighted on the ground near by. The ant started to run away with the pupa, but the fly pursued it, again impaled the pupa and started a tug-of-war with the ant. Neither side had any advantage, and then the fly rose again about three feet into the air with the pupa and ant and after a flight of about eighteen inches let them fall. The ant being discomposed by this procedure let go of the pupa, and no sooner had it done so than the fly seized it and, flying off with it triumphantly, settled near by and proceeded as in the previous case to suck the prey. This one again fell easily to my net, so that the flies are evidently keenly alert only when in the immediate vicinity of the ants. I subsequently noticed that the Diptera seemed to have certain preferences in regard to their prey, for I repeatedly noticed one poised over the ant column make an unsuccessful swoop and then fly, keeping level with the ant carrying the particular object which it had missed, making occasional rushes in an endeavor to secure it. Those I took had obtained ant pupæ, but I am sure they take other things from the drivers, probably portions of dead insects.

Further observations by Lamborn<sup>1</sup> in East Africa have shown that the Dorylinæ are by no means the only species of ants favored by the attentions of the African *Bengaliæ*. At Lindi, former German East Africa, a female *B. peuhi* Brauer and v. Bergenstamm was observed alighting near a column of *Crematogaster castanea* Smith which was passing up and down a baobab tree; the fly made various attempts to rob some of the ants of their food, tiny fragments of beetles; it was very alert, retiring immediately when any stray ant happened to come its way. *Bengalia gaillardi* Surcouf was seen in the same locality stealing food carried to the nest by workers of *Pheidole liengmei* Forel, *Camponotus* species, *Leptogenys stuhlmanni* Mayr, *Prenolepis longicornis* (Latreille), etc.; at Daressalaam this fly was watching for similar purposes the home-coming *Plagiolepis custodiens* (F. Smith).

The genus *Bengalia* is restricted to the Old World tropics and belongs in the Calliphorinæ. It differs conspicuously from the other members of this group in the structure of the proboscis, which is rigid, chitinized, strongly toothed at the apex, directed forward, and evidently

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<sup>1</sup>1920, Trans. Ent. Soc. London, (1919), Proc., pp. lii-lviii.



Fifty-one specimens of this interesting genus were taken hovering over the front ranks of a moving army of ants, in a *cafetal* at Paso de Telayo, during the last hour or two of daylight on March 29. In company with them were numerous specimens of *Hyalomyia* and some other small tachinids. The ants have been determined by Mr. Theo. Pergande as *Eciton foreli*, Mayr. . .<sup>1</sup> The column of ants was about 15 feet wide and 25 feet long, and moved slowly but surely in a straight line through the *cafetal*, swarming rapidly over the thick covering of dead leaves, branches, and other obstructions that strewed the ground under the coffee-trees. The specimens of *Stylogaster* hovered continually over the ants, now and again darting at them, without doubt for the purpose of ovipositing in their bodies. During the whole three months of my collecting in this locality, I saw not a single specimen of *Stylogaster* at any other time, but on this occasion, during the short time that I had before dark overtook me, I succeeded in capturing fifty-one specimens, by sweeping closely with the net over the front ranks of the ants.

From the accounts quoted above it is evident that both Bates and Townsend base their conclusions on mere surmises, since neither of them has succeeded in finding the eggs. Their observations merely show that *Stylogaster* is in some way associated with the columns of driver ants, though it is by no means certain that this is true for all the members of the genus. Some of the North American species are found as far north as Illinois and New York, in regions where foraging ants are altogether absent. Yet it is possible that the African species of *Stylogaster* are associated with the columns of the Dorylinae.<sup>2</sup> G. D. H. Carpenter, in Uganda, in his description of the frantic efforts made by cockroaches to escape from the columns of *Dorylus*, remarks: "I twice saw, hovering over these cockroaches, and occasionally suddenly pouncing down (apparently for the purpose of ovipositing) several of a small long-bodied insect—it might have been a dipteran or an ichneumon, but the hovering and darting flight suggested rather a syrphid. It was so extraordinarily active that I failed to catch it."<sup>3</sup>

In a recent account of his observations on army ants in British Guiana, Wheeler<sup>4</sup> observes that although he saw *Stylogaster* on several occasions accompanying the advancing armies of *Eciton burchellii* and darting at the ants or even at open spaces on the ground, there was nothing to convince him that these flies were ovipositing. Once he came upon a swarm of both sexes of *Stylogaster* hovering above a spot where

<sup>1</sup>According to Wheeler, a synonym of *Eciton burchellii* Westwood.

<sup>2</sup>Dr. H. Brauns, of Willowmore, wrote me recently as follows: "*Stylogaster* habe ich seiner Zeit einige Male in Westafrika (Cameroun, Gaboon) beobachtet. Die Thiere fielen mir dadurch auf, dass sie wie Falken über *Anomma* Zügen schwebten. In welchen Zusammenhang sie mit den Doryliden stehen, weiss ich nicht. Dass sie ihre Eier auf dem Raube von Doryliden, den diese mit sich schleppen, ablegen sollten ist kaum anzunehmen, da dieser alsbald verzehrt oder verfüttert wird." (Letter of June 5, 1920). I have collected one of the North American species (*Stylogaster neglecta* Williston) on flowers of *Clethra alnifolia*, *Monarda clinopodia*, *Helianthus strumosus* and *Eupatorium purpureum*.

<sup>3</sup>1915, Trans. Ent. Soc. London, (1914), Proc., pp. cviii-cix.

<sup>4</sup>1921, Proc. American Ac. Arts Sci., Boston, LVI, p. 206.

*Tracheloides* Aug. Morawitz (of which *Brachymerus* Dahlbom and *Fertonius* Pérez are synonyms) is regarded by Kohl in his able Monograph of the Palearctic Crabroninæ<sup>1</sup> as a species-group or subgenus of *Crabro* Fabricius. Only the two species mentioned above are known; they possess a large, much thickened head, with the face strikingly broad below, a peculiarity evidently adapted to their ant-hunting habits, since it makes the jaws with which they seize the ants much more powerful than is usual among species of *Crabro*. Indeed, most other members of this extensive genus prey on rather soft-bodied and harmless insects, chiefly Diptera.

3.—*Aphilanthops taurulus* Cockerell. Ainslie<sup>2</sup> found this philanthid wasp preying on the workers of *Pogonomyrmex barbatus* subspecies *rugosus* Emery in New Mexico.

4.—*Aphilanthops frigidus* (F. Smith). This interesting species of eastern North America has been very completely investigated by Wheeler<sup>3</sup> near Boston. Curiously enough, it selects only fertile females, or queens, of ants to provision its nests and seems to restrict its attacks to various species of the genus *Formica* (*Formica fusca* Linnæus and its variety *subsericea* Say; *F. pallidefulva* Latreille subspecies *nitidiventris* Emery; and *F. neogagates* Emery). It forms colonies of from thirty to sixty nests, located in open patches, roads or clearings in woods. The burrow descends with a very steep slope to a depth of six to eight inches, where it terminates in a small cell, there being two or three other cells on the sides. The *Formica* queens are captured during the short time of their nuptial flight, before they have lost their wings, and are merely stung and paralyzed. The wasp does not mutilate or malaxate her victims, which still move their palpi, legs, and antennæ either spontaneously or when touched, for several hours or even for a few days after they have been captured and placed in the nest. The wasp carries the ant under her body, supporting it by means of her middle and hind legs and holding its antennæ in her mandibles. Having dragged the ant a few inches into the burrow, she proceeds to cut off its wings, usually very neatly, although the stubs she leaves attached to the body are a little longer than in queen ants that have deâlated themselves; more rarely the wasp simply gnaws off the tips or apical halves of the wings. Wheeler believes that each female *Aphilanthops* secures several queen ants, usually five to seven, often belonging to more than one species, and

<sup>1</sup>Kohl, F. F., 1915, 'Die Crabronen der paläarktischen Region,' Ann. Naturh. Hofmus. Wien, XXIX, pp. 1-453, Pls. 1-xiv.

<sup>2</sup>Ainslie, C. N., 1909, 'A note on the habits of *Aphilanthops*,' Canadian Ent., XLI, pp. 99-100.

<sup>3</sup>Wheeler, W. M., 1913, 'A solitary wasp (*Aphilanthops frigidus* F. Smith) that provisions its nest with queen ants,' Journ. Animal Behavior, III, pp. 374-487.

stores them in two or three cells, from which they are taken as needed to feed a single larva. "The egg is evidently laid on an isolated ant which the mother wasp cuts in two in order that the larva may gain access to the nutritious contents of the thorax and gaster. Then the other ants are taken from storage and brought to the larva one by one as they are required, till all are consumed and the larva is ready to pupate."

*Aphilanthops* Patton is a strictly Nearctic genus of fossorial wasps, of which eleven species have been described, mostly of the western United States. It is highly probable that all will prove to be ant hunters, and an interesting field of study is here open to the myrmecologist.<sup>1</sup>

The prey of *Polybia scutellaris* (White), a social wasp of southern Brazil, consists mainly of winged termites, which are stored whole in the nest, often by the hundreds; but occasionally this wasp collects winged male ants too. In one case about a hundred males of *Dorymyrmex pyramicus* (Roger) and a few other male ants were found in its nest.<sup>2</sup>

### AMPHIBIANS<sup>3</sup>

The diet of many amphibians consists almost exclusively of various arthropods. Only living and moving prey is devoured; dead or motionless food has little or no attraction for them. In the frogs and toads the tongue, attached in front and free behind, is often the chief organ used in seizing the food, being thrown out with lightning-like rapidity; it is soft, extensile, coated with a glutinous secretion, and adheres firmly to the prey, which is swallowed whole. The teeth, when present, are used only for catching and holding the prey; they are absent in many genera. Digestion is very rapid. The American toad, *Bufo americanus* Holbrook, for instance, feeds continuously throughout the night, except when food is unusually plentiful; in twenty-four hours it consumes a quantity of insects equal to about four times its stomach capacity. In other words, the toad's stomach is practically filled and emptied four times in each twenty-four hours.<sup>4</sup>

<sup>1</sup>The species of the genus *Microbembex* store dead insects in their nests, a very unusual procedure among predaceous wasps; they can occasionally be seen collecting dead ants that have been thrown out at the entrance of ant nests. See Parker, J. B., 1917, Proc. U. S. Nat. Mus., LII, pp. 134-141.

<sup>2</sup>Wasmann, E., 1897. 'Beutethiere von *Polybia scutellaris* (White) Sause.,' Zool. Anzeiger, XX, pp. 276-279.

<sup>3</sup>I am under great obligation to Mr. C. L. Camp for valuable suggestions on the subject of ants as food of batrachians and reptiles.

<sup>4</sup>Kirkland, A. H., 1904, 'Usefulness of the American toad,' U. S. Dept. Agric. Farmers' Bull. No. 196, p. 6; reprinted with changes from Bull. 46, Hatch Exp. Stat. Amherst, Mass., 1897, pp. 1-30, Pl. II. See also Ritchie, A. S., 1860, 'The toad as an entomologist,' Canadian Naturalist, N. S., IV, pp. 174-178; Garman H., 1901, 'The food of the toad,' Kentucky Agric. Exp. Stat. Bull. 91; Hodge, C. F., 1898, 'The common toad,' (Worcester, Mass.); Storer, T. I., 1914, 'The California toad. An economic asset,' Univ. California Journ. Agric., II, pp. 89-91; Munz, P. A., 1920, 'A Study of the food habits of the Ithacan species of Anura during transformation,' Pomona Journ. Ent. Zool., XII, pp. 33-56.

Toads and frogs being more often seen while in search of food, the stomach contents of specimens in collections are frequently little or not at all digested and can then be easily identified; many insects with hidden habits may thus be obtained. Amphibians are in this respect of very great help to the collector of ants.

Numerical data relating to the food of these animals has not often been published, even for the species of temperate regions. Perhaps the most complete records of the kind are those in H. A. Surface's 'Report on the economic features of the amphibians of Pennsylvania.'<sup>1</sup> From this paper it may be seen that, while almost all salamanders, toads, tree-frogs, and frogs occasionally eat ants, these insects constitute an important item in the diet of certain species.

Food of Certain Amphibians in Pennsylvania (Surface)

	Number of Stomachs with Recogniz- able Food	Number of Specimens Eaten	Number of Ants	Percentage of Ants
<i>Plethodon cinereus</i> (Green)	260	583	182	30
" <i>glutinosus</i> (Green)	125	367	63	17
<i>Desmognathus fusca</i> (Rafinesque)	235	378	33	8
<i>Bufo americanus</i> Holbrook	52	150	20	13

Kirkland's paper referred to above contains the result of an examination of 149 stomachs of toads (*Bufo americanus* Holbrook) in Massachusetts; in this case 19 per cent of the total contents were ants; the percentage was higher in May, when ants formed 23 per cent of the food and were present in 70 per cent of the stomachs.

The Texan robber frog, *Eleutherodactylus latrans* (Cope), a land animal of secretive and nocturnal habits, probably feeds extensively on ants. J. K. Strecker<sup>2</sup> mentions that "the stomach of one example contained the elytra of a ground beetle and the remains of many spiders and ants."

True frogs of the genus *Rana* take very few or no ants, at least in North America, though, as may be seen below, the stomachs of certain of the African species contain a fair proportion of these insects, mostly in the winged phases. Surface, in Pennsylvania, found few or no ants in *Rana*, and this result is confirmed by C. J. Drake's very extensive study

<sup>1</sup>1913, Zool. Bull. Div. Zool. Pennsylvania Dept. Agric., III, Nos. 3 and 4, pp. 134-147.

<sup>2</sup>1910, Trans. Ac. Sci. St. Louis, XIX, No. 5, p. 82.

Enough is known, however, to make it certain that these animals are of prime importance in this respect.

While studying the amphibians of the Lang and Chapin collection, Mr. G. K. Noble, Assistant Curator of Herpetology at the American Museum, dissected the stomachs of a large number of specimens and has turned their contents over to me for identification. The results of these examinations will be published in detail in Mr. Noble's report. From the point of view of the myrmecologist they were of great interest, yielding a large number of remarkable forms; eighty different species, subspecies, and varieties were obtained in this way and, of these, forty were not otherwise represented in the collection upon which Prof. Wheeler's report is based; seventeen of these forms were new to science. Many of the ants found in the stomachs of amphibians are in an excellent state of preservation; others are considerably improved by a thorough cleansing with caustic potash. Future collectors in tropical countries are urged never to neglect this novel manner of increasing their material.

In the table below, I have condensed the results of the examination of 308 stomachs of the eleven species of Congo frogs and toads which apparently show a decided preference for ants; for five of these species ants constitute about 50 per cent or more of the total stomach contents. In addition, several species of Congo frogs had eaten isolated specimens of ants, which may, in some cases, have been swallowed accidentally together with mud, dead leaves, or vegetable matter, an abundance of

Stomach Contents of Congo Amphibians

	Number of Stomachs with Recogniz- able Food	Total Number of Insects Eaten	Number of Ants	Per Cent of Ants
<i>Bufo polycercus</i> Werner	53	759	406	66.66
“ <i>tuberosus</i> Günther	5	160	38	23.73
“ <i>funereus</i> Bocage	55	1292	705	54.56
“ <i>regularis</i> Reuss	31	963	484	50.25
“ <i>superciliaris</i> Boulenger	50	746	182	24.39
<i>Rana occipitalis</i> Günther	25	55	14	25.45
“ <i>ornatissima</i> Bocage	14	30	6	20.
“ <i>albolabris</i> Hallowell	19	42	25	59.28
“ <i>mascareniensis</i> Duméril and Bibron	24	40	11	27.50
<i>Hemisus marmoratum</i> (Peters)	22	1006	96	9.54
<i>Phrynobatrachus natalensis</i> (A. Smith)	10	47	20	42.55

which is often found in the stomach. For other species, however, the number of stomachs examined was too small to furnish reliable data; when more completely investigated, some of these may prove to be true ant-feeders.

A number of amphibians collected by the American Museum Congo Expedition and the forms of ants which could be identified by Prof. Wheeler among their stomach contents are listed below. Such records give an insight into the great variety of ants eaten by some of these animals and also, to a certain extent, into the preferences shown by individual species. I must, however, point out that much of the ant débris found in the stomachs was too poorly preserved to permit correct identification, at least with our present knowledge of African myrmecology. These lists could, therefore, be considerably lengthened. Nevertheless, in the case of the toads a sufficient number of specimens have been examined to show that ants are a very important article in their diet; a total of 1815 ants was found in 194 stomachs of the five species of Congo toads; these ants belong to 72 forms, six (or 8 per cent) of which are Dorylinæ, thirty (or 42 per cent) Ponerinæ and Cera-pachyinaæ, sixteen (or 22 per cent) Myrmicinæ, and nineteen (or 27 per cent) Formicinæ. Terrestrial ants seem to be taken almost exclusively and this fact undoubtedly accounts for the high proportion of the Ponerinæ represented.

*Xenopus mülleri* (Peters)

A common frog of the Sudanese and East African savannahs. Of ten stomachs examined, only one contained a single ant:

*Polyrhachis aërope* Wheeler.

*Xenopus tropicalis* (Gray)

A frog confined to the Rain Forest. Of eleven stomachs examined, two together contained five ants:

*Camponotus pompeius* subsp. *marius* Emery.

*Bufo regularis* Reuss

This widely distributed African toad occurs in the forest and in the savannah as well. Of thirty-eight stomachs examined, thirty-one showed recognizable food and nineteen of these contained ants:

*Dorylus nigricans* subsp. *burmeisteri* (Shuckard).

“ “ subsp. *sjaestedti* Emery.

*Platythyrea gracillima* Wheeler.

*Megaponera fœtens* (Fabricius).

*Bothroponera soror* (Emery).

- Anochetus bequaerti* Forel.  
*Pheidole kohli* Mayr, var.  
     " *megacephala* subsp. *melancholica* (Santschi).  
*Myrmicaria cumenoides* subsp. *opaciventris* (Emery).  
     " " " " var. *crucheti* (Santschi).  
*Crematogaster excisa* (Mayr).  
*Monomorium bicolor* Emery. -  
     " *afrum* var. *fullor* Forel.  
*Tetramorium guineense* subsp. *medje* Wheeler.  
*Plagiolepis tenella* Santschi.  
*Camponotus maculatus* (Fabricius).  
     " " subsp. *congolensis* Emery.  
     " " subsp. *solon* Forel.  
     " " subsp. *brutus* (Forel).  
     " *acvapimensis* Mayr.  
     " *rufoglaucus* subsp. *cinctellus* var. *rufigenis* Forel.  
     " *chapini* Wheeler.  
     " *polyrhachioides* Emery.  
*Polyrhachis militaris* (Fabricius).

#### *Bufo funereus* Bocage

This toad is commonly found in the Rain Forest and the outlying forest galleries. Of sixty-three stomachs examined, fifty-five contained recognizable food and forty-three of these ants:

- Dorylus emeryi* subsp. *opacus* Forel.  
     " *kohli* Wasmann.  
     " *nigricans* subsp. *arcens* (Westwood).  
     " *wilverthi* Emery.  
*Cerapachys cribrinodis* Emery.  
*Pallothyreus tarsatus* (Fabricius).  
*Megaponera fœtens* (Fabricius).  
*Bothroponera talpa* Ern. André.  
     " *pachyderma* (Emery).  
     " *soror* (Emery).  
*Phrynoponera gabonensis* (Ern. André).  
     " " var. *esta* Wheeler.  
     " " var. *fecunda* Wheeler.  
     " " var. *striatidens* (Santschi).  
*Euponera ingesta* Wheeler.  
     " *sennaarensis* (Mayr).  
*Plectroctena cristata* Emery.  
*Psalidomyrmex procerus* Emery.  
*Leptogenys stuhlmanni* subsp. *camerunensis* var. *opalescens* Wheeler.  
*Anochetus estus* Wheeler.  
     " *opaciventris* Wheeler.  
*Odontomachus assiniensis* Emery.  
     " " var. *furvior* Wheeler.  
     " *hæmatoda* (Linnæus).

- Pheidole batrachorum* Wheeler.  
*Myrmicaria eumenooides* subsp. *opaciventris* (Emery).  
 " " " var. *crucheti* (Santschi).  
*Meranoplus nanus* subsp. *soriculus* Wheeler.  
*Triglyphothrix gabonensis* Ern. André.  
 " *mucidus* Forel.  
*Cataulacus guineensis* F. Smith.  
*Engramma wolffi* Forel.  
*Plagiolepis tenella* Santschi.  
*Pseudolasius weissi* var. *sordidus* Santschi.  
*Camponotus maculatus* subsp. *solon* Forel.  
 " " subsp. *brutus* (Forel).  
 " *acvapimensis* Mayr.  
 " *pompeius* subsp. *marius* Emery.  
 " *wellmani* var. *rufipartis* Forel.  
 " *rufoglaucus* subsp. *cinctellus* var. *rufigenis* Forel.  
 " *viridus* subsp. *cato* (Forel).  
*Polyrhachis militaris* (Fabricius).  
 " *concava* Ern. André.

#### *Bufo tuberosus* Günther

A forest toad, much less common than the other species. Only five stomachs could be examined and each contained a number of worker ants:

- Paliothyreus tarsatus* (Fabricius).  
*Bothroponera soror* (Emery).  
 " *pachyderma* (Emery).  
*Phrynoponera gabonensis* var. *esta* Wheeler.  
 " " var. *fecunda* Wheeler.  
 " " var. *striatidens* (Santschi).  
*Euponera subiridescens* Wheeler.  
*Odontomachus assiniensis* Emery.  
*Triglyphothrix gabonensis* Ern. André.  
*Cataulacus guineensis* F. Smith.  
*Polyrhachis viscosa* F. Smith (?).

#### *Bufo polycercus* Werner

One of the three common forest toads of the Congo. Of the fifty-four stomachs dissected, fifty-three contained recognizable remains and thirty-one of these ants:

- Dorylus wilverthi* Emery.  
*Paliothyreus tarsatus* (Fabricius).  
*Megaponera fœtens* (Fabricius).  
*Bothroponera pachyderma* (Emery).  
 " " var. *funerea* Wheeler.  
 " *talpa* Ern. André.  
 " *soror* (Emery).



- Phrynoponera gabonensis* (Ern. André).  
 " " var. *esta* Wheeler.  
 " " var. *secunda* Wheeler.  
 " " var. *umbrosa* Wheeler.  
 " " var. *striatidens* (Santschi).  
*Euponera ingesta* Wheeler.  
 " *subiridescens* Wheeler.  
*Plectroctena cristata* Emery.  
 " *minor* Emery.  
*Psalidomyrmex procerus* Emery.  
 " *reichenspergeri* Santschi.  
*Leptogenys stuhlmanni* subsp. *camerunensis* var. *opalescens* Wheeler.  
 " *ergatogyna* Wheeler.  
*Anochetus opaciventris* Wheeler.  
*Odontomachus assiniensis* Emery.  
 " " var. *furvior* Wheeler.  
*Pheidole batrachorum* Wheeler.  
 " *megacephala* (Fabricius).  
*Crematogaster concava* Emery.  
*Triglyphothrix gabonensis* Ern. André.  
*Cataulacus guineensis* F. Smith.  
*Engramma wolffi* Forel.  
*Plagiolepis tenella* Santschi.  
*Pseudolasius weissi* var. *sordidus* Santschi.  
 " *bufonum* Wheeler.  
*Camponotus maculatus* subsp. *solon* Forel.  
 " " subsp. *brutus* (Forel).  
 " *pompeius* subsp. *marius* Emery.  
 " *vividus* subsp. *cato* (Forel).  
*Polyrhachis militaris* subsp. *cupreopubescens* var. *nkomožensis* Forel.  
 " *nigrita* Mayr.

### *Bufo superciliaris* Boulenger

A common toad of the Rain Forest in Cameroon, Gaboon and the Congo. Of fifty-six specimens examined in this respect, fifty showed recognizable remains of food in the stomach and thirty-five of these contained ants:

- Dorylus nigricans* subsp. *sjaestedti* Emery.  
*Pallothyreus tarsatus* (Fabricius).  
*Megaponera fœtens* (Fabricius).  
*Bothroponera talpa* Ern. André.  
 " *pachyderma* (Emery).  
 " *soror* (Emery).  
*Phrynoponera gabonensis* var. *esta* Wheeler.  
 " " var. *secunda* Wheeler.  
 " *bequaerti* Wheeler.  
*Euponera subiridescens* Wheeler.

- Plectroctena cristata* Emery.  
*Psalidomyrmex prgcerus* Emery.  
 " *obesus* Wheeler.  
*Odontomachus assiniensis* Emery.  
 " " var. *furvior* Wheeler.  
*Myrmicaria eumenoides* subsp. *opaciventris* Emery.  
*Tetramorium guineense* (Fabricius).  
*Engramma wolffi* Forel.  
*Pseudolasius bufonum* Wheeler.  
*Camponotus pompeius* subsp. *marius* Emery.  
 " *uwellmani* var. *rufipartis* Forel.

*Phrynobatrachus perpalmatus* Boulenger

A water frog of the forest region. Only eight of the stomachs examined contained recognizable remains of food and ants were found in one of these:

- Polyrhachis alluaudi* var. *anteplana* Forel.

Parts of many more ants were seen in the stomachs of the related savannah species *Phrynobatrachus natalensis* (A. Smith), but too poorly preserved for correct identification.

*Arthroleptis variabilis* Matschie

This is one of the typical frogs of the Cameroon, Gaboon and Congo Rain Forest. Seventeen of the stomachs examined contained recognizable food and two of these included ants:

- Pheidole batrachorum* Wheeler.  
*Aëromyrma* sp.

*Rana occipitalis* Günther

A large-sized frog, common in the vicinity of streams, ponds, and swamps throughout the forest and savannah, from Senegambia to Angola, Uganda and East Africa. All of the twenty-five stomachs examined, contained recognizable food and ants were present in ten cases:

- Dorylus nigricans* subsp. *sjæstedti* Emery.  
*Pallothyreus tarsatus* (Fabricius).  
*Megaponera fœtens* (Fabricius).  
*Bothroponera soror* (Emery).  
*Odontomachus hæmatoda* (Linnæus).  
*Myrmicaria eumenoides* subsp. *opaciventris* (Emery).  
*Camponotus maculatus* subsp. *congolensis* Emery.  
 " *acvapimensis* Mayr.  
 " *cæsar* Forel.  
 " *uwellmani* var. *rufipartis* Forel.  
 " *chapini* Wheeler.

*Rana albolabris* Hallowell

A characteristic frog of the Rain Forest, extending a little beyond the limits of the forest in swamps and along forest galleries. The

stomachs of twenty-three individuals were dissected and nineteen of these showed recognizable remains of food; ants were present in three cases only:

- Bothroponera pachyderma* (Emery).
- Odontomachus assiniensis* var. *aterrimus* Wheeler.
- Camponotus maculatus* subsp. *solon* Forel.

*Rana mascareniensis* Duméril and Bibron

Perhaps the most common frog throughout the larger part of the African continent. Of the thirty-nine stomachs examined, twenty-four contained recognizable remains, and a small number of ants, all of the winged phases, were found in five of them:

- Pheidole megacephala* (Fabricius).
- Camponotus viridus* subsp. *cato* (Forel).

*Rana ornatissima* Bocage

This frog is much rarer than the three preceding species; it is known from the savannahs south of the Rain Forest, from Angola to Southern Rhodesia and also from the northeastern Uele, where Lang and Chapin collected a number of specimens at Garamba. Of these, fifteen were examined for their food contents and fourteen contained recognizable remains; a few ants were found in a single stomach:

- Pheidole kohli* Mayr, var.
- “ *megacephala* subsp. *melancholica* (Santschi).
- “ *speculifera* Emery.

In addition, twenty stomachs of two other common Congo frogs (*Rana oxyrhynchus* A. Smith and *R. christyi* Boulenger) were dissected, but only a single winged ant was found. The pronounced aquatic habits of all species of *Rana*, which keep them in or near the water, evidently prevent them from feeding to any large extent on ants, except on individuals that accidentally drop into the water, as for instance, during their nuptial flights.

*Kassina senegalensis* (Duméril and Bibron)

A small frog occurring throughout the savannah country of Africa, with rather terrestrial habits and also said occasionally to ascend trees. A few ants were found in two of the nineteen stomachs dissected. The occurrence in one stomach of a number of workers of the hypogæic ant *Dorylus kohli* is interesting in connection with the burrowing habits of this frog.

- Dorylus kohli* Wasmann.
- Pheidole megacephala* subsp. *melancholica* (Santschi).

*Hemisis marmoratum* (Peters)

This little burrowing frog, of pronounced terrestrial habits, is found in the savannah country of a large part of Africa, north, south, and east of the Rain Forest. It lives mostly underground, and, according to Mr. Lang's observations, comes out of its burrows only after heavy rains. It is the most typical "ant-eater" of all Congo amphibians; twenty-two stomachs examined contained no other food than termites and worker ants, though termites were by far more abundant. True ants were found in four stomachs only:

*Dorylus kohli* Wasmann.

" *conradti* Emery.

*Tetramorium pusillum* var. *hemisi* Wheeler.

## REPTILES

Lizards often chew or lacerate their food to such an extent that the examination of their stomach contents gives but very general indications with regard to their diet. There can hardly be any doubt, however, that Formicidæ are part of the bill of fare of many of these reptiles. In Miss A. H. Pritchett's careful experiments,<sup>1</sup> ants, *Pogonomyrmex barbatus* subspecies *molefaciens* (Buckley) and *Pachycondyla harpax* (Fabricius), were eaten readily by *Sceloporus spinosus floridanus* (Baird), a common lizard of Texas. Another species, *Gerrhonotus infernalis* Baird, refused to eat *Camponotus maculatus* subspecies *sansabeanus* (Buckley) and *C. fumidus* variety *festinatus* (Buckley), but the author suggests that these ants were possibly too small to be noticed, as insects below a certain size are apparently not perceived by the large species of lizards. Concerning *Phrynosoma cornutum* (Harlan), Miss Pritchett writes: "The 'horned toads' were kept in cages with other lizards and also separately and were never seen to eat anything but ants. They are especially fond of the large agricultural ant, *Pogonomyrmex barbatus* Smith variety *molefaciens* Buckley" (p. 284).

In his paper on 'The horned lizards of California and Nevada of the genera *Phrynosoma* and *Anota*,' H. C. Bryant<sup>2</sup> says that ants, flies, and other insects constitute the principal diet of these genera and remarks: "Why the animal is never bothered by being stung internally by the ants it eats, seems hard to explain. Certainly the lining of the mouth and stomach must be particularly adapted to withstand the poisonous sting of insects, for when stung externally, the lizard shows no little discomfort" (p. 17). Unlike most other reptiles, the horned toad catches

<sup>1</sup>1903, Biol. Bull., V, pp. 271-287.

<sup>2</sup>1911, Univ. of California Publ. Zool., IX, No. 1, pp. 1-84, Pls. I-IX.

the insects on the end of its viscid tongue and swallows them alive, its feeding habits being indeed very similar to those of true toads. C. L. Camp<sup>1</sup> has published more detailed observations on the food of many California lizards. He found remains of ants in the stomach contents of the following species: *Uma notata* Baird, *Callisaurus ventralis ventralis* (Hallowell), *Uta stansburiana elegans* (Yarrow), *Sceloporus magister* Hallowell, *Phrynosoma platyrhinos* Girard, and *Cnemidophorus tigris tigris* Baird and Girard. In the case of one of the horned toads (*Phrynosoma*) examined, the contents of the stomach were: "fifteen parasitic nematodes, six Coleoptera, one orthopter, 145 red-headed ants, all apparently of the same species and swallowed whole, and one pebble" (p. 528). These ants belonged in all probability to one of the seed-storing species of *Pogonomyrmex*, for Mitchell and Pierce<sup>2</sup> also note that in Texas remains of *P. barbatus* (F. Smith) subspecies *molefaciens* (Buckley) were found several times in the excrement of the horned toad, *Phrynosoma cornutum* (Harlan), and "one colony was absolutely exterminated before the enemy left it."

The Australian horned dragon or moloch (*Moloch horridus*) is said by Saville Kent to feed exclusively on ants of the minutest size.

The small black evil-odored species [of ant], common in both South and Western Australia, was always a prime favorite with the specimens kept by the author, and wherever these ants abounded, in conjunction with a sufficiently warm temperature, no difficulty was experienced in maintaining these lizards in perfect health. . . . They would soon settle down to feeding in a row, and the number of ants an individual lizard would assimilate was something astonishing. On several occasions experimental reckoning elicited the fact that no less than from one thousand to fifteen hundred ants were taken in successive order at a single meal, each ant being separately picked up by a flashlike protrusion of the slender adhesive tongue.<sup>3</sup>

On examination of the stomachs of the lizards and chameleons collected by the American Museum Congo Expedition, Mr. K. P. Schmidt<sup>4</sup> found remains of ants, usually in a condition preventing any further identification, in the following species: *Lygodactylus picturatus gutturalis* (Bocage), *Agama colonorum* Daudin, *Bedriagaia tropidophilis* Boulenger, *Algiroides africanus* Boulenger, *Holaspis guentheri* Gray, *Ger-*

<sup>1</sup>1916, 'Notes on the local distribution and habits of the amphibians and reptiles of Southeastern California in the vicinity of the Turtle Mountains,' Univ. of California Publ. Zool., XII, No. 17, pp. 503-544, Pls. XIX-XXII. Through the courtesy of Mr. Camp I have been able to examine the stomach contents of a number of reptiles collected by him near the Turtle Mountains, Riverside Co., California. In the case of *Uma notata* the stomachs were almost entirely filled with heads and parts of the body of *Pogonomyrmex*, while in those of *Phrynosoma platyrhinos* there were heads of ants and also pieces of beetles.

<sup>2</sup>1912, Proc. Ent. Soc. Washington, XIV, p. 72.

<sup>3</sup>Saville Kent, W., 1897, 'The naturalist in Australia,' (London), pp. 85-86.

<sup>4</sup>1919, 'Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909-1915. Part I. Turtles, Crocodiles, Lizards, and Chameleons,' Bull. American Mus. Nat. Hist., XXXIX, pp. 385-624.

gray partridge, *Perdix perdix* (Linnæus), which is chiefly a grain-feeder. Of the fifty-six birds, forty-nine showed ants in their stomach contents, but in the majority of cases these insects were present in isolated specimens only. The following eight birds, alone, evidently exhibited a true myrmecophagous propensity:

*Dryobates major* (Linnæus). The greater spotted woodpecker is a typical ant-feeder; of twenty-three stomachs examined, fifteen contained ants, often in large numbers, belonging to the following six species: *Lasius flavus*, *L. niger*, *L. fuliginosus*, *Camponotus ligniperdus*, *Formica rufa*, and *Dolichoderus 4-punctatus*.

*Dryobates medius* (Linnæus). The middle spotted woodpecker feeds also largely on ants; of nine stomachs, six contained such insects, also often in abundance. The following species were recognized: *Lasius fuliginosus*, *L. alienus*, *Formica rufibarbis*, *F. rufa*, and *Myrmica lævinodis*.

*Dryobates minor* (Linnæus). Ants are also readily eaten by the lesser spotted woodpecker; five of the eight stomachs examined contained specimens, often in great numbers, of the following species: *Lasius alienus*, *L. fuliginosus*, *Camponotus sylvaticus*, and *Dolichoderus 4-punctatus*.

*Picus viridis* Linnæus. The main food of the green woodpecker consists of ants, which were present in all of the twenty stomachs analyzed, often the only contents and in considerable quantities (as many as 500 or 600 specimens in a single stomach). Ten species of ants were recognized: *Lasius alienus*, *L. flavus*, *L. fuliginosus*, *L. niger*, *Formica pratensis*, *F. rufa*, *F. rufibarbis*, *Camponotus vagus*, *Myrmica lævinodis*, and *Aphænogaster structor*.

*Picus canus* Gmelin. Only ants were found in the stomachs of the three specimens of the gray-headed green woodpecker examined; they belonged to five species: *Lasius alienus*, *L. flavus*, *Formica rufa*, *F. rufibarbis*, and *Camponotus vagus*.

*Dryocopus martius* (Linnæus). There were ants in five of the six stomachs examined of the great black woodpecker; often in abundance and of three species: *Lasius alienus*, *Camponotus ligniperdus*, and *C. vagus*.

*Jynx torquilla* (Linnæus). The wryneck subsists chiefly on ants; all the eighteen stomachs examined contained these insects, often in large numbers, six species being represented: *Lasius niger*, *L. alienus*, *Formica rufa*, *Camponotus sylvaticus*, *Myrmica lævinodis*, and *Tetramorium cæspitum*.

*Perdix perdix* (Linnæus). The common gray partridge feeds mainly on seeds and other vegetable substances, but it frequently picks up animals of various kinds. Of the 285 stomachs examined by Csiki, 177 (or 61.1%) also contained insects. The bulk of this insect food seems to have consisted of ants, which were found in 134 stomachs (or 47%), often in great quantities. *Lasius alienus* was present in 72 cases; *L. niger* in 57 cases; *Formica rufa* in 11 cases; *F. pratensis* in 2 cases.

All European observers agree that the green woodpecker, *Picus viridis* Linnæus, is one of the foremost ant-feeders. According to Wasmann's<sup>1</sup> observations in the Netherlands, this bird does not merely limit its myrmecophagous appetite to wood-boring ants (*Camponotus*), but frequently burrows into the nests of certain terrestrial species. In the spring and fall the excrement contains remains of many kinds, such as *Myrmica rubra*, *M. scabrinodis*, *Lasius niger*, *L. flavus*, *L. fuliginosus*, *Formica pratensis*, *F. rufa*, *F. rufibarbis*, and *F. sanguinea*, while in severe winters this woodpecker seems to feed almost exclusively on *Formica rufa* and *F. pratensis*, inserting its bill into their mound-shaped nests. W. C. Angus<sup>2</sup> also found that the stomach of one of these woodpeckers, shot in January in North Wales, contained *Myrmica scabrinodis*, "a common ant which nests on ground-hillocks, but never in trees."<sup>3</sup>

The very complete inventory of the food of the woodpeckers and their allies (Picidæ) in the United States published by Beal has led to the interesting results contained in the table below, in which the species are arranged in the order of their importance as ant-eaters. It may be seen that, for these birds, "ants constitute the largest item of animal food—28.41 per cent, considering the whole 16 species collectively—and are actually the largest item in the stomachs of 8 species. The Williamson sapsucker, the red-cockaded woodpecker, and the two flickers take the highest rank in this respect. Beetles stand next in importance, and amount to 20.42 per cent. These two items together form nearly half the food. The remainder of the animal food is composed of insects, with a few spiders, millepeda, and sowbugs, and occasionally a salamander, tree frog, lizard, or snail."<sup>4</sup>

<sup>1</sup>Wasmann, E., 1905, 'Zur Myrmecophagie des Gruenspechts,' Tijdschr. v. Ent., XLVIII, pp. 214-220. Wasmann likewise observed the chaffinch, *Fringilla caelebs* Linnæus, boring into a small nest of *Lasius niger* of which it picked up cocoons and workers as well.

<sup>2</sup>1885, Proc. Nat. Hist. Soc. Glasgow, N. S., 1, p. xviii.

<sup>3</sup>See also Leisewitz, W., 1905, 'Ueber die wirtschaftliche Bedeutung unserer Spechte,' Verh. Ornithol. Ges. Bayern, V. (1904), pp. 64-76.

<sup>4</sup>Beal, F. E. L., 1911, 'Food of the woodpeckers of the United States,' U. S. Dept. of Agric. Biol. Surv., Bull. 37, p. 10. See also C. V. Riley's account of 'Insects that woodpeckers eat' in Warren, B. H., 1890, 'Report on the birds of Pennsylvania,' 2d. Ed., (Harrisburg), pp. 176-178.

## Food of North American Picidæ

Name of Species	Number of Stomachs Examined	Per cent of Animal Food	Per cent of Ants
Williamson sapsucker, <i>Sphyrapicus thyroideus</i> (Cassin)	17	86.67	85.94
Red-cockaded woodpecker, <i>Dryobates borealis</i> (Viellot)	76	81.06	56.75
Red-shafted flicker, <i>Colaptes cafer</i> (Gmelin)	183	67.74	53.82
Flicker, <i>Colaptes auratus</i> (Linnæus)	684	60.92	49.75
Red-breasted sapsucker, <i>Sphyrapicus ruber</i> (Gmelin)	34	68.92	42.49
Pileated woodpecker, <i>Phlæotomus pileatus</i> (Linnæus)	80	72.88	39.91
Yellow-bellied sapsucker, <i>Sphyrapicus varius</i> (Linnæus)	313	49.31	34.31
Downy woodpecker, <i>Dryobates pubescens</i> (Lin- næus)	723	76.05	21.36
Hairy woodpecker, <i>Dryobates villosus</i> (Linnæus)	382	77.67	17.10
Lewis woodpecker, <i>Asyndesmus lewisi</i> Riley	59	37.48	11.87
Three-toed woodpecker, <i>Picoides americanus</i> Brehm	23	94.06	8.29
Nuttall woodpecker, <i>Dryobates nuttallii</i> (Gambel)	53	79.41	8.19
California woodpecker, <i>Melanerpes formicivorus</i> <i>bairdi</i> Ridgway	84	22.59	8.09
Red-bellied woodpecker, <i>Centurus carolinus</i> (Linnæus)	271	30.94	6.45
Arctic three-toed woodpecker, <i>Picoides arcticus</i> (Swainson)	28	88.69	6.35
Red-headed woodpecker, <i>Melanerpes erythro-</i> <i>cephalus</i> (Linnæus)	443	33.83	5.17
Total	3453		
Average		64.26	28.49

It would be worth while to consider in more detail the choice of food made by these ant-eating woodpeckers. Unfortunately, I have not found the needed information for some of the species included in the above list, such as, for example, the Williamson sapsucker; many of the other woodpeckers, especially those of the genera *Dryobates*, *Phlæotomus*, and *Melanerpes*, merely eat ants which they find in wood or underneath bark (*Camponotus* and *Crematogaster*). The flickers (*Colaptes*), however, are the ant-eaters *par excellence* among North American birds, for they have made ants their favorite food; they are also more terrestrial in



habits than the other woodpeckers and this explains how their ant diet includes not only wood- and bark-boring species, but also many others that nest in the ground (*Formica*, *Lasius*, *Myrmica*, *Aphænogaster*, *Solenopsis*, *Prenolepis*, etc.).

In one case a stomach and crop [of *Colaptes auratus*] were both filled with very small ants (*Crematogaster* species). The whole mass was divided with care into 16 parts as nearly equal as possible, and in one part 315 ants were counted, giving 5,040 in one meal of one flicker. In addition there were at least 100 pupæ. Two other stomachs and crops examined in the same way each gave a little over 3,000 ants. Probably each of the 100 stomachs in the collection contained nearly as much ant food as these, but the number of ants was less because they were of larger species. A large proportion of the ants eaten are of species that live in the earth, and these appear to be the principal food the flicker obtains on the ground. In every case where the stomach held a quantity of these small ants, a lot of fine sand revealed their source.<sup>1</sup>

In his study on 'The tongues of woodpeckers,' F. A. Lucas has the following interesting remarks which may be quoted in connection with our subject.

Considering the tongues in relation to food, we find that those of the various species of flickers (*Colaptes*) have the fewest terminal barbs and the longest dorsal tract of fine points; they are also among the longest. The members of the genus are particularly fond of ants, and the tongue seems especially adapted for probing ant hills. The function of the fine points on the upper part of the tongue seems to be to form a rough surface to which the sticky saliva will readily adhere and to which in turn the ants will be stuck. In this genus the submaxillary salivary glands reach the maximum size in the group.<sup>2</sup>

In North America the western meadowlark, *Sturnella magna neglecta* (Audubon), and the roadrunner, *Geococcyx californianus* (Lesson), may be taken as typical illustrations of occasional ant-feeders. The food of these birds has been investigated in California by H. C. Bryant.<sup>3</sup> About 2000 stomachs of the western meadowlark were examined, and 16.7 per cent of these contained remains of ants, which amounted to 3 per cent (volume) of the total food of all the specimens studied. Ants appear to be taken by this bird irrespective of size or kind. Of species identified, I may mention *Tapinoma sessile*, *Messor andrei*, *Pogonomyrmex californicus*, and species of *Camponotus* and *Formica*. In the case of the roadrunner, of which 84 stomachs were examined, a little over 4 per cent of the total food was made up of ants, bees, and wasps: one of these stomachs contained over 250 red ants (*Pogonomyrmex californicus*), along with a quantity of caterpillars, crickets, beetles, and grasshoppers;

<sup>1</sup>Beal, F. E., *op. cit.*, p. 54.

<sup>2</sup>1895, U. S. Dept. of Agric. Biol. Surv., Bull. 7, p. 38.

<sup>3</sup>1914, 'A determination of the economic status of the western meadowlark (*Sturnella neglecta*) in California,' Univ. of California Publ. Zool., XI, No. 14, pp. 21-24; 1916, 'Habits and food of the roadrunner in California,' *op. cit.*, XVII, No. 5, pp. 21-58, Pls. 1-1v.

another bird had eaten ten carpenter ants (*Camponotus* species). According to records in the United States Biological Survey; published by W. D. Hunter,<sup>1</sup> the following Texas birds are known to prey upon the agricultural ant, *Pogonomyrmex barbatus* subspecies *molefaciens* (Buckley): great-tailed grackle, *Megaquiscalus major macrourus* (Swainson); upland plover, *Bartramia longicauda* (Bechstein); burrowing owl, *Speotyto cunicularia hypogæa* (Bonaparte); Texas nighthawk, *Chordeiles acutipennis texensis* Lawrence; scissor-tailed flycatcher, *Muscivora forficata* (Gmelin); kingbird, *Tyrannus tyrannus* (Linnæus); redbird, *Cardinalis cardinalis* (Linnæus); and mockingbird, *Mimus polyglottos* (Linnæus).

Cleland's recent account of the food of Australian birds,<sup>2</sup> makes it clear that the rich ant fauna of that continent is preyed upon by a great many birds of different families. Of a total of 224 species examined with regard to their stomach contents, 73 were found to contain ants, though as a rule these insects were present in small quantities only. The following list contains such species as seem to show a preference for ants.

- Black-breasted plover.—*Zonifer tricolor* (Vieillot).
- Lesser golden plover.—*Charadrius dominicus* (P. Müller).
- Brown flycatcher.—*Micræca fascinans* (Latham).
- Flame-breasted robin.—*Petræca phœnicea* Gould.
- Scrub robin.—*Drymaædus brunneopygius* Gould.
- Coach-whip bird.—*Psophodes crepitans* (Latham).
- Blue wren.—*Malurus cyanocephalus* Sharpe.
- Grey shrike-thrush.—*Collyriocichla harmonica* (Latham).
- Black-backed magpie.—*Gymnorhina tibicen* (Latham).
- White-backed magpie.—*Gymnorhina leuco-nota* Gray.
- White-throated thickhead.—*Pachycephala pectoralis* (Gould).
- Yellow-breasted shrike-robin.—*Eopsaltria australis* (White).
- White-throated tree-creeper.—*Climacteris picumna* (Temminck).
- Brown tree-creeper.—*Climacteris scandens* Temminck.
- Noisy minah.—*Myzantha garrula* (Latham).
- Yellow-throated minah.—*Myzantha flavigula* Gould.

Most of the ants found in these stomachs were not identified. In the case of the *Micræca* and the species of *Myzantha*, remains of *Camponotus nigriceps* (Smith) and of a *Polyrhachis* were recognized. Two of the stomachs of *Psophodes crepitans* contained a large quantity of the heads and legs of ants, chiefly the "green-head ant" [*Rhytidoponera metallica* (F. Smith)]; some of the *Malurus cyanocephalus*, *Gymnorhina tibicen*, *Eopsaltria australis*, *Climacteris picumna*, and *C. scandens* had also fed on this or allied Ponerinæ. Bulldog ants (*Myrmecia* species)

<sup>1</sup>1912, U. S. Dept. Agric. Bur. Ent. Circ. No. 148, p. 6.

<sup>2</sup>Cleland, J. B., 1918, 'The food of Australian birds. An investigation into the character of the stomach and crop contents,' Science Bull. No. 15, Dept. of Agric. New South Wales, 112 pp.

numbers only. Certain Indian birds, however, feed entirely on ants and foremost among these are, again, the woodpeckers. Three stomachs of the northern rufous woodpecker, *Micropternus phæiceps* Blyth, contained exclusively ants: 1459 *Crematogaster subnuda* in the first; 2600 of the same ant in the second; 725 of this *Crematogaster*, 304 *Pheidole malinsi*, and 27 pupæ and larvæ of *Æcophylla smaragdina* in the third. Of 3921 insects taken by 16 specimens of another woodpecker, *Brachypternus aurantius* (Linnæus), 1738, or 44 per cent, were ants (*Camponotus compressus*, *Æcophylla smaragdina*, *Meranoplus bicolor*, *Myrmecocystus setipes*, and *Crematogaster subnuda*), and in several instances the bird's stomach contained nothing else. An interesting result was obtained with the wryneck, *Jynx torquilla* (Linnæus): seven stomachs contained 1540 insects, all but eight of which were ants, mostly of the species *Pheidole malinsi*. Another prominent ant-feeder in India is the brown shrike, *Lanius cristatus* Linnæus; of 111 insects taken by seven birds, 41, or 36 per cent, were ants (*Æcophylla smaragdina* and *Crematogaster subnuda*).

Similar observations on South and Central American birds would be extremely valuable, for it is surprising how few accurate data have been published, as yet, with regard to the food habits of most tropical birds. For this reason, I include a list of the Nicaraguan birds in the stomach of which Mr. W. De Witt Miller has found remains of ants.<sup>1</sup>

*Geococcyx velox* (A. Wagner). One stomach contained a mass of insects, including three fairly large ants; several other birds of this species showed no ants.

*Chloronerpes rubiginosus yucatanensis* (Cabot). Fragmentary remains of many ants were found in one stomach. The proventriculus and stomach of another individual were filled with ants, some of these being mostly yellowish and 10 mm. long; there was also one beetle. In a third case the stomach contained a large number of ants of at least two kinds, by far the majority belonging to a small yellowish species; also at least one small beetle. Many ants were present in the stomach of a fourth bird.

*Ceophlæus lineatus similis* (Lesson). Two stomachs examined contained numerous ants and bits of other insects.

*Centurus hoffmanni* Cabanis. In one case the stomach showed no other food than many ants of various kinds, while that of another bird was filled with fruit of a *Cecropia*.

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<sup>1</sup>I am greatly indebted to Mr. W. DeWitt Miller, Associate Curator of Ornithology in The American Museum of Natural History, for permission to use this information, and also for many valuable suggestions and criticisms on my account of birds as predaceous enemies of ants.

*Xiphocolaptes emigrans emigrans* Selater. Insects, including many ants, in one stomach; three other stomachs contained no ants.

*Saltator magnoides medianus* Ridgway. One stomach contained, among other things, a number of myrmecine ants.

*Amblycercus holosericeus* (Lichtenstein). One stomach was filled with insects, including at least one small black ant.

*Thamnophilus doliatus* (Linnæus). One stomach contained two small black ants among other insects; that of another individual was filled with fair-sized ants of at least two kinds, some black, some yellow; no ants were found in three other stomachs of this species.

*Pachysylvia decurtata* (Bonaparte). Two stomachs contained in one case one, and in the other four ants, among other insects.

*Pachyrhamphus cinnamomeus* Lawrence. One stomach was completely filled with insects, including two ants.

*Synallaxis pudica nigrifumosa* (Lawrence). One ant among many other insects, in one stomach.

*Hylocichla ustulata swainsoni* (Cabanis). Insects, including one ant head, were found in one stomach.

*Euthlypis lachrymosa* (Cabanis). The contents of one stomach consisted of insects, including ants.

*Cyclarhis flaviventris* Lafresnaye. Insects, including a few ants, were found in one stomach. Another bird contained no ants.

*Myiopagis placens accola* Bangs. One stomach showed a few insects, including one ant head.

*Salpinctes fasciatus* Salvin and Godman. In two stomachs examined a number of ants were found, together with other insects.

As Mr. Miller points out, it would seem that, except in the case of certain woodpeckers (*Chloronerpes*, *Ceophlæus*, and *Centurus*), ants are an exception in the food of the insectivorous birds of Central America. Perhaps the most pronounced ant-feeders of all Neotropical birds are the curious woodpeckers of the genus *Celeus*. G. F. Gaumer describes the habits of the common species, *Celeus castaneus* (Wagler), in Yucatan, as follows: "This bird has a very strong and peculiar odour, derived from its food, which consists exclusively of a small hymenopterous insect called the *Uss*. It is solitary, and lives in the deepest part of the forest. The specimens obtained were very tame and were watched for some hours before being shot; they jump nimbly about the trees, and are constantly catching the small insects which seem to be attracted to them by their odour."<sup>1</sup> I am informed by Mr. Miller that, according to Mr.

<sup>1</sup>Quoted by A. Boucard, Proc. Zool. Soc. London, 1883, pp. 452-453.

G. K. Cherrie's observations made in Central America, the "hymenopterous insects" in question are ants.<sup>1</sup>

*Phanicothraupis rubicoides* (Lafresnaye), one of the tanagers, is often credited with following swarms of ants in search of its food, as, for instance, by G. F. Gaumer<sup>2</sup> from observations made in Yucatan and by C. C. Nutting<sup>3</sup> in Nicaragua. The latter remarks: "Curiously enough, although a tanager, this bird is usually seen clinging to the tree-trunks, like the Dendrocolaptidæ, and hops about the ground like the Formicariidæ. Indeed it seemed to be living almost entirely upon ants. There were many places where the ground was actually swarming with these insects, and there *P. rubicoides* would congregate in large numbers, either picking up the ants from the ground, or climbing about the trunks of trees in pursuit of the same insect."

*Eucometis spodocephala* (Bonaparte), another tanager, and *Dendrocincla sancti-thomæ* (Lafresnaye), one of the Dendrocolaptidæ, were also seen by C. C. Nutting in Nicaragua, feeding largely upon ants (*op. cit.*, pp. 382 and 385).<sup>4</sup>

It is especially the Neotropical ant-thrushes, or Formicariidæ, that have been credited with habitually following the columns of the foraging ants (*Ecitonini*) in much the same manner as will later be described for the African ant-thrushes and doryline ants. R. Schomburgk<sup>5</sup> mentions that, in British Guiana, the moving armies of *Eciton* are always accompanied by large numbers of several species of birds, the most common of these being *Formicarius colma* (Boddaert) and *Pithys albifrons* (Linnæus). This traveller evidently believed that the birds were feeding on the ants themselves. H. W. Bates, speaking of his experiences with the foraging ants in Brazil, also writes that "when the pedestrian falls in with a train of these ants, the first signal given him is a twittering and restless movement of small flocks of plain-colored birds (ant-thrushes) in the jungle."<sup>6</sup> Belt's observations in Nicaragua are somewhat similar: "The numerous birds that accompany the army ants (*Eciton prædator*) are ever on the lookout for any insect that may fly up, and the heavy flying locusts, grasshoppers, and cockroaches have no chance of escape. Several species of ant-thrushes always accompany the army ants in the forest. They do

<sup>1</sup>Lüderwaldt (1909, Zeitschr. Wiss. Insektenbiol., V, p. 312) tells that the Campos woodpecker [*Colaptes ? campestris* (Vieillot)] ransacks the ground nests of *Camponotus rufipes* (Fabricius) in southern Brazil.

<sup>2</sup>Quoted by A. Boucard, Proc. Zool. Soc. London, 1883, p. 443.

<sup>3</sup>1883, Proc. U. S. Nat. Mus., VI, No. 24, p. 382.

<sup>4</sup>None of the few stomachs of *Phanicothraupis* and *Dendrocincla* from Nicaragua examined by Mr. Miller contained ants.

<sup>5</sup>Schomburgk, R., 1848, 'Reisen in British-Guiana,' (Leipzig), II, pp. 287-288 and 421.

<sup>6</sup>1863, 'The naturalist on the River Amazon,' (London), II, p. 357.

not, however, feed on the ants, but on the insects they disturb. Besides the ant-thrushes, trogons, creepers, and a variety of other birds, are often seen on the branches of trees above where an ant army is foraging below, pursuing and catching the insects that fly up."<sup>1</sup> It does not appear, however, that the food of the Formicariidæ has often been determined from actual examination of the stomach contents of these birds.

During his sojourn in Africa with the American Museum Congo Expedition, my friend Mr. J. P. Chapin made accurate investigations as to the food of birds, examining the stomach and crop contents of most of the specimens collected by him. He has kindly allowed me to use his observations, and some of his field notes are quoted in full below. Of about 6000 Congo birds examined by him in this respect, some 200, belonging to about 85 or 90 species, had included ants in their diet.

In the following account I have grouped the African ant-eating birds according to the interest they show in this kind of food and the manner in which they procure it. Data heretofore published bearing on the subject have been referred to, in so far as I have been able to ascertain in the extensive literature on African ornithology; in this, too, I have been very effectively aided by Mr. Chapin.

1.—In a first group may be placed birds that feed occasionally or accidentally on ants, without, however, showing much preference for this kind of diet. A great number, if not all, of the African insectivorous and omnivorous species should perhaps be included here; for most of them available records merely give "insects" in general as food. The following are the only species for which ants have been expressly mentioned as part of the diet.

*Glareola fusca* (Linnæus), according to v. Heuglin,<sup>2</sup> in Nubia pursues swarms of winged ants in the evening, as do other species of *Glareola*.

*Sarciophorus superciliosus* (Reichenow). Zech, in Togo, found ants in the stomachs.<sup>3</sup>

*Ædicnemus ædicnemus* (Linnæus), according to v. Heuglin,<sup>4</sup> feeds partly on ants in Nubia.

*Abdimia abdimi* (Lichtenstein) eats even ants, according to Hartmann,<sup>5</sup> and G. K. Marshall<sup>6</sup> in Rhodesia found, in the stomach of this

<sup>1</sup>1874, 'The naturalist in Nicaragua,' (London), p. 20.

<sup>2</sup>Heuglin, T. v., 1873, 'Ornithologie Nordost-Afrika's,' (Cassel), II, p. 982.

<sup>3</sup>Quoted by Reichenow, A., 1901, 'Die Vögel Afrikas,' (Neudamm), I, p. 191.

<sup>4</sup>Heuglin, T. v., 1873, *op. cit.*, II, p. 988.

<sup>5</sup>Quoted by Heuglin, T. v., 1873, *op. cit.*, II, p. 1104.

<sup>6</sup>1902, Trans. Ent. Soc. London, p. 350.

stork, beetles and "ants of the genus *Carebara*" (probably of the winged, sexual phases.)

*Melierax canorus* (Rislach). The stomachs examined by Oates, in Transvaal, contained large ants, rats and lizards.<sup>1</sup>

*Falco concolor* Temminck. Antinori observed in Eritrea flocks of this bird hunting winged ants (perhaps termites?).<sup>2</sup>

*Pogoniulus pusillus uropygialis* (Heuglin). v. Heuglin<sup>3</sup> found some ants among the stomach contents of this bird in Nubia.

*Irrisor senegalensis* (Vieillot), according to v. Heuglin,<sup>4</sup> eats ants among other insects in Nubia.

*Batis orientalis* (Heuglin). G. W. Bury noted, for a specimen collected in Northern Somaliland, that "the stomach was found to contain a large number of ants."<sup>5</sup>

*Batis molitor* (Hahn and Küster). Insects of various kinds, also ants, in the stomachs of Gazaland specimens.<sup>6</sup>

*Laniarius erythrogaster* (Cretzschmar), according to v. Heuglin,<sup>7</sup> eats ants among other insects in Nubia.

*Ploceus aureoflavus* A. Smith. Fischer<sup>8</sup> found in the stomach of this weaver-bird, in British East Africa, seeds and sometimes also ants and caterpillars.

*Nectarinia arturi* Selater. The crops examined by Swynnerton,<sup>9</sup> in Gazaland, contained flying ants, small flies and several large gnats.

*Chalcomitra kirki* (Shelley). The crop of one bird examined in Gazaland by Swynnerton<sup>10</sup> contained beetles and ants.

*Tarsiger stellatus* (Vieillot). The crops of two specimens examined in Gazaland by Swynnerton<sup>11</sup> contained berries, various insects and ants.

*Muscicapa cærulescens* (Hartlaub). Large black ants and beetles were found in the stomach of a specimen taken in Gazaland by Swynnerton.<sup>11</sup>

At Salisbury, Rhodesia, G. K. Marshall<sup>12</sup> found remains of ants in the stomachs of the following birds:

*Bradornis mariquensis* (A. Smith).

*Pratincola torquata* (Linnæus).

<sup>1</sup>Oates, F., 1881, 'Matabele Land and the Victoria Falls,' (London), p. 298.

<sup>2</sup>Antinori, O. and Salvadori, T., 1873, Ann. Mus. Civ. Genova, IV, p. 389.

<sup>3</sup>Heuglin, T. v., 1871, *op. cit.*, I, p. 762.

<sup>4</sup>1869, *op. cit.*, I, p. 216.

<sup>5</sup>Bannerman, 1910, *Ibis*, (9) IV, p. 312.

<sup>6</sup>Swynnerton, 1907, *Ibis*, (9) I, p. 70.

<sup>7</sup>Heuglin, T. v., 1871, *op. cit.*, I, p. 464.

<sup>8</sup>Quoted by Reichenow, A., 1904, 'Die Vögel Afrikas,' (Neudamm), III, p. 92.

<sup>9</sup>1907, *Ibis*, (9) I, p. 42.

<sup>10</sup>*Op. cit.*, p. 43.

<sup>11</sup>*Op. cit.*, p. 67.

<sup>12</sup>1902, Trans. Ent. Soc. London, p. 351.

*Monticola angolensis niassæ* Reichenow.  
*Saricola pileata* (Gmelin).  
*Dicrurus adsimilis divaricatus* (Lichtenstein).  
*Thamnozæa cinnamomeiventris* (Lafresnaye).  
*Crateropus jardinei kirkii* Sharpe.  
*Lophoceros leucomelas* (Lichtenstein).  
*Campothera bennetti* (A. Smith).  
*Crecopsis egregia* (Peters).

From Mr. Chapin's observations it appears that in the Belgian Congo swallows [*Riparia riparia* (Linnæus) and *Psolidoprocne nitens centralis* Neumann],<sup>1</sup> *Coracina pectoralis* (Jard. Selby), shrikes [*Nilaus afer* (Latham), *Corvinella corvina* (Shaw)], and certain kingfishers (*Halcyon pallidiventris* Cabanis) are very fond of catching sexual winged ants together with other flying insects, while francolins (*Francolinus lathamii* Hartlaub, *F. squamatus* Cassin, *F. icterorhynchus* Heuglin) and Guinea fowl (*Guttera plumifera schubotzi* Reichenow, *G. pallasi* Stone, *Phasidus niger* Cassin, *Numida pitilorhyncha* Lesson) often indiscriminately pick up worker ants from the ground with snails, beetles, seeds, and even pebbles. With regard to the two species of forest Guinea fowl, Mr. Chapin remarks that their flesh "is rather dry eating and has, in addition, a peculiar strong taste, due probably to something they eat, possibly the ants usually found in their crop." At Ngayu the crop and stomach of a black forest Guinea fowl, *Phasidus niger*, were filled with thick green leaves and driver ants. In the case of the savannah Guinea fowl, *Numida pitilorhyncha major* Hartlaub, ants were frequently found in the crop; usually, as in a specimen examined at Faradje in September 1911, these ants belonged to the large, black, termite-hunting species, *Megaponera fœtens* (Fabricius).

The following list contains the birds from the Belgian Congo which showed remains of ants in their stomachs. In most cases these insects were present only in small numbers, or the individuals taken belonged to the winged phases. In some of the pipits (*Anthus*) and thrushes (*Thamnozæa* and *Monticola*), however, worker ants and even their larvæ were sometimes present in large quantities; it is possible that these birds, and perhaps others in the list, may prove on further observation to be rather regular ant-feeders.

<i>Glareola melanoptera</i> Nordmann.	<i>Himantornis hæmatopus whitesidei</i> Sharpe.
<i>Galachrysis nuchalis emini</i> (Shelley).	<i>Ciconia ciconia</i> (Linnæus).
<i>Neotis denhami</i> (Children).	<i>Coturnix coturnix</i> (Linnæus).

<sup>1</sup>In a specimen of *Hirundo nigrita* G. R. Gray, from Gamangui, Mr. Chapin found that "the right metatarsus had been bitten by a driver ant, whose head still adhered to it, and all the lower part of the foot had died and dried up, without falling off."



<i>Coturnix delegorqueti</i> Delegorgue.	<i>Muscicapa striata</i> (Pallas).
<i>Milvus ægyptius parasitus</i> (Daudin).	<i>Stizorhina vulpina</i> Reichenow.
<i>Centropus grillii</i> Hartlaub.	<i>Oriolus larvatus lætior</i> Sharpe.
<i>Cuculus solitarius</i> Stephens.	<i>Onychognathus hartlaubi</i> Hartlaub.
<i>Cuculus jacksoni</i> Sharpe.	<i>Hyphantornis cucullata feminina</i> Grant.
<i>Lybius guifsobalito</i> Hermann.	<i>Malimbus nitens microrhynchus</i>
<i>Coracias abyssinicus</i> Hermann.	Reichenow.
<i>Eurystomus afer</i> (Latham).	<i>Pyromelana crassirostris</i> Grant.
<i>Eurystomus gularis</i> Vieillot.	<i>Estrilda atricapilla</i> Verreaux.
<i>Bucorvus abyssinicus</i> (Boddaert).	<i>Melanopteryx nigerrimus</i> (Vieillot).
<i>Ceratogymna atrata</i> (Temminck).	<i>Parmoptila jamesoni</i> (Shelley).
<i>Bycanistes sharpei</i> (Elliot).	<i>Anthus leucophrys gouldi</i> Fraser.
<i>Horizoceros granti</i> (Hartlaub).	<i>Pycnonotus tricolor</i> (Hartlaub).
<i>Irrisor erythrorhynchos</i> (Latham).	<i>Cinnyris superbus</i> (Shaw).
<i>Scopelus adolfi-friederici</i> Reichenow.	<i>Cinnyris splendidus</i> Shaw.
<i>Caprimulgus inornatus</i> Heuglin.	<i>Hedydipna platura</i> (Vieillot).
<i>Caprimulgus batesi</i> Sharpe.	<i>Eremomela badiceps</i> (Fraser).
<i>Macrodipteryx longipennis</i> (Shaw).	<i>Monticola saxatilis</i> (Linnæus).
<i>Cosmetornis verillarius</i> (J. Gould).	<i>Thamnozœa nigra</i> (Vieillot).

In the case of the weaver-birds included in the above list, it is evident that some of the species (*Parmoptila*, *Malimbus*, *Estrilda*, etc.) have a marked predilection for ants, since the crop and stomach very often contained their larvæ, pupæ, and workers. Mr. Chapin's note concerning a *Melanopteryx nigerrimus* obtained at Avakubi is worthy of quotation: "its stomach contained many of the large light brown ants<sup>1</sup> that bind together the leaves of mango, as well as those of other trees, with silky fibers produced by their larvæ."

2.—Birds that feed chiefly or to a very large extent on ants are of more interest to the myrmecologist, and some of them have developed peculiar habits in connection with this kind of diet.

a.—Swifts and bee-eaters seem to show, in tropical Africa, a marked preference for ants in the winged phases, which they catch in flight. The stomach of one of the most common swifts, *Micropus apus* (Linnæus), was frequently found by Mr. Chapin to be filled with brownish-black winged ants; many other species, such as *Micropus streubeli* (Hartlaub), *M. affinis* (Gray and Hardwicke), *Tachornis parvus* (Lichtenstein), *Chætura cassini* Selater, *C. ussheri sharpei* Neumann, *C. sabini* Gray, and *C. melanopygia* Chapin, have similar habits. Mr. Chapin observes that swifts feed mainly on winged ants, while swallows catch them only occasionally. The red-breasted bee-eater, *Merops*

<sup>1</sup>*Ecophylla longinoda* (Latreille). [J. B.]

*malimbicus* Shaw,<sup>1</sup> also shows a great predilection for winged ants; in the eight specimens shot near Monsembe, on the Congo River, from a flock of 175 to 200 which was resting in the top of a dead tree, the gizzard was well filled with such insects. Similar observations were made on related species at Avakubi (*Merops albicollis* Vieillot) and Bafwabaka [*Melittophagus mülleri* (Cassin)].

b.—A rather small group of insectivorous birds attack the nests of ants and feed on the workers as well as on the brood. This is a very common habit with many species of woodpeckers. Sjöstedt<sup>2</sup> relates that some of the Cameroon species seem to live chiefly on ants, which were the only insects he found in the stomach of *Campethera permista* (Reichenow). Kersting<sup>3</sup> found ants in the stomach of *Campethera nivosa* (Swainson) and v. Heuglin<sup>4</sup> in that of *Mesopicus schoensis* (Rüppell) and *Dendropicus obsoletus* (Wagler), brood as well as worker ants being present. Similar observations were made by Mr. Chapin on the following Congo species: *Campethera caroli* (Malherbe), *C. permista* (Reichenow), *C. balia* Heuglin, *C. abingoni chrysura* (Swainson), and *C. nivosa* (Swainson). His following note relates to a specimen of the last-named species from Avakubi: "the stomach contained larvæ and pupæ of a very small black ant that builds large brown nests in the trees.<sup>5</sup> From this it would seem that this woodpecker had been pecking holes in a nest."

A specimen of *Campethera abingoni* (A. Smith) obtained by Swynerton<sup>6</sup> in Gazaland had its stomach filled with hundreds of a small black tree-ant in all stages of development.

c.—Some birds of the African forests have developed the curious habit of following the columns of doryline driver ants, much as do the South American Formicariidæ I have previously mentioned. The earliest observations of the kind were made by Du Chaillu<sup>7</sup> in the Gaboon: "Hunting in the rear of the village (of Obindji) on the 15th [of April 1858], I shot a curious bird, the *Alethe castanea*—a new species. . . They fly in a small flock, and follow industriously the bashikoway ants [driver ants] in their marches about the country. The bird is insectivorous; and when the bashikoway army routs before it the frightened grasshoppers and beetles, the bird, like a regular camp-follower, pounces on the prey and carries it off. I think it does not eat the bashikoway."

<sup>1</sup>Hartert found winged ants, together with other insects, in the stomach of *Merops malimbicus* examined by him in Nigeria (1886, Journ. f. Ornithol., XXXIV, p. 593).

<sup>2</sup>1895, Kongl. Svenska Vetensk. Ak. Handl., N. S., XXVII, No. 1, pp. 54 and 56.

<sup>3</sup>Quoted by Reichenow, A., 1903, 'Die Vögel Afrikas,' (Neudamm), II, p. 170.

<sup>4</sup>Heuglin, T. v., 1871, 'Ornithologie Nordost-Afrikas,' (Cassel), I, p. 804 and 810.

<sup>5</sup>Evidently a species of *Crematogaster*. [J. B.]

<sup>6</sup>1907, *Ibis*, (9) I, p. 290.

<sup>7</sup>Du Chaillu, P. B., 1861, 'Explorations and adventures in equatorial Africa,' (New York), p. 319.

Reichenow<sup>1</sup> made similar observations on the same species of bird in Cameroon, but he found the stomachs of specimens examined by him filled with driver ants. He also claims that *Turdinus fulvescens* (Cassin) has similar habits.<sup>2</sup> According to Sjöstedt,<sup>3</sup> the following birds are found near the moving columns of *Dorylus* (*Anomma*) *nigricans* subspecies *arcens* in Cameroon: *Bleda notata* (Cassin), *B. syndactyla* (Swainson), *Alethe castanea* Cassin, *Criniger calurus* (Cassin), and *Neocossyphus poensis* (Strickland). This observer notes that *Bleda notata* on such occasions does not remain on the ground, but rather on the lower branches of trees and shrubs, whence it jumps down to the ants and returns at once to its perch. The stomach of *Neocossyphus poensis* was found to contain ants only, while that of *Bleda notata* contained ants and beetles. At Efulen, Cameroon, G. L. Bates<sup>4</sup> also saw *Alethe castanea* "in thickets where an army of driver ants covers the ground and bushes, as they are very fond of feeding on these ants, though they do not come into open places to do so." In another paper, Bates<sup>5</sup> writes: "Whenever you see a number of birds of different kinds flitting about near the ground in one place and twittering excitedly, you may be pretty sure there is an army of 'driver ants' at hand. Many different kinds of birds join in the chase of driver ants. I have even seen the small white-crested hornbill (*Lophoceros hartlaubi*) engaged in it." Another hornbill, *Ortholophus cassini* Finsch, was once seen by Bates<sup>6</sup> to join with smaller birds in pecking at a swarm of driver ants on the ground.

On Mount Ruwenzori, between 6500 and 9000 feet, R. B. Woosnam found *Alethe poliophrys* Sharpe "frequenting the forest zone and the lower edge of the bamboo. It appeared to be particularly fond of the soldier ants and might often be seen attacking a column of these insects as they crossed a path or open spot. Whether it really ate the ants or merely snatched away the eggs they were carrying, was a point we could never decide; probably the eggs were the attraction, for it seems difficult to imagine anything more unsatisfactory than a meal of angry soldier ants."<sup>7</sup>

<sup>1</sup>1875, Journ. f. Ornithol., XXIII, p. 20.

<sup>2</sup>Mr. Chapin did not find this to be the case with *T. fulvescens* in the Upper Congo.

<sup>3</sup>Sjöstedt, Y., 1895, 'Zur Ornithologie Kameruns,' Kongl. Svenska Vetensk. Ak. Handl., N. S., XXVII, No. 1, pp. 1-120, Pls. 1-x. In a later paper Sjöstedt further mentions certain woodpeckers of the genus *Campethera* and *Stiphornis gabonensis* Sharpe as occasionally following the columns of the dorylines in Cameroon, though not so regularly as the *Criniger* and *Alethe* ('Exped. Kilimandjaro, Meru, etc.,' II, 8, 1908, p. 111).

<sup>4</sup>Quoted by R. B. Sharpe, 1908, *Ibis*, (9) II, p. 128.

<sup>5</sup>Quoted by R. B. Sharpe, 1904, *Ibis*, (8) IV, p. 92.

<sup>6</sup>1905, *Ibis*, (8) V, p. 89. Under the name *Ortholophus albocristatus* (Cassin).

<sup>7</sup>Woosnam, quoted by O. Grant, 1910, *Trans. Zool. Soc. London*, XIX, p. 374

these birds were very shy and it was only after long waiting that I could shoot one.

"Now, what are the birds after? It is not, as a rule, the adult ants, for these are generally only eaten, if at all, in very small numbers. Nor is it their young, for they frequently do not carry any, and this circumstance has no relation to the presence or absence of birds. Is it the victims—other insects and the like—being carried by the ants? Surely there ought to be easier ways than this to procure the same food. Yet the three ant heads in the stomach of one of the *Neocossyphus rufus* might have come there in that way. Seizing some coveted morsel, the bird found, perhaps, that several ants had buried their jaws in it, but plucked off their bodies at, any rate, before eating it."<sup>1</sup> On another occasion, at Bafwabaka, the stomach of an immature *Neocossyphus p. præpectoralis* was found filled with driver ants; but in most of the other "ant-thrushes" examined for this purpose the food consisted mostly of small insects, with occasionally a driver ant. A number of stomachs of *Alethe* also contained the bones of small frogs.

Plate I (frontispiece) represents a typical association of three driver ant birds commonly found in the Ituri Forest following the columns of the dorylines: *Alethe c. woosnami* Grant, *Neocossyphus rufus gabunensis* Neumann, and *Bleda eximia ugandæ* van Someren.

#### MAMMALS

That many insectivorous and omnivorous mammals, such as moles, shrews, monkeys, and the like, will at times feed on ants can be expected after what we have learned above of the feeding habits of insectivorous birds; we know, however, but little about this from actual observation. We have the authority of John Muir that certain North American black bears are very fond of carpenter ants (*Camponotus*); they "tear and gnaw their home logs to pieces, and roughly devour the eggs, larvæ, parent ants, and the rotten or sound wood of the cells, all in one spicy acid hash."<sup>2</sup> Mr. C. L. Camp has kindly informed me that he once saw in the Yosemite National Park, California, bear-droppings containing masses of the chitinous remains of ants. Moles, too, must devour large numbers of worker ants and their pupæ, though I have found no

<sup>1</sup>Mr. Chapin also notes that, at Faradje, he once watched a chicken eating army ants.

<sup>2</sup>Muir, J., 1916, 'My first summer in the Sierra,' (Boston and New York), p. 46. C. H. Merriam (1884, 'The mammals of the Adirondack Region,' New York, p. 95) writes that the American black bear (*Ursus americanus* Pallas) "is *par excellence* an omnivorous beast, and his larder consists not only of mice and other small mammals, turtles, frogs, and fish; but also, and largely, of ants and their eggs, bees and their honey, cherries, blackberries, raspberries, blueberries and various other fruits, vegetables, and roots. . . . He delights in tearing open old stumps and logs in search of the ants that make their homes in such situations."

definite records thereof, except in the case of the American mole, *Scalopus aquaticus* (Linnæus). Scheffer<sup>1</sup> has examined one hundred stomachs of this animal in Kansas and found remains of ants in nineteen of them, these insects being then, as a rule, present in large numbers; one of the stomachs, for instance, contained 205 ants and 44 other insects; another, 250 ant puparia and 6 other arthropods.

So-called "ant-eaters" are found in practically all tropical regions, but the confusion so commonly made by casual observers between the true ants (Formicidæ) and the "white ants," or termites, in many cases makes it hard to decide from published accounts which of these mammals are truly myrmecophagous and to what extent. Moreover, but little information based on actual study has been published concerning their feeding habits and stomach contents. White ants, or termites, constitute, of course, an attractive food for almost every insectivorous animal, while true ants, as Beebe remarks, "are all flavored more or less strongly with formic acid, and must be an acquired taste."<sup>2</sup> Further interesting questions which cannot be answered at this time are whether the various ant-eaters prefer ants to other insects and whether they can make a selection between different species of ants. These points would be of importance in considering the possible use of these animals to combat the leaf-cutting ants of tropical America, as suggested by certain observers.

The echidnas, or spiny ant-eaters (*Echidna aculeata* Shaw and allies), of New Guinea, Tasmania, and Australia belong to the order Monotremata and are among the most primitive and odd-looking of present-day mammals. The Australian species, at least, is said by most observers to feed on "ants," though from the descriptions of G. Bennett<sup>3</sup> and Saville Kent it would appear that by this termites are meant as well as Formicidæ. Saville Kent, for instance, writes that when the echidnas are placed in contiguity to a teeming ant track, they take no notice of it, "appreciating the insects only under the conditions obtaining in the nests or hillocks. These edifices they would soon tear open with their powerful claws, exposing to view the white succulent nymphs, larvæ, and pupæ, or so-called eggs, upon which alone they concentrated their attention."<sup>4</sup>

<sup>1</sup>Scheffer, T. H., 1910, 'The common mole,' Bull. 168 Kansas State Agric. Coll. Exper. Stat., pp. 1-36; 1914, 'The common mole of the Eastern United States', U. S. Dept. Agric. Farmers Bull. 583, pp. 1-10. See also West, J. A., 1910, 'A Study of the food of moles in Illinois,' Bull. Illinois St. Lab. Nat. Hist., IX, 2, pp. 14-22.

<sup>2</sup>1918, Bull. Zool. Soc. New York, XXI, No. 1, p. 1561.

<sup>3</sup>Bennett, G., 1860, 'Gatherings of a naturalist in Australasia,' (London), pp. 147-150.

<sup>4</sup>1897, 'The naturalist in Australia,' (London), p. 19.

The echidna is chiefly nocturnal and shows many remarkable adaptations to its habit of feeding on subterranean insects. The face is drawn out into a long, tapering, cylindrical snout, terminating in a very small mouth. The tongue is elongated, very slender, and capable of being protruded for a considerable distance. The jaws are slender and entirely destitute of any kind of teeth, of which, moreover, no trace has been found in the young. The palate, however, and the back of the tongue are rough with small spines, presumably to hold the living prey. "For ants and their eggs form the staple food, and these the *Echidna* obtains by digging up the ant or termites' nests with its powerful limbs. Then the tongue covered with a sticky saliva is protruded; it becomes covered with ants, and is then quickly drawn back into the mouth."<sup>1</sup>

More circumstantial evidence concerning the food of the echidnas in Queensland is to be found in a short note by Bennett's son:

They are particularly partial to the white ants, which erect small mounds of clay about 18 inches in height. These they attack in a most systematic way, by working round the nest, by clearing away the earth and forming a trench where the nest joins the earth, and devouring all before them; and then they make a hole in the center and clear out the whole nest, leaving none behind to tell the tale of their visit. The soldier ant (a large stinging ant) they do not touch; their nests were close to the white ant mounds, but were untouched. The larger sugar ants, which raise mounds of sand about 16 inches high and 4 feet in diameter, they attack first, by lying on the mound with their tongue out and drawing in the ants that cross it; there they remain sometimes for hours. This, I have no doubt, is the time that they get the sand found in their stomach. They then make a hole from one side to the other, and devour the most delicate morsels coming in their way. In the daytime they do not move about much, beginning their search about a couple of hours before sundown.<sup>2</sup>

K. Dahl<sup>3</sup> also states that the Australian *Echidna aculeata* depends upon termites for its food.

Among the extensive order of marsupials, many of the insectivorous species must occasionally eat ants. One of them, the banded Australian ant-eater, *Myrmecobius fasciatus* Waterhouse, is often considered as belonging to a peculiar subfamily, the Myrmecobiinæ, and is said to feed on "ants" and perhaps also on other insects. This interesting animal offers, among the marsupials, all the adaptive characters of the South American ant-eaters: the elongate and pointed muzzle, the slender and extensive tongue, the stout fore limbs, and the long, curved, digging

<sup>1</sup>Lucas, A. H. S. and Le Souef, W. H. D., 1909, 'The animals of Australia,' (Melbourne), p. 148.

<sup>2</sup>Bennett, G. J., 'Observations on the habits of the *Echidna hystrix* of Australia,' Proc. Zool. Soc. London, 1881, pp. 737-739.

<sup>3</sup>1897, Zoologist. (4) I, p. 200. See also König, C., 1911, 'Der Ameisenegel,' Aus der Natur, VII, pp. 621-633.

The armadillos (*Dasypodidæ*), which range in many species over the tropical and temperate parts of South America, one of them even reaching Texas, are said to be omnivorous, feeding on roots, insects, worms, reptiles, and carrion; in how far this diet may include true ants is by no means easy to gather from the very scanty descriptions of the habits of these animals; in many cases termites are in all probability the chief food.<sup>1</sup> The snout of the armadillos is moderately elongate, and the tongue is long, pointed, extensile, though less so than in the *Myrmecophagidæ*.

It would thus appear that the pangolins or scaly ant-eaters (*Manidæ*; Pl. XXIV, fig. 2; Pl. XXV, figs. 1 and 2) of the Old World tropics are the only edentates whose myrmecophagous propensities are beyond doubt. These animals are at once recognizable by the large overlapping scales which cover the whole of the upper surface of the head, the upper surface and sides of the body, the whole of the tail, and the outer sides of the limbs; the legs are short and end in curved claws, those of the fore limbs being especially powerful. The snout is pointed and conical; teeth are entirely absent; the long, verniform, protractile tongue is flattened toward the tip and kept sticky with saliva abundantly produced by enormous submaxillary glands. The structure of the stomach shows further curious adaptations to their ant diet; in *Manis javanica*, for instance, most of the mucous membrane is transformed into a pavement epithelium of horny texture, raised into folds in the cardiac region near the œsophagus, while it forms horny teeth in the pyloric part, at the end of the great curve; opposite these pyloric teeth, at the end of the small curve, the middle line is swollen into an organ of trituration, covered with numerous horny teeth and moved by powerful underlying muscles. The gastric glands are united into a few voluminous glandular bodies which pour their abundant secretion into the stomach by way of wide glandular ducts. The insects are swallowed whole and reach the stomach together with saliva, sand, and small pebbles often as large as a pea; this mixture is then ground up by the peristaltic movements of the stomach, whose inner walls are effectively protected by the horny pavement epithelium; gastric juice is profusely poured over the stomach contents, which undergo a final grinding by the organ of trituration in the pyloric region.<sup>2</sup>

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<sup>1</sup>Lüderwaldt (1909, *Zeitschr. Wiss. Insektenbiol.*, V, p. 312) mentions incidentally that the armadillos in Brazil prefer to grub about in the earthen mounds of the stinging *Solenopsis geminata*.

<sup>2</sup>See Weber, M., 1904, 'Die Säugetiere.' (Jena), pp. 426-427.

Seven species are now generally recognized in this family and are all included in the genus *Manis*: four of these occur on the African continent, while the remaining three are found in the Oriental Region (Ceylon, India, Burma, southern China as far as Kianghsi, Formosa, and Sunda Islands). The ant-eating habit is common to all, though it has been investigated in only a very general way. I have been able to find but one record of the complete analysis of the stomach contents of one of these animals. It was made from a specimen of *Manis* (said to have been *temmincki*, but probably *gigantea* Illiger), the stomach of which was sent by Solon from the Lower Congo to Forel, who extracted from it the following ants,<sup>1</sup> several of which were at that time new to science.

*Dorylus (Anomma) emeryi* subsp. *opacus* Forel. Numerous workers.

*Pheidole punctulata* Mayr. Several workers and two soldiers.

*Crematogaster impressa* Emery. Very numerous workers and several males.

*Macromischoides aculeata* (Mayr). A few workers.

*Myrmecaria eumenoides* var. *congolensis* Forel. Very numerous workers.

*Rhoptromyrmex opacus* var. *estus* Forel. Very numerous workers, a number of males and a few females.

*Plagiolepis tenella* Santschi. Female.

*Oecophylla longinoda* (Latreille). Workers.

*Polyrhachys concava* André. A small number of workers.

*Camponotus manidis* Forel. A small number of workers.

*Camponotus foraminosus* subsp. *delagoensis* var. *sorptus* Forel. A very large number of workers, a goodly number of females and several males.

Büttikofer,<sup>2</sup> in Liberia, fed the smaller, arboreal species, *Manis longicaudata*, with larvæ taken from mushroom-shaped termite nests. Of the large, terrestrial *Manis gigantea*, he says that the anterior portion of the stomach of a specimen contained about six liters of termites, while the posterior portion was filled with an equal amount of driver ants. Vosseler<sup>3</sup> found that the excrement of a *Manis temmincki* Smuts which he observed alive at Amani in Usambara consisted entirely of the chitinous remains of driver ants.

The habits of the oriental species of the genus should not materially differ from those of their African relatives. Kreyenberg,<sup>4</sup> who observed *Manis javanica* in China, states that all stomachs examined by him contained large numbers of ants and their larvæ exclusively. And speaking of the same species in Borneo, Beebe<sup>5</sup> writes: "Ants, both stinging and harmless, form the entire food, although we must extend this general

<sup>1</sup>1909, Ann. Soc. Ent. Belgique, LIII, pp. 58-63.

<sup>2</sup>Büttikofer, J., 1890, 'Reisebilder aus Liberia,' (Leiden), II, pp. 393-395.

<sup>3</sup>1907, Zoolog. Beobachter, XLVIII, p. 197.

<sup>4</sup>1907, Zoolog. Beobachter, XLVIII, p. 184.

<sup>5</sup>Beebe, C. W., 1914, 'The pangolin or scaly-anteater,' Zool. Soc. Bull. New York, XVII, pp. 1141-1145.



specialized. In *M. gigantea* it has the form of a loop, consisting of two, broad, band-like projections distally united and reaching back half the distance from sternum to pelvis. In *M. tricuspis* and *M. tetradactyla*, however, two rod-like, cartilaginous projections extend outside the peritoneum much farther back and, turning upward to the right, are loosely fastened to the last ribs. The prehensile tongue also acts as an organ of touch and, due to its shape, can follow the intricate turns and windings of the galleries in ant and termite structures. This explains why the inmates and their larvæ are cleaned out as by enchantment. An adult male *M. tricuspis* pushed its tongue into the galleries of a sectioned ant nest for a distance of four inches, moving it just as easily sideways as up or down. After making room to insert its tiny snout, it sniffed into the tunnel, thereby still more inciting the inhabitants that, hurrying to the place of disturbance, were then lapped up so rapidly that it was difficult to see how well loaded the tongue was as it shot back and forth.

"The prey is disposed of so instantaneously that neither the ejection of formic acid, the powerful, pinching mandibles, the armature of spines, nor even the stings of the ants are of much avail. The giant ant-eaters, with their broader, more ribbon-like tongue, are more deliberate than the smaller species in feeding, but their methods are equally efficient. From the behavior of various forms observed it appears that they are not affected by the defensive weapons of any of the ants they feed upon. Probably these insects have little chance to make effective use of them before they are enveloped in slime, and later the gastric juices and the triturating action of the stomach render any further efforts impossible.

"The variety of ants taken by these pangolins proves that taste alone does not guide them in their choice, and I have already mentioned that our captives fed on termites with the same eagerness. Furthermore, the food, covered with slime, passes through the completely toothless mouth and throat so quickly that flavor is perhaps of little or no importance. In fact, the passage from mouth to stomach might be compared to a chute, and a process replacing mastication begins only after the food reaches the stomach.

"In spite of this apparent immunity of the scaly ant-eaters, we found that certain kinds of ants are evidently not preyed upon by at least some of the pangolins. Near one of our camps at Avakubi there was a nest of robber ants (*Megaponera fœtens*). When we inserted a grass-stalk into its entrance, the owners hurried out to attack the intruder. In a very few moments a *Manis tricuspis* lying rolled-up nearby was overrun by the

ants, which belabored it with their mandibles as well as with their painful stings. The pangolin became restless, unrolled by fits and starts, got to its feet, erected its scales, and hurried off to some distance. Then, again and again hooking its fore limbs into the ground, it dragged itself from spot to spot, at every pull exercising considerable pressure against the grass, thus endeavoring to free itself of the tormentors. Rolling up and unrolling and scratching with its claws exhausted its means of defense.

“Experiments with other captives of this species showed considerable variation in individual behavior. One taken near a column of army ants (*Dorylus*) merely made good its escape, another quickly broke up the well-ordered line. Sitting on its hind limbs and with its tail steadying its movements, the fore part of the body was swung about freely. The claws of the fore limbs were kept busy removing those of the fierce assailants that, in spite of the oft repeated shivering movements of the scaly armor, succeeded in gaining a hold. Lashing its sticky tongue through the confused crowds, the ant-eater lost no time in moving back and forth along the ant column as quickly as the dense clusters vanished into its mouth. Its hunger satisfied, it at once retreated, freeing itself of the few army ants that had managed to dig their mandibles into the soft parts of its hide. *M. tricuspis* fed freely on many other kinds of ants. Those we had alive at Avakubi, Medje, and Niapu were particularly fond of ants of the genus *Myrmecaria*. Brought within reach of such colonies, the pangolins always turned their attention to the deeper, open tunnels these ants construct across cleared spaces and trails. Here the steady stream of tiny travelers made their meals doubly easy. Curious was the habit of the ant-eaters, especially when sitting partly erect, of turning the outer edge of the tail down and suddenly sweeping into a heap all the fragments of ant or termite structures they had scattered about. This gave them a new chance of disposing of their victims that emerged again in numbers from the débris. Though undoubtedly nocturnal in habits, our captives had no objection to feeding during the day and only the direct rays of the sun interfered with the chances thus offered.

“While African pangolins have helped to enrich the stores of witchcraft both helpful and injurious, those of some parts of Japan, China, and Malaysia have furnished the folklore with a curious tale, slightly differing in details in the various regions, on their supposed feeding habits. According to the legend, the pangolin, after tearing open an ants' nest, erects its body scales and waits until as many ants as possible have

crawled beneath them. Suddenly the scales are pressed down hard, crushing the tiny prey to death; the ant-eater then goes into the water, erects its scales, and proceeds to enjoy a meal of dead ants floating on the surface.

“However great their reputation for slowness, under certain conditions the African species seen could proceed in a shuffling manner for a short distance at the rate of eighty yards a minute, the giant species being slightly faster. All four limbs and the tail take an active part, but walking on hind limbs or leaping was not observed. They can sit erect, steadied by their strong tail and pillar-like hind limbs, thus enabling them to carry out any movement with the fore part of the body and greatly increasing their ability to dig and feed. In walking, *M. tricuspis* and *M. tetradactyla* held their claws in a normal position, the tip of the claws striking the ground. The giant pangolins, however, walk on the “knuckles” of the fore limbs, so to speak, the claws being folded beneath and slightly turned inward so that only the longer, outer curve of the claw touches the ground.

“The strong, prehensile tail of the smaller pangolins, *M. tetradactyla* and *M. tricuspis*, is provided on the lower surface of the tip with a rough skin pad of great tactile sensibility. By means of this the long tail can rapidly explore the neighborhood for possible means of progress. It can grasp firmly even the slightest projection, thus enabling these ant-eaters hanging upside down to plunder ants’ nests even more easily than when sitting on a branch, for at any moment they can pull themselves out of reach of the attacking ants. By forcing the head up over the breast and belly they can hook the claws into their tail as into any nearby branch. These pangolins readily carry out a three-quarter twist with the forward part of the body, or turn back at a right angle to the surface on which they are climbing, and descend any slender tree or branch head downward by quickly shifting the grip of the prehensile tail.

“The smaller species, when suddenly frightened while climbing, may let themselves drop from any height, landing uninjured in a rolled-up condition, the flexible scales, backed by the resilient, strong panniculus carnosus, evidently absorb the shock. In the arboreal *M. tetradactyla*, the long tail, with its sharp-ridged and pointed scales on the under side, is dexterously used in getting about and often serves as stabilizer. As soon as the claws of the hind feet have gained firm hold in the bark the security of the position is greatly increased thereby. The body can then be bent even backward and the free fore limbs are put into action to widen the breach in the ant galleries as fast as the sticky tongue can empty them.

"The two giant species are terrestrial and fossorial in habits but are rather scarce. They alone have succeeded in holding their own over most of the Ethiopian Region. The Vaal-Orange River in the south and Abyssinia in the north are probably the limits of distribution for *M. temmincki*, and *M. gigantea* is known from the West African Rain Forest and the adjoining wooded galleries. The latter is the only large species we met in the Belgian Congo; specimens were taken at Bafuka, Niangara, Poko, and Niapu, the largest attaining five feet in length, the tail being less than half of this.

"Near the last-named place various burrows from which Pygmies had secured giant pangolins, both dead and alive, showed that the tunnels attain a length of fifteen feet and reach about five feet below the surface. In these forests the ant-eaters seemed to prefer the higher-lying, sloping sites for their permanent homes, evidently a safeguard against being drowned in a country with such a heavy rainfall. The heap of excavated soil near the open entrance seldom offers a clue to the real size of the irregular, winding burrow, as the weather rapidly effaces the traces of diggings carried on from time to time. Pygmy boys, with one end of a strand of rattan fastened to the waist and the other held by friends waiting outside, entered the burrows without hesitation and stated that there is a more spacious resting place at the very end of the tunnel shared often by an adult pair and their young. These boys, armed with only a knife, merely fastened the rattan around the live pangolin, which they prodded from behind while their companions pulled it slowly out of the hole. These otherwise harmless beasts, when touched while rolled up, suddenly switch their tail sidewise with such force that, if one's hand is caught between the rough body scales and the tail, it is seriously mutilated by the shearing action. Natives of the Ituri and Uele districts claim that the giant pangolins stay for weeks at a time in their burrows, but it is certain that at times they leave them several nights in succession to feed. One trailed to its underground home after a heavy rain was caught in nooses eighteen days later when trying to escape.

"One might think that animals so large and muscular would need great quantities of food, but this is only relatively true, for their sluggish habits considerably reduce the demands for nourishment. An adult male from Niapu measured 1530 mm. from snout to tip of tail, the latter accounting for 690 mm. The capacity of their stomach is relatively small, hardly more than two quarts (about two liters). In an adult female the stomach measured antero-posteriorly only 170 mm. and dorso-ventrally 70 mm. Büttikofer's remark, cited by Dr. Bequaert (p. 319), about a

"The stomachs of *M. tetradactyla* and *M. tricuspis*, as shown long ago for the latter by Klinckowström,<sup>1</sup> are also divided into two parts. The cardiac section is lined with horny pavement epithelium, the mucous membrane showing folds with numerous, wavy crossbars. The pyloric section, with its soft, gland-bearing mucous membrane, is sharply set apart. Though the distribution of various glands differs in the two species, the muscular portion of the pyloric section in both is much like that of *M. gigantea*. A mass of fine grit also helps pulverize the ants during the extended milling process.

"The numerous forms of the aardvark, *Orycteropus afer* (Pallas) (Pl. XXIV, fig. 1), are distributed over most of the Ethiopian Region and are equally common in the Savannah and Western Forest Provinces. Their food consists of white ants (termites), and true ants are only incidentally taken, as they often inhabit termitaria. In external characteristics the aardvark resembles a pig, about six and one-half feet in total length, with a slender head, long ears, and a heavy, tapering tail about two and one-third feet long. Its very muscular limbs with their enormous claws denote fossorial abilities. The mouth is small, the snout slightly protruding and rather easily moved. The nostrils can be opened and shut at will and the edges are set with a dense border of short, stiff bristles turned outward in such fashion as to prevent insects from entering the nose. The long, extensile tongue is of relatively normal shape and the rather flat-crowned, peculiar cheek-teeth are capable of crushing food. The stomach lacks the highly specialized triturating organs of the Manidæ, though strong, muscular walls are present in the pyloric section. The absence of stone and grit also indicates that the gastric juices play the most important rôle in the disintegration and digestion of food and are sufficient to assimilate the soft-bodied termites but not the well-chitinized ants. Numerous parasitic worms are thus enabled to live in the stomach.

"Of the many aardvark burrows seen near Faradje, those with one entrance were scarcer than those with two, but three and even as many as eight openings to a single retreat were recorded. In one case the three entrances to a burrow were as much as fifty feet apart. Many of the tunnels, which reached about five feet below the surface, were deserted; those inhabited seemed to indicate that the aardvarks occupy them at intervals and occasionally dig holes merely for shelter. At times these inoffensive animals are driven out of their lodgings by warthogs and py-

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<sup>1</sup>1895, Zool. Jahrb. Abt. Anat. Ontog., VIII, p. 495.

or rather they mix it with their rice as a condiment; it has a pungent acetic taste and smell which they evidently like." The same ant is used by the natives of North Queensland mashed up in water, like lemon squash, and forms the basis of a pleasant acid drink appreciated even by many European palates.<sup>1</sup>

Moreover, it is generally known that certain American Indians eat ants, as well as other insects, freely. This is especially true of the tribes that are but little inclined toward agriculture, periods of famine with them being rather frequent, due to the absence of permanent vegetable staples.<sup>2</sup> In his delightful book, 'My first summer in the Sierra,' John Muir<sup>3</sup> tells how the Digger Indians of California are fond of the larvæ and even of the adults of the large jet-black, wood-boring ants (*Camponotus*), of which "they bite off and reject the head, and eat the tickly acid body with keen relish." In his account of the honey ants of North America, McCook<sup>4</sup> remarks that the uses to which the Mexicans and the Indians of the southwestern United States put the replete of *Myrmecocystus* are various. "That they eat it freely, and regard it as a delicate morsel is beyond doubt. Prof. Cope, when in New Mexico, had the ants offered to him upon a dish as a dainty relish. The Mexicans (Lœw) press the insects, and use the gathered honey at their meals. They also are said to prepare from it by fermentation an alcoholic liquor. Again they are said (Edwards) to apply the honey to bruised and swollen limbs, ascribing to it great healing properties."

One finds in the narratives of Barrère,<sup>5</sup> de Azara,<sup>6</sup> Humboldt,<sup>7</sup> Rengger,<sup>8</sup> Richard Schomburgk,<sup>9</sup> and other travelers<sup>10</sup> frequent allusions to the fondness of many South American tribes for the large males and

<sup>1</sup>Saville Kent, W., 1897. 'The naturalist in Australia,' (London), p. 253.

<sup>2</sup>Sec Skinner, A., 1910. 'The use of insects and other invertebrates as food by the North American Indians,' Journ. New York Ent. Soc., XVIII, pp. 264-267.

<sup>3</sup>Muir, J., 1916. 'My first summer in the Sierra,' (Boston and New York), p. 46.

<sup>4</sup>McCook, H. C., 1882. 'The honey ants of the Garden of the Gods and the Occident ants of the American plains,' (Philadelphia), p. 32.

<sup>5</sup>Barrère, P., 1741. 'Essai sur l'histoire naturelle de la France Équinoxiale,' (Paris), p. 198. Speaking of an ant of British Guiana which he calls *Formica major, rolans, edulis*, this traveller writes: "Cette fourmi est passagère et paraît en grand nombre au commencement des pluies. Les nègres et les créoles mangent le derrière de cet insecte, qui est une sorte de petit sac, de la grosseur à peu près d'un pois chiche, rempli d'une liqueur blanchâtre, miellée, qui ne paraît être autre chose que les œufs qu'il dépose dans ce temps-là."

<sup>6</sup>de Azara, F., 1809. 'Voyages dans l'Amérique Méridionale,' (Paris), p. 199: "Les habitants de la ville de Santa Fé, qui est de ces côtés-là, vont à la chasse de ces fourmis ailées: on en prend la partie postérieure, qui est fort grasse, on la fait frire, et on la mange en omelette; ou bien après les avoir fait frire, on les passe au sirop et on les mange comme des dragées." After quoting this passage, Gallardo (1916, An. Mus. Nac. Buenos Aires, XXVIII, p. 344) adds that the gaster of the females of *Atta serdens* (Linnaeus), called *tanajára*, is still eaten by the Brazilians.

<sup>7</sup>Humboldt, A. de, 1822. 'Voyage aux régions équinoxiales du Nouveau Continent, fait par A. de Humboldt et A. Bonpland,' (Paris), VII, pp. 443-444.

<sup>8</sup>Rengger, A., 1835. 'Reise nach Paraguay in den Jahren 1818 bis 1826 von Dr. J. R. Rengger,' (Aarau), p. 253.

<sup>9</sup>Schomburgk, Rich., 1848. 'Reisen in British Guiana,' (Leipzig), II, p. 112.

<sup>10</sup>Sec Orton, J., 1876. 'The Andes and the Amazon,' 3d Ed., (New York), p. 301; Spruce, Rich., 1908, 'Notes of a botanist on the Amazon and Andes,' (London), I, p. 484.

queens of the common leaf-cutters, *Atta cephalotes* (Linnæus) and *A. sexdens* (Linnæus). Schomburgk vividly describes how these ants are collected by the Indians of British Guiana, when, with the first rain-storms, large numbers of the winged, sexual forms leave their mound-shaped nests. Their heads are pulled off as soon as they are caught, and the swollen gaster, filled with fatty tissue, is roasted or otherwise cooked; "thus prepared, these insects are considered even daintier than the larva of *Calandra palmarum*."

PLATE XXIV

Fig. 1. *Orycteropus afer* (Pallas). Freshly killed female, at Faradje, March 6, 1911. Anterior portion of the body, showing the elongated snout and the heavily built fore limbs with their powerful digging claws.

Fig. 2. *Manis gigantea* Illiger. Freshly killed female, at Niangara, April 26, 1913. Anterior view, showing the elongate snout and lengthened, heavy claws of the fore limbs.





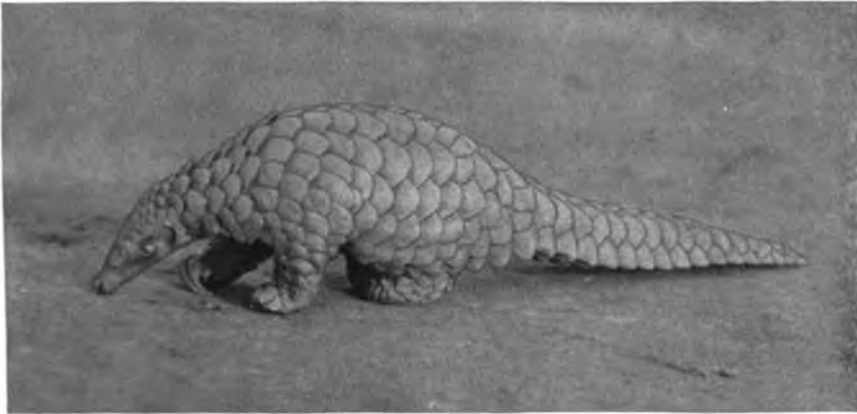
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The leaf-cutting ants of the tribe Attini, so abundant in tropical and subtropical America, are decidedly destructive to the vegetation and are rightly considered one of the worst pests to South American agriculture. Accounts of their depredations are found in practically all narratives of South American travellers. Though they attack many of the native herbs, shrubs, and trees, they often show a predilection for cultivated plants. It is no uncommon thing to find the saúvas, *Atta cephalotes* (Linnæus), so numerous in certain spots that the planters are forced to abandon their fields. Speaking of the ants in the Brazilian coffee districts, Van Delden (1885, pp. 297-298) writes: "The enemy most dreaded in the fazendas (plantations) is indubitably the saúva, or tana-jura, a dark-brown ant, two centimeters long, which undermines the ground by digging extensive passages and dens in all directions. It attacks all sorts of trees, the coffee-shrub among others, but has a decided preference for the orange and citron trees in the coffee gardens." H. W. Bates (1863) and others have noted that these ants often become troublesome to the inhabitants because of their habit of plundering the stores of provisions in houses at night.

The Attini are not represented in the Old World tropics, but possibly ants of other groups have developed similar habits there, though on a smaller scale. G. Aulmann (1912, p. 156) and Moorstatt (1914) mention that a leaf-cutting ant was observed in German East Africa at times causing considerable damage to cotton plants. The specific identity of this ant has not been ascertained, but it probably belonged to the genus *Messor*, which is known to collect pieces of grass in addition to seeds and grain (see Sjöstedt's observation quoted below, p. 359). King (1911) also notes that *Messor barbarus* (Linnæus), at Khartum, damages garden plants by biting off and carrying away the leaves, and adds that in cotton fields the sites of their nests are marked by bare patches devoid of vegetation. What use these ants make of the vegetable matter thus carried into their nests has not been investigated.

There are a few other cases on record of ants directly destroying living parts of plants. It is generally known that certain ants will injure buds and fruit in order to feed on the exuding sap (see Müller-Thurgau, 1892, pp. 134-135). Forel (1885, p. 338) mentions instances of *Tetramorium cæspitum* (Linnæus) attacking young roots of healthy sugar-beets at Vaux, Switzerland, many of the plants dying from the injuries received. J. Pérez (1906, pp. xxxii-xxxiv) records the havoc played by the same ant on the tubers of potato, near Bordeaux, more or less deep cavities being excavated and many young plants killed; *T. cæspitum*

was also found burrowing superficial galleries in the stems of living potato plants and attacking the roots of young cabbage and carrot.<sup>1</sup> In North America, *Solenopsis geminata* (Fabricius) and *S. molesta* (Say) often do injury to the soft parts of planted seeds, and the former also to strawberries (Webster, 1890) and other fruit. *S. molesta* has proved very injurious in gardens and fields; the chief damage is done to seeds of sorghum and corn, which are hollowed out undoubtedly for the purpose of extracting the oils (McColloch and Hayes, 1916; Hayes, 1920). According to Green (1900a) and G. R. Dutt (1912, p. 247), the Indian *Dorylus orientalis* Westwood is mainly or exclusively herbivorous, feeding on the bark of trees and the healthy tubers of plants, a habit the more remarkable since the majority of Dorylinæ are highly carnivorous. In Cameroon, certain ants have been seen attacking the fruits of cacao-trees: *Camponotus maculatus* subspecies *brutus* (Forel) gnaws the base of fruit-stalks where they are inserted into the trunk, licking up the sap at the wound, causing the fruits to drop off or dry; *Crematogaster africana* variety *winkleri* (Forel) gnaws away the skin of the cacao-fruit, often almost completely; while *Camponotus acrapimensis* Mayr and *Ecophylla longinoda* (Latreille) are accused of the same evil, though they cause but little damage (H. Winkler, 1905, pp. 129-137).

The greatest harm to the vegetation is undoubtedly done indirectly, both in tropical and temperate regions, by a host of species of ants that have a pronounced fondness for pasturing and guarding plant lice, scale insects, tree-hoppers, and other plant bugs on roots, stems, and foliage; all these Hemiptera suck the juices of plants, and their protection by the ants must, therefore, be regarded as pernicious. The "milking" habit among ants seems to be of very frequent occurrence, evidently because it offers so many advantages over direct feeding on plant-juices. Not only is the food supply much more abundant at any one time and within easier reach, but, in addition, the plant saps undergo chemical changes in the digestive tract of the Hemiptera, whose anal secretion, on which the ants feed, therefore contains a great amount of invert-sugar, instead of the much diluted cane-sugar of the plant. Many of the aphids attended by ants have undergone adaptive modifications of structure and behavior which show that their relations with ants have become of a mutualistic nature, and it is probable that the same will be found true for some of the ant-attended coccids and membracids of the tropics.

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<sup>1</sup>This habit of *Tetramorium cæspitum* in attacking subterranean parts of plants was known to Linnaeus, since he adds to the original description of this ant ("Syst. Nat.," Ed. 10, 1, 1758, p. 581): "Habitat in Europæ tubercibus." It is rather surprising that injuries by this ant have been so little noticed in later times. Concerning ants noxious in gardens, see also F. Heim (1894), Andersson (1901), and Cooley (1903).

Indeed, the association between phytophagous Hemiptera and ants offers a typical illustration of symbiosis in the strict sense, advantageous to both parties. The benefit that accrues to the ants has been explained above and needs no further comment; that derived by the Hemiptera, however, is of a more complex nature. It is obvious that the ants protect the plant bugs by driving away coccinellid beetles, ichneumon flies, and other enemies. In the case of aphids and coccids the ants frequently build tents or cowsheds over these insects, which thus continue to suck the juices of the plant while being "milked" by the ants and are, at the same time, protected from their enemies, from alien ants, and intemperies, and prevented from escaping to other plants.

The tent-building habit was discovered by P. Huber (1810, pp. 198-201) for *Lasius niger* (Linnæus) in Europe, and Forel (1874, pp. 204-205 and 420-422) gives an interesting account of it in his classical 'Ants of Switzerland.' *Lasius niger* has similar habits in North America (Wheeler, 1911b) and Japan (Stopes and Hewitt, 1909, pp. 1-6). This ant builds its tents of detritus or wood-fibres; while, according to Forel, certain species of *Myrmica* enclose their aphids in earthen cells, which communicate with the ground nest by means of covered galleries. Wheeler (*loc. cit.*) has described in detail the tent-building of the North American *Crematogaster lineolata* (Say) and I have found that several African members of this genus which attend coccids have similar habits. Certain North American species of *Lasius* (*L. flavus*, *L. niger*, and the species of the subgenus *Acanthomyops*) which live to a very large extent or exclusively on the excrement of root-aphids and coccids, remain throughout the year the constant companions of the lice, even hoarding in their nests during winter the eggs or the wingless, agamic form of the aphids and the fertile females of the scale insects. Forbes (1896), Webster (1907), and others have shown that the common North American *Lasius niger* variety *americanus* Emery guards the eggs of the corn root aphid (*Aphis maidi-radici* Forbes) throughout the winter, shifting them about, as it does its own young, to accommodate them to changes of weather and moisture. In spring, the young lice, on hatching from these eggs, are conveyed by the ants during fair weather to the roots of various weeds, being taken back to the burrows in bad weather or on cold nights. After the corn plants have started to grow, the young root lice, all of which belong to the wingless, agamic form, are transferred from the weeds to the roots of young corn, where they are tended throughout the spring and summer. It would thus appear that, without the aid of the little brown ant, this aphid is unable to reach the corn plants.

He also notes that certain common species which, in the nymphs at least, appear to exude the characteristic anal fluid when disturbed, nevertheless are not attractive to ants. He found the following species of Membracidae attended by ants in the vicinity of Ithaca, New York: *Thelia bimaculata* (Fabricius), *Telamona ampelopsidis* (Harris), *T. unicolor* Fitch, *Cyrtolobus vau* (Say), *Atymna castaneæ* (Fitch), *Ophiderma pubescens* (Emmons), *Vanduzeeia arquata* (Say), *Entylia bactriana* Germar, and *Publilia concava* (Say).

The following ants were actually observed by Funkhouser taking the secretion from the membracids: *Formica truncicola* subspecies *obscuriventris* (Mayr), *Formica exsectoides* Forel, *Camponotus pennsylvanicus* (DeGeer), *Crematogaster lineolata* (Say), and *Prenolepis imparis* (Say). All these ants seemed to make no distinction between the various species of tree-hoppers listed above and the mutual behavior of these insects was much the same in all the cases studied: "The ants stroke their charges with their antennæ, whereupon the membracids give off from the anal tube a liquid that issues in bubbles in considerable quantity. The anal tube of the membracid is capable of great evagination especially in the nymphs, in which it is long and cylindrical and usually tipped with a fringe of fine hairs. The honeydew is eagerly taken from the end of this tube by the ants. In many species the adults as well as the nymphs are sought, and the ants seem to be as attentive to one as to the other but the adults have not been observed to excrete the liquid to the same extent as the nymphs." (Funkhouser, 1917, p. 403.) The liquid sought by the ants "is colorless and transparent, rather heavy and somewhat sticky. When first exuded it is inclined to be frothy, due no doubt to bubbles of air which emerge with it, but it quickly clears on settling. It is practically tasteless even in comparatively large quantities, and many attempts to distinguish a sweet taste have proved unsuccessful. The term *honeydew*, therefore, commonly applied to the fluid, is hardly a descriptive one. It is very likely, of course, that the liquid may contain sugars not detected by the human tongue, and this would seem to be indicated by the fact that fermentation appears to begin if the substance is left exposed. No chemical analysis of honeydew has been made." (*Op. cit.*, p. 404.)

Miss Branch (1913, pp. 84-85) states that young *Entylia sinuata* seemed unable to molt successfully without the presence of ants. This fact led her to believe that the ants are necessary factors in the life of an individual membracid. Funkhouser's experiments, however, gave no support to this theory. Tree-hoppers of many species were reared

in the field and in the insectary, with and without ants, and no difference was noted in the length of the instars or success of the molting process.

Kornhauser (1919, p. 546) gives the following account of the manner in which *Thelia bimaculata* (Fabricius) is attended by ants. This membracid feeds on the sap of the common North American locust tree, *Robinia Pseudo-acacia* Linnæus. It deposits its eggs in slits in the bark, where they remain during the winter, hatching in early June. The first, second, and third instars occur on the branches, constantly attended by ants:

In my principal collecting fields [at Cold Spring Harbor, New York], *Formica truncicola* Nylander subspecies *obscuriventris* and *Cremastogaster lineolata* Say were the chief ants associated with *Thelia*. When tapped by the antennæ of the ants, the *Thelia* nymph or adult exudes from the anal tube a drop of clear fluid which is taken by the ant with great alacrity. Toward the middle of June, the ants build collars about the bases of the locust trees, and inside these collars in the cracks of the bark are to be found hundreds of *Thelia* nymphs of third to fifth instar, quietly feeding and undisturbed by the numerous ants in attendance. In this moist situation, protected from many of their enemies, the nymphs thrive. *Formica* builds the protecting collar of leaves, twigs, and bits of wood; *Cremastogaster* builds of sand grains cemented together. When one breaks the collar, many ants swarm out and attack the intruder, *Formica* biting one's fingers ferociously, while others grab the *Thelias* and drag them into underground passages. These pugnacious ants seem to have complete mastery of the *Thelia* nymphs.

Membracidæ are sometimes carried by ants into their formicaries (Enslin, 1911, pp. 19-21; W. M. Mann, 1915, p. 162), but they usually die soon, probably due to lack of food.<sup>1</sup>

Lamborn (1914) has described in detail several cases of trophobiosis between ants and coccids, membracids, jassids, and psyllids in Southern Nigeria. Regarding *Leptocentrus altifrons* Walker, a tree-hopper which is invariably ant-attended in its mature and larval stages, he writes as follows: "The solicitude of ants for the larvæ has a very definite object, for they are extremely partial to the fluid excreted at the anal extremity, and I remember seeing a *Camponotus akwapimensis* variety *poultoni* with the caudal whip of a membracid larva actually in its mouth." (Lamborn, 1914, p. 495.) I have on several occasions, in the Belgian Congo, collected ants which were in the act of attending tree-hoppers: so, for instance, in April 1912, at Elisabethville, Katanga, a number of workers of the common *Pheidole megacephala* subspecies *punctulata* (Mayr) were

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<sup>1</sup>Additional information concerning the relations between Membracidæ and ants is given by Belt (1874), Mrs. Rice (1893), Green (1900c), Froggatt (1902, p. 717), Baer (1903), Buckton (1903, p. 262), Poulton (in Buckton, 1903), Distant (1908, p. 209), Enslin (1911), Miss Branch (1913), Kershaw (1913), Lamborn (1914), and others.



busily engaged in licking the sweet excretions of some of these hemipterous insects feeding on a bush; again, at Welgelegen, Katanga, *Myrmecaria eumenoides* subspecies *opaciventris* variety *congolensis* (Forel) was found attending membracids fixed on the calyx of a malvaceous plant (Bequaert, 1913, pp. 427 and 428). Bell-Marley at Durban, Natal, observed that the common South African tree-hopper, *Ozyrhachis tarandus* (Fabricius), attracts great numbers of "small red ants." (Distant, 1908, p. 209.)

The nursing of scale insects by ants has repeatedly been noticed by Cockerell, Newstead, King, and others.<sup>1</sup> A rather interesting phase is offered in the case of various ants which keep coccids inside the swellings of myrmecophytes. Zimmermann found *Lecanium tenebricophilum* Green at Buitenzorg, Java, together with ants in living branches of *Erythrina lithosperma* Blume (Green, 1904, p. 204). In southern Europe, *Crematogaster scutellaris* (Olivier) and *Camponotus pubescens* (Mayr) often become harmful to olive trees by the care they bestow upon scale insects (Peragallo, 1882). Keuchenius (1914a and b) holds the view that *Ecophylla smaragdina* is very noxious to coffee plantations through its habit of keeping and protecting in its nests the green coffee scale, *Lecanium viride*, one of the most serious pests to the coffee tree. Gowdey (1917) also mentions that the root form of *Pseudococcus citri*, a parasite of coffee, orange, lemon, and cacao in Uganda, is attended by the ant *Pseudolasius gowdeyi* Wheeler.

Most of the wood-boring ants either accommodate themselves to pre-existent galleries made by other insects or attack dead wood only. Occasionally they find their way into houses. Forel (1874) and R. Brun (1913) have described cases in which populous colonies of the European *Camponotus ligniperdus* and *C. herculeanus* had excavated the beams, window-sills, and other wooden parts of buildings. Certain carpenter ants of temperate regions (*Camponotus ligniperdus*, *C. herculeanus*, *C. pubescens*, and others) extend their burrows into healthy wood (Forel, 1874); they may thus become very destructive in forests, the more so since they attract woodpeckers, which bore large access-holes through the perfectly healthy outside layers of the tree in order to feed on the carpenter ants and their brood. S. A. Graham (1918) describes how carpenter ants of an unidentified species are responsible for great damage to stand-

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<sup>1</sup>In India the lac-producing coccid, or lac insect, *Tachardia lacca* (Kerr), is frequently attended by ants, *Crematogaster subnuda* (Mayr) and *Camponotus compressus* (Fabricius), which may become a source of regular annoyance to the lac grower. In their eagerness to obtain "honeydew" the workers often nip off the white filaments, the two anterior of which are connected with the respiratory apparatus of the lac insect, the coccid being killed consequently (G. R. Dutt, 1912).

ing white cedar in Minnesota, at least twenty per cent of the trees cut showing ant injury to the stump. In this case, so far as observed, the ant never attacks a sound tree, but always gains entrance through a wound or decayed spot. When a colony has been established in a tree, the ants usually work well above the rotten area into the sound heartwood, honey-combing the tree with longitudinal galleries until there is often only a thin outer shell of solid wood. From the main nest they cut openings to the outside, frequently following a knot, through which the sawdust can be cast and through which the inhabitants may pass to and fro. Ants which make their galleries in the bark (such as many species of *Leptothorax*) usually do not burrow beyond the external dead layers and occasion little or no damage, except in cases where the bark itself is of economic value: *Camponotus herculeanus vagus* (Scopoli) and *Crematogaster scutellaris* (Olivier) are credited with destroying the bark of cork-oaks in southern Europe and North Africa (Maceira, 1904; Emery, 1908; Seurat, 1901; A. Krausse, 1913 and 1919).

Harvesting ants have often been accused of depredations in cereal fields, but these charges are apparently much exaggerated. Emery (1891, pp. 176-177), it is true, has observed in Italy that species of *Messor* actively engage in carrying off grain during the harvest. It does not seem, however, that the damage thus done could be very serious, since harvester ants collect mainly seeds of weeds and wild grasses. Yet in certain regions of North Africa, where colonies of *Messor* are very numerous, the grain these ants store away may amount to an appreciable portion of the harvest. Ducellier (1912) estimates that, in Algeria, *Messor barbarus* collects 50 to 100 liters of wheat from each hectare. J. Pérez (1903, pp. xxxiv-xxxv) has recorded cases in which *Messor barbarus* stole freshly sown carrot-seeds and also the ripe seeds of coriander in a vegetable garden near Bordeaux. Similarly, Koningsberger (1908, p. 99), in Java, blames *Plagiolepis longipes* (Jerdon) with stealing planted seeds of tobacco.

A few species of ants are commonly found in houses, boats, and ships; they are spread by commerce to considerable distances, and rapidly become cosmopolitan.<sup>1</sup> Such domestic species in the Belgian Congo include, among others, *Monomorium pharaonis* (Linnæus), *Tetramorium simillimum* (F. Smith), and especially the many forms of *Pheidole megacephala* (Fabricius); the last-named is the famous house ant of Madeira (O. Heer, 1852 and 1856), which has now established it-

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<sup>1</sup>Donisthorpe (1915, pp. 334-350) has given an interesting account of the exotic ants which have been introduced into Britain. His list includes fifty-one species, but only a small number of these have established themselves there; they are most commonly found in hothouses.

of ripe plantains, and rooted out cockroaches, spiders, and other suchlike denizens of a forest hut. So long as they were left unmolested, they avoided the human inhabitants; but when I attempted to brush them away they fell upon me by hundreds and bit and stung fiercely. I asked the Indian's wife if we had not better turn out awhile and leave them to their diversions. "Do they annoy you?" said she. "Why, you see it is impossible for one to work with the ants running over everything," replied I. Whereupon she filled a calabash with cold water, and going to the corner of the hut where the ants still continued to stream in, she devoutly crossed herself, muttered some invocation or exorcism, and sprinkled the water gently over them. Then walking quietly round and round the hut, she continued her aspersion on the marauders, and thereby literally so damped their ardour that they began to beat a retreat, and in ten minutes not an ant was to be seen.

Some years afterwards I was residing in a farm-house on the river Daule, near Guayaquil, when I witnessed a similar invasion. The house was large, of two stories, and built chiefly of bamboo-cane—the walls being merely an outer and an inner layer of cane, without plaster inside or out, so that they harboured vast numbers of cockroaches, scorpions, rats, mice, bats, and even snakes, although the latter abode chiefly in the roof. Notwithstanding the size of the house, every room was speedily filled with the ants. The good lady hastened to fasten up her fresh meat, fish, sugar, etc., in safes inaccessible even to the ants; and I was prompt to impart my experience of the efficacy of baptism by water in ridding a house of such pests. "Oh," said she laughingly, "we know all that; but let them first have time to clear the house of vermin; for if even a rat or a snake be caught napping, they will soon pick his bones." They had been in the house but a very little while when we heard a great commotion inside the walls, chiefly of mice careering madly about and uttering terrified squeals; and the ants were allowed to remain thus, and hunt over the house at will, for three days and nights, when, having exhausted their legitimate game, they began to be troublesome in the kitchen and on the dinner-table. "Now," said Doña Juanita, "is the time for the water cure"; and she set her maids to sprinkle water over the visitors, who at once took the hint, gathered up their scattered squadrons, reformed in column, and resumed their march. Whenever their inquisitions became troublesome to myself during the three days, I took the liberty to scatter a few suggestive drops among them, and it always sufficed to make them turn aside; but any attempt at a forcible ejection they were sure to resent with tooth and tail; and their bite and sting were rather formidable, for they were large and lusty ants. For weeks afterwards the squeaking of a mouse and the whirring of a cockroach were sounds unheard in that house.

In their general economy and behavior, the African Dorylini differ but little from the Ecitonini, as can be seen from various descriptions of their marauding columns quoted in Prof. Wheeler's Report of the Congo ants (pp. 46-49). It may, however, be noted that their armies are apparently much more populous than those of the ecitons and also more troublesome when invading human dwellings. A rather successful method of keeping them away from inhabited places consists in making a barrage of hot ashes across their highways.

Whoever has seen the almost fabulous numbers of individuals in the ant armies of the tropics can have no doubts as to the benefit they afford the vegetation by destroying caterpillars and other noxious insects. Since it is evidently the general impression that driver ants indiscriminately destroy all "pests" within their reach, I should like to call attention to some curious experiments with Dorylini made by Swynnerton (1916) in South East Rhodesia. His observations indicate how careful one must be in applying general formulæ to the interrelations of living beings. After giving an impressive account of the columns of driver ants (*Dorylus nigricans* variety *molestus* Gerstæcker) which "seize on any potential prey, from a minute beetle to a cow, that is so foolhardy as to approach them," Swynnerton describes with much detail his experiments to ascertain whether any non-flying insects are safe from these marauders. The unexpected conclusion was reached that these ants show strong preferences "readily taking some animals when they would not take others at all, and when failing in their attacks on yet others." Among the insects left unharmed by the ants of one of the columns were certain beetles (*Mylabris*, *Epilachna*) and caterpillars (*Amauris*, *Acræa*). "A small sciarid fly (*Apelmocreagis thoracica* Macq.) had been settled on the ground right amongst the ants, neither taking any notice of them nor drawing an attack. I captured and disabled it and placed it back amongst them, but tho numbers, I might say hundreds, inspected it, often passing their antennæ over it, all moved on and no attack whatsoever was made." The eggs and very young larvæ of most Rhopalocera experimented with were found to be quite unacceptable to driver ants.<sup>1</sup>

Swynnerton's experiments, however, do not materially detract from the total of the highly beneficial activity of the driver ants which, indeed, are a blessing to all tropical cultures. As Vosseler (1905, p. 298) states, "in a given time they destroy more insect vermin than all other insect-eating animals (birds, lizards, turtles, frogs, spiders, etc.) together, since they clean out to a certain depth the entire field invaded by them." The invasions of these Huns of the insect-world should be welcomed by all agriculturists in tropical regions, even if their pugnacious character and great numbers make them troublesome at times to human beings and domestic animals.

In Europe, foresters generally believe, apparently with good reason, that trees which attract ants or are surrounded by ant nests are less

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<sup>1</sup>Messrs. Lang and Chapin inform me that, according to their observations, driver ants are unable to take hold of the larvæ of *Dermestes*, evidently due to the abundant coating of hairs and also to the manner in which these larvæ can bend their body. They frequently witnessed the unsuccessful attempts of one or even several driver ants to grasp a *Dermestes* larva.

subject to the attacks of caterpillars and other noxious insects.<sup>1</sup> The very populous colonies of certain species of *Formica* prove most valuable in this respect. Forel has calculated that a large colony of the European *Formica rufa* daily destroys at least 100,000 insects. Certain plants possess various organs, such as nectaries and myrmecodomatia, which are often utilized by the ants. Whether these structures are intended merely to allure the ants which would thus form a body-guard to the plant, as Delpino and other botanists have believed, is a much discussed problem and will be considered more in detail elsewhere.

The protection afforded to the vegetation by many ants is so evident that it has been employed by some of the most progressive agricultural people, such as the Chinese and the Malays.<sup>2</sup> In Southern China and Indo-China it is an ancient custom to place the nests of certain insectivorous ants in the trees; in this way orange and mandarine trees are said to be kept free from caterpillars (McCook, 1882). Such use was recorded as early as 1640, and Emery identified the ant in question as *Æcophylla smaragdina*, the common silk ant or red tree-ant of the Old World tropics.<sup>3</sup> The Javanese of certain districts use ant nests, again probably those of *Æcophylla*, to protect their mango-trees from fruit-boring weevils, *Cryptorhynchus mangiferæ* (Fabricius), and, in order to give the ants a broader field for their activities, the various trees of a plantation are connected by means of bamboos (Vorderman, 1895).<sup>4</sup> The benefit derived from the presence of the predaceous *Æcophylla* is, however, partly offset by the fact that these ants usually keep coccids and peculiar caterpillars within their own nests, as shown by many observers (F. P. Dodd, 1902; Maxwell-Lefroy and Howlett, 1909, pp. 230-231; G. R. Dutt, 1912; Keuchenius, 1914a and 1914b).

Various attempts by agriculturists to make a more direct use of protection by ants have not thus far proved very successful. Perhaps many of these experiments have failed from lack of proper knowledge of

<sup>1</sup>Ratzeburg, 1844, III, p. 42; 1866, I, p. 143; 1868, II, p. 429. Judeich and Nitsche, 1895, I, n. 717.

<sup>2</sup>Popenoe (1921) has recently called attention to the use of certain unidentified ants by the Arabs of Yemen to combat insects noxious to date-palms. He quotes P. E. Botta [1841, 'Relation d'un voyage dans l'Yémen,' (Paris), p. 155] who says he verified the fact and who credits Forskål with having first observed it about 1764. In Forskål's posthumous work, however, edited by Niebuhr [1773, 'Descriptiones animalium quæ in itinere orientali observavit,' (Copenhagen), p. 83], under the name *Formica animosa* the following rather obscure statement appears: "Welcome to gardeners because of the useful animosity with which it pursues the 'Dharr' ants perniciously infesting *Phoenix dactylifer*. To this war it is led by heaping up 'Heml' (camel excrement) as its imperial reward." I have been unable to find additional information on this subject in Niebuhr's account of his travels with Forskål in Arabia fin Pinkerton, J., 1911. A general collection of the best and most interesting voyages and travels' (London), X, pp. 1-221].

<sup>3</sup>Emery, C., 1889, p. 15 of separate. Emery received his specimens from Bangkok. Dr. C. W. Howard recently sent Prof. Wheeler ants used for similar purposes by the Chinese near Canton; they also belong to *Æcophylla smaragdina*.

<sup>4</sup>In the Congo the silk nests of *Æcophylla* are very frequently found in fruit-trees and in coffee and rubber plantations.

ant behavior. The Guatemalan kelep-ant, *Ectatomma tuberculatum* (Olivier), introduced some years ago into Texas for the purpose of exterminating the cotton boll weevil (*Anthonomus grandis* Boheman), apparently has not in any way helped control this ill-reputed pest.<sup>1</sup> *Solenopsis geminata* (Fabricius), the "fire-ant" of the warmer regions of the world, apparently is a much more powerful enemy of the boll weevil (W. D. Hunter, 1907; W. E. Hinds, 1907). In certain parts of Brazil, the "formigas cuyabanas," *Prenolepis fulva* Mayr,<sup>2</sup> are considered very effective in fighting the leaf-cutting ants ("saúvas" or Attini), though there seems to be but little foundation for this belief (H. v. Ihering, 1905 and 1917; A. da Costa Lima, 1916). F. v. Faber (1909) claims that in Java "a black ant, 3 to 4 mm. long," but not otherwise identified, successfully controls the bugs of the genus *Helopeltis* in cacao plantations. Perhaps this is *Dolichoderus bituberculatus* Mayr, an ant which, according to de Lange (1910) and Moorstatt (1912), is used in Java to combat these same *Helopeltis* of cacao.

According to Rothney (1889, p. 355), two ants, *Monomorium salomonis* (Linnæus) and *Solenopsis geminata* (Fabricius), are deliberately introduced into warehouses in Madras to check the depredations of white ants. "This practice is not uncommon in Northern India and the natives of India are familiar with the kind of ant which should be brought in" (Maxwell-Lefroy and Howlett, 1909, p. 226).

Another service of ants which should not be overlooked by ecologists is their ceaseless activity in excavating, transporting soil particles, and hastening the decay of organic substances. Their multiple burrows, extending in all directions underground, bring about a very thorough ventilation of the soil and an easy and even distribution of moisture. They comminute and bring to the surface a large quantity of soil and subsoil, often from a considerable depth, and leave it exposed to the weathering action of the meteoric agents. Furthermore, they introduce into their subterranean excavations much organic matter which thus more readily decays and in turn yields acids that act upon the soil.

Owing to the hidden habits and minute size of most ants, their importance as geologic agents may be easily lost sight of, especially in temperate regions. In tropical and subtropical countries the result of their toil is often much more apparent, though it rarely approximates

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<sup>1</sup>See various papers by O. F. Cook (1904, 1905, and 1906) and their criticism by Wm. M. Wheeler (1904, 1905a, and 1906). A list of ants known to prey on the cotton boll weevil is given by W. Pierce (1912, pp. 69-73).

<sup>2</sup>Also called "*formigas cearenses*" or "*formigas paraguayas*"; various other species of ants are occasionally taken for "*cuyabanas*."

that produced by termites. Only certain species of *Formica* in temperate Europe and North America construct mound or hill nests of sufficient size or number to attract much attention; with them, the accumulations consist of a small part of excavated soil, most of the material being gathered in the vicinity by the workers. The conical mounds of the North American *Formica exsectoides* sometimes reach a meter in height and two to three meters in diameter at the base, while those of the European *F. rufa* often are much larger (over two meters high and eight to ten meters in diameter).

The crater-shaped or conical mounds of certain North American harvesting ants are partly made of earth brought from underground excavations. Those of *Pogonomyrmex barbatus* subspecies *molefaciens* may attain one to two meters in diameter and fifty centimeters in height, while in the common *P. occidentalis* they are but little smaller and often form extensive colonies (Headlee and Dean, 1908; Wheeler, 1910). *Ischnomyrmex cockerelli*, of the southwestern United States, surrounds the entrance to its nests with huge craters, from sixty centimeters to two meters in diameter and from 0.2 to 0.5 centimeters in height, built of coarse desert soil intermingled with pebbles sometimes two centimeters in diameter (Wheeler, 1910, p. 281).

The volume of material moved by some of the leaf-cutting ants (Attini) of tropical America is much greater than in any of the cases mentioned above. H. v. Ihering (1882), Gounelle (1896), and Branner (1896, 1900, 1910, 1912) have called attention to the importance of these insects as geologic factors. In certain parts of Brazil the ant hills of the saúva (*Atta* species, probably *cephalotes*) are so large and numerous that they become a remarkable feature of the landscape. At one place in the Rio Utinga region, in the interior of Bahia, where the forest had been cleared away so that the mounds were visible, Branner counted fifty-three of them within an area of 10,000 square meters. Their bases covered close to one-fifth of the total space under consideration and their volume was estimated at 2225 cubic meters. The cubical contents of the mounds, if evenly distributed over the entire 10,000 square meters, would have been 22.25 centimeters thick. In this case, the height of the ant hills varied from 1.2 to 4.5 meters, with an average of 2.5 meters. These were not the largest seen, for on the upper drainage of the Rio Utinga, Branner measured mounds of leaf-cutters five meters high and sixteen or seventeen meters in diameter at the base, each containing about 340 cubic meters of earth. The illustrations in Branner's latest papers (1910, 1912) remind one of strikingly similar landscapes with scattered termite

hills in many parts of tropical Africa (see Pl. XV). A considerable amount of living vegetable matter is carried by the leaf-cutting ants into the inner chambers of their nests, where it is cut up and worked in their mushroom-beds; vegetable substance is thus rapidly transformed into mineral matter and rendered available to new plant-growth.

True mound- or hill-building ants are not found in tropical Africa; many species, however, build small crater-shaped accumulations of earth at the entrance to their nest. Those of the seed-storing *Messor* are often very conspicuous in the arid parts of the continent; their craters sometimes measure a meter or more across and the earthen walls may reach twenty-five centimeters in height (Passarge, 1904, pp. 290-295; see also the photograph of a nest of *Messor* species taken by Mr. Lang on the Athi Plains, British East Africa, Pl. XXVI, fig. 1). The driver ants, when establishing their temporary abodes, often excavate considerable quantities of soil, as is shown by Mr. H. Lang's photograph of a nesting site of *Dorylus* (*Anomma*) *wilverthi* Emery (Pl. II).

The following chapters deal with many other activities by which ants come into direct contact with plants. They will further emphasize the importance of ants in the economy of nature, in which they must undoubtedly be regarded as the dominant insects (Wheeler). From the narrow point of view of human interests, by far the greatest number of ants are indifferent or negligible organisms, either because of their small size and scarcity of their colonies, or because they avoid the vicinity of man's activities. With regard to the comparatively few species that are of economic importance, "a consideration of all the facts forces us to admit, with Forel, that as a group ants are eminently beneficial and that for this reason many species deserve our protection. Some of our species, however, are certainly noxious, and these offer strong resistance to all measures for their extermination, owing to the tenacity with which they cling to their nesting sites, their enormous fertility and the restriction of the reproductive functions to one or a few queens that are able to resist destruction by living in the inaccessible penetralia of their nests" (Wheeler, 1910, p. 8).

#### Ants as Agents in the Pollination of Flowers

In Knuth's celebrated 'Handbook of Flower Pollination'<sup>1</sup> ants are dismissed with the brief statement that they "frequently occur as ravagers of flowers, for which reason Lœw has termed them *dystropous*."

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<sup>1</sup>English translation. (Oxford), 1906, I, p. 168.



Perhaps even in temperate zones this is not entirely true, and it is difficult to believe that, in Umbelliferæ and other flower associations with freely exposed nectar on which ants are most commonly met with, these insects are not at least effective agents of geitonogamy. In the tropics, moreover, ants are so abundant everywhere that very likely they are of even greater importance as carriers of pollen, the more so since many trees and shrubs of tropical forests bear flowers on their old wood on the very highways of the ants, so to speak. One might even venture to suppose that cauliflory is mainly of use to the plant in that the flowers are thus placed within easy reach of pollinating ants. Indeed, the question as to the origin and significance of cauliflory in tropical trees and shrubs has not thus far been satisfactorily answered. Wallace<sup>1</sup> regards it as an adaptation to pollination by butterflies, which, he says, keep to the undergrowth of the forest and rarely ascend to the crown of the trees. Haberlandt (1893, p. 132) argues that many of the caulinary flowers are dull colored and also otherwise but little adapted to Lepidoptera, and, from my personal experience in the Ituri forest, I must agree with him. I cannot recall a single instance in which I saw caulinary flowers visited by butterflies and I greatly doubt whether Wallace's explanation was founded on actual observation. In Haberlandt's opinion, cauliflory is merely the result of a tendency to a more complete division of labor, resulting in a sharper differentiation between the assimilating and the reproductive parts of the plant. Evidently A. F. W. Schimper (1903, p. 338) is also satisfied with a mere physiological solution when he supposes that the frequent occurrence of cauliflory among tropical trees is due to a weaker development or slighter degree of roughness of the bark.

The foregoing remarks will suffice to show that the relations between ants and cauliflorous plants are worthy of further attention. In his biological studies of tropical flowers, H. Winkler (1906) enumerates a number of plants in Cameroon which he asserts are pollinated by ants, though he does not enter into details nor describe any adaptations of the flowers to this peculiar mode of fecundation. It is interesting to note that most of the species thus mentioned by Winkler are cauliflorous trees or shrubs. The cacao tree (*Theobroma Cacao*) affords a classical illustration of cauliflory, its flowers being borne on both stem and main branches; in this case G. A. Jones (1912), from his experiments carried on in Dominica, West Indies, has reached the conclusion that ants are in all probability the chief agents of pollination.

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<sup>1</sup>1891, 'Natural selection and tropical nature,' (London). p. 244.

H. N. Ridley (1910, pp. 461-462) has made some interesting observations in Singapore on certain species of the anonaceous genus *Goniothalamus*, notably *G. Ridleyi* King, which produce their flowers in masses at the base of the tree.<sup>1</sup>

The flowers are of large size and dull reddish in color. They are almost invariably covered by a nest of very small black ants, which pile up powdery soil all over them, so that they are often quite concealed. It would, I think, be difficult for a bee or other insect to get to the honey of these flowers through the nest, yet I think no species of the genus fruits so regularly or heavily as does *Goniothalamus Ridleyi*. That the ants are distinctly attracted by the flowers, is clear from the fact that the flowers from the trunk which are too high up for the ants to cover with the nest are generally densely covered by a swarm of the insects. Owing, however, to the minuteness of the ants and the difficulty of making observations in such a mass of them, I have been unable to definitely decide whether the ants do actually fertilize the flowers by conveying the pollen from one to the other, but I can not see any other way in which the fertilization can be effected. The ants generally throw up the mounds over the flowers before the buds open, as if in anticipation of the honey within the flowers. In most species of the genus the flowers are borne on the branches or upper part of the stem, and are brighter in color, white or orange, and these are not haunted by ants, but doubtless fertilized by hymenopterous or dipterous insects. If the flowers of *G. Ridleyi* are, as I believe, fertilized by ants, their position at the base of the stem may be taken as a modification to that end. This, however, could not be classed as symbiosis, but rather as a modification for fertilization, as the main nest of the ants is apparently always underground near the tree.

### Ants and Extrafloral Nectaries

Under the term "extrafloral nectaries" botanists include all glands secreting saccharine substances located on the vegetative organs of plants, while the "floral nectaries" are similar nectar-secreting glands found on parts of the flower or of the inflorescence.<sup>2</sup> There is still considerable discussion as to the true significance of nectaries. In this connection it is rather interesting to observe that all earlier botanists regarded even the floral nectaries as having a physiological function. Some believed that the saccharine secretion accumulated in the flowers served to feed the embryo; others considered the nectaries as excretory organs, eliminating waste substances of no further use or perhaps even noxious to the plant. In later years the majority of naturalists have accepted none but an ecological explanation. That the nectar glands of

<sup>1</sup>M. S. Evans (1876) has described cross-pollination by means of ants in an unnamed rubiaceous shrub on the coast of Natal.

<sup>2</sup>Delpino (1874 and 1875c) proposed to replace these terms with "extranuptial" and "nuptial" nectaries respectively. A "nectary" was originally defined by Linnæus (1751, *Philosophia botanica*, p. 53) as that part of the flower which produces the honey: "*nectarium, pars mellifera flori propria*." Usage has extended the meaning of the word to apply to all glands of the plant producing sweet excretions. Caspary (1848, 'De nectariis,' Eberfeld) apparently first made the distinction between floral and extrafloral nectaries. The historical side of the question has been fully treated by G. Bonnier (1879).

flowers attract pollinating insects, which in turn assure or greatly facilitate cross-fertilization, is too well established a fact to be doubted. It is, however, by no means certain that these floral nectaries are not at the same time more directly useful to the plant in a physiological way.<sup>1</sup>

Ants are frequently seen busily visiting the extrafloral nectaries of certain plants. They are, for instance, seldom absent from the large stipular glands of certain species of *Vicia* (*V. sepium*, *V. sativa*, and *V. Faba*) in Europe (see Rathy, 1882, pp. 29-36; Hetschko, 1908). In North America the stipules of some species of *Cassia* are especially attractive to these insects. In the Belgian Congo, I have taken numbers of ants, together with many other Hymenoptera and Diptera, as they were sucking up the sweetish fluid secreted at the base of the leaf-blade of *Urena lobata* variety *reticulata* Guerke, a very common weed in native villages and cultures.<sup>2</sup> The foliar nectaries of several Javanese species of *Hibiscus* are also very inviting to ants (Kœrnicke, 1918). It is on similar observations that Delpino (1874, 1875, 1879), A. F. W. Schimper (1888), and Kerner von Marilaun (1876) based their ecological interpretation of extrafloral nectar glands. The following passage from Delpino's earliest paper (1874, pp. 237-238) may be reproduced in full, as it sums up his views:

What then is the function of the extranuptial nectaries, which are found on the caulinary leaves, on the bracts, and on the calyx? Though I reserve for another paper the publication of my studies of such and other extradichogamic relations between plants and insects, I do not hesitate to announce now that the chief function of these nectaries is to place the ants, wasps, and *Polistes* in the position of sentries and guards, to prevent the tender parts of the plant from being destroyed by larvæ. Where ants and wasps are present, larvæ cannot exist because they will be devoured. Thus certain plants have adopted the same means of defense and bait that we see used by the tribe of aphids, coccids, *Tettigometra*, and other cicadellids, which spontaneously place themselves under the powerful protection of ants. Still another function, though a subordinate one, can sometimes be carried on by the above-mentioned nectaries, namely that of keeping the ants from the nuptial nectaries by detaining them at the extranuptial nectar glands. Indeed we can ascertain the noxious effects of ants when they succeed in infesting the flowers. In the first place, ants have sedentary habits, remaining motionless for whole hours on the same flower: therefore, they are of no use in dichogamy. Secondly, ants are objects of fright and aversion to the natural pollinating insects of the plant, as for instance, flies, butterflies, and bees; hence, their presence on the flowers renders useless the dichogamic devices of these plants. I have repeatedly observed bees and bumble-bees avoid visiting flowers when they saw ants there. Which all makes it clear how plants under given circum-

<sup>1</sup>G. Bonnier (1879, p. 206) after a critical study of the subject, from an anatomical and a physiological viewpoint, concludes: "The nectariferous tissues, whether floral or extrafloral, whether or not producing a liquid externally, represent special food reserves directly connected with the life of the plant."

<sup>2</sup>See my notes on this plant in Rev. Zool. Afr., III, fasc. 1, 1913, p. 3.

stances may find great profit in producing extranuptial nectaries, either to secure permanent and bold guards against the invasions of larvæ or to lure the ants away from the flowers.

In some of his later publications Delpino has even proposed that all plants with extrafloral nectaries be regarded as myrmecophytes, and has followed this course in his elaborate 'Monograph of the Myrmecophilous Function in the Vegetable Kingdom' (1886-1889). Such an extreme view has not been accepted by many other naturalists, probably because it would extend the concept of myrmecophytism to include a very considerable portion of the world's flora.<sup>1</sup>

A. F. Schimper and Kerner von Marilaun fully endorse Delpino's theory and endeavor to give further evidence in its support. Kerner, for instance, has a clever explanation of how the involucrel nectar glands of certain Compositæ attract ants which defend the capitula against voracious beetles.<sup>2</sup> He has also built further on the idea that the extrafloral nectaries keep ants away from the flowers where they would come as "unbidden guests" to feed on the floral nectar without aiding in cross-pollination. He claims that ants climbing the plant thus find on their way up an ample and readily accessible supply of honey, and consequently do not trouble to go to the flowers.

Many objections can, however, be raised to Delpino's theory. First, myrmecologists will not readily admit Kerner's supposition as to the limitation of the ants' feeding propensities. As a matter of fact, these insects are sometimes found inside flowers of various types, and frequently so on those with freely exposed nectar, such as the Umbelliferae. In tropical regions at least, as I have suggested above, they should not be wholly disregarded as pollen carriers. Secondly, observation shows that the extrafloral nectaries, while present in a great number of species, are in many of them seldom if ever visited by ants. Thirdly, the visitors of extrafloral nectar glands especially attractive to insects frequently do not consist of ants only, but include various other Hymenoptera, Diptera, and Coleoptera, which are by no means deterred by the ants.<sup>3</sup> And lastly, it has not been sufficiently well established that the

<sup>1</sup>O. F. Cook's papers on the "kelep" ant offer a typical example of the lengths to which "myrmecophilism" may be carried by certain naturalists. According to this author (1904 *c.*, p. 666) the cotton-plant of eastern Guatemala has, through its extensive system of extrafloral nectaries, secured the active cooperation of the kelep or weevil-eating ant, *Ectatomma tuberculatum* (Olivier), against the boll weevil!

<sup>2</sup>The nectar glands at the involucrel bracts of certain Compositæ have been further investigated by v. Wettstein (1888) and Hetschko (1907). The last-named observer found that the sweet excreting bracts of the European *Centaurea montana* Linnæus are visited not only by ants (*Myrmica larinodis*, *M. ruginodis*, and *Lasius niger*) but also by other Hymenoptera (Apidae, Vespidae), Diptera, and Coleoptera.

<sup>3</sup>Hetschko (1908) gives a list of the visitors he observed at the stipular nectaries of *Vicia sativa* Linnæus. It includes, in addition to four ants (*Formica rufa*, *F. rufibarbis*, *Lasius niger*, and *Myrmica larinodis*), 24 species of Hymenoptera (6 Apidae, 4 Vespidae, 2 Sphegoidea, 10 Ichneumonidae, and 2 Tentredinidae), 21 of Diptera (8 Syrphidae, 12 Muscidae, and 1 Bibionidae), 8 of Coleoptera (3 Cantharidae, 2 Elateridae, 1 Phalacridae, and 2 Coccinellidae), and 1 of Hemiptera.

regions some individuals of the worker caste have developed into a special form of "repletes," which act as living reservoirs of liquid food for the purpose of tiding over periods of scarcity. Their "honey" is obtained from the excretions of various Hemiptera (see p. 336) and the sweet exudations of different plant organs and even of certain galls. A few years ago Wheeler published a complete account of the honey ants (1908*b* and 1910*b*, pp. 361-377), to which but little can be added at present.

Repletes have been described for the African *Plagiolepis trimenii* Forel,<sup>1</sup> discovered by Hutchinson in Natal. They are 6.5 mm. in length, of which the head and thorax together measure only 2 mm., and are said by Forel (1895) to have their gaster "distended with honey, like a round cyst, transparent, as large as a hemp seed, on which the chitinous laminæ of the segments appear like islands. The anterior portion of the first segment has a hollow depression into which the petiolar scale fits. With the aid of a lens it is possible to distinguish, below and behind, the stomach and gizzard with its reflected calyx, both of them displaced and flattened against the gastric wall." The gaster in these repletes is, according to the same author, nearly as fully distended as that of the North American *Myrmecocystus melliger*, and locomotion must be almost impossible for this insect.

The habit of using some of the members of the colony as honey pots will probably be discovered in certain other ants of the African deserts. Among other species it may be still in an incipient stage, as, for instance, in the case of *Acantholepis arnoldi* Forel in Southern Rhodesia. The nests of this ant are found in loose, sandy soil in the hottest places. They sometimes contain workers with gaster considerably swollen, as long as the head and thorax together, but not so rotund as in the repletes of *Myrmecocystus* or *Plagiolepis trimenii* (Arnold, 1920, p. 564).

#### Dispersal of Seeds by Ants

That certain ants gather seeds and preserve them in special granaries in their nests has been known since very ancient times. There are frequent allusions to harvesting ants, and even more or less accurate accounts of their activities, in the writings which have come down to us from the older civilizations along the shores of the Mediterranean.<sup>2</sup> Yet such keen myrmecologists of western Europe as Latreille and P.

<sup>1</sup>*Plagiolepis decolor* Emery, a very closely allied South African species, is, according to Forel, also a honey ant.

<sup>2</sup>These old accounts are given in the works of Moggridge (1873, pp. 5-11) and McCook (1879*a*, pp. 42-60).

Huber, unacquainted with the spectacular seed-storing habits of certain southern ants, discredited the assertions of the ancient writers. Though Sykes (1835) and Jerdon (1851) in India and Buckley (1861a) and Lincecum (1862) in North America had actually observed certain ants collecting large quantities of seeds, it needed the careful investigations of Moggridge (1873) in southern France and of McCook (1877 and 1879a) in Texas to dispel the skepticism of modern entomologists.

It is only more recently, however, that naturalists have come to appreciate the general importance of ants as seed distributors. Their rôle in this respect seems to have been first realized by Kerner von Marilaun (1895, pp. 866-867). Later F. Ludwig (1899, p. 38) definitely asserted that "ants do not only aid in scattering plant seeds, but that they play a prominent part in the dispersal of the indigenous (European) vegetation." In Sernander's comprehensive 'Monograph of European Myrmecochores' (1906b) one finds a detailed and critical history of the subject, together with an immense array of new and interesting observations. His conclusions show that in Europe a great many grasses and herbaceous plants rely almost exclusively, or at least to a large extent, on certain species of ants for the successful scattering of their seeds. Many of the more common ants, belonging to such ubiquitous genera as *Formica*, *Lasius*, *Tetramorium*, and *Myrmica*, gather seeds of various plants more or less consistently. To the phyteologist these widely distributed ants are perhaps factors of greater importance than the true harvesters. The latter, to be sure, are more spectacular in their performances, but they are restricted to certain desert or semi-arid regions and are evidently extreme cases, remarkable for the huge quantities of seeds stored in their granaries.

The ecological significance of seed-transporting ants can only be adequately realized upon closer scrutiny of the actual results of their activity in this line. Sernander's calculations, though based on moderate figures, show that the amount of seeds carried about by ants must be considerable. He found, for instance, that a single colony of *Formica rufa* transports during one season about 37,000 seeds and fruits. Observation also discloses that the seeds are in this way conveyed appreciable distances (100 to 200 feet) from the mother-plant. On their foraging excursions ants frequently drop or lose seeds along the road. Furthermore, many of the seeds finally stored in the recesses of the nest are sooner or later cast out near the entrance along with chaff and other débris from the ants' household, and a number of them are still able to germinate. Finally, with further investigation, the number of myrme-

cochores, or species of plants whose seeds are garnered by ants, increases steadily.<sup>1</sup>

One might reasonably surmise that in tropical countries too ants will be found to be efficient agents in the dispersal of the seeds and fruits of many species; but, as yet, this side of tropical ant behavior has been barely touched upon. O. Kuntze (1877, p. 24) mentions incidentally that in South America he saw ants carry off the seeds of papaw-trees (*Carica Papaya* Linnæus). R. H. Lock (1904) gives a short account of the dispersal in Ceylon of *Turnera ulmifolia* Linnæus by ants (*Pheidole spathifera* Forel) which are apparently attracted by the arillus of the seed. More recently, W. and J. Docters van Leeuwen-Reynvaan (1912) have carefully investigated the scattering of the seeds of *Dischidia Rafflesiana* Wallich and *D. nummularia* R. Brown, which are common epiphytes in Java. The pappiferous seeds of these Asclepiadaceæ bear a narrow, white caruncle of thin-walled cells filled with fatty and albuminous substances. When the fruits are ripe, they split open and the seeds are carried away by the wind; if they lodge on a branch or trunk, they germinate when sufficiently moistened, but such seedlings do not develop into adult plants. Plenty of healthy seedlings can, however, be found in the galleries of *Iridomyrmex myrmecodix* Emery, an ant which builds its nest on and in the bark of trees. Moreover, this ant has been seen in the act of transporting *Dischidia* seeds, to which it was probably attracted by the caruncles. These minute ants, being unable to grasp the seed itself, pull off the longer, fragile hairs of the pappus and by means of the shorter, stronger hairs, drag the seed into a slit in the bark or among the roots and stalks of other *Dischidiæ*. It may be noted that in Java the pitcher-shaped leaves of these species of *Dischidia*<sup>2</sup> are usually inhabited by the same *Iridomyrmex*, so that this is perhaps one of the clearest examples of true symbiosis between ants and plants. It would be important to investigate further whether the ants actually feed on the caruncles of the seeds. The case of *Dischidia* also suggests comparison with the "ant gardens" of the Amazon, which are considered in more detail elsewhere (p. 365).

Ule (1900, p. 123) records finding the pea-sized seeds of *Ipomœa pes-capræ* Linnæus lying in long rows on the sandy sea-shore at Copaca-

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<sup>1</sup>Speaking of the seed-transport by *Messor barbarus* in Arbe, an island in the Adriatic Sea, F. Neger (1910a, p. 139) writes: "If one would draw up a list of all the plants whose seeds or fruits are carried by *Messor* into its nests, this list would almost be equivalent to an enumeration of the flowering plants occurring on the island."

<sup>2</sup>Ridley (1910, pp. 462-465) concludes that *D. Rafflesiana* cannot be regarded as a true myrmecophyte: but the relations between the ants and the seeds of this plant escaped his notice, so that the question will bear still further study.

banana, near Rio de Janeiro; he saw leaf-cutting ants (*Attini*) moving along, each carrying one of the seeds into a hole. It would thus seem that the *Attini* also store seeds in their nests or perhaps use them in their fungus gardens.

H. Winkler's (1906, pp. 236-237) statements concerning the dispersal of seeds by ants in Cameroon do not enter into much detail and merely show that the rôle played by ants in this respect in tropical Africa should not be disregarded. He says that in the dispersal of "numerous dry fruits with small seeds, ants are undoubtedly also of significance, since no spot in the tropical Rain Forest is free from these insects. I have almost always found that the arilli on dropped seeds of *Blighia* and other Sapindaceæ had been eaten away by ants. I have, however, never seen flower-gardens (due to ants) in Cameroon."

#### Harvesting Ants

The reader will find a complete review of this fascinating subject in the chapter devoted to harvesting ants in Prof. Wheeler's ant-book (1910*b*, pp. 267-293). The following account, therefore, will deal with what little is known at present of the seed-storing ants in the Ethiopian Region.<sup>1</sup>

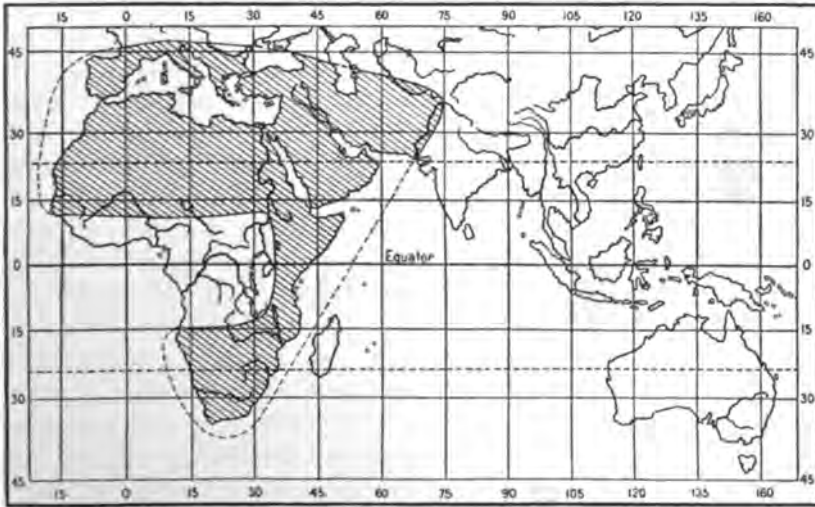
The typical Old World harvesters of the genus *Messor* are at home in the desert and semi-arid parts of the southern Palearctic, of the Ethiopian, and of the Indian Regions (Map 45). It is noteworthy that in Africa these ants, though widely distributed over the dry parts of the continent, avoid the moist West African Region (Engler's Western Forest Province), where seed-storing on a large scale is rendered practically impossible by the great moisture which prevails throughout the year, or at least for long periods, and would soon cause the stored seeds to sprout. Though *Messor* occurs as far north as Mossamedes and Bulawayo, as far west as the Great Rift Valley, and has recently been taken at Fort Crampel, French Congo, it has not been recorded from anywhere within the Congo Basin; yet it is not impossible that some of its forms might be found in Katanga. In East Africa this genus has the same general habits as in the Mediterranean Region (see Moggridge, 1873), as far as can be gathered from Sjöstedt's account of *Messor cephalotes* Emery, observed by him at the northern foot of Mt. Kilimanjaro:

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<sup>1</sup>Additional observations on the harvesting ant *Messor barbarus* subspecies *meridionalis* (Ern. André), in Macedonia, have recently been published by F. D. Döflein (1920).



At several spots one could see cleared spaces amidst the dry grass where every grass-stalk had been removed and the red-brown soil lay open to view, plane and clean as a well-attended garden plot. Such places were somewhat variable in size, mostly up to about 6 paces across and nearly circular. Heaps of fine grass-stalks cut to pieces (one to several liters; often 2 to 3 cm. long), together with grass panicles, were lying around. Scattered ants were wandering all over the place, the soldiers being especially striking on account of their big heads. The cleared place showed a large entrance, often more than finger-wide, into which the ants were dragging the stalk cuttings; more in particular I saw soldiers disappear with such cuttings through the entrance. The largest space I saw was 8 paces in diameter, with 4 or 5 separate entrances, one of which was larger than the others (as is the rule when there are many) and surrounded by an irregular, funnel-shaped depression, 15 to 20 cm. deep. The heaps of stalks, elsewhere clean and free from earth, were in this case mixed with soil and did not look as clean as usual. There were also holes in places along the path, into which the ants were dragging grass-stalks cut to pieces." (Mayr, 1907. pp. 14-15.)



Map 45. Distribution of *Messor*, a genus of harvesting ants. A subspecies of *M. barbarus* has recently been described from Fort Archambault, at about 9° 5' N., 16° 35' E.

Figure 1 on Plate XXVI represents one of these nesting sites of East African *Messor* from a photograph taken by Mr. H. Lang in the Athi Plains, British East Africa, during the R. Tjäder Expedition (July 1906). It is interesting to learn from Sjöstedt's experience with *Messor cephalotes* in East Africa and that of Neger (1910a) with *M. barbarus* in southern Europe that certain species of the genus *Messor* are leaf-cutting. What use these ants may have for the plant cuttings in their nests is as yet unknown.

one-half of the circle being generally deeper than the other, which may be due to the prevailing winds. These rubbish heaps when made by a populous colony sometimes reach very large dimensions, covering as much as one square foot of ground, and from one to three inches deep. The site of such a nest is very plainly indicated by these accumulations, since the husks are bleached almost white by the action of the sun. The nests of this ant appear to be very free of myrmecophilous insects and even the ubiquitous thysanuran is rarely to be found in them. The ants appear to have definite foraging grounds, to which access is obtained by well-marked and smooth paths leading from the nest in various directions." *Tetramorium setuliferum* Emery he describes (1917, p. 291) as "a harvesting and graminivorous species. The entrances to the nests are often surrounded by small accumulations of husks of a grass seed. These heaps are smaller than those of *Messor*, and much less tidily disposed."

The ponerine ants are well known for their predaceous habits and highly carnivorous diet. Yet one at least of these ants, the common African *Euponera sennaarensis* (Mayr), is to a large extent granivorous. Arnold (1913, p. 13; 1915, p. 7) found that the nest of this species in Rhodesia "often contains considerable accumulations of grass seed which may be used as food," though this ant is also a keen hunter of termites. Similar observations have been made on this species by K. Escherich in Abyssinia (Forel, 1910, p. 245) and by myself in Katanga (Bequaert, 1913, p. 421).

There is little doubt that certain ants derive at least part of their sustenance from the seeds which they carry into their nests. Yet it is by no means clear how they manage to utilize the various amylaceous, nitrogenous, and oily substances contained in the seeds, either for their own nourishment or as food for their brood. In the case of the many widespread species which use seeds only in small quantities, as an additional food supply, it would seem that the caruncle alone is bitten off, neither the coats of the seeds nor their contents being touched. This is, however, not the case with true harvesters, some of which have become almost purely granivorous and, as a rule, remove the entire kernel of the seed. In his experiments with a colony of *Messor structor* kept in an artificial nest, Emery (1899 and 1912b) found that this ant would more or less readily accept cooked or dried meat, various fresh mushrooms, husked rice, a variety of ripe and unripe seeds, plant buds, bread, and dry vermicelli. These substances would all be to a certain extent triturated

When carried out these masses are soft, damp, and bitter to the taste; their size varies from that of the head of a pin to that of a grain of pepper. Microscopic examination shows that they consist of comminuted parts of seeds, plant hairs, fibres, pollen, etc.<sup>1</sup> Neger calls these pasty masses "ant-bread-crumbs" and, although he never saw them being transferred, he supposes that they are eventually carried back into the nest by the ants. In a number of these crumbs he found spores and mycelium of a mould which he identifies with *Aspergillus niger*, having also obtained this fungus in a number of cultures made with fresh "ant-bread-crumbs" taken from worker ants. He formulates the hypothesis that the amylolytic and proteolytic action of this mould may help to render the crumbs more readily digestible so that they can be fed to the young as "larva-bread."

Emery (1912) completely rejects Neger's supposition that the starch and aleurone of the seeds need to be prepared by a ferment before being fed to the larvæ. He offered his colony of *Messor barbarus minor* wheat-paste made up in the form of small rings and found that this substance was readily accepted by the workers, who carried it into the moister part of the nest. There the rings were malaxated for some time and divided into small, twisted pieces, more or less irregular in shape, which were finally dumped into the drier chamber of the nest and never touched again by the ants. Fragments of this paste were also presented by the workers to the larvæ, the largest of which applied their mouth-parts to it just as to other food. Emery determined the weight and starch contents of fifty of these paste rings before and after malaxation by the ants. He infers from his figures that the workers either digested or fed to their larvæ at least 7.3 per cent of the starch and that they consumed also an unknown quantity of nonamylaceous substances, probably proteids; the latter he regards as a much more important aliment than the starch.

This brief consideration of the feeding habits of harvester ants may be properly concluded with Emery's remarks concerning the ethological significance of granivorous behavior among the Formicidæ:

The granivorous ants are derived from insectivorous ants. They represent an adaptation to the climatic conditions of dry prairies, steppes and deserts. When, owing to the summer droughts, insects become scarce and are no longer sufficiently numerous to satisfy the needs of the ants, the granivorous species substitute the living but dried seeds of plants, but at least the species I have observed will not refuse any

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<sup>1</sup>The composition of these pasty masses suggests great similarity with the pellets found in the infra-buccal pockets of many ants. Part of Neger's "ant-bread-crumbs" may well have consisted of such infra-buccal pellets, which, after being regurgitated by the ants, were merely discarded outside the nest.

insects that may be obtainable. The seeds, however, have the very great advantage that they keep for a long time; they can be accumulated in granaries, thus providing abundant provisions, not exactly for the winter, as the ancient sages maintained, but in general for any periods of scarcity.

### Ants and Epiphytes

Wherever in tropical and warm temperate regions the continued dampness of the air allows plants to thrive without being dependent on the soil for their water supply, epiphytes or air plants become an important and often very striking feature of the vegetation. They are especially abundant in the humid rain forest and are at their best in the mountain cloud forests of the tropics. The roots of these plants, boring into the many crevices on the tree's surface and retaining in their network decaying vegetable matter, rapidly loosen the outer layers of the bark and accumulate a cover of humus, affording favorable ecological conditions for a great variety of animals. Ants have not failed to recognize the nesting facilities here offered them by the many nooks and the uniform moisture and ventilation of this ærial root system. Indeed, the botanical collector in the tropics soon learns of the partiality of ants to the cover of humus on tree bark among and beneath the epiphytes.

Though the ethology of the various ants that live with epiphytes has been but little studied, there are a number of observations to show that the interrelations of these organisms are not always merely accidental but have in some cases produced reciprocal adaptation. The reader is referred to the Synopsis of Myrmecophytes (p. 494) for an account of the epiphytic *Myrmecodia*, *Hydnophytum*, and related rubiaceous genera which habitually harbor ants in the tubers of their rhizomes; similar pseudobulbs, inhabited by ants, are also known for a number of epiphytic ferns (p. 497.)

Ridley (1910, pp. 466-470), from observations in Singapore, has called attention to the fact that ants, mainly of the genus *Dolichoderus*, seem to be of considerable importance to the growth of certain epiphytic orchids. As soon as these plants start to grow, the ants bring up soil from the foot of the tree and fill the spaces between the roots, thus constructing shelters in which they raise their brood. This soil supplies nutritive substances to the roots and also keeps them cool and moist. From a comparison with young plants grown under different conditions, it would appear that the presence of ants among the roots is distinctly advantageous to the epiphyte, since seedlings not infested by ants are much weaker and suffer more from the drought. Though certain epiphytes, such as the orchid *Dendrobium crumenatum* Swartz and the ferns

*Asplenium nidus* Linnæus and *Platyserium bifforme* Blume, are apparently more attractive than others to ants, Ridley does not mention that any of these plants in Singapore grow only on arboreal ant nests.<sup>1</sup> According to Ule, a number of species of Brazilian ants have acquired the habit of selecting seeds of certain epiphytes, which they carry up trees and shrubs into the crevices on the bark and into the axils of the branches, where they cover them with soil. As the plants grow their entangled roots produce sponge-like ant nests with epiphytic shoots growing out on all sides, the whole resembling "witch-brooms" or bird nests. In certain parts of the Amazonian Rain Forest these aerial agglomerations of plants are so abundant as to form one of the striking features of the scenery. (Ule, 1901, 1905a, 1905d, 1906a, and 1908, pp. 435-436.)

Ule has described two main types of these so-called "ant-gardens." The largest are made by *Camponotus femoratus* (Fabricius) and placed high in the trees of the inundated forest; they consist of the following plants: *Philodendron myrmecophilum* Engler, *Anthurium scolopendrinum* Kunth variety *Poiteauanum* Engler, *Streptocalyx angustifolius* Mez, *Echnea spicata* Martius, *Peperomia nematostachya* Link, *Codonanthe Uleana* Fritsch, and *Phyllocactus phyllanthus* Link. The smaller gardens are more elegantly constructed and inhabited by species of *Azteca* (*A. traili* Emery, *A. ulei* Forel, and *A. olitrix* Forel); they are preferably placed in the lower trees and show the following flora: *Philodendron myrmecophilum* Engler, *Nidularium myrmecophilum* Engler, *Ficus paraënsis* Link, *Marsilea formicarum* U. Dammer, *Ectozoma Ulei* U. Dammer, *Codonanthe formicarum* Fritsch, and two Gesneriaceæ. Ule claims that, with the exception of *Anthurium scolopendrinum* and *Phyllocactus phyllanthus*, these "ant epiphytes" are so intimately connected with the ants that they are not found in the Amazon Basin in any other station. If Ule's conclusion be true, we have here a most remarkable instance of "selection" practiced by ants. As pointed out by Massart (1906), the results in this case show a striking parallelism with the effects of cultivation by man of crops and vegetables. By persistently caring through countless generations for the cultivated plants, man has gradually deprived them of most of their means of defense in competition with other plants and against the hardships of environment. Crops and vegetables, when left to themselves, are no longer able to hold their own in the

<sup>1</sup>Hart (1895) in Trinidad has also noticed the necessity for the presence of ants in the epiphytic clusters of certain orchids in order to assure the healthy growth of these plants. J. Rodway (1911, pp. 132-133 and 139) mentions that, in British Guiana, many of the epiphytic orchids (especially of the genera *Coryanthes*, *Gongora*, and *Oncidium*) shelter large communities of ants in the oval mass of their fibrous roots, the ants filling up the interstices to make a waterproof nest, so that the collector finds it very difficult to dislodge the plant without being severely bitten.

struggle with wild plants. Similarly, in the case of the plants domesticated by the ants in their "gardens," though it is certain that the seeds of these epiphytes are occasionally dropped elsewhere in the forest, they have lost the devices which allowed them to fight their rivals and are at present doomed unless cared for by the ants.

The partiality of certain ants to the clusters of *Tillandsia* and other epiphytic bromeliads was first noted by Wheeler (1901a, pp. 526-528, and 1901b) in Mexico. He relates his experiences as follows:

On accidentally pulling to pieces one of the large bud-like epiphytic tillandsias (probably *Tillandsia Benthamiana* Klotzsch), very common both in this and other localities about Cuernavaca, I was surprised to find it containing whole nests of ants, with their larvæ and pupæ snugly packed away like so many anchovies in the spaces between the moist overlapping leaves. A closer inspection showed that the ants had gnawed little holes through the leaves to serve as entrances to their chambers. These holes occasionally perforated a single leaf, but quite as often they threaded several leaves and extended to the very core of the bud. Sometimes a single colony of ants was divided up into companies, each occupying the space under a single leaf. But the most remarkable fact concerning these nests was the frequent occurrence of two or even three flourishing colonies belonging to different species in a single tillandsia, the whole habitable basal portion of which was rarely more than two to three inches long by one and one-half inches in diameter. Often these colonies were curiously intermingled in such a manner that there was no actual blending and the space under a single leaf was always occupied by ants of the same species, still, whole colonies or portions of a single colony were often completely surrounded by leaf spaces occupied by another colony.

Wheeler collected the following ants from these Mexican tillandsias: *Pseudomyrma gracilis* (Fabricius) variety *mexicana* Emery, *Crematogaster brevispinosa* (Mayr) variety *minutior* (Forel), *Leptothorax petiolatus* Forel, *Cryptocerus aztecus* Forel, *C. wheeleri* Forel, *Camponotus rectangularis* Emery variety *rubroniger* Forel, and *C. abdominalis* F. Smith variety. Though the tillandsias appear to suffer no injury from their tenants, Wheeler is not inclined to regard this association of plants and ants as a case of symbiosis, because at least four of the seven species enumerated above occur also under other conditions in the neighborhood of Cuernavaca.

Wasmann (1905a, p. 210, Pl. VIII, fig. 1) also describes and figures an interesting carton nest of *Crematogaster sulcata* (Mayr), from Rio Grande do Sul, Brazil, which was interwoven in a pensile cluster of epiphytic tillandsias. Calvert (1911), in Costa Rica, found the clumps of epiphytic bromeliads frequently inhabited by ants, especially by the large black species *Odontomachus hastatus* (Fabricius) "with enormously developed jaws, bent near the tip, which are carried wide open and measure one-quarter inch from tip to tip: occasionally they would be

jassids and membracids and collect the secretion of extrafloral nectaries. Examination of such "compound nests" revealed that all the superficial galleries, and they alone, are stuffed with *Crematogaster* and their brood, whereas only the center, or core, of the garden is occupied by the *Camponotus* with their larvæ and cocoons. The galleries of both species, however, open into one another so that the adult ants undoubtedly move about together more or less.

The conclusions drawn by Wheeler from his observations differ in several important particulars from Ule's. The frequent parabiosis of *Crematogaster* and *Camponotus* shows that Ule's distinction of gardens on the basis of the size of the ants inhabiting them does not hold in British Guiana. Moreover, though the same plants do not occur in all gardens, no preference of certain ants for certain plants could be detected. All the species of ants found in the ant-garden biocœnose may also nest elsewhere, but it must be admitted that *Camponotus femoratus* shows a decided preference for the garden nest, so that we have here a very regular and intimate ethological relationship between an ant and certain epiphytes. According to Wheeler the ant-gardens are not started in the manner implied by Ule, viz., by means of the ants either putting seeds into crevices or accumulating a certain amount of humus at some spot on a tree or bush and then collecting and planting the seeds in the mass. It is more probable that the young ant epiphytes originally grow in small accumulations of earth or detritus, which are ultimately settled by colonies of the ants. That the amount of humus is gradually increased by the ants with the growth of the colony admits of no doubt, and it is possible that as the accumulation becomes greater, it may be sown with seeds falling from the original plant. Furthermore, it is practically certain, from what we know of the habits of ants, that new gardens cannot be seeded from old ones, as Ule maintains, for this would be too great a task for the single fecundated queens which start the new colonies. Ule's experiments with ants transporting the seeds of these epiphytes do not furnish conclusive proof that the insects actually sow the plants, for ants will often carry all sort of portable organic bodies into their nests, only to cast them out later when they find them useless. And lastly, Ule records no convincing observations in support of his contentions that the ants actually cultivate the growing plants. Wheeler believes, therefore, that it is advisable to suspend judgment for the time being as to the provenience and significance of the plant elements in the ant-garden biocœnose of tropical America.

The association of ants with certain species of *Dischidia*, a genus of epiphytic Asclepiadaceæ in the Oriental Region, has been treated in detail in a preceding chapter (p. 357) and other aspects of it are considered in the sequel (p. 520).

#### Gall-inhabiting Ants

The habit of sheltering their brood within old galls produced by various insects is very common with ants and is worthy of careful study for several reasons. In the first place, certain species of ants are so frequently found in galls that this location of their nests has become part of their normal behavior. Secondly, most galls have such regular shape and structure that often they look like normal productions of the plant; when settled by ants they may then simulate true myrmecodomatia and become a source of confusion in the study of myrmecophytism. Thirdly, the gall-inhabiting behavior of ants can help us to understand the origin and meaning of myrmecophily proper in plants. And, finally, as shown by Prof. Bailey's histological studies, certain myrmecodomatia occupy a somewhat intermediate position between normal plant structures and galls, since the intervention of the ants results in the production of hyperplasias or abnormal tissues by the plant.

Gall-inhabiting ants are rarely met with in the colder regions of the globe, where the rigor of winter prevents these insects from acquiring true arboreal or epiphytic nesting habits. Patton (1879), however, recorded finding in Connecticut, nests of *Leptothorax curvispinosus* Mayr (= *Stenammas gallarum* Patton), with queen, workers, and larvæ, in deserted, dead galls of *Gelechia gallæsolidaginis* Riley on the stems of goldenrod (*Solidago* species) and in those of *Cynips spongifica* Osten Sacken on oaks; and H. Ross (1909) has mentioned the frequent occurrence in southern Germany of *Crematogaster brevispinosa* Mayr variety *minutior* Forel in old oak-galls.

On the other hand, the gall-inhabiting behavior becomes part of the normal habits of many species of ants in the xerophytic and warmer parts of the southern Nearctic and Palearctic Regions. Wheeler (1904a, pp. 155-158; and 1910b, pp. 208-212) has written a most entertaining account of the ant-fauna of the spherical, woody galls produced by the cynipid *Holcaspis cinerosus* Bassett on the twigs of the Texan live oak. *Crematogaster lineolata* (Say) subspecies *læviuscula* Mayr and its variety *clara* Mayr merely use them as temporary shelters for the workers, but *Leptothorax obturator* Wheeler, *L. fortinodis* Mayr, *Camponotus caryæ* (Fitch) variety *decipiens* Emery and its subspecies *rasisis* Wheeler,



stalk. Often the swelling is symmetrically developed, especially when occurring on a petiole, but in many cases it bulges more on one side of the support. Two galls may be placed close, one above the other, or even partly united. A cross-section of a young swelling shows the typical structure of a pith gall: a spacious central cavity, completely closed and surrounded by the hypertrophied fibrovascular tissues of the stem. In young galls I always found a single larva of a lace-bug belonging to the genus *Copium* (Tingitidæ) feeding inside the cavity on the pith cells along the wall. When the *Copium* reaches the adult stage, the "ripe" gall splits open, allowing the bug to escape. Such old, empty galls may eventually be invaded by ants, but I have never observed this myself. I am, therefore, fully satisfied that the swellings of *Clerodendron formicarum* are true insect galls. That they are not real myrmecodomatia is moreover indicated by their irregular distribution over various parts of the plant.<sup>1</sup>

We now come to a consideration of the so-called myrmecophilous acacias of Tropical Africa. These plants present a rather difficult problem, and, though I myself am convinced that they are not true myrmecophytes, the facts in the case are still far from being satisfactorily elucidated. Unfortunately, I have never had an opportunity to study them in the field.

While travelling across the deserts of Nubia and Sennaar in 1867, G. Schweinfurth discovered a curious, shrubby *Acacia*, which he described and figured under the name *Acacia fistula* (1867, p. 344, Pls. IX and XIII). Some of the thorns of this plant were considerably swollen, hollowed out, and pierced by an orifice; the wind playing on these empty swellings produced a whistling noise, the plant being therefore called "Ssoffar," or flute, by the natives. Schweinfurth did not record the occurrence of ants in the swellings<sup>2</sup> but stated that the small, circular orifice was pierced "by the escaping insect," the swellings being, in his opinion, true insect galls, a view endorsed by Ascherson (1878, p. 44).

Many travellers have since remarked upon the abnormally swollen thorns of certain East African acacias and have also called attention to the fact that they are frequently settled by ants. According to Harms' recent account<sup>3</sup> the following African species of the genus *Acacia* have been found with ant-inhabited swellings:

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<sup>1</sup>Various species of *Copium* produce galls on several Central African *Clerodendrons*; they most frequently affect the flowers. *Copium stolidum* Horvath, for instance, very commonly deforms the flowers of *Clerodendron spinescens* Guerke.

<sup>2</sup>Keller (1892 a, p. 137), however, asserts that Schweinfurth found ants inside the swollen thorns of this *Acacia fistula*, though he did not mention the fact in his paper.

<sup>3</sup>In Engler, 1915, "Die Pflanzenwelt Afrikas," III, 1, pp. 368-373; see also Harms, 1914, Engler's Bot. Jahrb., LI, pp. 361-365.

*Acacia fistula* Schweinfurth and *A. zanzibarica* (Sp. Moore). In Harms' opinion these two forms are hardly specifically distinct from the common African *A. seyal* Delile.

*A. drepanolobium* Harms.

*A. formicarum* Harms. This is probably Sjöstedt's "Flötenakazie" from the Masai-steppe.

*A. pseudofistula* Harms.

*A. malacocephala* Harms.

*A. Bussei* Harms.

The exact nature of the swollen thorns of these plants has been somewhat disputed. As mentioned before, Schweinfurth and Ascherson regarded them as true galls. This opinion is further supported by the thorough researches of Keller (1892a) and Sjöstedt (1908), as well as by the more recent observations of Glover Allen (Wheeler, 1913, p. 130, footnote), H. Winkler (1912, p. 65), and H. Schenck (1914, p. 453). Sjöstedt was unable to discover the maker of the galls; yet he believes that they may owe their development to the sting of some dipterous or hymenopterous insect. Glover Allen, however, found that the enlarged thorns of *Acacia fistula* (from the Nilotic Sudan) consist, when young, "of a solid mass of green, succulent tissue, with a single small larva inside, as in a typical insect gall"; and H. Winkler discovered in German East Africa a beetle-larva in a swollen *Acacia* thorn that was entirely intact. Alluaud and Jeannel are, it seems, the only observers inclined to believe that the ants themselves produce the galls,<sup>1</sup> but their own observations hardly support this view.

During his travels in British East Africa with R. Tjäder, in 1906, Mr. H. Lang made some observations on gall-bearing acacias growing in large numbers on the Athi Plains. One of his photographs of these curious plant deformations is reproduced on Plate XXVI, fig. 2. From information he kindly gave me, I am led to agree with Sjöstedt and others that the swellings are true insect galls.<sup>2</sup> They are not found on all specimens of the same species of *Acacia*, even in one locality: while on some plants practically all the thorns are swollen, others nearby bear hardly any galls; furthermore, their size is quite variable and their shape rather irregular. Mention may still be made of the fact that,

<sup>1</sup> "En somme, nous ne pouvons pas affirmer avec certitude quels sont les rapports exacts du *Cremastogaster vulcania* avec l'*Acacia* sur lequel on le trouve, mais ce que nous avons vu nous pousse fortement à croire que ce sont bien les *Cremastogaster* qui provoquent par leur intervention à l'extrémité des rameaux jeunes, la formation des galles, qui entretiennent leur accroissement, puis le moment venu les perforent pour y installer leur nid" (Santachi, 1914, p. 98).

<sup>2</sup> Some authors admit that the swellings of the thorns of African acacias are not due to ants, yet call them ant-galls ("Ameisengallen"). This misleading term should be avoided, because it conveys the erroneous idea that the ants are responsible for the production of the galls. Even the myrmecodomatia of true myrmecophytes are normally produced by the plant without the intervention of ants; though, when inhabited by these insects, some tissues in certain species may show a peculiar hyperplasia.

*Crematogaster (Decacrema) solenopsides* subspecies *flavida* (Mayr), in thorn galls of *Acacia Bussei*, Usambara (Sjöstedt, 1908); the variety *gallarum* (Santschi) was taken in galls of an acacia at Mindouli, French Congo.

*Cataulacus intrudens* (F. Smith), in thorn galls of *Acacia Bussei*, Usambara (Sjöstedt, 1908); originally described from thorns of *Acacia*, in Natal

*Tetraponera penzigi* (Mayr), in thorn galls of *Acacia drepanolobium*, near Kahe, in the plain at the foot of Mt. Kilimanjaro, and in West Usambara (Sjöstedt, 1908).

*Tetraponera natalensis* F. Smith was taken from thorns of a species of *Acacia* in Natal (F. Smith, 1876).

According to Kohl (1909, p. 151), H. Schinz found ants inside hypertrophied thorns of *Acacia horrida* in South Africa.

As would be expected from the fortuitous production of galls on plants, none of the ants mentioned in the preceding pages seems to restrict the location of its nest to galls. They are evidently all arboreal species which are in the habit of sheltering their brood in hollow branches or cavities of trees.

### Fungus-growing Ants

Allusion has been made above to the depredations of the South American leaf-cutting, or parasol, ants. Though the destruction wrought by these insects was familiar to the indigenes and early colonists, what use is made of the vegetable matter carried into their nests is a discovery of comparatively recent date. H. W. Bates in his classical 'Naturalist on the Amazon' (1863, I, pp. 23-26) describes the activities and earth-works of the large South American leaf-cutter, *Atta cephalotes* (Linnaeus), in great detail. In his opinion, "the leaves are used to thatch the domes which cover the entrances to their subterranean dwellings, thereby protecting from the deluging rains the young broods in the nest beneath." Lincecum (1867), Norton (1868), and B. R. Townsend (1870), who studied the smaller Mexican and Texan parasol ants, all overlooked the most important peculiarity in the behavior of these insects.

Belt (1874) was the first to understand the true significance of the leaf-gathering habit. He definitely states that the parasol ants use the leaves "as a manure, on which grows a minute species of fungus, on which they feed;—that they are, in reality, mushroom growers and eaters." He then proceeds to describe the interior of the nests of the species of *Atta* studied by him in Nicaragua.

The chambers were always about three parts filled with a speckled, brown, flocculent, spongy-looking mass of a light and loosely connected substance. Throughout these masses were numerous ants belonging to the smallest division of the workers, which do not engage in leaf-carrying. Along with them were pupae and larvae, not gathered together, but dispersed, apparently irregularly, throughout the flocculent

mass. This mass, which I have called the ant-food, proved, on examination, to be composed of minutely subdivided pieces of leaves, withered to a brown color, and overgrown and lightly connected by a minute white fungus that ramified in every direction throughout it. I not only found this fungus in every chamber I opened, but also in the chambers of the nest of a distinct species that generally comes out only in the night-times. . . . When a nest is disturbed, and the masses of ant-food are spread about, the ants show great concern to carry away every morsel of it under shelter again.

Belt's observations were subsequently confirmed by Fritz Müller (1874), Tanner (1892), A. Möller (1893), Sampaio (1894), H. v. Ihering (1894 and 1898), Urich (1895a-b), Swingle (1896), Forel (1896a-c, 1897), Wheeler (1901b, 1905b-c, 1907, 1910b, etc.), Gældi (1905a-b), J. Huber (1905, 1907, 1908), and others. It is now an established fact that the Attini, a tribe of myrmicine ants restricted to America, are all intimately associated with fungi, which they cultivate on an appropriate substratum and which in turn supply these insects with their only food.<sup>1</sup> They are the only ants known to be strictly vegetarian. Various stages in the development of the fungus-growing behavior may still be recognized among the many forms of the tribe.<sup>2</sup> The different members of the lower genus, *Cyphomyrmex*, and probably also of *Myrmicocrypta*, make a small, crude nest; they collect caterpillar excrement on which they grow a flocculent mycelium with well-developed food-bodies, or bromatia (called "kohlrabi-heads" by A. Möller); their gardens are only a few centimeters in diameter, of irregular shape, and lie on the floors of small dilations in the rough earthen galleries of the nest. *Apterostigma*, *Sericomyrmex*, *Mycetosoritis*, and *Trachymyrmex* all excavate more regular nests and construct pendent mushroom gardens on a substratum of insect excrement and vegetable débris. The gardens of *Apterostigma* are sometimes provided with a special mycelial envelop, but those of all other Attini are naked. *Mølleri* and *Acromyrmex* make one or more large gardens on the floors of the nest-chamber. And, finally, the *Attæ*, s. str., which include the true parasol ants, the largest and most powerful species of the tribe, collect large quantities of leaves, flowers, and other vegetable substances for their gardens; their nests attain huge dimensions and comprise a number of large chambers, each with a sessile mushroom garden of triturated plant fragments, permeated with fungus hyphæ.

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<sup>1</sup>The genus *Proatta*, recently discovered by v. Buttell-Reepen in Sumatra, was originally placed by Forel among the Attini, but later separated by the same author to form a tribe of its own. There is nothing to show that this Sumatran ant has developed fungus-growing habits.

<sup>2</sup>The habits of the genus *Blepharidatta* Wheeler are unknown.

The origin of new colonies among the Attini and the method of transferring fungus culture from the maternal to the daughter colony have been investigated by H. v. Ihering (1898), Gœldi (1905a), and J. Huber (1905, 1907, and 1908). The deãlated, fertilized female of *Atta sexdens* (Linnæus) often starts a new colony alone; she digs a burrow in the soil and forms at a depth of 20 to 30 cm. a chamber in which she deposits within a few days a little packet of eggs. Even at that time one finds beside the eggs a flat heap of loose white substance, only 1 to 2 mm. in diameter, which is the earliest rudiment of the fungus garden. On searching for the origin of the fungus germs with which this new garden is established, v. Ihering discovered that every *Atta* queen, on leaving the parental nest, carries in her infrabuccal pocket a loose pellet of debris containing also hyphæ from the fungus gardens. This fact was confirmed by J. Huber, who successfully reared an *Atta* colony from its inception to the appearance of the first workers. The day following the nuptial flight the female disgorges this pellet on the floor of the newly dug chamber; to keep the fungus alive she frequently manures parts of it with liquid excrement from the tip of her gaster. In this early stage of the colony the queen does not feed on the fungus but eats a great number of her own eggs. The first larvæ, too, are fed directly on eggs thrust into their mouths by their mother. Shortly after hatching, the first workers usurp the functions of the mother ant, which henceforth degenerates into an egg-laying machine. They manure the garden with fecal droplets and feed the larvæ with their mother's eggs, while they themselves feed on the bromatia meanwhile developed on the hyphæ. A few days later the workers start to extend the formicary; they also break through the surface of the soil and return with new material for the fungus garden. In the meantime, the bromatia have become so abundant that they can be fed to the larvæ. Huber also observed that the founding of a new colony by a queen is often unnecessary, because fertile females of *Atta sexdens* are readily adopted by strange workers of their own species, thus adding to the strength of existing formicaries.

The systematic position of the fungi grown by the Attini is still disputed. A. Möller is apparently the only botanist to have made a special point of studying this problem. His attempts, however, to raise any fruiting form from mycelial cultures started with portions of the fungus gardens of ants were unsuccessful. But he found in four instances an agaricine mushroom, which he called *Rozites gongylophora*, growing on extinct or abandoned *Acromyrmex* nests. From the basidiospores of this plant he succeeded in raising a mycelium resembling in all respects that of

the ant-gardens. Three of the species of *Acromyrmex* did not hesitate to eat portions of this mycelium and also of the pileus and stem of the *Rozites*. Möller therefore identified the fungus grown by *Acromyrmex* with his *Rozites gongylophora* and in this he has been followed by most other investigators. Wheeler (1910b, pp. 327-328), however, maintains that Möller's observations are far from conclusive. He believes that the fungi cultivated by the ants may be more closely related to the moulds (Ascomycetes) than to the toadstools (Basidiomycetes). He has even described the peculiar fungus grown by the Texan *Cyphomyrmex rimosus* (Spinola) variety *comalensis* Wheeler as *Tyridiomyces formicarum*, assigning it provisionally to the Exoascaceæ (Wheeler, 1907, p. 772).<sup>1</sup>

There can be little doubt that the highly specialized fungus-growing behavior of the Attini must have been gradually derived from some more primitive fungus-eating habit. How this developed is at present a matter of conjecture, but it may be expected that other ants will show vestigial fungicolous habits. When these have been properly studied, they may, taken in addition with what is known of the ethology of other fungus-growing insects, give us a proper clue to the possible evolution of the complicated ethology of the Attini.

A condition very near the primitive fungus-growing behavior is perhaps exemplified in the remarkable carton nests of the European *Lasius fuliginosus* (Latreille). I quote the following description from Donisthorpe's recent volume on 'British Ants' (1915, p. 193):<sup>2</sup>

These nests are often very large, having the appearance of a huge sponge, and consist of a number of irregular cells separated from each other by thin carton walls, which are rather brittle and generally black in color, but sometimes light brown, according to the amount and the color of the earth used in their construction. The carton contains a quantity of a fungus which was named *Septosporium myrmecophilum* by Fresenius (1852, p. 49, Pl. vi, figs. 29-31). Saccardo (1886, p. 538) describes it as *Macrosporium myrmecophilum*, but considered it might be identical with *Cladotrichum*, and Lagerheim (1900) came to the conclusion that it was really a *Cladotrichum*, and called it *C. myrmecophilum*. I supplied Dr. Jessie Baylis Elliot of the Birmingham

<sup>1</sup>Spegazzini has also given descriptions of fungi taken from the gardens of various Attini in Argentina. He regards *Bergellinia ? belli* Spegazzini (1899, p. 311) as one of the Discomycetes. *Rhizomorpha formicarum* Spegazzini (1899, p. 352) is probably the sterile form of one of the Xylariaceæ. Both these fungi were found in the mushroom gardens of *Acromyrmex lundii* (Guérin). *Monilia formicarum* Spegazzini (1910, p. 414), described from the nests of *Atta hyalrix*, is one of the many imperfect fungi of unknown affinities. Prof. Wheeler has kindly sent to me for publication the following extract from a letter written by Mr. Carlos Bruch, dated La Plata, Argentina, July 16, 1921: "You will, no doubt, be interested in the discovery of the mushrooms which are cultivated by some of the Argentinian Attini. *Acromyrmex lundii* cultivates *Xylaria micrura* Spegazzini; *A. (Mallerius) heyeri*, *Poroniopsis bruchi* Spegazzini; and *Atta wollenweideri* a gigantic agaricus, *Locelina mazzuchii* Spegazzini. This year I found on the culture substratum that had been carried out into their hills by the ants hundreds of *Poroniopsis* in every nest. Masses of substratum which I had sifted for guests two months previously were completely covered by the mushrooms. The damp autumn months this year were particularly favorable to the development of the mushrooms mentioned." *Xylaria* and *Poroniopsis* are both Pyrenomycetines (Ascomycetes) of the family Xylariaceæ. *Locelina* is one of the Hymenomycetines (Basidiomycetes) and placed in the family Agaricaceæ. *Rozites* is also a genus of themenomycetines.

<sup>2</sup>I have inserted in parenthesis the dates and pages of the references.

University with various samples of *D. fuliginosa* carton, and she has proved, by making cultures, etc., that the fungus it contains is a *Cladosporium*, and so should be called *Cladosporium myrmecophilum* (J. B. Elliot, 1915, p. 138, Pl. VIII, figs. 1-4). The "raison d'être" of this fungus is probably twofold; the hyphæ may act as food for the ants and their brood—it forms a delicate bluish mould on the walls of the cells and under the microscope it may be seen to have been bitten off by the ants—and the mycelium helps to strengthen the walls of the nest. The ants most probably cultivate this fungus intentionally, as no other species of fungus is found in these nests, but it would not alone supply sufficient food for the teeming myriads that form the population of a large colony.

No definite proof has apparently been given that the fungus in the carton nest of *Lasius fuliginosus* contributes to the diet of the ants, but Donisthorpe remarks that "the great difficulty experienced in rearing *fuliginosa* larvæ in captivity—when no carton is present—would seem to show that the fungus is necessary as food, though the ants feed on other substances as well." Adlerz (1913, p. 63) and Donisthorpe (1915, p. 229) have shown that *Lasius umbratus* (Nylander) also builds carton nests with inner walls covered by the hyphæ of a fungus. Dr. J. B. Elliot (1915, pp. 139 and 142, Pl. II, figs. 5-10) described the hyphæ found in one of these nests in England as a variety *myrmecophilum* of *Hormiscium pithophilum* (Wallrich), a fungus which is usually found in thick, superficial patches of mycelium on the leaves of pines, firs, and yews.<sup>1</sup>

According to Dr. J. B. Elliott (1915, p. 142), the species of fungus associated with the carton of *Lasius fuliginosus* is always the same, which also holds true in the case of *L. umbratus*. "Since the fungus exists in the carton as a pure culture, all 'foreign' fungi are doubtless 'weeded' out, as in the fungus gardens of the white ants and the leaf-cutting ants, for many varieties of fungus spores must be introduced into the nests by the passing of insects in and out."

It seems likely that certain, at least, of the many tropical ants which construct nests either of carton or of more loosely agglutinated plant-fibres, will eventually show similar associations with fungi. Farquharson (1914), in Southern Nigeria, several times found fungus hyphæ growing on the aerial shelters composed of chewed wood and built over coccids by a species of *Crematogaster*. But it is very doubtful whether the ants had anything to do with this fungus. Perkins suggested that the mycelium in this case may merely have grown on the excreta of the coccids or even on the scale insects themselves. The roughly woven

<sup>1</sup>These fungi from the nests of *Lasius fuliginosus* and *L. umbratus* are all conidia-bearing or sterile mycelia of uncertain systematic position.

nests of the African *Macromischoides aculeatus* (Mayr) are frequent on leaves in the forest. They have been described by Santschi as lined with a mycelium bearing fructifications. Prof. Wheeler's examination of nests of this species (p. 190) argues for the probability that this fungus has no relation with the ants, being but one of the many fungi which in the moist tropical forest grow over dead vegetable matter. *Chromosporium formicarum* Ferdinandsen and Winge (1908, p. 21, Pl. II, fig. 11) is another imperfect fungus found by Raunkjær on the island of St. John, West Indies. Its brown-yellow conidia covered the walls of galleries in a decaying log occupied by unidentified ants. The writers assume that the ants feed on these conidia, but this will need actual confirmation.

A few words may be said about the peculiar fungi found growing on the inner walls of the myrmecodomatia of certain ant-plants. Miehe (1911*b*, pp. 331-341) made the interesting discovery that some of the galleries in the pseudobulbs of the Javanese *Myrmecodia tuberosa* and *Hydnophytum montanum* are lined with mycelium. This is found only in tubers inhabited by ants; the free tips of the hyphæ are evidently bitten off by these insects and in some places the sods of mycelium are trimmed to an equal level. Miehe believes that the fungus grows on the excrement of the ants, but he evidently discards the idea that the insects feed on it. If they cut the hyphæ down, it is merely, he thinks, because too thick a carpet would soon obstruct the galleries of the formicary. He thus regards the fungus as a mere intruder of no use to the ants. The presence of fungi inside myrmecodomatia seems to be very general, since Prof. Bailey found a more or less luxuriant growth inside the cavities of all the myrmecophytes of which he could obtain suitable material (See Part V). The mycelia are sporadically distributed in most cases, but their aërial portions show unmistakable evidences of having been cropped by the ants. In one of the species of *Plectronia* (*P. Laurentii*) and in the *Cuvieræ* there are dense mats of delicate, white hyphæ, which remind one forcibly of the "ambrosia" cultivated by certain wood-boring beetles and gall-midges, of which I shall have more to say below. In a recent paper, Bailey (1920) fully discusses the question whether the mycelia of the myrmecophytes are eaten by the ants and whether they are cultivated by them or are merely adventitious.

The pellets in the infrabuccal pockets of ants inhabiting myrmecophytes usually contain numerous spores and also fragments of hyphæ which appear to have been removed from the walls of the domatia. This might be considered as indicating that the ants feed to a greater or less



extent upon the fungi. But the evidence appears much less conclusive when viewed in the light of Bailey's discovery that the infrabuccal pellets of almost all ants tend to contain spores and fragments of hyphæ. This is as true of the entomophagous *Ponerinæ* and *Pseudomyrminæ* as of the more or less omnivorous *Myrmicinæ*, *Dolichoderinæ*, and *Formicinæ*; of ants of temperate as of tropical regions; and of species which nest in the ground or in carton or silk domatia as of those which live in decaying plant tissue. On the other hand, such is not the case with the crops and stomachs of imaginal ants. If any of the ants actually feed upon fungi, they must triturate the spores and mycelia, or compress them, and drain off the liquid or semi-liquid contents. Under such circumstances, one would expect to find torn or ruptured spores and finely divided fragments of hyphæ in the infrabuccal cavity. This was not so, however, in any of the pellets analyzed by Bailey; the spores and fungus filaments were intact and still retained their protoplasmic contents. All the evidence at hand favors Janet's (1896, p. 15; 1899) contention that the function of the infrabuccal pocket is to serve as a receptacle for food-residues and detritus. Bailey therefore concludes that, though many ants are closely associated with fungi, there is no sufficient proof that any of the *Formicidæ*, other than the *Attini*, are fungivorous. The cropping of the hyphæ which cover the inner walls of myrmecophytes does not indicate necessarily that these fungi are eaten by ants.

In most myrmecodomatia the growth and sporadic distribution of the hyphæ suggest that the mycelia are purely adventitious. Only in the case of the localized luxuriant growths of "ambrosia" in *Cuviera* and *Plectronia Laurenti* are there indications that the ants may actually be fungus-farmers; the mycelia appear to be more or less pure cultures and are closely associated with the detritus of the ant colonies. Yet it is by no means certain that even these results are not obtained quite unintentionally on the part of the ants. The environmental conditions within the myrmecophytes undoubtedly facilitate the growth of fungi which must be kept within bounds by a constant cropping of the mycelia or they might interfere with the activities of the insects. Unless all fungi are equally resistant to continued cropping and react similarly in the peculiar conditions within the domatia, certain species will tend to become dominant. Should a particular form gain the upper hand and grow actively, it would probably be transferred to new nests by the queens, since the infrabuccal pockets of imagines almost invariably contain fragments of hyphæ or spores. Thus "pure cultures" of fungi may have been brought about through the activities of the ants, but

quite incidentally and without utilitarian purpose on the part of the insects. Such considerations are certainly of great interest in a discussion of the probable origin of the remarkable fungus-growing and fungus-feeding habits of the highly specialized *Attini*. If mats of hyphæ growing in particular luxuriance on the detritus (pellets, feces, etc.) of the colony were found by the ants to be edible, it would be a comparatively simple matter for these insects to increase the volume of their primitive fungus gardens by adding extraneous material, such as insect excrement or vegetable débris, to the original compost.

The systematic affinities of the fungi found flourishing on the inner walls of myrmecophytes have not been investigated. They probably represent imperfect forms of some of the higher *Ascomycetes*.

It is interesting to compare the fungus-growing behavior of the *Formicidæ* with like activities of other insects. Such are known at present to exist among the termites, or *Isoptera*, certain wood-boring beetles of the families *Scolytidæ* and *Lymnæxylonidæ*, and a number of gall-making *Cecidomyidæ*.

That certain termites cultivate mushrooms in their nests was known long before similar observations were made with regard to ants, fungus gardens of the former having been accurately described in 1781 by Smeathman in his celebrated 'Account of the Termites.' Yet the true meaning of these gardens was not realized till after the fungicolous *Formicidæ* had been more fully investigated. Even at present, many aspects in the behavior of fungus-growing termites, such as the manner in which they feed on the mushroom and the origin of fungus gardens in their new nests, are still obscure. So much is certain — that their fungus-growing behavior differs from that of the *Attini* in several important particulars as summarized by Wheeler (1907, pp. 784-785).

In the first place the termites use their own excrement as a substratum, moulding it into the form of a sponge containing numerous habitable chambers and galleries. This substance is, of course, much harder and more compact than the comminuted leaves, etc., employed by the *Attini*. Second, the fungus grown on this substratum forms bromatia (the spherules or oñial heads) of a very different type from those found in the gardens of the *Attini*. And third, the termites that are in the habit of growing fungi are not exclusively mycetophagous like the *Attini*, but subsist also and probably very largely on dead wood, twigs and leaves.

According to Bugnion (1914a, p. 171), the larvæ and the royal pair alone are nursed with the bromatia of the fungus, while the adult workers and soldiers feed directly on vegetable fibres and cells. It may further be mentioned that the fungus-growing habit is by no means general in the

order Isoptera, but is restricted to certain paleotropical genera, such as *Microtermes* Wasmann and *Termes* Linnæus, which are regarded as the most specialized members of the group. As in the case of the fungus gardens of the Attini, the identity of the fungi grown by the termites is far from being known beyond question. The fungous sponges found in the termitaria are evidently imperfect forms of higher mushrooms, which have been ascribed to certain Basidiomycetes (Agaricaceæ) by Holtermann (1899), Doflein (1905*b*), and Petch (1906).

The so-called "ambrosia beetles" are all wood-boring Coleoptera whose larvæ do not feed directly on the fibres of the wood but on the bromatia of a fungus which the adults cultivate on the walls of their galleries. The best-known of these are certain Scolytidæ, which furthermore resemble ants and termites and differ from most other Coleoptera in that the adult beetles live in societies and care for and feed their larvæ. Perhaps the most interesting points in this case are that, so far as known, the food of each species of fungus-growing scolytid is limited to a certain kind of ambrosia and only the most closely related species have the same food fungus; also that the origin and further growth of the fungus is entirely under the control of the beetle. When the mother beetle leaves the old burrow to excavate new brood galleries, wherein to deposit her eggs, she transports with her the germs of the ambrosia fungus. Strohmeyer (1911) discovered lumps of mycelium adhering to the dense brushes of hair found on the head of the females of certain exotic Scolytidæ, these brushes being totally absent in the males; he believes that the fungus is transferred in this manner to the new burrows. In other ambrosia Scolytidæ, however, the females show none of these hair brushes, so that the fungus must be carried in some other way. According to Neger (1908*a-d*) the conidia of certain of these mushrooms form a mucilaginous mass which adheres readily to any part of an insect passing over it. In some cases part of the bromatia is preserved in the digestive tract of the adult beetle, and voided in the new burrow (Schneider-Orelli, 1913). The ethology of another wood-boring beetle, the European *Hylecæus dermestoides* (Linnæus), one of the Lymexylonidæ, has been studied by Neger (1908*a-d*, 1909*b*, and 1914) and more in detail by Germer (1912). These investigators have found that the larva, which burrows in dead tree stumps, never feeds on the wood itself. The walls of its galleries are overgrown with a mycelium producing globular bromatia and thick-walled spores, which are cropped off by the larva together with some of the hyphæ. Since the female of *Hylecæus* lays her eggs on the bark of stumps and dies shortly after oviposition,

contain forms which attack living insects. In some other groups, such as the Saprolegniaceæ and the Pythiaceæ, certain species are commonly met with on dead insects; these are, however, mere saprophytes and cannot be properly included among the entomogenous fungi.

From the data collected in this chapter, it is evident that ants are remarkably immune from the attacks of parasitic fungi; only a few species of such ant parasites are known and these are rarely encountered. This is the more surprising since ants exist everywhere in great abundance and have probably been collected and studied in larger numbers than any other group of insects.

At first sight ants would seem to be particularly favorable hosts for such parasites since these insects are in the habit of huddling together in masses in warm subterranean galleries, where the fungi might be supposed to develop luxuriantly and transmit their spores from ant to ant with great facility. Further consideration of the matter, however, leads to the conclusion that other habits of the ants must, in all probability, tend to suppress or render impossible the development of the fungi, except under unusual conditions. All ants devote a great deal of time and attention to cleaning their own integument and that of their nestmates. They are, indeed, forever combing and scraping the surfaces of their bodies with their tongues and strigils, so that fungi must find it difficult to gain a precarious foothold in their nests, to say nothing of an opportunity to proliferate. And even on the rare occasions, when this happens, important organs like the mandibles, antennæ, labium, maxillæ, palpi and eyes are kept scrupulously free from parasitic growth. (Wheeler, 1910a, p. 85.)

The ENTOMOPHTHORACEÆ constitute part of the very extensive class of alga-like fungi or Phycomycetes. By far the majority of the species of this family parasitize living arthropods, though a few genera grow on living or dead plants. "They are distinguished by the production of numerous hyphæ of large diameter and fatty contents, which, in the insect forms, ultimately emerge from the host in white masses of characteristic appearance and produce at their extremities large conidial spores which are violently discharged into the air and propagate the disease. The common house-fly fungus is perhaps the most familiar example of the kind, and no one can have failed to notice the affected flies in autumn or late summer adhering to looking-glasses or window-panes surrounded by a smoky halo of discharged conidia. In addition to these conidia the propagation of the fungus, after long periods of rest, may be provided for by the formation of thick-walled resting spores adapted to withstand successfully the most unfavorable conditions. These resting spores, which may be either sexual (zygospores), or asexual (azygospores), finally germinate and produce conidia that are discharged in the usual fashion and serve to infect fresh hosts." (Thaxter, 1888,

p. 136.) The parasitic forms in this family usually attack soft-bodied insects, such as flies, caterpillars, moths, butterflies, aphids, etc.; the infection results from contact with a conidial spore, which, adhering to the host, enters its body by means of a hypha of germination. These fungi have never been observed on ants, perhaps because they have not been properly looked for, though it is quite possible that the heavy, chitinous integument and the customary cleanliness of ants protects them against infection by such parasites.

The HYPOCREACEÆ belong to the class Ascomycetes, and among them several species of *Cordyceps* afford "by far the most conspicuous examples of entomogenous plants, many of which are of large size, or brightly colored" (Thaxter, 1888, p. 135). In this case, the polycellular mycelium pervades the tissues of the host, which is rapidly killed, and often produces asexual spores or conidia, borne on external hyphæ variously agglutinated or united. In this imperfect, more common condition, they are often described under the generic designation of "*Isaria*" and are then placed, together with other similar imperfect fungi, in the family Stilbaceæ. The mycelium finally produces outside the body of the insect a boll-shaped or club-like organ or fructification, carried on a stalk sometimes several inches in length. The swollen portion of this external stroma bears numerous ascocarps or perithecia containing the spores, which are formed within elongate cells, the asci. As many as eleven species of *Cordyceps* have been described from ants, but some of these are very imperfectly known, especially with regard to the structure of the asci and spores, so that they are much in need of further study. Furthermore, all *Cordyceps* seem to be little or not particular in the choice of their host, the same species often growing indifferently on insects of several orders.

#### **CORDYCEPS** E. Fries

*Cordyceps* E. FRIES, 1818, 'Observ. Mycol. Flor. Suec.,' p. 316.

#### **Cordyceps australis** (Spegazzini)

*Cordyceps unilateralis* subspecies *australis* SPEGAZZINI, 1881, An. Soc. Cientif. Argentina, XII, p. 80 (of separate).

*Cordyceps australis* SACCARDO, 1883, 'Syll. Fungorum, Pyrenomyc.,' II, p. 571.

SPEGAZZINI, 1889, Bol. Ac. Nac. Ciencias Córdoba, XI, p. 536. M. C.

COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 34. MASSEE, 1895, Ann.

of Botany, IX, p. 15; 1898, Revue Mycologique, XX, p. 86. A. MÖLLER, 1901.

'Phycom. u. Ascom. Unters. aus Brasilien,' p. 218, Pl. vi, figs. 92 and 93.

*Cordyceps australis* P. HENNINGS, 1902, Hedwigia, XLI, p. 10.

This species seems to be rather common in southern Brazil, where it was originally discovered near Apiahy on *Pachycondyla striata* Smith by Puiggari, and later seen three times on the same species of ant at Blumenau by A. Möller. It has also been found in southern Brazil on various beetles.

#### ***Cordyceps japonensis* Hara**

*Cordyceps japonensis* HARA, 1914, *Botan. Magazine*, Tokyo, XXVIII, pp. 348 and 351, fig. I.

*Cordyceps* species, HARA, 1913, *Nawa's Insect World*, Gifu, Japan, XVII, p. 472, figs. A-D.

Described from Japan: Province Mino, Kawauye-mura and Province Mino, Kakumuno-ga-hara (K. Hara Coll.); growing on an unidentified ant, to judge from the description, a species of *Camponotus*.

#### ***Cordyceps formicivora* (Schröeter)**

*Torrubia formicivora* SCHRÖETER, 1894, in Cohn, 'Kryptogamen-Flora von Schlesien,' III, 'Pilze,' 2, p. 276.

*Cordyceps formicivora* SACCARDO, 1895, 'Syll. Fungorum,' XI, p. 366.

Growing from the thorax of *Camponotus ligniperdus* (Latreille) on the Warthaberg, Frankenstein, Silesia (Schröeter Coll.).

#### ***Cordyceps Lloydii* Fawcett**

*Cordyceps Lloydii* FAWCETT, 1886, *Ann. Mag. Nat. Hist.*, (5) XVIII, p. 316, fig. SACCARDO, 1891, 'Syll. Fungorum,' IX, p. 1000. M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 36, fig. 9. MASSEE, 1895, *Ann. of Botany*, IX, p. 20; 1898, *Revue Mycologique*, XX, p. 90. C. G. LLOYD, 1919 (June), *Mycological Notes*, No. 59, p. 856, fig. 1437.

This fungus was originally described from a specimen growing on *Camponotus abdominalis* (Fabricius), = *C. atriceps* (F. Smith), and found on the banks of the Puruni River, British Guiana (G. A. Lloyd Coll.). C. G. Lloyd has recently recorded it from Uganda, where it was obtained by W. Gowdey, growing on a dead worker of *Paltothyreus tarsatus* (Fabricius) attached by means of its mandibles to the stalk of a plant: "The fungus is a very minute, white club with a small capitate head and seems to agree very well with the original figure." To judge from C. G. Lloyd's photographs, this parasite is very different from the *Cordyceps* commonly found in the Belgian Congo on the same ant, *Paltothyreus*, and referred below to *C. myrmecophila* (Cesati).

**Cordyceps myrmecophila** (Cesati)

- Hypocrea* (*Cordyceps*) *myrmecophila* CESATI, 1846, in Klotzsch, 'Herb. Mycol., Centuria XI, cura L. Gravenhorst,' No. 1033 (exsiccata with description). D. v. SCHLECHTENDAL, 1846, Botan. Zeitung, IV p. 877. CESATI, 1855, *ibid.*, XIII, p. 75.
- Campylothecium myrmecophilum* CESATI, 1846, in Klotzsch, 'Herb. Mycol., Centuria XI,' No. 1033.
- Hypocrea myrmecophila* BERKELEY AND BROOME, 1851, Ann. Mag. Nat. Hist., (2) VII, p. 186.
- Cordyceps myrmecophila* CESATI, 1858, in Klotzsch, 'Herb. Mycol., Ed. Nov., Centuria VIII, cura L. Rabenhorst,' No. 719 (exsiccata with description). D. v. SCHLECHTENDAL, 1858, Botan. Zeitung, XVI, p. 302. M. J. BERKELEY, 1860, 'Outlines of British Fungology,' p. 382. W. NYLANDER, 1869, Notis. Sällsk. pro Fauna et Flora Fenn. Förhandl., X, p. 88, Pl. II, figs. 4a-d (separate in 1868). SACCARDO, 1883, 'Syll. Fungorum, Pyrenomyc.,' II, p. 566. G. MASSEE, 1886, Grevillea, XV, No. 73, p. 2. M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 31, fig. 6. MASSEE, 1895, Ann. of Botany, IX, p. 14; 1898, Revue Mycologique, XX, p. 85. RABENHORST, WINTER AND PAZSCHKE, 1890, 'Fungi Europæi,' No. 3649 (exsiccata). F. J. SEAVER, 1910, 'North American Flora,' III, pt. 1, p. 54. STITZ, 1911, Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08), III, p. 377, footnote. C. REA, 1914, Trans. Brit. Mycol. Soc., IV, pt. 2, (1913), pp. 199, 203, and 213.
- Cordyceps* (*Entomogena*) *myrmecophila* CESATI, 1861, Commentario della Soc. Crittogam. Italiana, I, No. 2, p. 61, Pl. IV, figs. II, 1-4.
- Torrubia myrmecophila* M. C. COOKE, 1871, 'Handbook of British Fungi,' II, p. 771. PHILLIPS AND PLOWRIGHT, 1875, Grevillea, III, p. 126.
- Cordyceps myrmecophila* P. HENNINGS, 1904, Hedwigia, XLIII, 4, p. 248. STITZ, 1916, Ergebn. Zweit. Deutsch. Zentr. Afr. Exp. 1910-11, I, p. 371.

This is the most frequently observed fungous parasite of ants, being recorded from the tropical and temperate parts of both hemispheres and attacking many kinds of insects besides ants. It was discovered by Cesati in 1846, at Brescia, in Lombardy, Italy, some three hundred individuals of the same nest being infested by the fungus<sup>1</sup>; the species of ant was not recorded at the time, but W. Nylander in 1869 identified Cesati's specimens—from Klotzsch' exsiccata—as *Formica fusca* Linnæus. W. Nylander mentions it also as occurring in Finland (Jalguba on Lake Onega; A. Kuhllhem Coll.), growing out of the anterior part of the pronotum of *Formica rufa* Linnæus. It was again noted by Hennings from Brazil (Rio Juruá, Juruá-Miry; E. Ule Coll.) on *Dinoponera grandis* (Guérin).

In tropical Africa it seems to show a predilection for the common large ponerine ant, *Paltothyreus tarsatus* (Fabricius). Stitz (1911, p.

<sup>1</sup>"Ce fut un cimetière de fourmis tout entier qui se parait de cette jolie Sphériacée." (Cesati, 1855, p. 75.)

sionally to this species (Fig. 77), though it may be undescribed. It was growing on a dead worker of *Camponotus (Myrmothrix) abdominalis* (Fabricius), fixed on a leaf of a low bush in the forest near the Tropical Research Station of the New York Zoological Society.

***Cordyceps subunilateralis* (P. Hennings)**

*Cordyceps subunilateralis* P. HENNINGS, 1902, Hedwigia, XLI, p. 168; 1904, Nerthus, Pl. 1, fig. 9.

*Cordyceps subunilateralis* P. AND D. SACCARDO, 1905, 'Syll. Fungorum,' XVII, p. 826.

From the confluence of the Para and Surinam Rivers, Dutch Guiana, on the thorax of an unidentified ant (J. Michaëlis Coll.).

***Cordyceps unilateralis* (L. and C. Tulasne)**

*Torrubia unilateralis* L. AND C. TULASNE, 1865, 'Selecta Fung. Carpologia,' III, p. 18, Pl. I, figs. 3-4. BERKELEY AND COOKE, 1876, Journ. Linn. Soc. London, Botany, XV, p. 394.

*Cordyceps unilateralis* SACCARDO, 1883, 'Syll. Fungorum, Pyrenomyc.,' II, p. 570. FAWCETT, 1886, Ann. Mag. Nat. Hist., (5) XVIII, p. 317. THAXTER, 1891, Botan. Gazette, XVI, p. 203. M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 33, fig. 7. MASSEE, 1895, Ann. of Botany, IX, p. 15; 1898, Revue Mycologique, XX, p. 86. SPEGAZZINI, 1912, An. Mus. Nac. Hist. Nat. Buenos Aires, XXIII, p. 76.

This is a rather generally distributed parasite of ants, and it attacks other insects too. Originally described from Brazil on *Atta cephalotes* (Linnaeus), it was again found there on the same ant by Traille.<sup>1</sup> Fawcett records it on *Camponotus abdominalis* (Fabricius), = *atriceps* (Smith), also from Brazil, and on *Echinopla melanarctos* Smith and *Polyrhachis merops* Smith, both collected by A. R. Wallace at Tondano, a village in the island of Celebes. Thaxter found it in North America on an ant which was not further specified at the time, but is, according to Prof. Wheeler's identification, *Camponotus herculeanus* (Linnaeus) subspecies *pennsylvanicus* (De Geer) from North Carolina.<sup>2</sup> Finally, Spegazzini mentions it from an unidentified ant found at Puerto León, Misiones, Argentina.

The external part of this *Cordyceps* consists of a black, very slender, thread-like stroma, 13 to 20 mm. long and  $\frac{1}{4}$  to  $\frac{1}{2}$  mm. thick at the base,

<sup>1</sup>An unidentified *Cordyceps* is figured by J. R. Inda (1907, p. 4, fig. 2) on a leaf-cutting attine ant from Cuarnava and Jolapa, Mexico.

<sup>2</sup>According to information kindly given by Prof. Wheeler, there are also in Prof. Thaxter's collection unidentified *Cordyceps* on *Camponotus herculeanus* subspecies *pennsylvanicus* variety *noveboracensis* (Fitch) from Maine, and on *C. abdominalis* (Fabricius) from Trinidad. An unidentified *Cordyceps* has also been mentioned on *Camponotus sexguttatus* from Brazil by Fawcett (1886, p. 317).



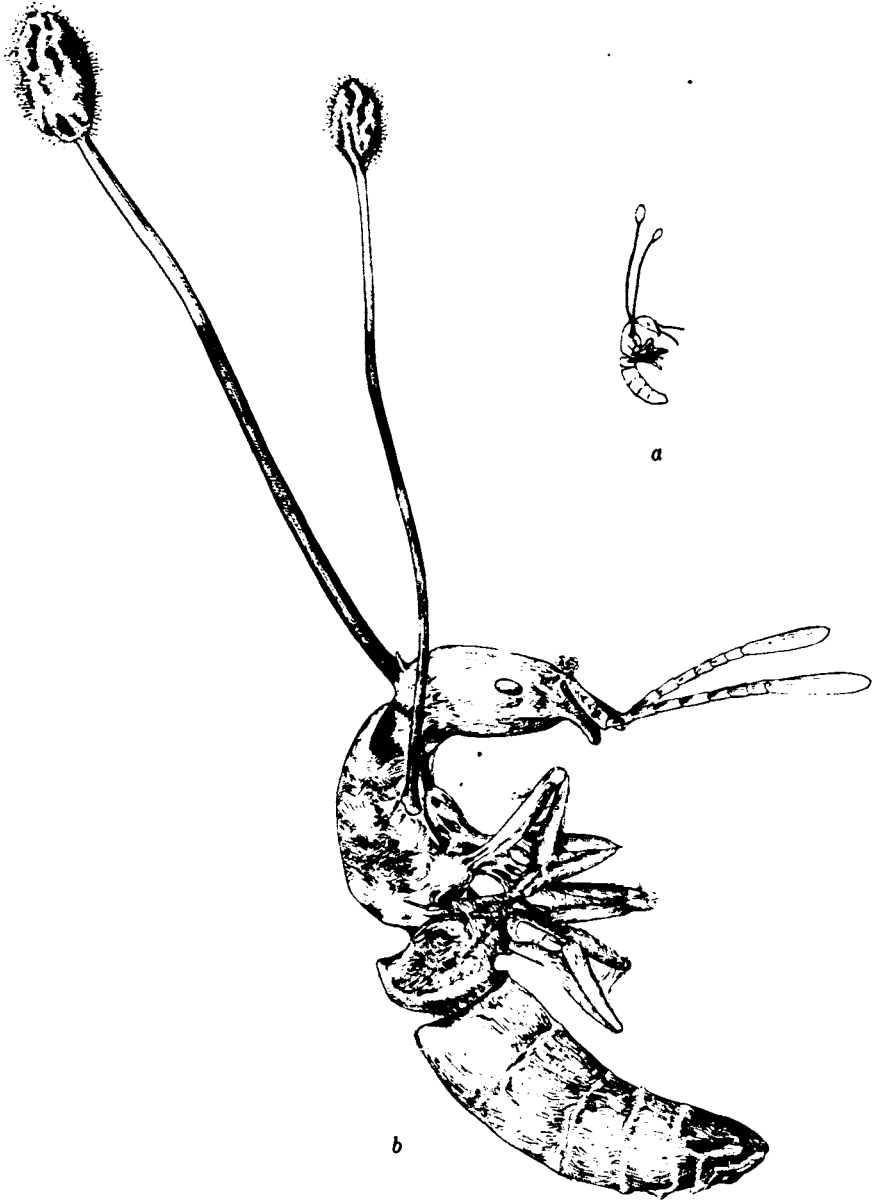


Fig. 79. *Isaria myrmicida* C. G. Lloyd, growing on *Pachycondyla striata* F. Smith, at Tijuca, in the vicinity of Rio de Janeiro, Brazil: a, natural size; b,  $\times 7$ .

***Isaria myrmicidæ* C. G. Lloyd**

*Isaria myrmicidæ* C. G. LLOYD, 1920, Mycological Notes, No. 62, p. 915, Pl. CXLIII, figs. 1636 and 1637.

The above name is given by C. G. Lloyd to a parasite found in Brazil by J. Rick on an unidentified ant; his figure evidently represents the petiole and gaster of a ponerine, perhaps of the same species of *Pachycondyla* mentioned below as host of this fungus. The brief description reads as follows: "This is not a *Cordyceps* as would appear from the photograph but an *Isaria* which is only named for convenience in the museum. Our figure (Fig. 1636) enlarged six-fold tells all to be told about it. Fig. 1637 is natural size. The stem is about a centimeter long, slender and black. The head is cylindrical and white. Spores are 'pip-shape,'  $2 \times 8$ ."

Fig. 79 shows a parasite of *Pachycondyla striata* F. Smith,<sup>1</sup> which is evidently Lloyd's "*Isaria myrmicidæ*." The drawing was made from a specimen in the Herbarium of the New York Botanical Garden kindly loaned to me by Dr. N. L. Britton and Dr. F. J. Seaver. It was obtained by J. N. Rose and P. G. Russell in 1915 at Tijuca, in the vicinity of Rio de Janeiro, Brazil.

***Stilbum formicarum* Cooke and Massee**

*Stilbum formicarum* COOKE AND MASSEE, 1889, Grevillea, XVIII, No. 85, p. 8.  
M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 38, Pl. 1, fig. 12.

An undetermined species of ant, sent from Cheltenham, Victoria, Australia, was bearing upon its body a little *Stilbum*, with elongated slender stems, from five to eight millimeters in length, black, and flexuous, slightly thickened towards the base, and bearing at the apex an obovate, pink-colored capitulum or head, with elliptical conidia ( $10\mu$  long and  $3\mu$  broad). Several of these fungi occurred on the body of each dead insect.

The genus *Stilbum* comprises imperfect fungi, usually placed in a family STILBACEÆ. Most of the species are saprophytic and only a few have been found on insects. It is quite possible that the Australian form mentioned here represents the conidial form of some ant-attacking *Cordyceps*, and I have, therefore, thought it convenient to mention it in connection with the Hypocreaceæ.

<sup>1</sup>The ant was identified by Prof. Wheeler.

Mycolog. France, XXIX, p. 511. SPEGAZZINI, 1914, Redia, X, (1915), p. 29, Pl. I, fig. 2. REHM, 1903, Ascomyceten, No. 1451 (exsiccata).

This is apparently the only fungous ant parasite commonly found in Europe. Originally described from Linz on the Rhine, Germany, where Wasmann found it on *Myrmica lævinodis* Nylander, it was observed by Rick on the same ant at several other localities in Luxemburg (Belle Vue), Germany (Berncastel on the Moselle), and Austria (Feldkirch and Garina in the Vorarlberg). Spegazzini mentions it from Italy on *Myrmica scabrinodis* Nylander (Fig. 80a-b).

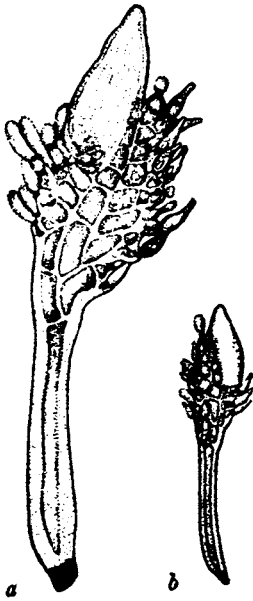


Fig. 80. *Rickia Wasmannii* Cavara, a parasitic fungus of *Myrmica lævinodis* Nylander in Europe. Mature individual: a,  $\times 600$ ; b,  $\times 290$  (after Thaxter, 1908).

Donisthorpe (1912, p. 5; 1913, p. 96; 1915, p. 154) mentions the discovery at Rannoch, England, of a nest of *Leptothorax acervorum* (Fabricius), all the ants of which were covered with a fungus, though quite alive. The specimens, unfortunately, were lost, but the author thinks that the fungus was probably a species of Laboulbeniaceæ.

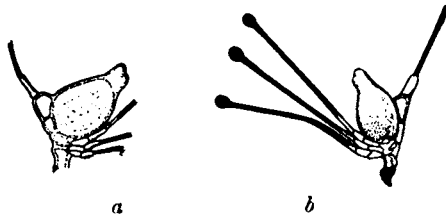


Fig. 81. *Rickia formicicola* Spegazzini, a parasitic fungus of *Prenolepis silvestrii* Emery in Argentina. Two mature individuals,  $\times 300$  (after Spegazzini, 1917).

### ***Rickia formicicola* Spegazzini**

*Rickia formicicola*, 1917, SPEGAZZINI, An. Mus. Nac. Hist. Nat. Buenos Aires, XXIX, p. 665, fig. núm. 195.

This species (Fig. 81) was found in the island of Santiago, La Plata, Argentina, growing on *Prenolepis silvestrii* Emery.

### ***Laboulbenia formicarum* Thaxter**

*Laboulbenia formicarum*, 1902, THAXTER, Proc. American Ac. Arts Sci. Boston, XXXVIII, p. 39; 1908, Mem. American Ac. Arts Sci. Boston, XIII, No. 6, p. 359, Pl. LVIII, figs. 14 and 15. WHEELER, 1910, Psyche, XVII, pp. 83-86. J. BEQUAERT, 1920, Bull. Brooklyn Ent. Soc., XV, p. 71.

This parasite (Fig. 82a-b) attacks various species of North American ants; strange to say, it has only been recorded thus far from the vicinity of Boston, where it appears to be rather common. Thaxter discovered it at Cambridge, Massachusetts, on *Lasius niger* variety *americanus* Emery and *Formica subpolita* variety *neogagates* Emery. Wheeler found the same fungus infesting nearly all the nests of *Lasius niger* variety *neoniger* Emery, on the seashore at Ellisville, Massachusetts, and gives some interesting details with regard to the ecology of the infested colonies.

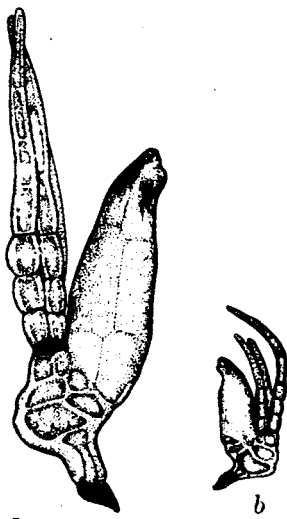


Fig. 82. *Laboulbenia formicarum* Thaxter, a fungous parasite of various North American ants. Mature individuals: a,  $\times 625$ ; b,  $\times 280$  (after Thaxter, 1908).

On the beach itself, which consists of a deep layer of pure sand, there are colonies of *Formica fusca* variety *argentata* Wheeler, *Myrmica scabrinodis* Nylander variety *sabuleti* Meinert, *Tapinoma sessile* Say and *Lasius neoniger*. The last is far and away the most abundant and its workers are of large size. None of the ants in this locality, including the *neoniger*, was found to be infested with *Laboulbeniaceæ*. On the border of the salt meadow, however, immediately adjoining the beach, where the soil is moist, consisting of a mixture of rather sour, decomposing humus mixed with sand, and probably not infrequently wetted by the spray and occasionally even submerged at very high water, the only ant is *L. neoniger*, but its colonies are less populous than those on the beach, the workers are distinctly smaller and are practically all infested with the *Laboulbenia*. Passing over from this zone of infestation to the pasture land adjoining the salt meadow, the variety *neoniger* is replaced by *L. niger* L. variety *americanus* Emery which is the form of the species commonly occurring in higher and dryer pastures and fields. None of the workers of this form, which lacks on the scapes and legs the erect hairs so conspicuous in the variety *neoniger*, was found to be infested with the

fungus. It would seem, therefore, that while *neoniger*, unlike any of the other ants, is able to exist in a depauperate condition in the damp, sour soil at the edges of salt meadows, it does so only at the risk of becoming infested with *Laboulbenia formicarum*. Indeed, the infestation of the ants in this strip of littoral at Ellisville is often so excessive that they resemble hedgehogs, fairly bristling with tufts of the fungus. (Wheeler, 1910a, p. 84.)

Though *Laboulbenia formicarum* may occur on all parts of its host, it appears from Wheeler's observations that it grows most abundantly on the abdomen, middle and hind femora and tibia, and posterior portions of the head. The thorax and coxæ, as a rule, are entirely free from the fungus; the clypeus and gula are generally free, and this seems to be invariably the case with the mandibles, antennal funiculi, palpi, labium,

maxillæ, and eyes. In a very few specimens, one or two of the little plants were seen on the antennal scapes, but, as a rule, these organs are perfectly clean.

In August 1919, I took a worker of *Formica pallide-fusca* subspecies *schaufussi* Mayr infested with *Laboulbenia formicarum* at Forest Hills near Boston. I was, however, unable to locate the nest to which this individual belonged, but this observation shows once more that this fungus, though restricted to ants, attacks indifferently many species (Bequaert, 1920). Prof. Thaxter has also informed Prof. Wheeler that he has taken this *Laboulbenia* on various species of *Formica*, at Cambridge, Massachusetts.

Several so-called "imperfect fungi"—incompletely developed, conidia-bearing or sterile stages of various Ascomycetes—are known to attack insects, and some of these have been seen on ants. I have mentioned above *Stilbum formicarum* Cooke and Masee and have also alluded to the *Isaria* stage of *Cordyceps*, which may be expected on ants, since so many species of the latter genus have been found in the ascibearing stage on these insects. H. Bischoff (1912) has mentioned the finding by Quiel, at Potsdam, Germany, of two nests of *Formica rufa* heavily infested with fungous growths, about the size of a pin-head and attached mainly to the thorax, more rarely to other parts of the body. The ants were apparently but little hampered by their parasites. From cultures obtained with these fungi, Bischoff concludes that they belonged to several species, among them a *Mucor* (of the *spinulosus* group), a *Penicillium*, and a yeast with sexual reproduction; characteristic brown hyphæ present in the tufts on the ants, were not obtained in the cultures. More recently, Thaxter (1914, p. 239) found in the vicinity of Cambridge, Massachusetts, a fungus forming blackish incrustations on various parts of ants, and giving rise to a few short, colorless, erect branches; the exact nature of this plant has not been determined, nor is the name of its host mentioned.<sup>1</sup>

Thaxter (1891, p. 203, Pl. xx, figs. 1-9) has described, under the name *Desmidiospora myrmecophila*, a new genus and species of fungus which was growing luxuriantly on a large black ant fastened to the under side of a rotting log in Connecticut.<sup>2</sup> The hyphæ, much branched and septate, covered the host in a white flocculent mass; they emerged

<sup>1</sup>J. Leidy (1884) has recorded finding in Pennsylvania a *Camponotus pennsylvanicus* under the bark of a decaying tree: it was infected with a fungus which spread through every part of the body. This may have been a saprophytic fungus which had invaded the ant after death.

<sup>2</sup>This ant has recently been identified by Prof. Wheeler in Prof. Thaxter's collection as *Camponotus herculeanus* subspecies *pennsylvanicus* (DeGeer). Prof. Thaxter also possesses the same fungus from New Hampshire, growing on the subspecies *pennsylvanicus* and its variety *noreboracensis* (Fitch).

especially from between the abdominal segments, enveloping the insect more or less completely and extending a short distance over the substratum. The spores are of two kinds, the microconidia being minute ( $12 \times 2 \mu$ ), hyaline, subfusiform, and produced at the apex of subulate lateral basidia; while the macroconidia are much larger, terminal, brown, flat, multilocular, irregularly lobed, up to  $\frac{1}{10}$  mm. broad ( $80-100 \times 68-90 \mu$  and  $12-14 \mu$  thick). Thaxter remarks that it is not impossible that this fungus is an imperfect form of some *Cordyceps* or possibly parasitic on an immature *Isaria* or *Cordyceps* previously developed within the insect. As it is, Thaxter places *Desmidiospora* among the Hyphomycetes and Lindau<sup>1</sup> regards it as genus of the Mucedinaceæ. Some years ago Patouillard (1892) described, under the name *Hirsutella entomophila*, a curious fungus found growing on a beetle in Ecuador. At first sight it resembled an *Isaria*, but Patouillard thought he had observed that the spores were borne on basidia; he, therefore, included this parasite among the Basidiomycetes, placing it in the Clavariæ. Recently, however, Speare (1920) has shown that this, as well as similar fungi, do not produce true basidia and must be removed from the Basidiomycetes. It is rather a definite form of imperfect fungi, probably a stage of one or more species of *Cordyceps* or related genera. In the same paper, Speare remarks apropos of *Desmidiospora myrmecophila* Thaxter (p. 65): "While its resting spores are anomalous in character, and although no structures analogous to the synnemata of *Hirsutella* were described, its subulate sporophores and fusoid spores are of the same type as the corresponding organs of the form under consideration."

A snowy white mould, *Sporotrichum minimum* Spegazzini (1881, pt. 4, p. 123 of reprint; Saccardo, 1886, p. 101; M. C. Cooke, 1892, p. 37), also one of the Mucedinaceæ, was found in Argentina upon the putrescent body of *Acromyrmex lundii* (Guérin), in a rotten trunk. It was diffused over the insect, at first in a powdery and then a cottony white stratum, forming minute tufts. The threads were creeping and densely interwoven, branched, very slender (scarcely  $2 \mu$  in diameter), sparingly septate, hyaline, with conidia scattered here and there.

It is possible that both this *Sporotrichum* and Thaxter's *Desmidiospora myrmecophila* are mere saprophytes, which have grown over the ant after the death of the insect.

*Hormiscium myrmecophilum* Thaxter, another imperfect fungus found on ants, is described by Thaxter (1914, p. 238, Pl. XIX, figs. 22-25) as follows: "Filaments nearly hyaline, becoming brownish, darker near

<sup>1</sup>In Engler and Prantl, 1900, Die Natürl. Pflanzenfam., I. Abt. 1\*\*, p. 454.

living in symbiosis with their host. Special devices, often of a complicated nature, assure their transmission within the insect egg from one generation to another, so that they have become normal constituents of all the members of certain species, genera, families, or even higher groups of insects. Some of these micro-organisms float freely in the lymph, and in many cases great numbers of them also fill the plasma of certain fat-cells, thus forming so-called "mycetocytes." The mycetocytes may occur isolated in various parts of the body, or they may be grouped together and even more or less fused into special fungous organs, the "mycetoms." Sometimes micro-organisms of two or even three different kinds live within separate cells of the same host, either quite apart from one another or in compound mycetoms. Typical illustrations of intracellular mycoses are presented by certain hemipterous insects. In particular, all the Homoptera possess such intracellular, hereditary symbionts; their mycetoms are often enclosed within a pigmented epithelium and connected with special branches of the tracheal system of the insect (P. Buchner, 1913).

Intracellular symbionts also occur in certain ants, and it is probable that their presence in these insects is more frequent than is known at present. They were first seen by Blochmann (1884, 1888) in *Camponotus herculeanus* subspecies *ligniperdus*, densely filling cells which this investigator regarded as belonging to the epithelium of the intestine. According to Buchner's recent researches (1919) the intracellular organisms of that ant are really contained in special mycetocytes placed in a continuous layer beneath and between the true epithelial cells of the mid-gut. They are present in all individuals in the form of tiny, thread-like bodies, 10 or 12  $\mu$  long, generally regarded as bacteria. At the beginning of the sexual maturity of the insect, some of the symbionts leave their mycetocytes, in the worker as well as in the queen. They invade the egg-follicles from all sides and penetrate the egg, the entire plasma of which at first becomes densely filled with bundles of bacteria placed parallel to one another; but, as the egg grows, these organisms are pushed to its posterior pole. Blochmann found similar, but smaller (4 to 5  $\mu$ ), organisms in *Formica fusca*, where they occupy two groups of cells in the adipose tissue. According to Buchner (1918, p. 77, footnote), intracellular bacteria live in many species of *Camponotus*, such as *C. senex* (F. Smith), *C. maculatus* subspecies *congolensis* Emery, *C. maculatus* subspecies *brutus* (Forel), *C. maculatus* subspecies *atramentarius* Forel, *C. rectangularis* subspecies *rubroniger* Forel, and perhaps in all the members of that genus. But they are absent in many other ants, as, for instance, in *Myrmecina latreillei* Curtis.

## 2. A REVIEW OF AFRICAN MYRMECOPHYTES

For all practical purposes, ant-plants or myrmecophytes may be briefly defined as plants which during life are continuously inhabited by certain species of ants. This definition, however, calls for certain explanatory remarks which will be found in the introduction to the general review of recorded ant-plants (p. 494). What is known of the ecology of African myrmecophytes has been brought together in the present chapter, in addition to my own field observations. For the convenience of the entomologist, I have compiled from the taxonomic literature the technical descriptions of these plants. To most students they will, I fear, not be much more helpful than they were to me; but descriptive botany seems able to offer nothing better. In themselves, they afford sufficient apology for the fact that in so many cases a correct identification of the plant in question can not be made.<sup>1</sup> It is to be hoped that the absence of a specific name will not render the observations recorded entirely valueless, since more often than not future field workers will be able to recognize the plants by some of the peculiarities shown in the drawings or mentioned in the text.

Being more familiar with the African flora, I may be permitted to call attention to a few general features of myrmecophytism as suggested by a consideration of African ant-plants. Certain of these remarks may also apply to myrmecophytes of other regions, while some perhaps could not be generalized without modification.

(a) Though over 30,000 species of flowering plants have been described thus far from the Ethiopian Region, only 42 of them can be regarded as more or less well-defined or probable myrmecophytes. In not more than 20 of these cases have the relations to ants been established from actual observation; for the remaining 22 species myrmecophily is merely surmised from analogy with what is known of their near relatives.<sup>2</sup> In other tropical parts of the world, the number of plants with special accommodations for sheltering ants is somewhat higher (about 116 species in the Neotropical and 109 species in the Indomalayan, Papuan, and Australian Regions), but it must be remembered that their floras are much richer than that of the Ethiopian Region, so that their proportion of myrmecophytes is but little if any higher. The compara-

<sup>1</sup>In the case of plants collected by me, numbers are given referring to my herbarium specimens which are now in the hands of Prof. E. De Wildeman, Director of the Brussels Botanical Garden. Some of these specimens have been identified by that authority and their study will undoubtedly be completed in the near future.

<sup>2</sup>Sixteen myrmecophytes are at present known from the Belgian Congo. According to the latest data available, 6372 species of Spermatophyta, belonging to 1261 genera, had been described from that region at the end of 1918 (Goossens, V, 1919. 'Aperçu de nos connaissances actuelles sur la flore du Congo belge.' Bull. Agricole du Congo Belge, X, pp. 154-161).



tively small number of myrmecophytes is rather surprising considering the abundance and variety of tropical plant life and the many opportunities which ants must have had to become acquainted with it.

■ (b) The African myrmecophytes belong to a few taxonomic types, represented by 7 families and 12 genera, as follows:

Leguminosæ	<i>Schotia</i> , with 1 species.
Euphorbiacæ	<i>Macaranga</i> , with 2 species.
Sterculiacæ	<i>Cola</i> , with 3 species.
	<i>Scaphopetalum</i> , with 2 species.
Flacourtiacæ	<i>Barteria</i> , with 5 species.
Apocynacæ	<i>Epitaberna</i> , with 1 species.
Verbenacæ	<i>Vitex</i> , with 2 species.
Rubiaceæ	<i>Uncaria</i> , with 1 species.
	<i>Sarcocephalus</i> , with 1 species.
	<i>Randia</i> , with 3 species.
	<i>Plectronia</i> , with 6 species.
	<i>Cuviera</i> , with 15 species.

*Schotia*, *Cola*, *Scaphopetalum*, *Barteria*, *Epitaberna*, and *Cuviera* are precinctive Ethiopian genera, while the others are either also represented in the Oriental and Indomalayan Regions (*Macaranga*, *Sarcocephalus*, *Plectronia*) or tropicopolitan (*Vitex*, *Uncaria*, *Randia*). The family Rubiaceæ leads the list with the largest number of myrmecophilous species (26, belonging to 5 genera), which is true also in other tropical regions. For *Barteria*, *Epitaberna*, and *Cuviera*, myrmecophytism is to all appearances one of the generic peculiarities, probably being present in all the members.

It is a curious fact that in the Ethiopian Region and elsewhere some of the largest families of the vegetable kingdom, in which differentiation into species has been most active, show very few (Leguminosæ, Orchidacæ) or no cases of myrmecophily. As illustrations of the latter may be mentioned the Gramineæ, Cyperacæ, Liliacæ, Labiatæ, and Compositæ.

(c) True myrmecophytes are restricted to the sections of the earth situated between the tropics, a fact easily accounted for by the uniform temperature which prevails there and permits ants to establish their perennial abodes within the rather thin walls of plant tissues. I already have shown (p. 371) that the so-called ant acacias of the dry East African plains and *Clerodendron formicarum* of the savannah country are by no means myrmecophytes. When these cases are eliminated, all African ant-plants known at present occur only in the permanently moist and evergreen Rain Forest of the western and equatorial parts of the continent. All the Oriental and Indomalayan and the vast majority of the Neotropical myrmecophytes grow similarly in the moist tropical forest areas.

The one notable exception is presented by the true ant acacias of Central and South America (p. 510), which do not grow in the forests, but only in the open country or savannahs and along road-sides, and in some cases even prefer semiarid regions.

(d) The African myrmecophytes are all perennials and of a woody texture, either bushes, low trees, or woody creepers. This also holds true for the ant-plants of southern Asia, Malasia, and tropical America, though the types there are somewhat more varied, including, for instance, typical epiphytes. It is essential to the prosperity of the ant colonies that their permanency be assured for many years, a condition which, of course, could not be provided by annual or biennial plants. In addition, the woody texture of the walls adds considerably to the solidity of the domatia and to the protection of the formicaries. In a number of cases (*Cola*, *Scaphopetalum*), but not all, the leaves and stems of plants inhabited by ants are abundantly covered with long, stiff hairs.

(e) The structures offered as myrmecodomatia by the ant-plants show but little diversity, are usually of a very simple type, and affect few organs of the plant. There is nothing here comparable with the intricacy and endless variety of adaptations presented by entomophilous flowers to pollinating insects. The following types of myrmecodomatia have been recognized in Africa.

1.—The stipules persist for some time and are much swollen, their recurved margins enclosing a pouch-like cavity: *Macaranga saccifera*. A more primitive condition of stipular myrmecodomatia is illustrated by the *Uragoga* described on p. 453.

2.—The leaves produce pouches at the base of the blade: species of *Cola* and *Scaphopetalum*.

Swollen stipules and leaf pouches may be regarded as myrmecodomatia of a very primitive type. They are not much sought by the ants, probably because they do not offer enough solidity and permanency as shelters for formicaries. In the few cases in which I observed ants using the swollen stipules of *Macaranga saccifera* and the foliar pouches of *Cola Laurentii* and *Scaphopetalum Thonneri*, the colonies were very small and the ants timid.

3.—The stems of the plant are externally normal, but hollowed out practically their entire length: *Vitex Staudtii* and *Barteria Deweyrei*.

4.—The stems present fistulose swellings either in the middle of the internodes (*Randia Lujæ* and *R. myrmecophyla*), in, above, or below the nodes (*Uncaria*, *Sarcocephalus*, *Plectronia*, and *Cuviera*), or at the base of certain branches (*Barteria fistulosa*).

are no swellings and the normal stems are filled with pith. Penzig believes that the ants trim the growing upper end of the branch in order to enter the pith and are thus responsible for the dichotomous inflorescence of this species. I am rather inclined to think that the galleries are bored by some insect larva and are only settled by ants after being left by their maker.

Annibale (1907a) mentions two other African Bignoniaceæ, *Kigelia africana* (Lamarck) and *Newbouldia lævis* (P. de Beauvois), as "myrmecophilous" because he found nectaria on the under side of the leaves. In addition, herbarium specimens of *Newbouldia lævis* examined by him were hollow in the upper part of the flowering branches, the cavities having one or two apertures at the base. The author assumes that these hollows are natural formations of the plant and are settled by the ants, which pierce the exit holes. He does not state that these insects were actually found in the branches, and the explanation offered above for similar cavities in *Stereospermum* is probably also true here.

*Grumilea venosa* Hiern (Rubiaceæ). Belgian Congo. "Bush of about 2 m., always inhabited by numerous black ants" (Dewèvre; see De Wildeman and Durand, 1901, p. 130).

*Microdesmis puberula* J. D. Hooker (Euphorbiaceæ). Belgian Congo. "Ém. Laurent regarded this plant as a myrmecophyte; indeed some of the branches on specimens collected at Bombaie and provided with witch-brooms, are excavated with galleries; but the myrmecophytic character is not much pronounced." (De Wildeman, 1910, 'Études Flore Bas- et Moyen-Congo,' III, 2, p. 250.)

In addition to the ants indicated in the general account of African myrmecophytes which follows, Father Kohl collected at Stanleyville and in nearby localities a number of species "in myrmecophilous plants" which have not been identified thus far in the literature. I subjoin a list of these insects, compiled from Forel's recent paper (1916) on the ants collected in the Belgian Congo by Kohl:

- Crematogaster ruspolti* variety *atriacapis* (Forel).
- C. sjöstedti* subspecies *kohliella* (Forel).
- C. nigeriensis* variety *wilniger* (Forel).
- C. kasaiensis* (Forel).
- C. kohli* (Forel).
- C. solenopsides* subspecies *flavida* variety *convexiclypea* (Forel).
- Monomorium oscaris* subspecies *springualense* variety *paternum* Forel.
- M. exiguum* subspecies *flavescens* Forel.
- Leptothorax evelynæ* Forel.
- Tetramorium simillimum* subspecies *isipingense* variety *dumezi* Forel.

*Engramma laurenti* variety *congolense* Forel.  
*Prenolepis grisoni* Forel.

### Leguminosæ

Though this is one of the four or five largest families of plants and contains many of the more common bushes and trees of the tropics, only very few of its members are known to be myrmecophytes. After the elimination of the East African so-called "ant acacias," which, as I have shown elsewhere, do not possess true myrmecodomatia, there remains in Africa only one genus that possibly presents biocenotic associations with ants.

### SCHOTIA Jacquin

*Schotia* JACQUIN, 1786, 'Collectanea Austriaca ad Botanicam Chemiam et Historiam Naturalem Spectantia,' I, p. 93. OLIVER, 1871, 'Flora of Tropical Africa,' II, p. 309. HARMS, in Engler and Prantl, 1897, 'Die Natürl. Pflanzenfam.,' Nachträge zu III, pt. 3, p. 196.

*Theodora* MEDIKUS, 1786, 'Theodora speciosa, ein neues Pflanzengeschlecht,' p. 16. TAUBERT, 1894, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' III, pt. 3, p. 138.

"Unarmed trees or shrubs. Leaves abruptly pinnate, with coriaceous often small leaflets; stipules small. Flowers red or purple, clustered in short often dense panicles, heads or racemes. Bracts and bracteoles caducous or subsistent. Calyx-tube turbinate, campanulate or narrowly infundibuliform; segments 4, much imbricate. Petals 5, slightly unequal, clawed or sessile, longer or shorter than the calyx, imbricate. Stamens 10, free or shortly coherent below; anthers uniform, dehiscent longitudinally. Ovary stipitate with elongate style and small terminal stigma; ovules 4 to 8 or 10, or more. Legume oblong, often falcate, compressed, coriaceous, dehiscent or subdehiscent. Seeds exalbuminous" (Oliver, 1871).

This genus belongs to the subfamily Cæsalpinioidæ, in which the flowers are not of the papilionaceous type usual in the family, but possess a rather spreading, zygomorphous corolla; in the bud the upper sepals and petals are covered by the lower. *Schotia* is restricted to tropical and southern Africa and contains twelve species, one of which is supposed to be myrmecophytic.

### *Schotia africana* (Baillon)

*Humboldtia africana* BAILLON, 1870, 'Histoire des Plantes,' II, p. 99, footnote (Tropical West Africa).

*Schotia humboldtioides* OLIVER, 1871, 'Flora of Tropical Africa,' II, p. 310. HARMS, 1915, in Engler, 'Die Pflanzenwelt Afrikas,' III, pt. 1, p. 454, fig. 249.

*Theodora africana* (Baillon) TAUBERT, in Engler and Prantl, 1894, 'Die Natürl. Pflanzenfam.,' III, pt. 3, p. 138.

"A glabrous tree of 25 to 30 feet; extremities (in our specimens) tumid immediately under each node, narrowing gradually nearly to the middle of the internode. Leaves  $\frac{1}{2}$  to 1 ft. long, 2- to 4-jugate, glabrous; leaflets thinly coriaceous, the

lowest pair near the base of the leaf, obliquely elliptic-oblong, narrowly acuminate, base very oblique rounded;  $4\frac{1}{2}$  to 6 in. long,  $1\frac{3}{4}$  to  $2\frac{1}{3}$  broad; petiolule 0 to 1 line. Racemes solitary, or 2 or 3 from the axils,  $1\frac{1}{2}$  to 2 in. long, densely many-flowered. Bracteoles broadly ovate, about  $\frac{1}{2}$  line long. Flowers patent, on pedicels of about 1 line. Calyx  $\frac{2}{3}$  to  $\frac{3}{4}$  in. long, puberulous or glabrate, the tube but slightly exceeding the limb. Petals oval or ob-lanceolate narrowed at base, slightly longer than calyxlobes. Filaments glabrous, very shortly unequally coherent at the base. Ovary and gynophore pilose; ovules 4 to 5. Legume unknown.

"This plant so much resembles species of the Indian genus *Humboldtia*, that in the 'Genera Plantarum' (of Bentham and Hooker) it is referred to as an African species of that genus. Except in the long narrow calyx-tube and fewer ovules, I do not find any technical character of importance to distinguish it from the other *Schotia*. The minute bracteoles, which persist until flowering, do not enclose the young bud" (Oliver, 1871).

Cameroon: River Cameroon (Mann).

According to Harms (1915), who figures the swellings, *Schotia africana* is a tree of the Rain Forest of Cameroon, Spanish Guinea and Gaboon; the internodes of young branches are often swollen towards the upper node and hollow inside. The wall is pierced with a hole through which ants gain access to the inner cavity. This supposed myrmecophyte should be carefully studied in the field. Though having all the appearances of myrmecodomatia, its swellings may still be mere insect galls inhabited by ants after being left by their makers, as is so often the case in the tropics.

### Euphorbiaceæ

#### MACARANGA DuPetit-Thouars

*Macaranga* DUPETIT-THOUARS, 1806, 'Gen. Nov. Madagascariensia,' p. 26. PAX, 1890, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' III, pt. 5, p. 59. PRAIN, 1912, in Thiselton-Dyer, 'Flora of Tropical Africa,' VI, 1, p. 932. PAX, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 298.

Trees or shrubs. Leaves alternate, petiolate, simple or lobed; their base often palminnerved and sometimes peltate, occasionally penninnerved. Spikes or racemes axillary or lateral or sometimes forming a terminal panicle. Flowers dioecious, rarely monoecious, apetalous. Male flowers small, clustered. Female flowers solitary. Bracts distinct or minute, entire or lobed or fimbriate. Male flower: calyx globose, closed in bud, splitting into 3- to 4-valvate lobes; stamens sometimes few (1 to 3), often numerous (10 to 30); filaments short, free, very rarely united or as if branched; anthers short, terminal, usually 4-celled, 4-valved, sometimes 3-celled, 3-valved, rarely 2-celled; no rudimentary ovary. Female flower: calyx truncate or shortly toothed, ultimately wide-cupular or obliquely spathaceous; ovary 2- to 3- (rarely 4- to 6-) celled; styles short, stout, entire, free or slightly united at the base, rarely long, slender or united in a globose mass; ovules in each cell solitary. No disk. Capsule breaking up into 2-valved cocci or occasionally, when 1-chambered, almost indehiscent. Seeds globose; testa crustaceous; albumen fleshy; cotyledons broad, flat. (After Prain, 1912.)

The genus *Macaranga* includes over 170 species of trees and shrubs distributed in Africa and its islands, Indomalaya, and the Australian and Polynesian Regions. Some forty species have been described from Tropical and South Africa, fourteen of which are recorded from the Belgian Congo. It is probable that a number of the African species are more or less associated with ants, since several of the Indomalayan forms exhibit various mutualistic relations with these insects. Ridley is even inclined to believe that in some species of this genus symbiosis of the ants and the plant appears to be as complete as possible (see p. 516).

Two of the African species, *M. saccifera* Pax and *M. Schweinfurthii* Pax, have persistent pouch-like stipules which are occasionally occupied by ants. Ém. Laurent noticed that in another species, *M. dibeleansis* É. De Wildeman,<sup>1</sup> the leaves attract ants, probably by means of the nectaries at the base of the blade; the stipules are more or less concave, not at all pouch-like, and soon deciduous, so that this species probably is not a true myrmecophyte.

#### ***Macaranga saccifera* Pax**

*Macaranga saccifera* PAX, 1894, Engler's Bot. Jahrb., XIX, p. 93, Pl. I. TH. DURAND AND H. SCHINZ, 1896, Mém. Couronnés Ac. Roy. Belgique, LIII, 4, p. 246. É. DE WILDEMAN AND TH. DURAND, 1900, 'Contributions Flore du Congo,' II, p. 57; 1901, 'Reliquiæ Dewevreanae,' p. 212. É. DE WILDEMAN, 1905, 'Mission Émile Laurent,' fasc. 2, p. 130, Pls. XXXIX-XLI; 1908, 'Études Flore Bas- et Moyen-Congo,' II, 3, p. 283. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 496. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 149. É. DE WILDEMAN, 1910, 'Compagnie Kasai, Miss. Perm. Ét. Scient.,' p. 330. ENGLER, 1910, 'Die Pflanzenwelt Afrikas,' I, p. 644, fig. 555. PRAIN, 1912, in Thiselton-Dyer, 'Flora of Tropical Africa,' VI, 1, p. 934. PAX, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 312, fig. 51. É. DE WILDEMAN, 1919, C. R. Ac. Sci. Paris, CLXIX, p. 394.

"A shrub or tree; branches armed with spines, densely tawny-pubescent. Leaves long-petiolate, rounded-ovate, deeply 3-lobed; lobes obovate-oblong or triangular, acute; margin repand or toothed; base narrowly deep-cordate; 8 to 10 in. long, nearly as wide, subcoriaceous, gland-dotted beneath, with a pair of marginal glandular processes at the junction with the petiole; petiole 6 in. long; stipules converted into large coriaceous acute flask-shaped sacs. Male flowers in axillary panicles; bracts ovate, acute, subtending several flowers, buds globose. Female flowers unknown" (Prain, 1912).

Pax (1914) distinguishes two forms:

Variety *α. genuina* Pax and K. Hoffmann, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 312, fig. 51.

<sup>1</sup>Described by De Wildeman, 1908, in 'Études Flore Bas- et Moyen-Congo,' II, pt. 3, p. 281. See also H. Kohl, 1909, p. 150.

"Leaves rather densely glandular underneath. Rachis sparsely pilose; young bracts densely imbricate, almost entire."

French Congo: Libreville (Klaine).

Belgian Congo: Lower Congo: in the Cataract District between Matadi and Leopoldville (Laurent). Kwango: Madibi (Sapin). Kasai: Mukenge (Pogge); Kondué; Batempa; between Lusambo and the Lomami River (Ém. and M. Laurent). Upper Congo: Eala (Pynaert; M. Laurent); Bokakata (Dewèvre); Bumba (Seret); Injolo (Seret; M. Laurent). Eastern Congo Forest: Patalongo near Yambuya (M. Laurent); Panga (December 19, 1913; J. Bequaert; Coll. No. 1552); in the forest between Walikale and Lubutu (village of Mosekowa, January 21, 1915; J. Bequaert; Coll. No. 6700).

Variety *β. dentifera* Pax and K. Hoffmann, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 313.

"Leaves sparsely glandular underneath. Rachis pubescent; bracts more loosely imbricate, denticulate."

Cameroon: Lomie (village of Bumba); Molundu (Mildbraed).

#### **Macaranga Schweinfurthii Pax**

*Macaranga Schweinfurthii* PAX, 1894, Engler's Bot. Jahrb., XIX, p. 92. TH. DURAND AND H. SCHINZ, 1896, Mém. Couronnés Ac. Roy. Belgique, LIII, 4, p. 246. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 496. PRAIN, 1912, in Thiselton-Dyer, 'Flora of Tropical Africa,' VI, 1, p. 935. PAX, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 313.

*Macaranga rosea* PAX, 1899, Engler's Bot. Jahrb., XXVI, p. 328. É. DE WILDEMAN, 1908, 'Études Flore Bas-et Moyen-Congo,' II, 3, p. 283. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 496. PRAIN, 1912, in Thiselton-Dyer, 'Flora of Tropical Africa,' VI, 1, p. 935. MILDBRAED, 1912, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 456.

*Macaranga Lecomtei* BEILLE, 1908, Bull. Soc. Bot. France, LV, Mém., 8, p. 78.

*Macaranga calophylla* PAX, 1909, Engler's Bot. Jahrb., XLIII, p. 221.<sup>1</sup>

"A shrub or tree, sometimes very lofty, reaching 150 feet in height (Chevalier); trunk and branches armed with spines, branches glabrous. Leaves long-petiolate, ovate, shallowly 3-lobed; lobes oblong or triangular, acute; margin irregularly toothed; base narrowly deep-cordate; 6 to 18 in. long, nearly as wide, membranous, becoming firmer with age, gland-dotted beneath, with a pair of glandular processes at the junction with the petiole; petiole 8 to 16 in. long; stipules large, ovate, acute, 1¼ in. long. Male flowers in lateral panicles fasciated in the axils of fallen leaves; bracts concave, thick, entire, subtending many flowers. Stamens 2 to 5 (usually 3). Female flowers in short lateral racemes; pedicels short, stout. Sepals ovate, obtuse. Ovary glabrous, 2- to 3-celled; stigmas spreading. Capsule usually 2-coccous; cocci ½ in. across" (Prain, 1912).

French Sudan: Darbanda in the Boro Valley (Chevalier).

Southern Nigeria: Oban (Talbot).

Cameroon: Tibati; Songalong (Ledermann); Bipindi (Zenker); Johann-Albrechtshöhe (Büsgen).

<sup>1</sup>The synonymy accepted here is from Pax's recent monograph of the Euphorbiaceæ (1914).

French Congo: Brazzaville (Chevalier).

Belgian Congo: Upper Congo: Eala (Pynaert); Ikenge (Huyghe). Kasai: Mukenge (Pogge). North-eastern Congo: Beni (Mildbraed); Mangbetu Country at Munza's (Schweinfurth).

Angola: Bamba (Monteiro); Ambriz (Welwitsch).

Anglo-Egyptian Sudan: Niam Niam Country near the river Diagbe and near the river Djur (Schweinfurth).

Uganda: very common (Scott-Elliot; Bagshawe).

Prain still thinks that *M. rosea* differs from *M. Schweinfurthii* in the shape of the basal sinus of the leaf, which is open in the former and narrow in the latter; Pax (1914), however, believes that both are forms of the same species.

According to Pax (1914), the stipules of *M. Schweinfurthii* are persistent, 3 to 5 cm. long, 2 to 3 cm. broad, slightly saccate at the base, obliquely inserted, acuminate, membranous, glabrous, shortly connate at the base. It is quite possible that, although much less pouch-like than in *M. saccifera*, they may occasionally be occupied by ants, though this has never been observed.

#### ECOLOGY OF *Macaranga saccifera*

This species is one of the common elements of the undergrowth in the Rain Forest of the Congo, in the eastern district of which I frequently observed it. Growing preferably in low-lying, rather swampy portions of primary forest, it is often found along the banks of rivers or at the edge of brooks. All the specimens I saw were low bushes, rarely over three feet high and generally smaller. Since, however, none of them were in flower or with fruit, they may have been juvenile or dwarfed. The very conspicuous, persistent stipules, placed in pairs at the base of the petiole, are always much swollen, saccate or flask-shaped, about 1 to 3 cm. long, and end in a curved, acuminate apex (Fig. 83). Their texture is more or less coriaceous and hispid hairs are scattered over the outer surface. In each stipule the free, lateral margins are curved close to each other, leaving a very narrow, upper slit as entrance to the pouch. At the foot of the leaf-blade occur two folds, one on either side of the petiole, covering nectaries which I have seen visited by ants. De Wildeman formerly supposed that these folds might shelter mites or even be myrmecodomatia, but I doubt whether such is the case.

That the stipular pouches of *Macaranga saccifera* were occasionally used by ants was merely surmised by Pax on account of the analogy of these organs with similar structures of other myrmecophytes. É. Laurent, however, found ants inside the pouches of the specimens which he collected in the Kasai District, Belgian Congo, and this observation



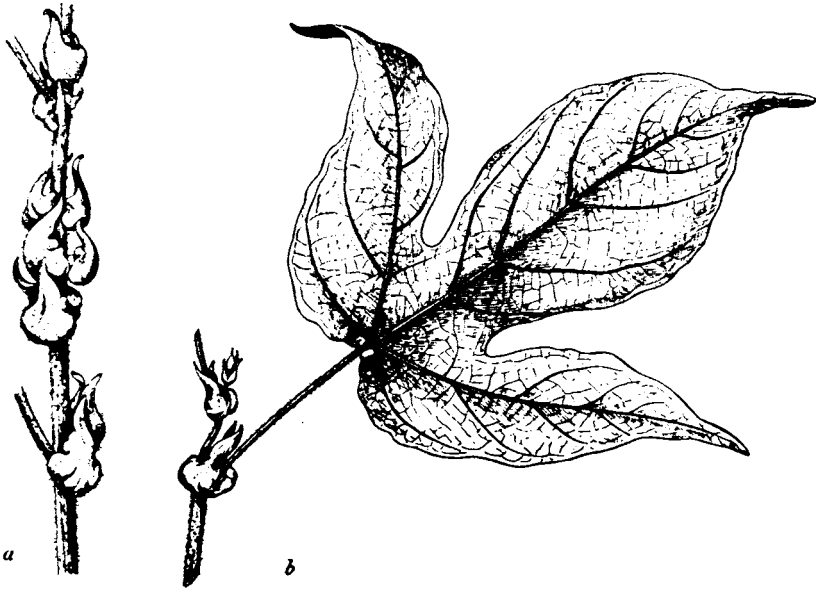


Fig. 83. *Macaranga saccifera* Pax: a, portion of branch with pouch-like stipules; b, extremity of branch with stipules and a leaf seen from above showing the two folds at base of blade. About one-half natural size (after De Wildeman, 1905).

has quite recently been confirmed for my herbarium plants by É. De Wildeman (1919b) who, moreover, points out that *M. saccifera* shelters ants only under certain circumstances. The latter author also mentions that *M. saccifera* has been cultivated for several years at the Brussels Botanical Garden, where it still continues to produce its saccate pouches though these are never utilized by ants.

On only one occasion have I found ants inside the stipular pouches of this plant. Near the village of Mosekowa, between Walikale and Lubutu, in January 1915, a few specimens of *Crematogaster* (*Atopogyne*) *africana* subspecies *tibialis* Santschi occupied some of the stipules. In each case the upper slit leading inside the pouches was not closed with fibres or carton, and no coccids were found with the ants. Since no young or pupæ were present, these pouches can not be regarded as the real nest of the ants, but merely as temporary shelters or annexes. In my opinion, this plant belongs to a very primitive stage of myrmecophily, when compared with some of the other African ant-plants. For this very reason, however, its relations to the ants deserve to be more fully investigated.

### Sterculiaceæ

#### COLA Schott and Endlicher

*Cola* SCHOTT AND ENDLICHER, 1832, 'Meletemata Botanica,' p. 33. MASTERS, 1868, in Oliver, 'Flora of Tropical Africa,' I, p. 220. K. SCHUMANN, 1895, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' III, pt. 6, p. 99; 1900, 'Sterculiaceæ Africanae,' in Engler, 'Monogr. Afrik. Pflanzenfam.,' V, p. 110.<sup>1</sup>

*Educardia* RAFINESQUE, 1814, Specchio delle Scienze, Palermo, I, p. 158 (not *Educardia* Salisbury, 1808).

*Lunanea* A. DE CANDOLLE, 1825, 'Prodromus Regn. Veget.,' II, p. 92.

Trees, shrubs or bushes. Leaves entire or lobed, often polymorph, rarely digitate; glabrous, hairy or scaly. Flowers in axillary panicles or clusters, sometimes out of the old wood. Flowers through abortion unisexual or polygamous. Calyx cup-shaped or campanulate, 4- or 5-cleft. Petals absent. Staminal column sometimes very short, bearing at the top a ring of 10 to 12 anthers, disposed in one or two, regular rows; anther-cells (theæ) parallel or superposed. Ovary 3- to 10-celled, with as many styles as cells. Ovules numerous in each cell. Fruit of 4 or 5 leathery or woody oblong carpels, ultimately splitting lengthwise. Seeds numerous, obovoid, exalbuminous; cotyledons thick, sometimes deeply bifid; radicle next to the hilum. (After K. Schumann.)

This large genus is restricted to the continental part of the Ethiopian Region. About one hundred species have been described, most of which grow in that portion of Africa defined by Engler as the "Western Forest Province" and twenty-five of them occur in the Belgian Congo. A few very closely allied forms possess at the base of the leaf-blade a pair of small pouches which are occasionally inhabited by ants. In addition, these myrmecophilous species differ from their relatives in having branches and leaves covered with numerous long, stiff, erect hairs of a brown or brownish red color; the other members of the genus being glabrous.

#### *Cola Dewevrei* De Wildeman and Durand

*Cola Dewevrei* É. DE WILDEMAN AND TH. DURAND, 1899, Bull. Soc. Bot. Belgique, XXXVIII, 2, p. 184; 1901, 'Reliquiæ Dewevreanæ,' p. 24. É. DE WILDEMAN, 1907, 'Mission Émile Laurent,' fasc. 4, p. 406, Pl. CXXVII. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 62. É. DE WILDEMAN, 1920, 'Mission de Brieri au Mayumbe,' p. 191.

"A low shrub, 1 to 2 m. high. Branches hollow, terete, with long pilosity. Leaves trilobate, deeply cordate at the base, abruptly acuminate at the apex, shiny on upper and under sides, pilose, especially on the veins. Secondary veins arcuately anastomosing toward the margin and uniting with the reticulate finer venation, a little prominent above, more strongly so below. Petiole very long, more or less grooved above, with long pilosity, 6 to 32 cm. long. Leaves 13 to 25 cm. long and 15 to 24 cm. broad. Stipules linear-lanceolate, dropping, pilose, about 6 to 11 mm. long and 1 to 1.5 mm. broad. Flowers yellow, fasciculate, axillary, subsessile, bracteate. Calyx

<sup>1</sup>According to the rules of botanical nomenclature the name *Cola* should be replaced, it seems, either by *Educardia* or by *Lunanea*, since the latter two are not pre-occupied and evidently have priority.

5-lobed, ferruginous tomentose externally, brown and less pilose inside, about 11 mm. long; its lobes 2 to 3 mm. long, acute, with more or less reflexed tips. Androecium of the male flowers stipitate, smaller than the calyx, with subglabrous stipe, 4 mm. long; the anthers placed close together, parallel and united into a ring which is about 15 mm. high" (De Wildeman and Durand, 1899).

Belgian Congo: Mayombe: Lemba River (Dewèvre).

It would seem from the descriptions that the later *C. Laurentii* De Wildeman and the earlier *C. marsupium* K. Schumann are not specifically distinct from *C. Dewevrei*. According to De Wildeman (1907, p. 406), the leaves of *C. Dewevrei* have a different shape from those of *C. Laurentii*, with basal lobes almost touching each other. In these *Colæ*, however, the form of the leaves varies to such an extent even on the same plant that this character is by itself unsatisfactory for the distinction of the species. The existence of foliar pouches is not mentioned in the original description of *C. Dewevrei*, but De Wildeman's figures of that species published in 1907 show them distinctly.

#### **Cola Laurentii De Wildeman**

*Cola Laurentii* É. DE WILDEMAN, 1907, 'Mission Émile Laurent,' fasc. 4, p. 403, fig. 68, Pls. CXXXV, CXXXVI, and CXXXVII; 1908, 'Études Flore Bas- et Moyen-Congo,' II, 3, p. 304. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 63. H. KOHL, 1909, *Natur u. Offenbarung*, LV, p. 148. A. ENGLER, 1912, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 506. É. DE WILDEMAN, 1919, *Bull. Jard. Bot. Bruxelles*, V, p. 358.

"A small tree with cylindric branches densely villose; with brownish, elongate, spreading hairs which drop late. Leaves with more or less lengthened petioles, which are cylindrical, hispid with spreading hairs, 5 to 35 cm. long. Leaf-blade 3-lobed or nearly 5-lobed, cordate at the base; the midlobe about two thirds the length of the leaf, which varies from 11 to 36 cm.; the midlobe is oblong, rather suddenly acuminate at the tip, acute; lateral lobes about of the same shape, a little shorter and narrower than the terminal lobe, which reaches a length of 23 cm. and a width of 13.5 cm. Leaf-blade paler on the under than the upper side or about the same color, with 7 basal veins, the lateral ones often united at the base. Leaf-blade coriaceous, glabrous, except on the veins of both sides, especially on those of the under side which are very prominent and bristling with stiff hairs. Between the midrib and the first lateral vein on each side of it there is a small pouch strongly projecting on the upper side; the two veins between which this pouch is formed are united at the base by a plate of tissue. Stipules filiform, hispid, rather dropping, about 2 cm. long, acute. Flowers fasciculate at the axils of the leaves; the rachis about 1 cm. long; the bracts linear, acuminate, hispid, about 2 mm. long; the pedicels villose, a little over 1 mm. long. Calyx campanulate, about 8 mm. long; with 4 to 5 lobes one-third the length of the tube; calyx densely villose, brownish on the outer side, with more scattered hairs internally. Male flowers with an uniseriate androecium, composed of three a little over 2 mm. long, borne on a slender, feebly elevated androgynophore which is 3 to 4

mm. long and shorter than the calyx-tube. Female flower with a densely villose, ovoid ovary; the style shorter than the ovary, with spreading stigmata which are as long as the calyx-tube. Staminodes reduced, surrounding the base of the ovary. Fruits red, 5 to 6 cm. long including the acumen, with 4 to 5 seeds" (De Wildeman, 1907).

Belgian Congo: Lower Congo: Sabuka (M. Laurent); between Boma and Yanga (R. Verschuren). Kasai: Dibele; Kondué (Ém. and M. Laurent); forest of the Sankuru (Luja). Upper Congo: Eala; Yakusu (Ém. and M. Laurent); Yambinga (M. Laurent); Dundusana (F. Reygaert); Barumbu (November 3, 1913; J. Bequaert; Coll. No. 1081). Eastern Congo Forest: Yambuya (M. Laurent); Basoko (Ém. and M. Laurent); Fariala between Mawambi and Avakubi (f. *integrifolia*; Mildbraed); between Lubutu and Kirundu (village of Uchibango, February 1, 1915; J. Bequaert; Coll. No. 6790); Stanleyville (March 1915; H. Lang).

De Wildeman classified as "form *intermedia*" plants of this species in which entire and trilobed leaves are found on the same branch together with all intermediate shapes; his "form *integrifolia*" includes specimens in which all the leaves are entire, ovate-cordate at the base and as much as 35 cm. long and 18 cm. broad; in this last form pouches are also feebly developed along the midrib in the axils of the first or first and second lateral veins, above the large basal pouches.

In recording the form *integrifolia*, Engler (1912, p. 506) also mentions that in his opinion *C. Laurentii* is not specifically distinct from *C. marsupium*.

#### ***Cola marsupium* K. Schumann**

*Cola marsupium* K. SCHUMANN, 1891, Ber. Deutsch. Bot. Ges., IX, pp. 68-70; 1900, 'Sterculiaceae Africanae,' in Engler, 'Monogr. Afrik. Pflanzenfam.' V, p. 113, Pl. XII, figs. A-D. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 148.

"A shrub or tree, with slender, terete branches, the younger ones flattened and strongly hispid, later glabrescent. Leaves with long, terete, hispid petioles; oblong or obovate-oblong, shortly and very sharply acuminate, cordate at the base; with 7 or even 9 veins; provided with a pair of pouches forming basal swollen domatia between the midrib and the lateral veins; covered with rather long hairs on the veins on both sides, rather rigidly herbaceous. Stipules filiform, hispid, persistent for a long time. Flowers short pedicellate, axillary, fasciculate, placed either at the extremity of branches which are rather sparsely leaved below or on leafless branches. Bracts and bracteoles linear, acuminate, hispid. Calyx campanulate; its upper third split into 4 or 5 ovate, acute lobes; tomentose outside, papillate inside. Male flower: andræcium uniseriate of 16 to 20 thecæ, raised on a gracile, glabrous column. Female flower: ovary subglobose, pentamerous, tomentose; the style glabrous, straight, 5-lobed; 8 ovules in each cell; follicles short stipitate, fusiform.

"The shrub reaches a height of 1 to 2.5 m.; the tree as much as 10 m. The foliate, flowering branches are 3 to 3.5 mm. thick at the base and 20 to 25 cm. long; they are rough, being covered with simple, spreading, brown red or brown hairs, which are thickened into a tubercle at the base. The petiole is 1.5 to 15 cm. long and covered with the same pile. The blade has a length of 6 to 30 cm. and a width of 3 to 13 cm.

above the middle; in addition to the basal veins, it is crossed on each side of the midrib by only 5 to 6 stronger veins, which are a little more prominent on the under side, as is also the reticulate venation; sometimes the blade is somewhat gibbous; in life it is dark green, brownish green when dry. The basal pouches can be entered from the under side; they are not always present, but usually found on the larger leaves. The stipules are 1 to 1.5 cm. long and covered with brown hair. The bracts of the flowers are usually somewhat broader than the stipules, but otherwise similar. The yellowish green calyx is 5 to 7 mm. long. Male flower: andrœcium 1.5 mm. long, as well as the androgynophore. Female flower: calyx slightly larger; ovary 6.5 mm. long, surrounded at the base by a ring of staminodes 2 mm. high. The fruit is red, but perhaps not entirely ripe" (K. Schumann, 1900).

Cameroon: Abo (Buchholz); Johann-Albrechtshöhe: in the Senge Mountains (Staudt).

French Congo: Maveli Mountains near the Sibange Farm (Dinklage).

It seems probable that the three forms described above, *C. Dewevrei*, *C. Laurentii*, and *C. marsupium*, all belong to one species, for which the name *C. marsupium* K. Schumann should be retained. This is, however, a question to be decided by botanists and, in order to avoid any possible confusion, I have here used the name *C. Laurentii* for the plants observed by me in the Belgian Congo, because the description of that species fits them most nearly.

#### ECOLOGY OF *Cola Laurentii*

This plant is rather common in the Congo Basin, where it prefers the drier, more elevated parts of the primitive Rain Forest. It usually grows as a shrub of moderate size (1 to 2.5 m. high), more rarely as a small tree (as much as 10 m. high) and flowers in both forms. The leaves are, as mentioned above, of variable size and shape, usually elongate-oval, with cordate base; the margin may be entire, or slightly or deeply lobate. The pair of basal, elongate-oval pouches on the leaves are more or less developed; wholly absent in certain cases, in others they may attain 15 mm. in length and 5 mm. in width; on the average they are 4.5 to 9 mm. long, 1.5 to 4 mm. broad and 6 mm. high. Placed at the base of the blade close to the midrib, they project on the upper side of the leaf and on the under side have a narrow slit their entire length.

The general aspect of *C. Laurentii* is illustrated on Plate XXVII, Figure 2, by a photograph of a branch, with flowers and fruit, made by Mr. H. Lang at Stanleyville, while the shape of the myrmecodomatia is seen in Text Figure 84. As mentioned by Ém. Laurent (De Wildeman, 1907, p. 405), the pouches are only occasionally occupied by ants. They were empty on most of the many plants which I examined. On one occasion, near the village of Uchibango, between Lubutu and Kirundu (February 1915), ants belonging to the dolichoderine *Engramma kohli*

"Shrub about 2 m. high, covered with brown pile towards the apex of the branches, the stem otherwise glabrous. Leaves alternate, obovate, subcordate at the base, abruptly and sharply acuminate at the apex, entire; greenish-gray above, greenish-brown below, subcoriaceous, not shiny above; glabrous or sparsely pilose near the veins; 14 to 20 cm. long, 4.5 to 6.5 cm. broad beneath the apex, about 2 cm. broad near the base; petiolate, the petiole 5 to 6 mm. long, thick, silky. Leaves asymmetric, unilaterally constricted towards the base, which bears on the upper side a small pouch acuminate towards its tip and opening below in the axil of the penultimate lateral vein. On each side of the midrib there are about 8 lateral veins, projecting slightly on the upper, more strongly on the under side and arcuately anastomosing before the margin; a conspicuous, dense network of anastomosing venules. The basal lateral vein and the midrib, nearly meet on one side of the leaf, and unite by a secondary vein, enclosing thus the opening of the pouch. Stipules subulate, more or less persisting, 5 to 12 mm. long, fasciculate, each cluster 10 to 20 mm. long, branched, axillary, pedicellate, the pedicel 5 to 7 mm. long, bracteate; the bracts subulate, ciliate. Sepals 5, free almost to the base, oblong, velutinous externally, more or less keeled, with three veins. Petals 5, subequal with the sepals, oblong, with recurved apex, hood-shaped, longitudinally striate. Tube of the stamens membranous, pentagonal, sulver-shaped, with 5 fertile edges, the intervening lobes sterile; the fertile lobes opposite the petals. Petals covering the stamens in the bud; there six for each phalange; the three subsessile; sterile lobes briefly tridentate, the median tooth obtuse, the lateral teeth narrow. Ovary oblong, 5-celled. Style entire, erect or slightly curved at the apex. Fruit red, stellate, 7 mm. long and about 3.5 mm. broad, with a prominent, horned apex; it is divided into 5 distinct cells, each of which contains 4 seeds, inserted on a central placenta.

"Differs from *S. Thonneri* in the leaves and fruit, and in the number of ovules or seeds contained in each of the cells of the ovary or fruit" (De Wildeman and Durand, 1901).

Belgian Congo: Eastern Congo Forest: forest at Matchacha (Dewèvre),<sup>1</sup> Kasai: Kondué (Luja).

Dewèvre wrote the following field-notes for his specimens: "calyx green; corolla orange-yellow with red stripes; coronula (or stamen-tube) with red edges; anthers brown; the leaves have at the base a fold inhabited by numerous red-brown ants with black abdomen." Luja found *Engramma lujæ* Forel in the pouches of *S. Dewevrei* at Kondué.

### **Scaphopetalum Thonneri** De Wildeman and Durand

*Scaphopetalum Thonneri* É. DE WILDEMAN AND TH. DURAND, 1897, Bulletin de l'Herbier Boissier, V, June, p. 521, Pl. XXI; 1901, Bull. Soc. Bot. Belgique, XXXIX, 2, p. 96. É. DE WILDEMAN, 1907, 'Mission Émile Laurent,' fasc. 4, pp. 400-402, figs. 66 and 67, Pls. CXXI and CXXII; 1907, *ibid.*, fasc. 5, p. cccxv, fig. XII. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 66. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 110, Pl. I. A. ENGLER, 1912, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 503. É. DE WILDEMAN, 1919, Bull. Jard. Bot. Bruxelles, V, p. 356.

<sup>1</sup>To judge from Dewèvre's itinerary, this locality is situated on the banks of the Congo River (Lualaba) between Ponthierville and Nyangwe; I have not found it on any map.

length of 30 to 40 cm. and a width of 12 to 15 cm.; they may be gradually tapering at the apex, abruptly constricted into an acumen, or even sub-obtuse.

ECOLOGY OF *Scaphopetalum Thonneri*

This species is in many places a common bush of the undergrowth in the primitive, rather dry, and often very shady Rain Forest. Its stems are irregularly branched and never grow very high, usually reaching 1 to 2 m., more rarely as much as 4 m. The young branches are densely covered with stiff, erect, brownish-red hairs, a peculiarity which is often found among myrmecophytes, though far from being the rule. While I have observed this plant in many places and at various seasons, I have but seldom seen it with flowers. These are inconspicuous, yellowish green, with the petals carmine red on the inner side.

The peculiar pouch at the base of the leaf-blade is shown on Plate XXVII, Figure 1, from a photograph taken by Mr. Lang. Such an ascidium is present on all the leaves of the plant, though its size is variable. As a rule, it consists of a very elongate, club-shaped evagination of the blade on the upper side, laterally near the midrib, and opens on the under side by a narrow slit its entire length. This pouch may be 25 to 50 mm. long and is very narrow in the distal half or two-thirds; nearer the base of the leaf it swells rather suddenly and reaches a width of 6 to 8 mm. The slit on the lower surface of the pouch is placed between the midrib and the first lateral vein, which, on that side of the leaf, is deflected from its normal, oblique course and runs close to and parallel with the midrib the whole length of the slit. Furthermore, at the distal end of the opening the deflected lateral vein is connected with the midrib by means of a short cross-vein. As a result of this peculiar structure, the base of the leaf becomes asymmetric, the pouch-bearing side being usually much narrower and tapering more gradually towards the petiole, while the opposite side expands into a broad, semi-cordate lobe which covers the branch. The leaves are apparently arranged alternately in two rows and are more or less horizontal, nearly in one plane. When a branch is seen from above with the extremity farthest from the observer, all the leaves to the right have the pouch on their right half, while those to the left have the pouch on the left half. This arrangement of the leaves and ascidia, more or less distichous in appearance, is well illustrated on the plate.

In most cases the pouches of this plant are empty, but on two occasions, at Barumbu and Yambuya, in November 1913, I found unidentified ants in them. These insects had established regular formicaries

therein, with a queen, larvæ, and pupæ, and had even brought coccids into the cavities; furthermore, they had closed the slit almost completely with a tent of brownish vegetable fibres. At Niapu, in January 1914, Mr. H. Lang collected two species of *Engramma*, *E. kohli* Forel and *E. lujæ* Forel, from the ascidia of this *Scaphopetalum*. So far as recorded, the ants which inhabit these pouches are small and timid; they do not emerge from their retreats when the plant is disturbed and contribute little or nothing to the protection of their host. The leaves of *Scaphopetalum Thonneri* are frequently injured by phytophagous insects, even when their pouches are occupied by ants.

While drawing up the original description, De Wildeman and Durand found a few ants in the pouches of the specimens collected by Thonner and thus recognized the myrmecophily of this species. Émile Laurent's short field-notes are to be found in the account of the plants he collected (De Wildeman, 1907).

#### Flacourtiaceæ

Only one genus of this family, *Barteria*, is definitely known to contain true myrmecophytes. Certain species of other genera have been found in association with ants, but there is reason to believe that they had been settled only by accident. The best-known of these is the African *Buchnerodendron speciosum* Guerke,<sup>1</sup> a common bush or small tree of the primary Rain Forest, also found in forest galleries along streams in the Savannah. On a specimen observed at Romée, near Stanleyville, H. Kohl (1909, pp. 109-110) found that "the branches, 1 m. in length, were all hollow to within 5 cm. of their tips and inhabited by small black ants, *Crematogaster excisa* Mayr.<sup>2</sup> Two or three apertures led into the cavity. I did not find coccids on the inner walls of these branches, several of which I cut open, though such were seen in the axils of the leaves where they were actively attended by the ants." Kohl, however, believes that this plant was only accidentally occupied by ants, an opinion with which I am in complete agreement. I have repeatedly found this *Buchnerodendron* growing under a variety of conditions and, though my attention was especially directed to its possible relations with ants, I never saw any of these insects inside its branches.

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<sup>1</sup>Described in Engler's Bot. Jahrb., XVIII, 1894, p. 161, Pl. iv.

<sup>2</sup>Forel (1909b, p. 69 and 1916, p. 408) identified this ant found by Kohl inside *Buchnerodendron speciosum* as *Crematogaster impressa* Mayr.



In the original description of *Caloncoba Laurentii* (De Wildeman and Durand)<sup>1</sup> the branches of this tree are said to be fistulose and the following notes are given: "*C. Laurentii* is myrmecophilous; the stem is hollow for a long distance and pierced with exit holes at various levels, either at the cicatrice of a leaf base or at any other point along the internode. There were several ants inside the specimens we saw." Gilg, who, it seems, examined some of the type material, did not find the stems hollow nor pierced with orifices, and concluded that one of the branches had been accidentally settled by ants, probably in a former burrow of some wood-boring larva.

#### BARTERIA J. D. Hooker

*Barteria* J. D. HOOKER, 1860, Journ. Linn. Soc. London. Botany, V, p. 14. MASTERS, 1871, in Oliver, 'Flora of Tropical Africa,' V, p. 510.

Tree or shrubs, rarely over 20 m. high, usually much lower, with thick, horizontal branches. Leaves large, leathery, alternate, oblong or oval, subacuminate, almost entire, with short, thickened petioles. No stipules, the decurring base of the leaf forming a raised line on both sides of the stem. Flowers dichlamydeous, hermaphrodite, subsessile, arranged in dense axillary or supra-axillary tufts or rows, rarely solitary; surrounded by overlapping bracts which completely enclose the flower-bud. Calyx-tube short, deeply divided into 5 oblong-lanceolate, overlapping, white sepals, which are silky at the outer side. Petals 5, inserted on the inner edge of the calyx-tube, similar to the sepals, white. Corona duplicate, emerging from the throat of the calyx-tube; outer row membranous, jagged at the edge, about half the length of the petals; inner row much smaller, consisting of a ring of thick, fleshy tubercles. Stamens numerous, monadelphous at the base, emerging from the base of the calyx-tube; filaments in two rows; anthers linear-oblong, introrse. Ovary sessile, globose, surmounted by a single, thick style, which terminates in a large, mushroom-shaped stigma. Ovules numerous, inserted on 3 or 4 parietal placentas. Fruit a coriaceous, ovoid, indehiscent berry; seeds ovoid, compressed, with a crustaceous, coarsely pitted testa.

The genotype, *B. nigrilana* J. D. Hooker, was discovered by Barter at the mouth of the Niger, during the Baikie Niger Expedition (1859). The genus is strictly Ethiopian with a small number of species peculiar to the Rain Forest and extending but little beyond it into the forest galleries of the neighboring grass-lands. The area of its distribution, indicated by the interrupted line on Map 19, falls entirely within the limits of the "Western Forest Province" as defined by Engler. That *Barteria* is thus far unknown from the forests of Upper Guinea, west of

<sup>1</sup>'Contributions Flore du Congo,' I, 1899, p. 8 (Coquilhatville). According to Gilg (Engler's Bot. Jahrb., XL, 1908, p. 463), this is merely a synonym of *Caloncoba Welwitschii* (Oliver), a common bush or low tree in the forests of Cameroon, Gaboon, Belgian Congo, and Angola. The synonymy of *C. Laurentii* and *C. Welwitschii* is accepted by Th. and H. Durand in their 'Sylloge Flore Congoles,' 1909, p. 37. I have very often observed *C. Welwitschii* and never seen it associated with ants.

"Leaves 22 to 24 cm. long, 6 to 7 cm. broad. Petiole about 6 to 8 mm. long, canaliculate above. Sepals 2.8 to 3 cm. long, 10 to 11 mm. broad. Anthers about 3 mm. long" (E. G. Baker, 1905).

Uganda: Musozi on the shore of Lake Victoria, type locality (Bagshawe). This is very close to Bukoba, the type locality of *B. Stuhlmannii* which perhaps is merely a synonym of *B. acuminata*.

### **Barteria Dewevrei** De Wildeman and Durand

*Barteria Dewevrei* É. DE WILDEMAN AND TH. DURAND, 1899, 'Contributions Flore du Congo,' I, p. 8; 1901, 'Reliquiæ Dewevreanae,' p. 97. É. DE WILDEMAN, 1906, 'Mission Émile Laurent,' fasc. 3, pp. 247-249, Pl. xxxii; 1908, 'Études Flore Bas- et Moyen-Congo,' II, p. 316. GILG, 1908, Engler's Bot. Jahrb., XL, p. 480. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 108. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 223.

"Tree 5 to 6 m. high, branched, glabrous. Leaves oblong-elliptic, green above, paler underneath, brown when dried, acuminate, attenuate at the base into the petiole, which is very short, thick, blackish, not stipulate, decurrent; the blade 27 to 34 cm. long and about 11 cm. broad; with about 14 nerves below and above on each side, uniting before the margin; the under side with a feebly prominent, reticulate nervation. Flowers 2 to 4 together, axillary, sessile, bracteate at the base, the bracts numerous and closely imbricate, cupuliform, brown, smooth. Sepals 5, white on the inner side, rufous-velutinous on the outer side, oblong, united at the base, acuminate, about 3.5 cm. long and 1.5 cm. broad. Petals little longer than the calyx, white, oblong-obtuse, about 3.5 cm. long and 1.4 cm. broad. Stamens inferior, numerous, in several rows, coalescent at the base, with white filaments and yellow anthers, about 3 mm. long. Ovary globose, green, glabrous, with a heavy style and a very large, conico-globose, 5-lobed, yellow stigma (according to Dewèvre). Fruit globose, 2.5 cm. broad, with three parietal placentas" (De Wildeman and Durand, 1899).

Judging from the descriptions, this species is a near relative of *B. nigritana*. De Wildeman and Durand compare it with that species, and in a later publication De Wildeman (1908, p. 248) writes that *B. Dewevrei* is "perhaps only a variety" of *B. nigritana*. Gilg (1908, *loc. cit.*), however, says: "this species is very closely allied to *B. fistulosa* Mast., yet, I presume, distinct from it. The broad, thick, leathery leaves are different, as also the larger flowers, and above all is the fact that the flowers are inserted as a rule 3 or 4, rarely 5, together in the axils of the leaves."

Only known thus far from the Belgian Congo: Lower Congo: Sabuka (Ém. and M. Laurent); Leopoldville (March 26 and May 19, 1915; J. Bequaert; Coll. Nos. 7173 and 7663). Kasai: Dima; cliffs of Batempa; along the Sankuru; Kondué; Bena Dibele; Olombo (Ém. and M. Laurent); Bena Makima; Bombaic (Lescrauwaet). Middle and Upper Congo: Bolombo; Inongo (Ém. and M. Laurent); Bangala, type locality (Dewèvre; Hens). Eastern Congo Forest; Yalutcha; Yanonge (H. Kohl).

***Barteria fistulosa* Masters**

*Barteria fistulosa* MASTERS, 1871, in Oliver, 'Flora of Tropical Africa,' V, p. 511. K. SCHUMANN, 1890, Verh. Bot. Ver. Brandenburg, XXXI, 2, p. 121, footnote. A. ENGLER, 1892, Engler's Bot. Jahrb., XIV, p. 392. WARBURG, 1894, in Engler and Prantl, 'Die Natürl. Pflanzenfam.' III, pt. 6a, p. 27, fig. 2B. É. DE WILDEMAN AND TH. DURAND, 1901, 'Reliquiæ Dewevreanæ,' p. 98 (type and variety *macrophylla*). H. WINKLER, 1906, Engler's Bot. Jahrb., XXXVIII, pp. 259-260. É. DE WILDEMAN, 1906, 'Mission Émile Laurent,' fasc. 3, pp. 250-258, Pls. XCI and XCI; 1907, 'Études Flore Bas- et Moyen-Congo,' II, 1, p. 57; 1908, *ibid.*, II, 3, p. 316. H. WINKLER, 1908, Aus der Natur, III, p. 661. GILG, 1908, Engler's Bot. Jahrb., XL, p. 480. H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 97-108. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 223. ENGLER, 1910, 'Die Pflanzenwelt Afrikas,' I, 2, p. 642, fig. 553B. J. GILLET AND E. PÂQUE, 1910, 'Plantes Principales Kisantu,' p. 81. GILG, 1913, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 568. É. DE WILDEMAN, 1920, 'Mission de Briey au Mayumbe,' pp. 104, 203, and 255.

"A small tree with angular, smooth or lenticellate, fistular branches. Leaves leathery, 10 to 12 in. long, 3 to 4 in. wide, oblong, obtuse, glabrous, 1-nerved, somewhat narrower at the base which is decurrent along the branch. Stipules 0. Flowers sessile, in linear clusters emerging from the stem between it and the decurrent edges of the leaf, each encircled at the base by numerous overlapping leathery shiny chestnut-colored oblong obtuse or boat-shaped bracts, increasing in size from below upwards. Flowers smaller than those of *B. nigritana*. Sepals and petals downy on the outside, lanceolate, wavy at the margins. Corona and inner organs of the flower as in the last-named species, but smaller. Anthers apiculate.

"The so-called decurrent leaves would probably be more correctly described as congenitally adnate to the branch for some distance. The manner in which the flowers emerge from between the sides of the base of the leaf and the stem is very curious" (Masters, 1871).

De Wildeman and Durand's variety *macrophylla* (1901) was based on specimens with larger leaves (25 to 35 cm. long; 14 to 15 cm. broad); but, as De Wildeman observed later, this variety cannot stand, because the shape and size of the leaves in this species are extremely variable: "the normal obovate-elliptic shape, rather broadly cuneate at the base, may change in terminal leaves into elongate obovate-lanceolate, very long-cuneate at the base and reaching a length of 27 cm. by a width of 7 cm. In other forms. . . broadly obovate, shortly attenuate leaves reach a length of 38 cm. and a width of 16 cm." ('Mission Émile Laurent,' p. 249.)

According to H. Winkler (*op. cit.*, p. 260, footnote) there are two forms of *B. fistulosa* in Cameroon: "In one of them the lateral hollow branches inhabited by the ants are longer, the leaves are larger and inserted on the branch by a broader base. In this form the fruits are mostly divided into four, while in the other form they often consist of 5, or even 6, carpels. There was also a clear and characteristic difference in the shape of the seeds; while in the first variety they are 6 to 7 mm. long, 3.5 to 4 mm. wide and 2 mm. thick, the seeds of the other which were the same length measured only 3 mm. in width or even less, being thus much more slender."

Fernando Po, type locality (Mann).

Cameroon: Victoria (Wederbauer; Winkler); Barombi (Preuss; Staudt); Bipindi (Zenker).

Belgian Congo: Lower Congo: Tumba (Ém. and M. Laurent); Kisantu (Gillet); Thysville (June 4, 1915; J. Bequaert). Kwango: Madibi (Leserauwaet). Kasai: Dima; Manghe; Lomkala; Olombo (Ém. and M. Laurent); Bachi-Shombe (Leserauwaet). Middle and Upper Congo: Ibali; Inongo; Eala; Botuma; Bolombo (Ém. and M. Laurent); Coquilhatville (Dewèvre); Lake Leopold II (Body); Betutu (Bruneel); Barumbu (October 28 and November 17, 1913; J. Bequaert; Coll. Nos. 1003 and 1209). Eastern Congo forest: Stanleyville (Dewèvre; February 1915, J. Bequaert and H. Lang); Romée; Yangandi; Yalutcha; Yanonge (H. Kohl); Avakubi (January 17, 1914; J. Bequaert); Penge and at many places in the forest between Penge and Irumu (February 1914; J. Bequaert; Coll. No. 2339); Moera near Beni; between Mawambi and Avakubi (Mildbraed); in the forest between Walikale and Lubutu (January 1915; J. Bequaert). Mr. H. Lang also photographed at Medje what is evidently this species. Mayombe: Ganda Sundi (de Briey).

Winkler (1906, pp. 259-260) has published some interesting morphological and ethological notes on *Barteria fistulosa* studied by him at the Botanical Garden of Victoria, Cameroon.

One of the flowering periods,—if there be more than one—starts in March. The large white flowers are crowded together side by side on the broad base of the leaves. They seem to open with dawn and the anthesis apparently lasts a few hours only. I have not found nectar in them and never observed pollinating insects; bugs and little beetles which are often found in the flowers, have, I presume, hardly to be considered as such; nor, as it seems to me, the ants which inhabit the tree. The fruits ripen about 3 months after the flowering. They have the shape of a walnut, and are 3.5 to 4 cm. long with a diameter of 27 to 30 mm. They are flattened on two sides at the base by pressure against one another. They have four distinct protuberances at the apex, the stump of the style being placed between the four grooves. The fruits which I picked were covered at their base by the brown, closely appressed calyx;<sup>1</sup> however, the latter apparently remains on the tree when the ripe fruit drops. The consistency of the fruits can best be compared with that of a celluloid ball. The numerous, parietal placentas are arranged on four longitudinal bands. Each seed is enveloped by an arillus-like pulp, which has an agreeable, sweet-sour flavor; the pulp of the various seeds fills the fruit with a slimy mass. The seed is flattened, of rounded-rhomboid shape, with a small umbilicus and a network of dimples on the surface. To be sure the seeds are scattered by animals, which trace the pulp. The genets which I kept in captivity preferred these to almost all fruits. I have found, on fruits still adhering to the tree, holes the size of a hazelnut or an entire half of the pericarp lacking; the seeds together with the arillus had disappeared. Traces of bites could be distinctly recognized on a number of fruit envelopes which I found at some distance from one of the trees; they certainly were not from a bird's bill, but from teeth, probably of fruit-eating bats.<sup>2</sup> When compressed, and consequently also when bitten, the fruits split open at the top in the form of a cross between the grooves; but they open by themselves only when rather intensively drying.

<sup>1</sup>The author evidently means the involucre of bracts, not the true calyx.

<sup>2</sup>In the African Rain Forest fruit bats undoubtedly are important agents in scattering the seeds of many fruit-bearing trees. See the remarks on this subject by H. Winkler (1906, p. 236) and H. Lang and J. P. Chapin (1917, Bull. Amer. Mus. Nat. Hist., XXXVII, p. 484).

***Barteria nigritana* J. D. Hooker**

*Barteria nigritana* J. D. HOOKER, 1860, Journ. Linn. Soc. London, Botany, V, p. 15, Pl. II, figs. 1-5.

*Barteria nigritana* MASTERS, 1871, in Oliver, 'Flora of Tropical Africa,' II, p. 510. H. WINKLER, 1906, Engler's Bot. Jahrb., XXXVIII, p. 260, footnote. GILG, 1908, Engler's Bot. Jahrb., XL, 1908, p. 479; 1913, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 568.

*Barteria Braunii* ENGLER, 1892, Engler's Bot. Jahrb., XIV, p. 392. WARBURG, 1894, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' III, pt. 6a, p. 27, fig. 2A. ENGLER, 1910, 'Die Pflanzenwelt Afrikas,' I, 2, p. 642, fig. 553A.

"A small tree or shrub with stout branches, covered with rusty down, and marked on either side with a raised line continuous with the base of the leaves. Leaves coriaceous glabrous, 6 to 10 in. long, 2 to 3 in. wide, oblong, subacute, crenulate or entire; unicostate, rounded at the base or tapering into a short, thick leaf-stalk. Stipules deciduous. Flowers large, 1 to 1½ in. in diameter, sessile or subsessile in axillary tufts, each tuft consisting of 2 to 4 flowers, each of which is invested in a series of overlapping coriaceous chestnut-colored acute or cuspidate bracts. Flower-tube very short, glabrous. Sepals 5, somewhat coriaceous, oblong-lanceolate or obtuse, downy and golden brown on the outer side, smooth and whitish within. Petals oblong, wider than the sepals and about equal to them in length, white. Stamens hypogynous or slightly perigynous; filaments slender. Ovary smooth; style simple, as long as the filaments and terminated by a large conical or cushion-shaped stigma. Fruit ovoid, about the size of a pigeon's egg, coriaceous, reddish, 1-celled, with numerous compressed pitted seeds attached to parietal placentas" (Masters, 1871).<sup>1</sup>

Southern Nigeria: Nun River, type locality (Barter); Bonny River (Mann); Old Calabar (Thomson).

Cameroon: Batanga (Dinklage); Kribi (Zenker).

Spanish Guinea: on the coast of Bata near Campo (Busse).

French Congo: on the Gaboon River near Libreville (Mildbraed).

As pointed out by Gilg this species seems to be restricted to the coastal forest belt ("eine echte Seestrandspflanze") which grows inland of the mangrove formation along the Gulf of Guinea. Similar patches of dense forest are to be found immediately landward to the mangroves in the estuary of the Congo, but I have never seen any *Barteria* there.

***Barteria nigritana* variety *uniflora* De Wildeman and Durand**

*Barteria nigritana* variety *uniflora* É. DE WILDEMAN AND TH. DURAND, 1900, 'Contributions Flore du Congo,' II, p. 24; 1900, Bull. Herbarium Boissier, (2) I, p. 22.

É. DE WILDEMAN, 1904, 'Études Flore Bas- et Moyen-Congo,' I, p. 169. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 109. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 224.

<sup>1</sup>J. D. Hooker's original diagnosis is as follows: "Frutex robustus, habitu *Smeathmanniæ*, foliis 6-10" long., 2-3" lat., nervis primariis numerosis. Stipulæ deciduæ, non visæ. Flores sessiles, circiter 1-1¼" diametro, iis *Smeathmanniæ* subimiles. Bractæe numerosæ arcte imbricatæ, alabastrum maturum velantes, late ovatæ cuspidato-acuminatæ. Petalæ calyce paulo longiora. Stamina perplurima. Ovarium glaberrimum. Fructus magnit. ovi columbæ."

"A high tree, with thick branches, which are striate, ferruginous-pubescent, marked on either side with a raised line connecting the leaf-bases. Leaves alternate, shortly petiolate; the petiole 5 to 6 mm. long and 3 mm. broad; oblong, subacuminate, 11 to 17 cm. long and 3.7 to 5.5 cm. wide, entire, shiny above and below, dark above, paler below, the upper side subglabrous or with a few scattered hairs; the under side with short, sparse, brown pilosity, especially on the veins; lateral nerves a little prominent above and below, arcuately anastomosing towards the margin and prominent in the more or less recurved margin. Flowers sessile, solitary in the axils of the leaves; at the base with closely imbricate bracts, which are scarious, brown, pilose externally, embracing. Calyx with ovate-lanceolate lobes, ferruginous pilose on the outer side, glabrescent on the inner side, acuminate, 3 cm. long and 12 mm. wide. Petals equal to the sepals but completely glabrous. Corona erect, membranaceous, fimbriate-lacerate at the apex. Stamens numerous, with connate filaments. Ovary globose, with parietal placentas, and numerous ovules; style solid; stigma very large, 6 to 7 mm. broad, conico-globose" (De Wildeman and Durand).

Belgian Congo: Lower Congo: Forest of Talavanje, type locality (Cabra); Kisantu (J. Gillet).

It seems doubtful whether this form is really a variety of *B. nigritana* in view of its occurrence inland far from the coastal belt. It may possibly be specifically distinct or constitute a form of *B. Dewevrei*, a species commonly found in the Lower Congo. From the description, it appears very similar to *B. Stuhlmannii*.

#### **Barteria Stuhlmannii Engler and Gilg**

*Barteria Stuhlmannii* ENGLER AND GILG, 1908, Engler's Bot. Jahrb., XL, p. 479.

*Barteria nigritiana* WARBURG, 1895, in Engler, 'Pflanzenwelt Ost-Afrikas,' C, p. 278 (not *nigritana* Hooker).

"Shrub or tree with fistulose branches, which are densely and very shortly fulvous-pilose when young. Leaves ovate or ovate-oblong, very seldom oblong; acute or often shortly and broadly acute-acuminate at the apex, rounded toward the base, though narrowed at the very base into a 6 to 8 mm. long petiole, on both sides of which there is a 3 to 4 mm. wide wing; leaves obsolete sinuate-denticulate, or more often subentire, with cartilaginous margin, glabrous above (except on the median nerve), very sparsely and shortly pilose below, leathery, with 13 to 15 pairs of lateral nerves which run almost straight to near the margin where they unite by curves; with numerous transverse nerves running parallel to each other and strongly prominent on both sides; other reticulate veins almost absent. Flowers solitary or occasionally by twos in the axils of the leaves. Bracts enclosing the flower in an involucre, coriaceous, with scattered fulvous pilosity on the back. Outer sepals entirely covered on their outer side with dense fulvous pile, which on the back of the inner sepals forms only a median vertical line; otherwise glabrous, oblong, with very acute apex. Petals a little shorter than the sepals, but similar in shape, very tender; glabrous. Outer corona membranous, glabrous, about half the length of the petals, unevenly incised and fimbriate; inner corona much shorter, thickened, forming a raised ring which is distinctly but feebly emarginate and furrowed. Stamens numerous, coalescent at the base into a tube. Ovary short, turbinate, glabrous, with 4 parietal placentas. Style elongate, reaching the anthers, thick, gradually thinner upwards, ending in a very

thick, head-shaped stigma. Fruit subglobose; the pericarp parchment-like or chartaceous, fragile; seeds numerous, inserted on 4 parietal placentas, oblong, yellowish, with pitted testa.

"The winged petiole is 6 to 8 mm. long and, with both wings spread, 7 to 9 mm. wide. The swollen, hollow stalk is 6 to 10 mm. thick. The blade of the leaf is 16 to 19 cm. long, 7 to 9 cm. broad. The bracts which enclose the base of the flowers are 7 to 9 mm. long and equally wide. The outer sepals are about 2.5 cm. long, 1 cm. wide;

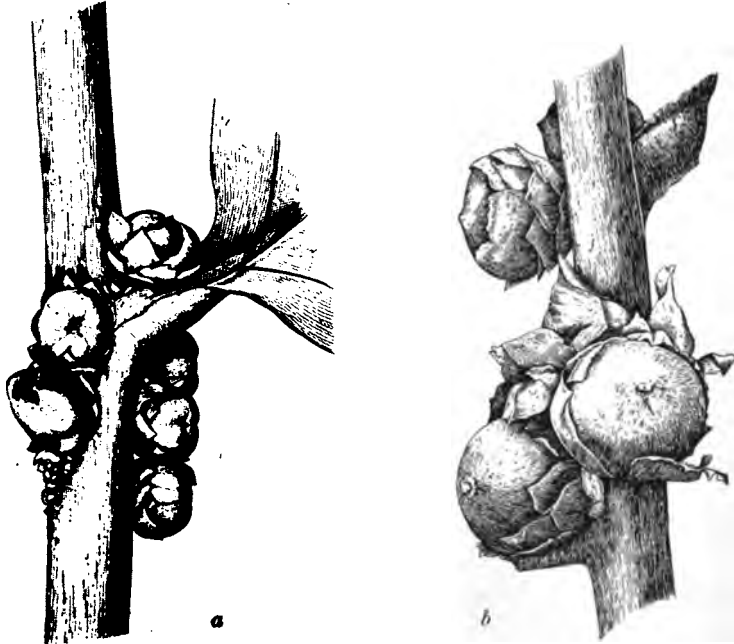


Fig. 85. a, *Barteria fistulosa* Masters: portion of branch with fruits along decurrent leaf base; b, *Barteria Dewevrei* De Wildeman and Durand: portion of branch with fruits clustered in axile of leaves (after De Wildeman, slightly modified).

the inner ones decrease gradually. The petals are about 2.2 cm. long, 8 to 9 mm. broad. The style is about 1.5 cm. long, the stigma 4 mm. long and 3 mm. thick at the base. The fruit has a diameter of about 2.5 cm. The seeds are 5 mm. long, 3 mm. wide and 1.5 mm. thick" (Engler and Gilg, 1908).

German East Africa: Bukoba, type locality (Stuhlmann).

This plant will, I believe, prove to be identical with *B. acuminata* E. G. Baker (see above, p. 425), described from Musozi on Lake Victoria, which is practically the same locality as Bukoba.

During my travels in the Belgian Congo, I came across two species of *Barteria*, *B. Dewevrei* and *B. fistulosa*. The latter is by far the more common and can be best recognized by the very peculiar way in which it

they stop growing, lose their foliage, and gradually dry up; finally, these dead members are dropped by a histological process similar to that causing the leaves to fall. One always finds, therefore, a number of dead branches scattered over the ground at the base of this *Barteria*. Whether there is a law of periodicity or other rule governing this peculiarity cannot be decided at present, but so much is sure: the few flowering branches remain on the stem until after the fruits are ripe.

The lateral branches of *Barteria fistulosa* are of two kinds. The sterile branches—and, as noted, these are in the great majority—present at a short distance from their base an abrupt and conspicuous swelling which continues almost uniformly to near the apex with only slight constrictions at the nodes (Plate XXVIII, Fig. 2; Text Fig. 86). Except in

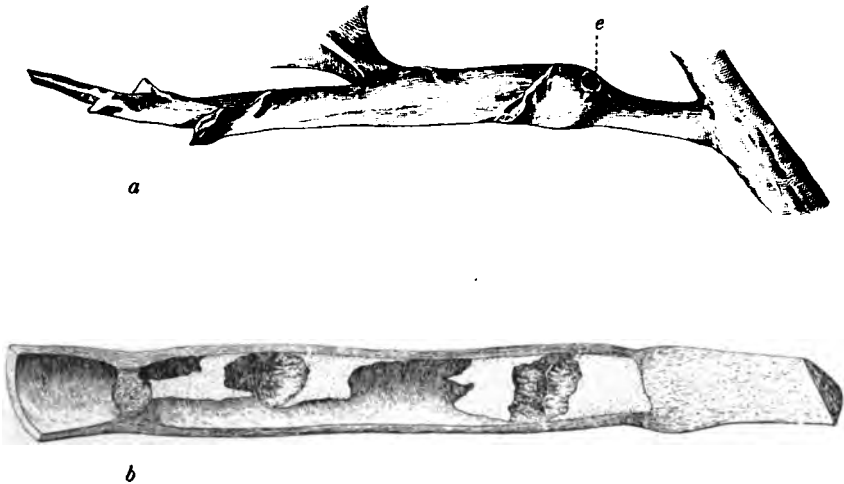


Fig. 86. *Barteria fistulosa* Masters: a, lateral branch suddenly swollen beyond its base, where it shows the circular opening (e) gnawed by the ants and leading into the domatium; about one-half natural size (after De Wildeman); b, part of longitudinal section of very young swollen lateral branch, showing gradual drying up of pith before ants gain access to the cavity; drawn from life at Barumbu, October 1913; natural size.

very young plants, these swellings are nearly always hollow and inhabited by ants. The flowering branches appear only at certain seasons and on older trees; they are normal, not swollen, yet frequently hollowed out and also occupied by ants.

From an examination of very young specimens and others not inhabited by ants, I found that the trunk and normal, flowering branches are filled with pith and remain so unless excavated by the ants. The swollen branches (Fig. 86), on the contrary, become hollow naturally.



When young, their various internodes are at first only slightly swollen and entirely filled with soft, greenish, parenchyma; soon, however, the enlargement becomes more pronounced; the pith turns pale brownish, gradually dries and what remains finally forms brownish membranes on the inner walls or irregular partitions in a spacious cavity (Fig. 86b). The ant-chamber is thus ready for occupancy before the insects touch the branch. On uninhabited plants the sterile branches show no orifice, nor any depression or scar on their outer surface that might mark the spot where the entrance to the cavity will later be pierced by the ants. Moreover, the walls of the limb are soft and easily pressed down with the fingers, so that they must offer but little resistance to the powerful mandibles of the *Pachysimæ*.

The larger specimens of *Barteria fistulosa* that one commonly meets in the forest are, as a rule, settled by a populous colony of the large, black *Pachysima æthiops* (Emery),<sup>1</sup> the true body-guard of the tree. As soon as any portion of their host plant is disturbed, they rush out in numbers and hastily explore the trunk, branches, and leaves. Some of the workers usually also run over the ground about the base of the tree and attack any nearby intruder, be it animal or man. All observers agree that the sting of the *Pachysima* is exceedingly painful and is felt for several hours. Its effects can best be compared with those produced by female velvet ants (Mutillidæ; see Kohl's remarks reproduced in Prof. Wheeler's Report, p. 115). Consequently these ants are greatly dreaded by the natives and there remains little doubt that they afford a most effective protection to their host plant.

Trees inhabited by *Pachysima* are generally healthy and free from the attacks of most phytophagous insects. On specimens untenanted by ants, however, the leaves are often badly eaten by caterpillars, as I observed in two instances at Barumbu in October, 1913. On both of these trees there were also several nests of the weaver-ants, *Ecophylla longinoda* (Latreille), and numerous workers of a small *Crematogaster* running over the branches and leaves. At Penge, in February, 1914, another uninhabited *B. fistulosa* showed the live wood of its trunk badly bored by adult bostrychid beetles. On the other hand, the *Pachysimæ* are not always successful in keeping smaller parasites from their host. At Barumbu a tree occupied by a populous colony of *P. æthiops* showed numerous cecidomyid galls on its leaves. They were small fleshy swellings of the parenchyma, about equally protruding on both sides of the

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<sup>1</sup>Probably sometimes also by *Pachysima latifrons* (Emery).

leaf, and irregularly scattered. Inside of them was a single chamber containing one gall-midge larva and surrounded by a wall of coarser tissue in the center of a solid, juicy, parenchymatous mass.<sup>1</sup>

An older, inhabited *Barteria fistulosa* may be regarded as the home of a single colony of *Pachysima* which has resulted either from the gradual growth of a small nest founded by one female, or from fusion of several nests started independently by a number of females. Both modes are possible, but the second is probably the more common. At Avakubi, in January, 1914, I had an opportunity to examine a very young *Barteria fistulosa* not over one meter high, with but six short, horizontal branches, all of which were swollen beyond the base in the usual way. Only a few of the distended internodes were settled by ants and each was a closed, separate cavity containing one deälated *Pachysima* queen; no workers, larvæ, or eggs were present. After the nuptial flight the *Pachysima* females had evidently entered the hollow internodes by gnawing through the wall. They had not again left the cavity, for the entrance was partly plugged up by callus growth. When disturbed, these gravid queen ants made no attempt to defend themselves, behaving in this respect very differently from workers. It is also interesting to note that some of the *Pachysima* females were dead and that in one such case another minute ant, of an unidentified species, had established its nest in the same internode with the remains of a dead *Pachysima* queen. A colony of *Pachysima æthiops* in a somewhat more advanced stage was found in a young *Barteria fistulosa* at Barumbu in November, 1913. A queen ant, surrounded by an abundance of eggs and young larvæ, was found inside each of a series of swollen internodes, all still separated by the nodal partitions. Here, too, a growth of callus had partly closed the entrance which had been further plugged with dried particles of pith evidently brought there by the female. Since the older *Barteria* is finally occupied by one single colony, all the members of which live and work peacefully together and enter indifferently the various domatia, the initial formicaries in all probability fuse into one. The workers in such a formicary not only enlarge the exit holes, which are usually placed at the base of the swelling toward the upper face of the branch, but also clean the cavities of the remains of dried pith and pierce the partitions between the various internodes. Each lateral branch finally forms one continuous gallery.

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<sup>1</sup>Lamborn (1914, p. 493) notes that he once found larva and pupa of *Tinthia lambornella* Durant, an egeriid moth, in an internode of a *Barteria* in Southern Nigeria; this cavity was separated from the adjoining internodes, both of which were inhabited by *Pachysima æthiops*.

The origin and growth of new colonies of *Pachysima* in *Barteria* deserves to be further investigated in the field. Perhaps such a study will show us typical examples of secondary pleometrosis, or founding of an insect society through fusion of a number of colonies each started independently by a fertile female. H. v. Ihering (1907) believes *Cecropia adenopus* is settled in this manner by *Azteca mülleri*. Furthermore, in his opinion, all but one of the fertile queens inhabiting the same tree are eventually killed by the workers, a conclusion drawn from the presence of a sole queen in each adult *Cecropia*. It will be important to look into conditions in this respect in the *Pachysima* formicaries of *Barteria*.

The *Pachysimæ* undoubtedly derive certain advantages from living inside *Barteria*. The hollow, nearly horizontal branches provide very convenient nesting chambers, where the brood is kept in safety under almost ideal conditions of aëration, temperature, and humidity. Whether the ants also procure part or all of their food from the host is still doubtful. Kohl has often seen the workers actively licking nectaries at the insertion of the leaves, and also gnawing the young bark and the epidermis on the upper and under sides of the blades; they are particularly fond of the very young flowers, which they frequently destroy almost completely. Certain other insects live in the domatia with the ants, the most common of these companions being coccids (*Pseudococcus citri* variety *congoënsis* Newstead) which, I am inclined to think, are not brought in by the ants, but migrate inside the swellings of their own accord. I have found this to be also the case with scale insects living in the myrmecodomatia of *Cuviera*. Even in very young *Barteriæ*, of which only a few internodes are occupied by queen ants and their brood, one discovers coccids in the cavities. Another interesting inquiline of *Barteria* is a minute phorid fly, *Hypocera tristis* H. Schmitz, noticed by Father Kohl near Stanleyville in swellings of *Barteria fistulosa* occupied by *Pachysima æthiops* (Wasmann, 1915a, p. 320, footnote).

Whether the coccids of *Barteria* are really attended by *Pachysima* for the sake of their excretions remains uncertain. Wheeler and Bailey (1920, pp. 261-262) have dissected the pellets contained in the infra-buccal pockets of workers and the trophothylaces of larvæ of *Pachysima æthiops* and *P. latifrons*. They were much the same in both species and consisted of pieces of coccids or whole, crumpled-up bodies of young scale insects, fungus spores, bits of mycelium, portions of plant-tissue evidently gnawed from the walls of the cavities, pollen-grains, etc. In a few of the pellets Prof. Bailey found small nematodes resembling the species of *Pelodera* described by Janet as living both as parasites in

the pharyngeal glands of certain European ants and as free organisms in the detritus of the nest.

A thorough investigation of the feeding habits of both adult and larval *Pachysimæ* in *Barteria* will be the most important problem to be studied in the future. In this connection, it may be well to note a peculiarity to which my attention was directed by my friend, Mr. J. P. Chapin, during our stay at Avakubi in January, 1914. When *Barteria fistulosa* inhabited by *Pachysima* occurs in rather dense forest, one frequently notes about its base an open patch, fifteen to twenty feet in diameter, where most of the heavy undergrowth has been cleared away. Only a few, low herbaceous plants and often also the slender leaf-stalks of the common marantaceous forest reed, *Sarcophrynium Arnoldianum* De Wildeman, are left standing. The ground at the foot of the tree is partly covered with fallen leaves and dead branches of the *Barteria*. One can always find a few *Pachysima* workers running over this open space, for a purpose unknown to me, perhaps in search of insects which may form part of their diet.<sup>1</sup> I merely venture the supposition that the ants themselves are instrumental in preventing the growth of heavy vegetation near the base of their shelter, perhaps by nipping the tender shoots of the young plants.<sup>2</sup> One can readily imagine that such a clearing would be of use to the ants in their hunts for other insects, making the capture of their prey so much easier and quicker. Incidentally, *Barteria* too may be benefited, since it is saved competition with more vigorous species of trees or shrubs, which, if allowed to thrive near its trunk, would soon interfere with its growth. The shade given by *Barteria fistulosa* is so slight that this factor alone could not account for the absence of woody vegetation within a radius of six to eight feet from its base.<sup>3</sup>

As soon as the leaves of *Barteria fistulosa* fall, the branches begin to dry up, but remain on the tree for several weeks before being shed as described above. Then, however, they are not occupied by the *Pachysimæ*, which pay no further attention to them, one proof more of the strict, obligatory relations existing between these ants and the host plant. The empty, dried swellings may be temporarily occupied by other, small

<sup>1</sup>My observations do not agree on this one point with those of Father Kohl, who believes that *Pachysima* never leaves *Barteria* "since they do not undertake hunting parties for strange insects."

<sup>2</sup>With regard to this interesting point I quote the following passage from Kohl's paper (1909): "Some natives assured me that the *Simæ* (= *Pachysimæ*) occasionally trim to half its height the low vegetation which surrounds their host plant. I once observed similar, partly cut low plants in the vicinity of my Mission, but I did not guess the possible agent of this."

<sup>3</sup>Ule (1907, p. 131) also remarks that *Pseudomyrma dendroica* Forel and *P. triplaris* Forel, which live inside stems and branches of *Triplaris Schomburgkiana* along the Jurua River, Brazil, run down to the ground, where in a circle a few meters wide no other vegetation is allowed to grow.

species of ants. At Barumbu, in October, 1913, I came across a *Barteria fistulosa* whose living branches were inhabited by *Pachysima æthiops*, while the dead twigs, still attached to the tree, contained small colonies of a *Crematogaster*. These little ants were apparently not molested by their large neighbors, but, when the tree was disturbed, they remained safely inside, while the *Pachysimæ* rushed forth and ran feverishly over the plant.

The myrmecophytic nature of *Barteria fistulosa* was first recognized by K. Schumann (1890, p. 121, footnote) on herbarium specimens collected in Cameroon. Some of the swellings cut open by him still contained a few *Crematogasters*. Its relations with ants were studied in the field by A. Dewèvre (De Wildeman and Durand, 1901, p. 98), Émile Laurent (De Wildeman, 1906, pp. 250-258), H. Winkler (1906, p. 59), and H. Kohl (1909, pp. 97-108). Mention is made in Prof. Wheeler's Report (p. 114) of some of these earlier observations which agree in most details with my own.

The following ants have been found thus far in the swellings of *Barteria fistulosa*, but the two species of *Pachysima* alone can be regarded as obligatory guests of the plant. The others are all accidental tenants which nidify in other places also; they are usually met only on plants or in branches which for some reason or other have been left by the *Pachysimæ*.

*Pachysima æthiops* (F. Smith). The large, black ant which is the regular inmate of *Barteria fistulosa*, was first collected in this plant by Father Kohl, near Stanleyville (1909, p. 106), and sent by him for identification to Forel (1916, p. 403). Both Mr. Lang and I commonly found the same species at Medje, Ambelokudi, Barumbu, Avakubi, etc.<sup>1</sup> The scale insect *Stictococcus formicarius* Newstead was found by Kohl near Stanleyville with these ants (Newstead, 1910, p. 19).

*P. latifrons* (Emery). Specimens of this species obtained by Mr. H. Lang at Niangara were probably taken from *Barteria fistulosa*.

*Tetraponera anthracina* (Santschi). Near Stanleyville (H. Kohl; see Forel, 1916, p. 403). I found several workers of this species at Thysville (June 1915) running over the leaves and twigs of a *Barteria fistulosa* whose swellings were free of ants; I did not find their nest.

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<sup>1</sup>*Pachysima æthiops* was originally described from South Africa, without indication of collector. No species of *Pachysima* has since definitely been recorded from that part of the continent. Since the genus is restricted to *Barteria* and *Myrmecia*, which are not known to occur south of 7° S. lat., there is a question whether Smith's type was wrongly labeled. It is, however, not so clear how he could have received West African specimens of *P. æthiops* at a time (1877) when hardly any myrmecological collections had been made in Equatorial Africa. I am rather inclined to believe that Smith's type was obtained in the forests of Natal from a myrmecophyte which has since escaped notice.

The hollow branches of the two specimens of *B. Dewevrei* examined contained colonies of *Crematogaster africana* variety *schumanni* (Mayr), with a queen, workers, and brood; also some coccids which were usually in a small, scar-like depression in the wall. In one tree some of the branches contained insect larvæ, a lepidopterous pupa, and an adult beetle, but these were in cavities quite separate from those inhabited by ants.

Dewèvre, who discovered this species in the Bangala region, on the Upper Congo, mentions finding ants in its hollow branches (De Wildeman and Durand, 1901, pp. 97-98). A few notes on its relations with ants were also made by Ém. Laurent (De Wildeman, 1906, pp. 247-250) and H. Kohl (1909, pp. 108-109). The following ants have been found in its myrmecodomatia:

*Pachysima æthiops* (F. Smith). Dima (Ém. Laurent; see H. Kohl, 1909, p. 108); Yalutcha and Yanonge (H. Kohl, 1909, p. 108).

*Crematogaster africana* (Mayr) variety. Dima (Ém. Laurent; see H. Kohl, 1909, p. 108).

*C. africana* variety *schumanni* (Mayr). Leopoldville (J. Bequaert).

### Apocynaceæ

#### EPITABERNA K. Schumann

*Epitaberna* K. SCHUMANN, 1903, Engler's Bot. Jahrb., XXXIII, 2, p. 316.

"A bush with branches thickened and hollow below the nodes. Leaves large, short petiolate, lanceolate, short acuminate. Flowers diclinous, showy, axillary; their pedicel with a pair of lower bracteoles, simulating interpetiolar stipules, and also with a second pair of bracts below the ovary. Sepals large, foliaceous, subinequal, alternating with very large, linear, solitary glands. Corolla very large, infundibuliform; its lobes ample, curled along the margin, their sides in the bud inflexed and covering each other dextrorsely; its throat with variegated hairs. Stamens inserted near the throat, without any stiff appendage at the base, acute and not appendiculate at the apex. Ovary perfectly inferior, pentapterous, 2-celled; with numerous ovules inserted on a thickened placenta; disc annular; style thickened and bilobed at the apex. Fruit unknown.

"Only one species is known.

"The genus is a relative of *Tabernæmontana*, from which it differs in its completely inferior ovary and in the large sepals" (K. Schumann, 1903).

This is the only genus of the large family Apocynaceæ which has thus far been recognized as a myrmecophyte and the true nature of its relations with the ants has apparently not been further investigated on living specimens. It contains only one species.

***Epitaberna myrmæcia* K. Schumann**

*Epitaberna myrmæcia* K. SCHUMANN, 1903, Engler's Bot. Jahrb., XXXIII, 2, p. 317.

"Branches thickened at the nodes, quadrangular, glabrous. Leaves short petiolate, lanceolate, amplex; short and sharply acuminate, acute at the base, glabrous above; slightly hairy on the under side in youth and later on with scattered pile on the midrib. Flowers short pedunculate. Ovary glabrous. Sepals lanceolate, acuminate, large, glabrous. Corolla with a tube extending hardly beyond the calyx; glabrous outside; densely villose at the throat on the inner side; the lobes broadly elliptic, acuminate, curled along the margin, twice the length of the tube, lanceolate in the bud. Stamens linear, enclosed. Style glabrous, filiform, thickened at the apex.

"The flowering branches, 15 cm. long, are 2 mm. thick in the middle of the internodes; the upper part of the internodes is swollen into a spindle-shaped cavity with thin walls, which is as much as 5 cm. long and 9 mm. in diameter and serves as a myrmecodomatium. The heavy, glabrous petiole is grooved on the upper side and at most 5 mm. long. The blade has a length of 11 to 28 cm. and a greater width of 5.5 to 11 cm. in the middle; it is crossed on each side of the midrib by 6 to 10 stronger veins, which are prominent on both sides; in dried condition it is dark green above, pale green below. The flowers do not always present an ovary, there being male and female flowers; but otherwise they do not differ from each other. The peduncle is 5 mm. long, and the inferior ovary about the same length. The green sepals reach a length of 2.5 cm. The tube of the white corolla, with its chrome-yellow throat, is 2.2 cm., and its lobes 5.5 cm. long. The stamens are inserted at 15 mm. above the base of the corolla; the anthers are 7 mm. long. The style measures 1.3 cm.

"The plant is remarkable, representing a new case of myrmecophily. I myself have collected the ants from the wool of the throat of the corolla. This is the first case of completely epigynous flowers among the Apocynaceæ; accordingly the fruit is probably also syncarpous" (K. Schumann).

Cameroon: Bipindi (Zenker).

*Epitaberna myrmæcia* probably occurs throughout the forest of southern Cameroon and Spanish Guinea. According to Stitz (1910, p. 131), Tessmann found inside the caulinary swellings of this plant, the large *Pachysima æthiops* (F. Smith) (= *spininoda* André) which the Pangwe call "engunkun," much fearing its sting in the belief that it causes fever.

Tessmann, in his account of the Pangwe of southern Cameroon and Spanish Guinea, describes how the tribe uses this myrmecophyte in one of their religious ceremonies. During the initiation to the "Sso-cult" of the Yaunde, the candidates are obliged to pass for several days through a succession of tests, one of which is as follows. Nests of stinging ants, especially those of *Plagiolepis carinata* Emery, and branches of *Epitaberna myrmæcia* inhabited by *Pachysima æthiops*, are hung or placed in a low hut built for that purpose near the village. This place soon swarms with ants; pods of *Mucuna pruriens* covered with dangerously itching hairs are also thrown inside. The neophytes are then brought there and,

after being much frightened by howling and threats, are forced to crawl in succession through the ant-hut where they are, of course, fearfully stung.<sup>1</sup>

### Verbenaceæ

#### CLEODENDRON Linnæus

*Clerodendron* LINNÆUS, 1753, 'Species Plantarum,' Ed. 1, II, p. 637. BRIQUET, 1895, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' IV, pt. 3a, p. 174. J. G. BAKER, 1900, in Thiselton-Dyer, 'Flora of Tropical Africa,' V, 2, p. 292.

"Trees or shrubs, sometimes scandent. Leaves opposite, rarely ternately verticillate, entire or toothed. Cymes axillary or terminal, lax or dense. Flowers small or large, various in color. Calyx not accrescent; tube campanulate; lobes 5, equal, longer or shorter than the tube. Corolla-tube cylindrical; lobes 5, obovate, spreading or slightly reflexed, subequal or unequal. Stamens 4, inserted below the throat of the corolla-tube; filaments long, filiform, involute in bud; anthers ovoid or oblong, with parallel cells. Ovary imperfectly 4-celled; cells 1-ovuled; style long, bifid at the apex. Fruit a globose drupe with a fleshy pericarp and 4 smooth or rugose pyrenes. Seed oblong, exalbuminous" (J. G. Baker, 1900).

This is a very large genus, numbering some 200 species and distributed between the tropics in the Old World; over 150 have been described from Africa, 35 of which have been recorded from the Belgian Congo. They are very common at the edges of the forest and along rivers, where the creeping species often are one of the striking elements in the landscape, on account of their beautiful, showy flowers. The species of the savannah are most frequently low shrubs or erect or trailing herbs.

A number of species of *Clerodendron* have been found associated with ants, but the few published observations are too fragmentary to show whether any of the forms are true myrmecophytes. Among the African representatives, *Clerodendron excavatum* É. De Wildeman<sup>2</sup> is myrmecophilous according to certain observers, while others assert that its hollow stems are merely filled with water. At all events, ants were never found inside the stems of that plant.

At Penge, in January, 1914 (Coll. No. 2205), I collected on the bank of the Ituri River in the dense undergrowth of the forest a low bushy *Clerodendron* which may possibly be *C. excavatum* É. De Wildeman. The plant was 3 to 4 m. high and divested of leaves at that season of the year. Some of the branches, however, were covered with numerous, white, showy flowers, obliquely directed downward. No swellings nor domatia could be found, but the internodes of stem and branches were normally

<sup>1</sup>Tessmann, G., 1913, 'Die Fangwe,' II, pp. 46-47.

<sup>2</sup>Described, 1909, in 'Études Flore Bas- et Moyen-Congo,' III, 1, pp. 132-134, Pl. XI; 1912, *ibid.*, III, 3, p. 468.



hollow, due to the early resorption and drying up of the pith. Many of the hollow internodes contained nests, with a fertile queen, workers, brood, and newly hatched winged sexual forms of a small, unidentified ant. The insects entered and left by a circular entrance pierced through the wall about half-way between two nodes. In certain cases the partition at the nodes had not been removed, whereas in others the entire limb formed one continuous nesting cavity. An internode of one of the living branches was occupied by a nest of a small solitary bee belonging to the genus *Allodape*.

In a recent note De Wildeman (1920) directs attention to several African *Clerodendrons* with fistulose stems, such as *C. excavatum* De Wildeman, *C. angolense* Guerke, and *C. cavum* De Wildeman. The last named was described from specimens which I collected in the Savannah country of the northeastern Belgian Congo, near Boga (July 12, 1914; Coll. No. 5002), between Beni and Kasindi (August 9, 1914; Coll. No. 5205), and near Rutshuru (September 4, 1914; Coll. No. 5534). It is a low bush of the open grass-land, with white flowers; I never observed ants living in or on it.

Following the description of his *Clerodendron formicarum*, Guerke mentions that he saw a specimen obtained by Stuhlmann near Bukoba. Ants of the genus *Crematogaster* were living in its hollow stem, the walls being pierced by a circular hole. Guerke, however, was doubtful as to the specific identity of this Uganda specimen and the typical *C. formicarum* from Angola and the Kasai. The latter is a low, semi-herbaceous plant, 25 to 30 cm. high, which, as I have shown elsewhere, is not the myrmecophyte its name would imply. Stuhlmann's specimen from Bukoba was a rather high, much-branched shrub, with smaller flowers and there is a possibility that it belonged to *C. cavum* De Wildeman, collected by me in several near-by localities.

#### VITEX Linnæus

*Vitex* (Tournefort) LINNÆUS, 1753, 'Species Plantarum,' Ed. 1, II, p. 638. J. BRIQUET, 1895, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' IV, pt. 3a, p. 170. J. G. BAKER, 1900, in Thiselton-Dyer, 'Flora of Tropical Africa,' V, p. 315.

"Trees or shrubs, with glabrous or hairy branches. Leaves opposite, usually compound, digitate, rarely simple. Cymes dichotomous, axillary or forming a terminal panicle. Flowers whitish, yellowish, lilac, or blue. Calyx campanulate or funnel-shaped, 5-toothed or nearly truncate, accrescent. Corolla-tube short or long, sub-cylindric or funnel-shaped, straight or slightly curved; limb obliquely patent, sub-bilabiate. Stamens 4, didynamous, inserted in the corolla-tube and usually exserted from it; anther-cells nearly parallel or divergent. Ovary at first imperfectly

2-celled, usually finally 4-celled; ovules solitary, laterally attached; style filiform, bifid at the apex. Drupe with a more or less fleshy mesocarp and a hard, 4-celled endocarp. Seeds obovate or oblong, exalbuminous" (J. G. Baker, 1900).

This diagnosis should be amended to include creepers also. Apart from the myrmecophilous species of the Ituri Forest described below, the creeper form was apparently thus far unknown in the genus. J. Briquet,<sup>1</sup> it is true, incidentally mentions *Vitex pycnophylla* K. Schumann as a creeper, but, so far, I have failed to find a species of that name described.<sup>2</sup>

The genus *Vitex* contains over one hundred species in the tropical and subtropical parts of both hemispheres. A large number of these are found in Tropical Africa, some twenty being recorded from the Belgian Congo. It is rather closely allied to *Clerodendron*, from which it can only be separated with certainty by the structure of the fruit. While in *Vitex* the endocarp of the drupe forms a single 4-celled nutlet, in *Clerodendron* each fruit contains two 2-celled or four 1-celled nutlets. In addition, all known forms of *Clerodendron* have simple leaves, either entire, toothed, or more or less lobed, whereas in *Vitex* compound, digitate leaves are the rule and simple ones the exception.

Two of the African species are definitely known to be myrmecophilous, but probably other tropical members of the genus also have associations with ants.

#### ***Vitex Staudtii* Guerke**

*Vitex Staudtii* GUERKE, 1903, Engler's Bot. Jahrb., XXXIII, 2, p. 299.

"Tree or shrub<sup>3</sup> with quadrangular branches. Leaves 5-foliolate, with very long petioles; the leaflets petiolulate, obovate, attenuate at the base, with entire margin, ending in a very long apex, rough above, glandular below. Inflorescences terminal, thyrsoidal, loose; peduncles puberulent. Calyx cupuliform, with truncate or obsoletely 5-toothed margin.

"The branches are sharply quadrangular, entirely glabrous, hollow. The opposite leaves are 5-foliolate, with a petiole 10 to 18 cm. long. The leaflets have a petiole of 5 to 20 mm.; that of the median leaflet longer than the others; they are obovate, twice as long as broad on the average, without the apex 10 to 14 cm. long and 5 to 7 cm. wide; narrowed at the base into the petiole; with entire margins; prolonged into a tip which is suddenly constricted at the base and 1 to 3 cm. long; the upper side with very short, scattered, coarse hairs; under side glabrous, but densely covered with minute, golden yellow glands. The thyrsoid inflorescences are terminal, as much as 30 cm. long, very loose with far spreading branches, which are quadrangular like the petioles, and glabrous or with feeble downy hairs toward the

<sup>1</sup>In Engler and Prantl, 1895, 'Die Natürl. Pflanzenfam.,' IV, pt. 3a, p. 133.

<sup>2</sup>The name is not recorded in the Index Kewensis nor in any of its Supplements.

<sup>3</sup>"Arbor vel frutex." This should be amended to "creeper." See remarks at end of description.

apex; the subdivisions of the inflorescence are pseudo-umbels of 6 to 20 flowers. The peduncles are 2 to 4 mm. long, covered with fine downy hair and bear about the middle of their length 2 lanceolate, easily dropped, downy bracts, 2 to 4 mm. long. The calyx is broadly cupuliform, 3 mm. long, with a truncate or very indistinctly 5-toothed margin. The corolla is greenish-white, covered with yellow glands outside, with curved tube.

"The species belongs in the section *Agnus Castus* and more definitely in Briquet's *Terminales*-group. Among related forms, *V. Buchanani* Baker differs in the smaller, hairy leaves; *V. quadrangula* Guerke also is more strongly pilose. *V. thyrsiflora* Baker too belongs in this group, but is known to me only by the description according to which the leaves are pubescent on the under side also and the calyx apparently is more distinctly toothed. The present species is furthermore characterized by being inhabited by red ants; the hollow branches usually show at the nodes the almost circular orifices which are characteristic of so many ant-plants" (Guerke, 1903).

Togo: not rare in the forest (Baumann).

Cameroon: Yaunde (Zenker and Staudt).

Belgian Congo: Northeastern Congo Forest: Avakubi (January 1914; Lang, Chapin, and J. Bequaert; Coll. No. 1803); Medje (July 1914; Lang and Chapin); Penge (January 31, 1914; J. Bequaert; Coll. No. 2216); between Penge and Irumu (village of Nduye, February 20, 1914; J. Bequaert); Kilo (June 30, 1914; J. Bequaert; Coll. No. 4894).<sup>1</sup>

*V. Staudtii* must also occur in Spanish Guinea, since its peculiar host, *Viticicola tessmanni* (Stitz), was originally found at Alen, Spanish Guinea, by Tessmann.

With the exception of the indication "tree or shrub," Guerke's diagnosis of *V. Staudtii* agrees perfectly with a myrmecophilous creeper obtained by me in the Ituri Forest and of which dried branches were also brought back by Messrs. Lang and Chapin. In the hope of identifying this plant, I have carefully read the numerous published descriptions of African *Vitex* and there is a reasonable certainty that the Ituri creeper is either identical with or very closely allied to *Vitex Staudtii*.<sup>1</sup> The designation "tree or shrub" is, I believe, due to the fact that Guerke based his description on a few herbarium specimens, which gave not the slightest indication that the species was a creeper; moreover, all other members of the genus known thus far are either trees or erect shrubs.

#### ***Vitex yaundensis* Guerke**

*Vitex yaundensis* GUERKE, 1903, Engler's Bot. Jahrb., XXXIII, 2, p. 296.

"Tree, with very long petiolate, 5-foliolate leaves. Leaflets short petiolulate, oblong-ovate, cuneate at the base, with entire margin, very glabrous on both sides. Flower-cymes axillary, with very long peduncles. Bracts linear. Calyx turbinate, 5-toothed, with deltoid teeth. Tube of the corolla hardly raised above the calyx.

<sup>1</sup>Mr. Chapin informs me that he saw this myrmecophilous creeper also near Ngayu.

<sup>2</sup>The first indications as to the taxonomic position of this curious myrmecophyte were given by Prof. I. W. Bailey, who, from histological examination of the stems, concluded that it belonged to the *Verbenaceae*, most probably in the genus *Vitex*.

"A tree 6 to 8 m. high, with quadrangular, glabrous branches. The leaves are 5-foliolate, borne on a petiole 15 to 22 cm. long, which is glabrous with a flattened groove above. Leaflets with a petiole 1 to 2 cm. long; elongate-ovate, narrowed at the base into the petiole; with entire margin; long acuminate, herbaceous, entirely glabrous on both sides. Parallel lateral veins very numerous, as many as 25 on the median leaflet. The median leaflet reaches a length of 24 cm. and a width of 9 cm.; the two lateral leaflets nearest it are a little smaller, reaching a length of about 20 cm.; the two external leaflets are only 14 cm. long and 7 cm. wide, being in proportion broader than the two lateral leaflets. The inflorescences are placed in the axils of the upper leaves and borne on peduncles 16 to 20 cm. long; they are loose, compound double cymes (dichasia) with strikingly long ramifications. The bracts are sessile, linear, long acuminate, with fine downy hair, as much as 15 mm. long on the lower ramifications; shorter on the upper ramifications. The peduncles are 2 to 3 mm. long and covered with fine downy hair. The calyx when expanded is top-shaped, downy, 3 mm. long, 5-toothed; the teeth are triangular with even sides, rather acute, 1 mm. long and about as wide at the base. The corolla has a very thick, glabrous tube, which is only 4 mm. long; the limb is distinctly bilabiate and 5-lobed; the two posterior lobes are ovate, obtuse, downy, 1 mm. long; the two lateral ones have a similar shape and pilosity, but are 2 mm. long; the anterior one is spatulate, somewhat emarginate, 4 mm. long, pilose at the base and on the middle line, otherwise glabrous. The flower is greenish-yellow; the anterior lobe violet.

"The species belongs near the very large leaved *V. grandifolia* Guerke and *V. bipindensis* Guerke, but differs in the squarrose, very loose inflorescences, and also in the remarkably numerous lateral veins of the leaves. The plant is certainly inhabited by ants, as one can conclude from the characteristic circular openings at the nodes of the branches" (Guerke, 1903).

Cameroon: Yaunde (Zenker).

#### ECOLOGY OF *Vitex Staudtii*

My attention was first called to this remarkable myrmecophyte by my friend, Mr. J. P. Chapin, at Avakubi, in January, 1914. Knowing my interest in ant-inhabited plants, he directed me to a swampy, wooded spot on the banks of the Ituri River, about five miles upstream from that locality, where there were many specimens of a creeper in the undergrowth of the forest. When the stems of this plant were slightly touched or otherwise disturbed, large numbers of slender, reddish ants rushed out of the hollow stalks ready to attack. I later came across the same creeper on several occasions during my travels in the Ituri Forest, and it appears to be fairly common throughout that region. On the other hand, I never saw it along the Semliki River or in the primitive forest between Lake Kivu and the Lualaba.

All the specimens observed by me were growing in very moist places, usually in parts of the forest flooded after heavy rains. The older plants consist of a long, flexible, woody main stalk, about 15 to 20 mm. thick at the base, or occasionally more. This stem begins to

branch feebly and irregularly a short distance from the ground and climbs freely among bushes and low trees, sometimes to a height of 8 to 10 meters. Its upper part is much more abundantly ramified and spreads leaves and flowers over the crown of the supporting vegetation. The compound, digitate leaves, of three to five nearly sessile leaflets, are borne on long petioles and placed opposite each other in decussate rows. Young branches and those on the upper part of the plant are quadrangular their whole length, with four slightly convex or nearly flat sides and more or less winged angles. These four winged ribs are continuous along the limb, at the nodes running on both sides of the petioles. Older branches show the ribs much less pronounced, the surfaces between becoming more convex, but often they still possess fairly pronounced wings, which can even be traced along the main stalk. Stem and branches show no sign of swellings. I have never seen the flowers, but the fruit is small, spheroidal, dry, hard, and of a pale orange-yellow color when ripe.

Adult plants were always inhabited by ants, invariably of the species *Viticicola tessmanni* (Stitz). The insects enter and leave their nests through a few orifices arranged in pairs at the nodes, nearly opposite each other and between the points of insertion of the leaves (Fig. 88a). The aperture, usually more or less crater-shaped, is placed at the top of a slight elevation which is produced by a peculiar ring of sclerenchyma, as shown by Prof. Bailey (see Part V, p. 591). On examining a very young specimen of this *Vitex* still free of ants, I was unable to find a depression, elevation, or scar on the surface to indicate the points where the insects would later gnaw entrance holes. Prof. Bailey's histological study shows that the most favorable situation for the nodal apertures is midway between the points of attachment of the leaves (see Part V, p. 592). The location of exits in *Vitex Staudtii* compares to a limited extent with that in *Cecropia adenopus*, in which, however, the entrances are always pierced above the axils of the leaves but in a section of the stem which is practically devoid of tough tissues (Schimper, 1888). In *Cecropia* the location of this diaphragm of softer tissues is marked externally by a roundish depression or prostoma, at the upper end of a shallow groove running upward from the insertion of the petiole; the ants of *Cecropia* always locate the entrance to the hollow stems in the depressed prostoma. How in *Cecropia*, *Vitex Staudtii*, and other similar cases the ants discover the spots particularly favorable for apertures and why they practically restrict their attacks to these parts of the stem are questions which cannot be satisfactorily answered at present. It

has been suggested (Wheeler, 1913, p. 136) that ants may be able, through their extremely delicate tactile (or rather chordonotal) sense-organs, to select the thinnest spot in the wall of a cavity for perforation. Their sense of smell may also warn them against gnawing parts of the stem containing certain distasteful substances.

A longitudinal section of the stalks (Fig. 88b) discloses many features of further interest. In the first place, adult plants occupied by an ant colony are hollowed out nearly from top to bottom, all the internodes and various branches freely communicating with one another. The entire plant shelters one ant community, containing, in addition to one or more deälated queens, a number of fertile, ergatoid, wingless females. The formicaries of *Viticicola tessmanni* in the stems of *Vitex Staudtii* are thus splendid examples of polygynous insect societies. As in the case of *Pachysima* colonies in *Barteria*, they probably originate through secondary pleometrosis, or subsequent fusion of several isolated colonies, each started by a fecundated queen in the various limbs. A young specimen of *Vitex Staudtii*, scarcely 1 m. high, growing near the village of Nduye, between Penge and Irumu, was particularly instructive in this connection. Each of the lower internodes on the side-branches was occupied by a fertile, deälated female of *Viticicola tessmanni*, together with brood at various stages of development; no workers were present.

The ants clean out most of the medullary tissue nearly the entire length of the internodes, leaving only a peripheral layer of it for a short distance a little above the node. This remaining pith partly constricts the cavity and is probably left to keep the brood of the ants from dropping below the node, thus helping to distribute it regularly over the various internodes of the vertical stems and also preventing it from obstructing the apertures at the nodes. On a level with this inner circle of tissue the walls of the stem are also slightly thicker than in the other parts of the internode. At Kilo, in June, 1914, I saw a very young *Vitex Staudtii* composed of an unbranched, leaved, erect, thin stem about two feet high and unoccupied by ants. The central cylinder of the whole plant was filled with soft medullary tissue. It is possible that this substance dries up by itself, causing the stems to be hollow without the intervention of ants. In nature, however, this must be rarely the case, for, in adult plants housing a colony of *Viticicola*, pith is found only in the topmost internode of very young branches which are still green and soft; the ants steadily work upward through the nodes and excavate the interior before it has begun to dry.

The inner walls of the hollow stalks also show a peculiar series of depressions or narrow channels, the like of which is not known for any other myrmecophyte. These lateral cavities perforate the xylem and end blindly just under the cambium; they are arranged at irregular intervals, one above the other, in two longitudinal rows. The rows are opposite each other and their position shifts at every node, so that they always run on the sides corresponding with the upper pair of apertures of every internode. The number of channels in a row varies with the length of the internode, in some cases there are fifty or more, but often fewer. It occasionally happens that one of these lateral galleries perforates the bark, and this supplementary exit hole then produces the same projecting ring of sclerenchyma which surrounds the normal, crater-like apertures at the nodes. Since no trace of lateral cavities is found in young internodes where the pith has not yet been removed by the ants, we must conclude that they are excavated by the workers of *Viticicola*. They are not used by the inmates for their eggs or very young larvæ. Coccids are not found in these channels and, furthermore, are absent from the hollow stalks of *Vitex Staudtii*. It was at first believed that the channels assist in the aëration of the hollow interior, but this is disproved by Prof. Bailey (see Part V, p. 586). He found that the bark outside the depressions presents no lenticels or patches of aërenchyma for the exchange of gases. On the contrary, the overlying tissues are compact and, in old stems, there are disks of impervious sclerenchyma located just opposite the blind ends of the cavities. Moreover, Prof. Bailey discovered that the channels are not natural gaps in the woody portion of the wall, but are excavated by the ants in peculiar cores of delicate, un lignified cells, that are symmetrically distributed in certain radii of the stem and surrounded by abnormal tissues similar to those presented by heteroplasmatic zoococidia. The arrangement of the galleries in two rows below the apertures of the upper node results from the fact that in *Vitex Staudtii* the principal water-conducting passages in each internode are largely confined to those sides of the stele which pass out to the leaves at the next (higher) node. The lateral cavities are excavated in the sides of the stele poorly supplied with vessels and, furthermore, located in those portions of the xylem which are devoid even of a narrow fringe of small primary tracheæ.

Prof. Wheeler has given a detailed description of *Viticicola tessmanni* (Stitz), the obligatory guest of *Vitex Staudtii*, in its various adult phases and larval stages. My observations in the field furnish no clue as to the possible food of these insects, but the ants are evidently adapted

Specimens collected by Dewèvre in the Belgian Congo (Leopoldville; Bokakata) bear the following note: "Arbuste de 2 m. environ, toujours habitée par de nombreuses fourmis noires." (De Wildeman and Durand, 1901, p. 130).

#### **Uragoga species ?**

In the forest bordering one of the affluents of the Congo near Leopoldville, I came across a semiherbaceous, low bush, which I provisionally refer to the genus *Uragoga* (May 18, 1915; Coll. No. 7656). The flowers are white, with greenish spots on the teeth of the corolla; the fruit is a red berry. At each node, between the points of attachment of the leaves, there are two curious, persistent stipules, occupying the entire width of the stem (Fig. 89). They are convexly swollen to the upper side and the free margin is recurved downward, the whole forming an inverted cup or pouch broadly open below. Coccids were usually found inside this cavity and the ants, *Crematogaster striatula* variety *obstinata* (Santschi), had built a tent of vegetable material over the inferior opening of the stipules. I did not find eggs, larvæ, or pupæ of these ants inside the stipules, which I therefore regard not as myrmecodomatia but merely as "kraals" to shelter the scale insects. Yet this case suggests useful comparison with the stipular pouches of *Macaranga saccifera* and other more typical ant structures of plants.

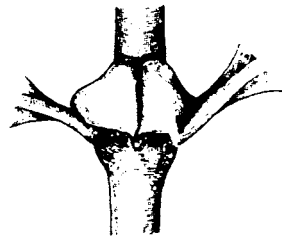


Fig. 89. *Uragoga* species? Swollen stipules at base of a pair of leaves; drawn from life at Leopoldville, May, 1915; twice natural size.

#### **UNCARIA Schreber**

*Uncaria* SCHREBER, 1789, in Linnaeus, 'Gen. Plant.,' Ed. 8, I, p. 125. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 41. HAVILAND, 1897, Journ. Linn. Soc. London, Botany, XXXIII, p. 73.

*Ourouparia* AUBLET, 1775, 'Histoire des Plantes de la Guiane française,' I, p. 177, Pl. LXVIII. K. SCHUMANN, 1891, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' IV, pt. 4, p. 57.

*Agylophora* NECKER, 1790, 'Elementa Botanica,' I, p. 145.

Climbing shrubs with opposite, interpetiolar, fugacious stipules; the lower part of the terminal branches with axillary recurved hooks, often spirally rolled up and placed opposite each other; in some cases these hooks still bear a few aborted, opposite leaves. On older branches the recurved hooks are often replaced by heavy, woody thorns. Leaves usually leathery, rarely herbaceous; the stipules entire or bifid. Flowers pedicelled or sessile, crowded into loose, globose heads, without intervening bracteoles. Flower heads placed in the axils of the upper leaves, either singly or in decussate panicles. Calyx salver-, or bell-, or funnel-shaped; the calyx-tubes





Fig. 90. *Uncaria africana* G. Don. Extremity of branch with capitulum of fruits (after Bentham, 1849).

Sierra Leone, type locality (G. Don; Afzelius; Barter; Scott Elliot; Johnston).  
Nigeria (Vogel).

Cameroon.

Spanish Guinea: Rio Muni (Mann).

Belgian Congo: Lower Congo; banks of the Lukungu River (Dewèvre); Kisantu (Gillet); Inkisi River (Vanderyst). Kasai: Linkanda (Gentil). Upper Congo: Mondombe (Jespersen). Northeastern Congo forest: Mangbetu Country (Schweinfurth); Uele region (Seret); Barumbu (November 3, 1913; J. Bequaert; Col. No. 1069); Penge (January 27, 1914; J. Bequaert; Coll. No. 2136); between Penge and

Irumu (village of Tete, February 22, 1914; J. Bequaert; Coll. No. 2658); between Walikale and Lubutu on the Oso River (village of Mandimbo, January 18, 1915; J. Bequaert; Coll. No. 6664).

Uganda.

Angola: Golungo Alto—"in the primitive forests of Sobato de Mussengue" and "in the very dense, primitive forest of Quibanga" (Welwitsch).

Also known from Madagascar and the Comoros.

Haviland distinguishes several varieties:

Variety (1). Flowers subsessile. Upper part of the calyx-tube 4 mm. long. Sierra Leone, Niger, Mangbetu.

Variety (2) *madagascariensis* (*Ouroparia madagascariensis* Baillon, 1879, Bull. Soc. Linn. Paris, I, p. 228). Flowers subsessile. Upper part of the calyx-tube 2 mm. long. Malagasy Region.

Variety (3) *angolensis* Haviland. Flowers pedicellate. Upper part of the calyx-tube 4 mm. long. Angola.

Variety (4). Flowers pedicellate. Upper part of the calyx-tube 2 mm. long. Cameroon.

The variety *angolensis* Haviland is described more in detail by Hiern (1898) as follows:

An arborescent shrub, glabrous except the inflorescence. Trunk in some cases more than 100 ft. long and 6 in. in the lower part, climbing to a very great height and then hanging down; branches patent, fuscous, rather glossy, tetragonal. Leaves opposite, elliptical, narrowly acuminate at the apex, obtusely narrowed or nearly rounded at the base, thinly coriaceous, glossy, dark green above, paler beneath, 2 to 4  $\frac{1}{2}$  in. long,  $\frac{1}{2}$  to 1  $\frac{3}{8}$  in. broad; lateral veins about 6 on each side of the midrib, slender; petiole  $\frac{1}{8}$  to  $\frac{1}{4}$  in. long. Stipules ovate, small, somewhat hairy on the inner face, nearly deciduous. Spines axillary, mostly crooked,  $\frac{1}{4}$  to  $\frac{3}{4}$  in. long. Flower heads terminating the branches, shortly pedunculate, globose, about 2 in. in diameter. Flowers golden-tawny, about  $\frac{3}{4}$  to  $\frac{7}{8}$  in. long (including the exerted style), very numerous, crowded. Pedicels about  $\frac{1}{8}$  to  $\frac{1}{6}$  in. long in flower,  $\frac{3}{8}$  in. long in fruit, tomentellous. Bracts 0. Calyx silky-tomentellous with short upward hairs, somewhat constricted above the ovary, greenish-fuscous; tube broader than the ovary, campanulate, funnel-shaped,  $\frac{1}{6}$  to  $\frac{1}{5}$  in. long, shortly 5-cleft, lobes thickly lanceolate. Corolla  $\frac{1}{2}$  to  $\frac{3}{8}$  in. long; tube slender, except the base clothed outside with downward tawny short silky-tomentose hairs,  $\frac{1}{3}$  in. long; limb much broader than the tube, hemispherical,  $\frac{1}{2}$  to  $\frac{1}{4}$  in. in diameter, golden-tawny tomentose outside, glabrous inside, deeply 5-lobed; segments about  $\frac{1}{4}$  in. long, obovate-oblong, rounded at the apex with an apiculus. Stamens 5, about half as long as the corolla-lobes, glabrous, introrse, inserted on short, flattened filaments at the base of the corolla-limb. Ovary ellipsoidal, tomentose, rather thicker than the base of the calyx-limb, much thinner than the top of the calyx-limb. Style filiform, exerted about  $\frac{1}{4}$  in. beyond the corolla, glabrous below, stigmatose and rather thickened in the upper part towards the clavate stigma. Young fruit subglabrous, about  $\frac{3}{8}$  in. long,  $\frac{1}{6}$  in. thick, narrowed at both ends especially towards the base.

This species probably occurs throughout the African Rain Forest. In a recent note, De Wildeman (1919) calls attention to the myrme-

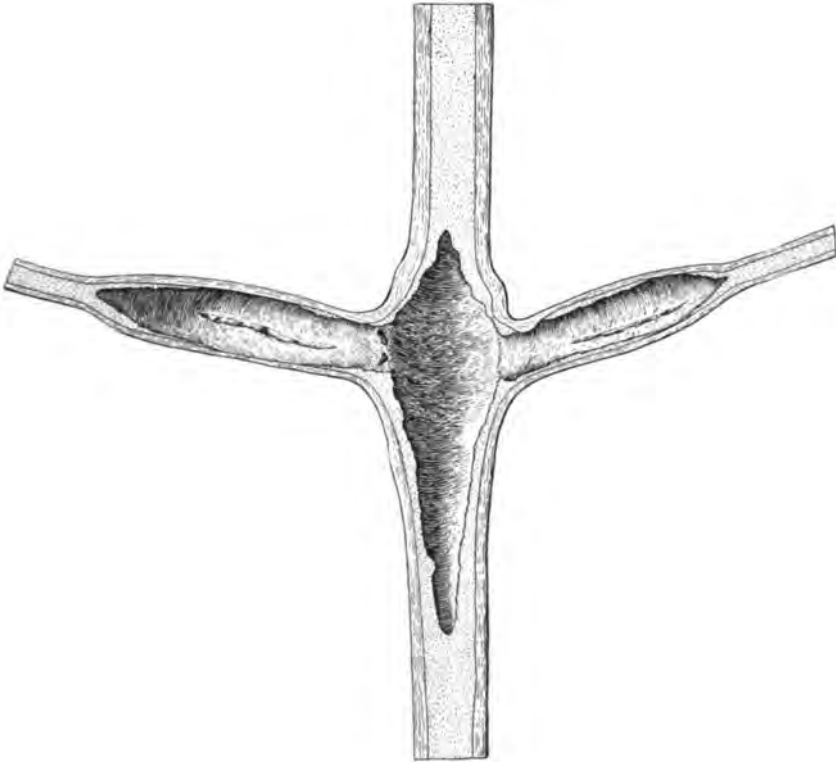


Fig. 91. *Uncaria africana* G. Don. Longitudinal section of myrmecodomatium at a node, showing three cavities communicating with one another; the aperture is not figured. Drawn from life at Barumbu, November, 1913; natural size.

cophytism of certain African plants of this genus. He proposes, provisionally, the varietal name *myrmecophyta* De Wildeman for specimens which I collected in the Ituri Forest at Penge and between Penge and Irumu, without, however, giving characters by which this new variety could be differentiated from the typical form. I am inclined to believe that myrmecophytism is normal for *Uncaria africana* throughout its range and has merely been overlooked thus far. When terminal branches alone are collected, there may be no indication of the peculiar myrmecodomatia in herbarium specimens, even should such have been present on lower parts of the plant. Ant-inhabited parts of plants are also frequently avoided by botanical collectors. Moreover, it is possible that the myrmecodomatia are absent or but little pronounced in certain individuals or at certain stages of growth.

ECOLOGY OF *Uncaria africana*

Here (Figs. 90 and 91) we have one of the many climbing bushes or "scramblers"—as Schimper proposed calling them—which frequently form tangles of vegetation over the low trees at the edge of clearings and along river banks. While the trunk and main branches are straight and stiff as in ordinary bushes, all or part of the lateral branches are limp and pliable. The latter either hang down freely or work their way upward, keeping hold of the other trees by means of the spirally curved hooks and woody thorns, which are placed in pairs above the nodes and are evidently modified branches. The leaves are glabrous, as well as the branches at the extremity of some of which the flowers or fruits form head-clusters.

The myrmecodomatium of this *Uncaria* consists of the enlarged and hollow basal internodes of two opposite, lateral branches, the cavities in this pair of swellings communicating with the hollow, very slightly swollen node of the main branch (Fig. 91). The middle chamber is more or less club-shaped, 5 to 6 cm. long and 10 to 20 mm. wide in the upper half; it is dug farther into the pith below than above. The two lateral cavities are 3 to 6 cm. long and 6 to 10 mm. broad.

All the specimens I had opportunity to study in the field were inhabited by ants of the genus *Crematogaster*, which were identified as *C. excisa* subspecies *andrei* (Forel) in the case of the plants found near the Oso River, between Walikale and Lubutu in January, 1915. The myrmecodomatia contained not only the queen, workers, and brood of the ants, but also numerous coccids. These scale insects were invariably located in the lateral swellings and fixed at the bottom of two deep, opposite, longitudinal grooves in the inner wall. One or more circular exit holes are pierced by the ants through the sides of the lateral cavities. Often the depressions occupied by the coccids are open to the exterior by means of irregular slits through which the ants enter and leave. It would thus seem that these grooves are gnawed by the ants, probably on account of some special hyperplasias formed in that region of the walls. The coccids merely select the grooves for nutritive, juicy tissue to be found there and continually renovated by the attacks of the ants.

On the plants examined by me at Barumbu in November, 1913, there were a number of young branches whose basal internodes, though distinctly swollen, were still filled with juicy pith tissue. In another instance, between Walikale and Lubutu, the basal swellings of many older branches were not yet inhabited by ants, presenting no exit holes; nevertheless, they were entirely hollow inside, so that the cavities of

ECOLOGY OF *Sarcoccephalus* SPECIES

This myrmecophyte was first met with in the Ituri Forest, near the village of Banana between Penge and Irumu (February 24, 1914; Coll. No. 2605) and was again seen near the village of Masongo, between Walikale and Lubutu (January 15, 1915; Coll. No. 6629). It is a low, erect tree or shrub, rarely over 8 meters high, usually much smaller (3 to 4 m.). The straight trunk bears, from its foot on, regularly spreading, opposite, decussate branches. The leaves are opposite, large and very broad, usually purplish-red on the under side, especially when young. The terminal part of the branch bears, between the points of attachment of the leaves, striking, broad stipules which, however, are early deciduous.<sup>1</sup> It never happened that I saw flowering plants, but the fruit is a spheroidal, solid ball, 9 to 10 cm. in diameter, placed at the extremity of a side branch, on a short, recurved pedicel. All the specimens observed grew on swampy, rather open spots of the primitive forest, either at the edge of a brook or in the water.

It is quite possible that this species has been described before, perhaps under a related genus of Rubiaceæ, but it agrees with none of the diagnoses seen so far. Its relation with ants would easily escape notice,

for the myrmecodomatia are inconspicuous and, when not actually occupied by insects, could often be discovered only upon sectioning the branches. Externally, they consist (Fig. 92) of a very slight, often imperceptible swelling on the upper half or two-thirds of the internode. Inside, the central cylinder is hollowed out into a spacious cavity, 6 to 8 cm. long and 5 to 7 mm. wide at the top. Domatia inhabited by

ants have a circular aperture a short distance below the node.

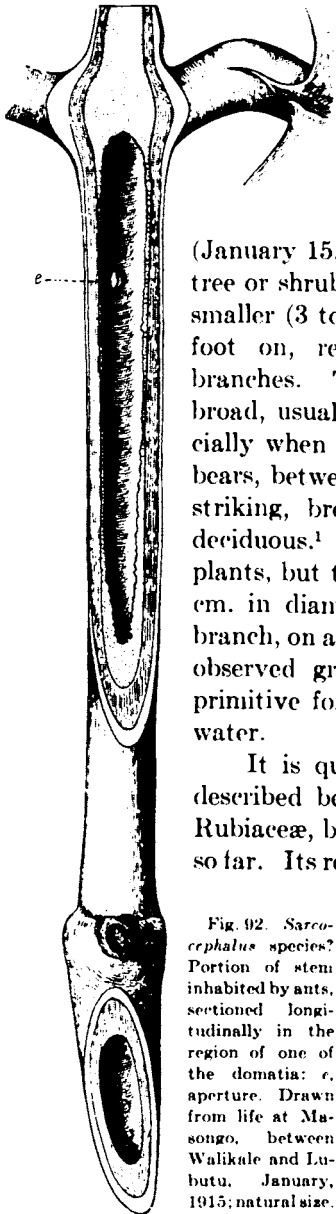


FIG. 92. *Sarcoccephalus* species? Portion of stem inhabited by ants, sectioned longitudinally in the region of one of the domatia: e, aperture. Drawn from life at Masongo, between Walikale and Lubutu, January, 1915; natural size.

<sup>1</sup>In the common African *Sarcoccephalus sambucinus* the stipules are small (4 mm. long) and persistent; but they are large and caducous in many other species of the genus.

Sections made of a number of young specimens of this myrmecophyte not yet settled by ants showed that in this case, too, the swollen upper portion of the internodes becomes hollow of its own accord through the drying up of part of the medullary tissue; such cavities have no exit holes. In this species the lower internodes of the main trunk and side branches are neither transformed into domatia nor in the least swollen and remain completely filled with pith. Very young plants show no trace whatsoever of ant-chambers and on an adult tree the size and shape of the myrmecodomatia becomes more pronounced toward the upper branches.

In both localities where I observed this *Sarcocephalus* a number of specimens were inhabited by small ants of the genus *Crematogaster*. Those taken from the domatia of the plants between Walikale and Lubutu were identified by Santschi as *C. africana* subspecies *winkleri* variety *fickendeyi* (Forel), a form commonly found nesting in other places. These insects had established regular colonies in the cavities, with a queen, workers, and brood; coccids were also among them, fixed on the inner walls.

#### RANDIA Linnæus

*Randia* (Houston) LINNÆUS, 1753, 'Species Plantarum,' Ed. 1, II, p. 1192. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 93. K. SCHUMANN, 1891, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' IV, pt. 4, p. 75.

Erect or scandent, spinous or unarmed shrubs or trees, with opposite or verticillate, often leathery leaves; stipules rather short, solitary, entire, more or less heath-like. Flowers large or medium-sized; solitary, few together, or corymbose; as a rule apparently axillary or terminating short lateral branches, or terminal. Calyx-tube ovoid or turbinate, ribbed or cylindrical; the limb usually tubular, truncate, toothed, lobed, or spathaceous; lobes sometimes foliaceous. Corolla white or yellowish, or more greenish; campanulate, funnel-shaped, or salver-shaped; tube in some species much elongated; limb spreading or reflexed, dextrorsely contorted in the bud. Anthers sessile or subsessile, narrowly linear, inserted at or near the throat or mouth of the corollar tube, included or exerted. Disk annular or cushion-shaped. Ovary 2-celled. Ovules very numerous, immersed in the fleshy placentas. Style strong, glabrous or hairy; stigma club- or clapper-shaped, entire, bidentate or bilobed, sulcate. Berry 2-celled, usually many-seeded; the testa of the seed leathery or membranous.

This genus is close to *Pouchetia* A. Richard and *Oxyanthus* de Candolle; still more so to *Gardenia* Ellis, which it often resembles in general habitus. *Gardenia* has the ovary completely one-celled for the whole length; this character, however, is not always easy to decide upon because in certain species of *Randia*, as, for instance, *R. physophylla*, the ovary is incompletely divided into two cells.

About 150 species have been described, by far the majority being found in the Oriental and Ethiopian Regions and a few in Tropical America. In the Belgian Congo the genus is well represented by some twenty-five species. They are trees or bushes with large, showy flowers, growing mostly in the Rain Forest or in the forest galleries along the streams of the Savannah.

Three of the African species are associated with ants; they all belong to that section of the genus in which the lobes of the calyx are elongate, slender, subulate, and not leaf-like. *R. physophylla* K. Schumann is characterized by the presence of glandular cavities at the base of the leaf-blade (Fig. 94). The two others, *R. myrmecophylla* É. De Wildeman and *R. Lujæ* É. De Wildeman, possess caulinary myrmecodomatia and, in addition, agree in the following characters:

Trees or shrubs with glabrous branches, feebly flattened at the nodes; the internodes often swollen, spindle-shaped; the swellings being hollow, usually pierced by one or more orifices and inhabited by ants; the leaves are opposite, or apparently verticillate, three of them being placed at about the same level; blade obovate, acuminate, constricted at the base into a rather thick, short petiole.

They can be separated as follows on characters mentioned in their descriptions:

- Flowers erect, placed by twos or fours in the axils of the leaves, about 22 cm. long; tube of the corolla glabrous externally. Leaves smaller, with acarodomatia in the axils of the lateral veins..... *R. Lujæ* De Wildeman.
- Flowers pendent, solitary, terminal, much larger; the corolla alone 22 to 25 cm. long, shortly tomentose externally. Leaves larger, the blade as much as 30 cm. long and 15 cm. broad, without acarodomatia. *R. myrmecophylla* De Wildeman.

#### **Randia Lujæ De Wildeman**

*Randia Lujæ* É. DE WILDEMAN, 1904, C. R. Ac. Sci. Paris, CXXXVIII, p. 914; 1904, 'Notices sur des Plantes utiles ou intér. Flore du Congo,' I, pt. 2, pp. 282-284; 1907, 'Études Flore Bas- et Moyen-Congo,' II, p. 159; 1910, *ibid.*, III, pt. 2, p. 286; 1912, *ibid.*, III, pt. 3, p. 487. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 259. H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 155 and 158. É. DE WILDEMAN, 1920, 'Mission de Briey au Mayumbe,' pp. 43, 88, 222, and 264.

"Large tree with glabrous branches, the internodes often thickened toward the base and pierced by one or two orifices leading into a cavity inhabited by ants. Leaves obovate, acuminate, narrowed at the base into a short and rather thick petiole; blade rather coriaceous, darker colored above than below, 20 to 25 cm. long, 5 to 12 cm. broad, glabrous on both sides, with an acumen of 15 mm. Lateral veins numbering about 9 on each side of the midrib, anastomosing into a curve before reaching the margin, little or not prominent above, prominent on the under side; in the axils of the origin of the lateral veins there are acarodomatia excavated in the tissue of the nervure and opening by a pore at the under side of the blade, more or less visible on

the upper side as feeble swellings. Flowers by twos, erect, sessile or subsessile, about 22 cm. long; calyx about 17 mm. long, glabrous, with 5 ribs ending in 5 subulate, irregular teeth; corolla with a long linear, glabrous tube, rather abruptly widening in its upper part, the broadened portion about 22 mm. long; ending in 4 ovate-lanceolate, acute lobes of about 3 mm.; glabrous externally, sparsely villous internally. Stamens partly exerted, extending beyond the broadened funnel of the corolla for about 11 mm. Fruit globose, voluminous, over 15 cm. in diameter" (É. De Wildeman, 1904).

Belgian Congo: Kasai: forest along the Sankuru River, type locality (Luja). Middle and Upper Congo: Lukolela (Clacssens); Lokelenge (Bruneel); Bianga (Bellefroid). Mayombe: Ganda Sundi (de Briey).

According to De Wildeman (1910, p. 286) the leaves are often placed in verticils of three; the flowers frequently by fours; the fruit is grayish, subspherical, with 5 more or less conspicuous ribs. This species is close to *Randia maculata* de Candolle, = *R. longiflora* (Salisbury), but differs in the presence of acarodomatia in the axils of the lateral veins and the ant-swellings of the internodes.

#### ***Randia myrmecophyla* De Wildeman**

*Randia myrmecophyla* É. DE WILDEMAN, 1907, 'Études Flore Bas- et Moyen-Congo,' II, pt. 2, p. 160, figs. 5-8, Pls. xxxviii-xxxix; 1908, *ibid.*, II, pt. 3, p. 346; 1907, 'Mission Émile Laurent,' V, pp. ccxxiii-ccxxiv, figs. IX, XI.

*Randia myrmecophila* TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 260.

*Randia myrmecophila* H. KOHL, 1909, *Natur u. Offenbarung*, LV, pp. 158-160, fig. 5.

"Shrub with glabrous branches, which are flattened at the nodes, and swollen toward the apex of the more or less lengthened internodes. Internodes hollowed over part of their length, sheltering ants and coccids. Leaves opposite or pseudo-verticillate by threes, petiolate; the petiole flattened above. Stipules very broad, triangular, acuminate, about 4 mm. long. Flowers solitary, the calyx with 5 linear teeth. Corolla with a cylindric tube, widened in its upper part, with 5 lobes which are rounded at their apex. Anthers inclosed. Style with a club-shaped stigma, not or little exerted.

"Variety *typica* De Wildeman (1907, p. 160).

"Petiole 15 to 25 mm. long, short tomentose, flat above. Blade of the leaves cuneate at the base, rounded-cuneate at the apex, glabrous above, velutinous-tomentose on the under side, with 11 or 12 lateral veins on each side of the midrib, 20 to 40 cm. long and 9 to 13.5 cm. broad. Calyx short tomentose externally, becoming glabrous with age, densely villose and silky inside; its tube, including the ovary, about 2.5 cm. long, with conspicuous ribs ending beyond the truncate margin in 5 linear teeth, 5 to 13 mm. long. Corolla with its tube 22 to 25 cm. long, shortly tomentose externally; more heavily villose inside, except in its widened, glabrous part which is 9 cm. long; lobes villose on both faces, 5.5 cm. long and of about the same width, partly overlapping in the bud. Fruit ovoid, 10 cm. long, 8 cm. in diameter, with 5 feeble ribs.

"Variety *subglabra* De Wildeman (1907, p. 163).

"Petiole 8 to 15 mm. long, sparsely and short tomentose, flat on the upper side. Leaf-blade rather broadly cuneate at the base, glabrous and shiny above, glabrous and dull on the under side, except on the lateral veins of which there are 12 or 13 on each



side of the midrib; 18 to 23 cm. long and 7.5 to 12.5 cm. broad. Calyx short tomentose externally, becoming glabrous with age; densely silky-villose inside; its tube including the ovary about 2.5 to 2.8 cm. long, often split on one side; ribs conspicuous, ending beyond the truncate margin into 5 linear teeth, 16 mm. long. Corolla with a tube of 21 to 22 cm., the lobes about 4 cm. by 4 cm.; the villosity as in the form *typica*.

"Variety *glabra* De Wildeman (1907, p. 163).

"Petiole 15 to 30 mm. long, glabrous. Leaf-blade long cuneate at the base, glabrous on both faces, shiny above, dull below; with about 14 lateral veins on each side of the midrib; 18 to 26 cm. long and 6 to 10.5 cm. broad. Calyx glabrous externally; the tube including the ovary about 2 cm. long (in the bud), the teeth 6 to 15 mm. long" (De Wildeman, 1907).

Belgian Congo: Kasai: Bombaie (É. and M. Laurent). Middle and Upper Congo: Eala, type locality (Pynaert; M. Laurent; variety *typica*); Coquilhatville (M. Laurent; variety *subglabra*). Eastern Congo Forest: Yambuya (M. Laurent; Solheid; variety *subglabra* and variety *glabra*); Avakubi (January 13, 1914; J. Bequaert; Coll. No. 1917).

De Wildeman's figure of a flowering live plant (1907, p. 160, fig. 5) shows that the very large, solitary, terminal flowers are pendent. According to the same author, it belongs to the group of *R. malleifera* (Hooker), which species, however, differs in the absence of ant-swellings, the smaller corolla with much denser and longer tomentum on the tube, and the villosity of the stem.

#### ***Randia physophylla* K. Schumann**

*Randia physophylla* K. SCHUMANN, 1899, Engler's Bot. Jahrb., XXVIII, pt. 1, p. 64.

É. DE WILDEMAN, 1903, 'Études Flore Bas- et Moyen-Congo,' I, p. 81; 1907, *ibid.*, II, pp. 74 and 164; 1912, *ibid.*, III, pt. 3, p. 487. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 260.

"Leaves very short petiolate or sessile, oblong, short and sharply acuminate, broadly cuneate at the base, subcordate and auriculate below, the earlets excavated and glandular; leaves very glabrous on both sides, resinous and very shiny. Ovary, to judge from the fruit, globose, glabrous and scabrous. Calyx tubular and irregularly 5-lobed, the lobes costate and scabrous. Corolla pentamerous, each of the 5 lobes divided in the upper part into obovate, obtuse, carnoselaciniae. Anthers curved, broad. Style exerted for a long distance out of the corollar tube; subclavate and sulcate in its upper part. Berry globose, crowned by the calyx.

"The petiole is hardly 3 to 4 mm. long. The blade has a length of 30 to 35 cm. and a width in the middle of 12 to 14 cm.; it is crossed on each side of the midrib by 23 to 25 heavy lateral veins, which are visible on both upper and under surfaces; the leaf is shiny chestnut-brown in dried condition. The two semiglobose glandular cups at the base of the leaf are 5 mm. deep. The glands of the stipules must secrete an abundance of resin, for it fairly drenches the leaves and forms a crust at the base of the petiole. The calyx has a length of 3 to 3.5 cm. The corolla is very fleshy, 18 to 19 cm. long, of which 15 cm. is the length of the tube. The stamens are 1.3 cm. long. The style exceeds the corollar tube by about 3 cm. The berry has a diameter of 2.5 cm." (K. Schumann, 1899).

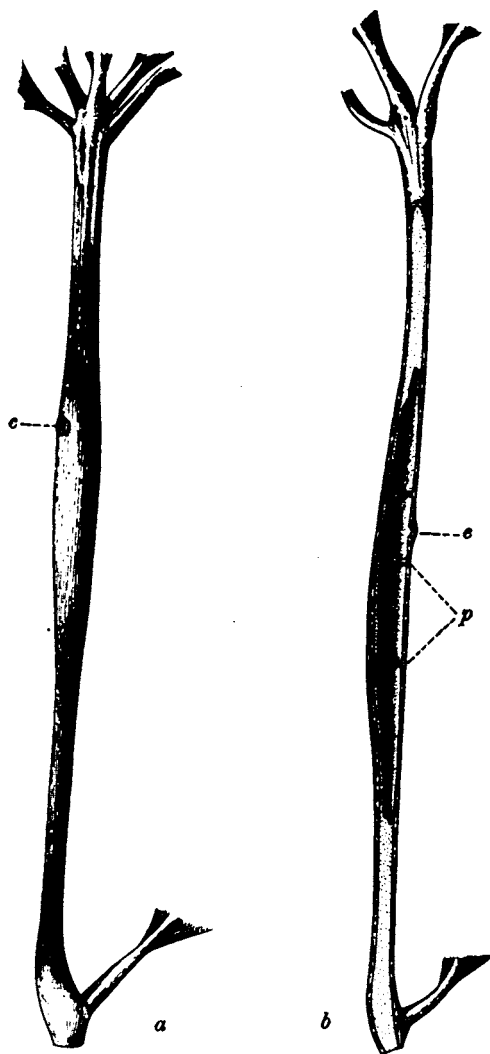


Fig. 93. *Randia myrmecophyla* De Wildeman: *a*, portion of branch showing swollen internode inhabited by ants; *b*, longitudinal section of this internode; *e*, entrance to cavity; *p*, partitions built by ants. Drawn from life at Avakubi, January, 1914; one-half natural size.

partitions; even then, there would usually be only one external aperture to the domatium. By means of these dividing walls the ants undoubtedly make a much more efficient use of the hollow internodes, for it has been observed that in such cases the larvæ and pupæ are kept toward the

nodes in the narrower upper and lower stories. Coccids are also common companions of the ants in this *Randia*.

*Crematogaster rugosa* is a small and timid ant and probably does not give its host much protection. Even when the branches containing formicaries are shaken, the inmates do not leave their retreats. The specimen near Avakubi, though settled by ants, had its leaves badly eaten by phytophagous insects.

Ém. Laurent, the discoverer of this *Randia*, recognized its myrmecophily in the field. He found an unidentified ant and coccids in the swollen internodes. I am not aware that additional information on this plant has been published since, but Kohl in later years has collected from its domatia specimens of *Camponotus foraminosus* Forel and *Cataulacus weissi* Santschi (Forel, 1916, pp. 427 and 443).

#### ECOLOGY OF *Randia physophylla*

I found a specimen of this species in a forest gallery near Leopoldville, in April, 1915. It was a small tree, with very large leaves, about 46 cm. long and 27 cm. wide, on short petioles (1 cm.). The young leaves, before complete expansion, are viscose, being covered with a resinous, sticky substance. The large, showy flowers are erect; their calyx ends in broad lobes; the corolla, about 26 cm. long, is dirty white in its upper part and greenish white in the tubular, lower portion. The egg-shaped fruit is 6 cm. long without the persistent calyx, 4 cm. thick, and deprived of ribs.

This species has no swellings on its branches and the stem is never hollow nor inhabited by ants. At the base of the leaf-blade (Fig. 94), on both sides of the midrib, there is an evagination of variable size, convex on the upper surface of the leaf, broadly open below. On some blades it consists of a mere inflation of the leaf-base, whereas in others it may be 4 to 6 mm. deep and pouch-like, 5 to 8 mm. long and 6 to 7 mm. broad. In all cases, however, on looking into it from the under side, one finds in the bottom, close to the midrib, a conspicuous pale brown gland which secretes a sweet substance. On some of the leaves of the specimen I examined near Leopoldville, a number of ants, *Crematogaster africana* subspecies *laurenti* variety *zeta* (Forel), had taken possession of these distended nectaria, closing the opening on the under side with a tent of fine, agglutinated, dark brown vegetable fibres. Frequently they were accompanied by coccids. Never having seen queens or brood of the ants in the leaf swellings, I can not regard these structures as forming part of the nest. Ants of the same variety occasionally build fibrous shelters over coccids which are fixed on the fruits of this *Randia*.

From the foregoing it is evident that *Randia physophylla* is not a true myrmecophyte in the sense generally meant by this term. Yet its relations with ants are not without interest, for here we have a primitive stage leading to the production of true ant-pouches such as those of *Scaphopetalum Thonneri*, *Cola Laurentii*, and certain South American Melastomaceæ.

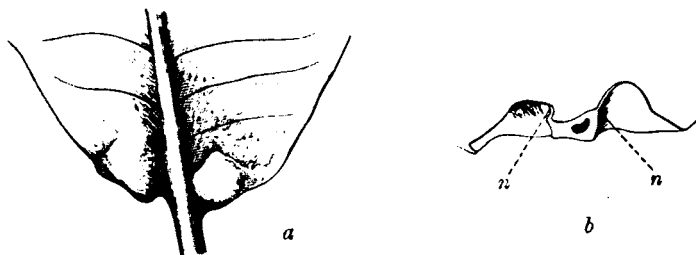


Fig. 94. *Randia physophylla* K. Schumann: a, base of leaf-blade with the two swellings, seen from above, natural size; b, cross section of this base, one and one-half natural size; the nectarium is placed in n. Drawn from life at Leopoldville, April, 1915.

#### PLECTRONIA Linnæus

*Plectronia* LINNÆUS, 1767, 'Mantissa Plant.,' I, p. 52. K. SCHUMANN, in Engler and Prantl, 1891, 'Die Natürl. Pflanzenfam.,' IV, pt. 4, p. 91.  
*Canthium* LAMARCK, 1783, 'Encyclop. Méthod.,' I, p. 602. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 132.

Shrubs or trees, often climbing or clambering bushes, occasionally spinous, with opposite leaves and branches, and acuminate stipules from a broad, often sheath-like base. Frequently some of the branches are sarmentose, hooked or winding; or the plant emits whip-like shoots, often many meters long, somewhat compressed, leafless or with small leaves, furnished with heavy, more or less recurved spines; these shoots trail along the ground or work their way up the trees. Flowers small, axillary, in dense cymes or umbels, or short panicles or clusters. Calyx-tube short, turbinate, campanulate, or hemispherical; limb short, 4- or 5-toothed or cleft, or subtruncate, deciduous. Corolla coriaceous; tube rather short, exceeding the calyx, glabrous outside, hairy with a ring of deflexed pilose hairs or rarely glabrous inside; throat rather constricted or dilated, often bearded; lobes 4 or 5, rarely 6, ovate or lanceolate, reflexed, usually glabrous, valvate in the bud (toward the apex sometimes induplicate-valvate). Stamens 4 or 5, rarely 6, exerted, inserted at the mouth of the corolla; filaments short; anthers ovate, or oval, or lanceolate, acute or obtuse, usually subsagittate at the base, as a rule glabrous, fixed at the back. Ovary 2-celled, fleshy. Style flexuous, filiform or thickened, exerted or equalling the corolla, usually glabrous. Stigma capitate, calyptriform or mitre-shaped, sometimes bifid at the tip, often sulcate. Ovules solitary, pendulous, orthotropous, the micropyle directed upward. Fruit a drupe, didymous, subdimidiate, or globose, 2-celled or by abortion 1-celled; stones 2 or 1, sometimes subrugose. Seeds pendulous, solitary, nearly straight or curved, sometimes bent into the form of a horseshoe round the placenta; testa membranous; albumen fleshy, sometimes ruminated; embryo cylindrical, nearly straight or curved, axile; cotyledons short, radicle superior.

***Plectronia glabriflora* (Hiern)**

*Plectronia glabriflora* (HIERN) K. SCHUMANN, 1895, in Engler, 'Pflanzenwelt Ostafrikas,' C, p. 386. H. KRAUSE, 1911, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-1908),' II, p. 326.

*Canthium glabriflorum* HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 140; 1898, 'Catalogue Afr. Plants Welwitsch,' II, p. 474. K. SCHUMANN, 1891, Ber. Deutsch. Bot. Ges., IX, pp. 61-62. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 162.

*Canthium polycarpum* SCHWEINFURTH Mss., 1877, ex Hiern, in Oliver, 'Flora of Tropical Africa,' III, p. 139.

"An unarmed tree, 40 to 50 feet high, with palm-like habitus; branches erect-patent, obtusely angular, glabrous or somewhat hispid. Leaves oval, shortly and abruptly acuminate, with a broad somewhat excavated base, thinly coriaceous, scabrous-hispid or glabrate above, turning reddish when dry, more or less hispid on the veins beneath, 3 to 5 by  $1\frac{1}{2}$  to  $2\frac{1}{2}$  in.; lateral veins about 7 to 8 pairs; petiole  $\frac{1}{8}$  to  $\frac{3}{8}$  in., hispid or glabrate; stipules ovate,  $\frac{1}{8}$  to  $\frac{1}{2}$  in. long (exclusive of the style), on short puberulous or glabrate pedicels, many together, in dense dichotomous globose panicles of 1 to  $1\frac{1}{2}$  in. diameter; common peduncle glabrate or puberulous, short or ranging up to  $\frac{1}{2}$  in., spreading, sometimes unilateral. Calyx-tube glabrous; limb truncate or obscurely toothed, glabrous or ciliate. Corolla glabrous outside, bearded inside; lobes 5, subobtusely. Disk glabrous. Stigma elongate-calyptiform, much exserted" (Hiern, 1877).

San Thomé: at 1000 feet (Mann; Welwitsch).

Southern Nigeria: Old Calabar (W. C. Thomson).

Cameroon: Barombi (Preuss).

Belgian Congo: Kwidjwi Island near Mgaturu in the forest (Mildbraed). Northeastern Region: Nabambisso River in the Niam-Niam Country (Schweinfurth).

Angola: Malange (Buchner).

Preuss, who observed this species in Cameroon, calls it an "ant-plant." According to Schumann (1891), the ants live inside the hollow stem and probably also in the horizontal branches. No other observations have been made on this form and its description is reproduced here chiefly on account of its possible identity with *P. Laurentii*.

***Plectronia Laurentii* De Wildeman**

*Plectronia Laurentii* É. DE WILDEMAN, 1906, 'Mission Émile Laurent,' III, pp. 294-296, Pls. xcviij-xcix; 1907, 'Études Flore Bas- et Moyen-Congo,' II, pt. 2, p. 174; 1908, *ibid.*, II, pt. 3, p. 348; 1910, *ibid.*, III, pt. 2, p. 294. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 268. H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 160-161.

"Shrub reaching a height of about 2.25 m., with quadrangular stems showing opposite the leaves a groove pierced with openings which allow ants to enter the internodal cavity. Branches spreading, glabrous when full-grown. Leaves opposite, petiolate; the petiole reaching a length of 2 to 3 cm., ciliate on the sides; the blade wedge-shaped, rounded or almost subcordate at the base, very broadly cuneate or acuminate at the apex, more or less coriaceous, 7 to 28 cm. long and 6 to 16 cm. broad,

with 8 to 12 lateral veins on each side of the midrib. Leaf-blade with scattered hairs; appressed on the upper side, somewhat more abundant on the under side, especially on the veins, which are villose, scabrous, and ciliate on the margins. Stipules triangular, subapiculate, about 1 cm. long. Inflorescences axillary, opposite, reaching a length of 5 to 6 cm. and about equally broad. Common peduncle short, glabrous, 3 to 8 mm. long, with dichotomous ramifications which bear below each bifurcation a more or less regular ring of bracteoles. Flowers fasciculate at the end of the ramifications; the pedicel short, slender, accrescent on the fruit and sometimes reaching a length of 5 mm. Calyx with feebly widened limb, superficially denticulate, glabrous. Corolla about 2 mm. long, glabrous externally, with 5 lobes. Style unknown in adult condition. Fruit flattened, subreniform, 6 mm. high, 9 mm. broad, and 4 mm. thick, sometimes one-celled by abortion" (De Wildeman, 1906).

Belgian Congo: Middle and Upper Congo: Bokala; Irebu; Chumbiri; Bolengi; Eala (M. Laurent); Lukolela (Pynaert); Bolombo; Nouvelle-Anvers; Malema (É. and M. Laurent). Eastern Congo Forest: Romée (H. Kohl); Tshopo River near Stanleyville (March 6, 1915; J. Bequaert; Coll. No. 7042); between Walikale and Lubutu (village of Pale, January 12, 1915; J. Bequaert; Coll. No. 6585); Paku (Seret).

It would seem from the description that *Plectronia glabriflora* (Hiern) is rather closely allied to, if not identical with, *P. Laurentii*; it is hardly to be expected that a plant so commonly found throughout the Congo Basin is absent from Cameroon and Angola.

#### ECOLOGY OF *Plectronia Laurentii*

The following notes were made on specimens in the forest region between Walikale and Lubutu (near the village of Pale, January, 1915; Coll. No. 6585) and along the Tshopo River near Stanleyville (March, 1915; Coll. No. 7042). This plant is a bush or small tree, about 4 to 7 meters high, with an erect, straight trunk, bearing from a short distance above the ground regularly opposite, nearly horizontal branches. The most striking feature is the squareness of the limbs which, on the younger parts of the plant, show four very pronounced longitudinal grooves interrupted at the nodes only. Above the nodes, where the myrmecodomatia are located, the depressions expand into four broad, flat sides, the stem being almost regularly square on a cross-section. Older branches often become more cylindrical, only slight traces of the longitudinal furrows being left. The leaves are short petiolate, large and broad, as much as 28 cm. long and 16 cm. wide. The stipules drop off early. While the stalk and limbs are glabrous and smooth, the leaves are slightly hairy and somewhat rough.

Both the trunk and lateral branches of *P. Laurentii* were inhabited by ants, of the form *Crematogaster africana* subspecies *laurenti* (Forel) in the case of the specimens from the Tshopo River, and of the variety

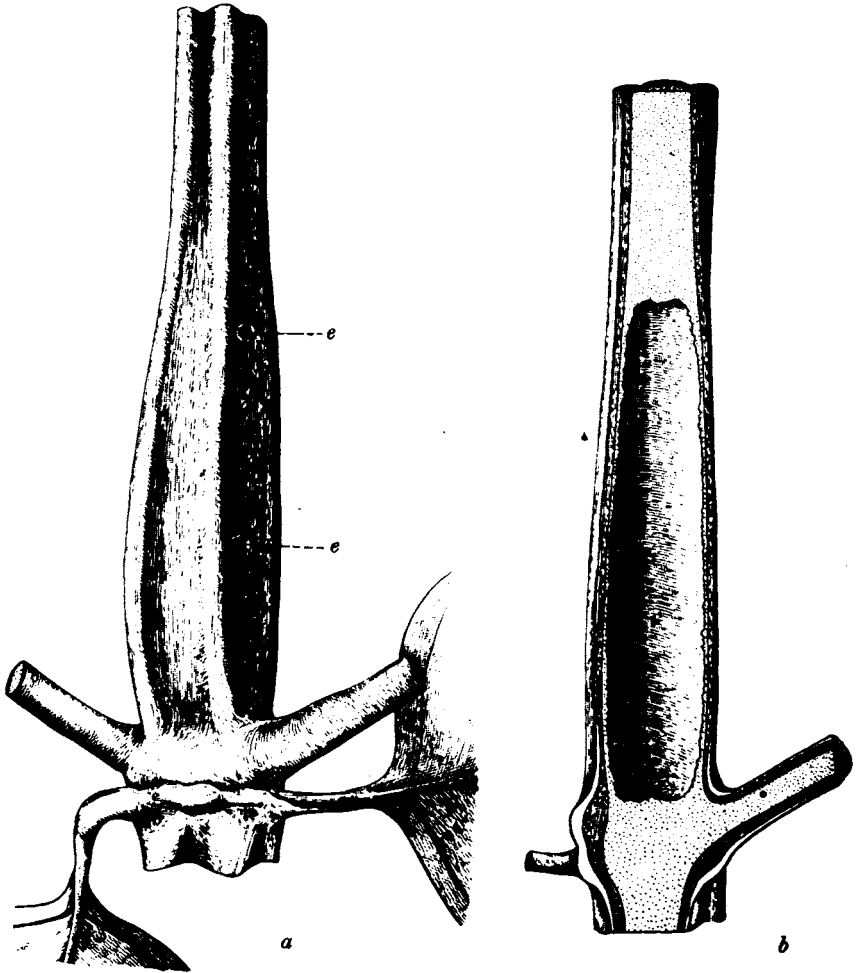


Fig. 95. *Plectronia Laurentii* De Wildeman: a, portion of branch with swelling above node inhabited by ants, showing apertures (e) to the domatium; b, longitudinal section of this myrmecodomatium. Drawn from life at Pale, between Walikale and Lubutu, January, 1915; natural size.

*zeta* (Forel) of that race in those found between Walikale and Lubutu. The older stalks of the plants are not much swollen, but the medullary cylinder is almost completely excavated, even the partitions at the nodes being occasionally perforated. In younger branches the various myrmecodomatia are more distinct; they are then moderately pronounced, quadrangular swellings, with the flat sides separated by slightly raised, obtuse ridges (Fig. 95a and b). They usually extend the basal two-thirds

of each internode and very gradually disappear in the upper part toward the node. The internal cavity is quite spacious, 6 to 7 cm. long and 10 to 15 mm. wide. An examination of very young shoots shows that the swellings are normal productions of the plant and that the cavities originate through the drying of the pith before the ants gnaw apertures. Hollows inhabited by these insects present a number of small, circular exit holes, which in my specimens were commonly located on any one of the sides. According to Kohl (1909, p. 161), they are placed on the surfaces facing the lower leaf pair, but this is far from being the rule. Many swellings, especially on the younger branches, have only one aperture; more commonly there are 2 to 4 entrances to each cavity, and in some cases as many as 12 to 15.

At least on the younger portions of the plant, every domatium contains a complete ant colony, with a queen, workers, and brood. Frequently coccids also are present and those found by Kohl near Stanleyville, together with *Crematogaster*, in the swellings of *P. Laurentii* have been described by Newstead (1910, p. 18) as *Hemilecanium recurvatum*. A number of such scale insects were also fixed on the outer surface of the stem, especially near the nodes, within tents of plant-fibres built by the ants and often communicating with their cavities. Kohl (1909, p. 161) further mentions that some of the internodes of a *Plectronia* in that locality were occupied by small, white caterpillars, while others were inhabited by ants.

*Plectronia Laurentii* was discovered at various places along the banks of the Middle and Upper Congo by Ém. Laurent, who has given in his field-notes a good account of its relations with ants (De Wildeman, 1906, pp. 294-296). Much additional information on this species has been published by H. Kohl (1909, pp. 160-161). These observations agree in most details with mine.

The ants, all of the genus *Crematogaster*, found associated with *P. Laurentii* are evidently facultative inhabitants of these plants. The following forms have been recorded thus far:

*Crematogaster africana* (Mayr), variety. Belgian Congo; found by Ém. Laurent (Kohl, 1909, p. 161).

*C. africana* subspecies *laurenti* (Forel). Found by Laurent at Bokala (Kohl, 1909, p. 160), by Kohl at Isangi and Stanleyville (Forel, 1909, p. 60), and by myself near the Tshopo River.

*C. africana* subspecies *laurenti* variety *zeta* (Forel). Between Walikale and Lubutu (J. Bequaert) and in the Congo (Kohl; see Forel, 1909, p. 70).



*C. africana* subspecies *winkleri* (Forel). Belgian Congo (Kohl); see Forel, 1909, p. 69).

*C. africana* subspecies *winkleri* variety *fickendeyi* (Forel). With regard to this variety Forel (1916, pp. 409–410) writes:

Kohl has collected various forms transitional between the race *winkleri* and the variety *fickendeyi*, on one occasion in a nest, probably usurped, of *Tetramorium aculeatum*, also in myrmecophilous plants or in termitaria. His No. 68 bears the following interesting remark: "Ant from plants. Lives in and on the myrmecophyte *Plectronia Laurentii* De Wildeman. Five meters above the ground the trunk bore a carton nest, 40 to 50 cm. high, of this ant. But it inhabits at the same time all the hollow branches of the plant. Makanga on the Okiavo River." One may conclude from this that there is no absolute contrast between the carton nest of *buchneri* and the habit of living in hollow stalks.

#### ECOLOGY OF UNIDENTIFIED AFRICAN SPECIES OF *Plectronia*

In addition to the species just studied, I have found caulinary swellings inhabited by ants on a number of rubiaceous plants which are provisionally regarded as belonging to the genus *Plectronia*. It is possible, however, that one or more may be species of related genera, such as *Vangueria*, *Grumilea*, or *Psychotria*. At any rate, I have been unable to identify them with any of the described African Rubiaceæ and they may even represent forms new to science. Their correct identification will undoubtedly be made later when the study of my herbarium, now in the hands of Mr. De Wildeman, Director of the Brussels Botanic Garden, is more advanced.

*Plectronia* species A.—This species was first observed on the forested banks of the Aruwimi River near the village of Bafwalipa, between Bomili and Avakubi (December 29, 1913; Coll. No. 1696). It also occurred in the Ituri Forest, near the village of Tete, between Penge and Irumu (February 22, 1914; Coll. No. 2567), and, in company with Mr. Lang, I came across it again along the Tshopo River near Stanleyville (March 6, 1915; Coll. No. 7043). It is a climbing, much-branched bush of the forest, with simple, opposite, short petiolate or sessile leaves, which are asymmetric and cordate at the base. There were no thorns or spines on the specimens I examined. The entire plant—leaves and stems—is abundantly covered with long, erect, brownish hairs. The flowers are small and clustered in corymbs in the axils of the leaves.

Myrmecodomatia (Fig. 96) are found on some of the branches only. They consist of spindle-shaped swellings on the lower third of an internode, are about 30 mm. long and 8 mm. thick, and placed immediately above the node. The domatium is a spacious, rather thin-walled cavity. When inhabited, it is almost wholly cleaned of medullary tissue and com-

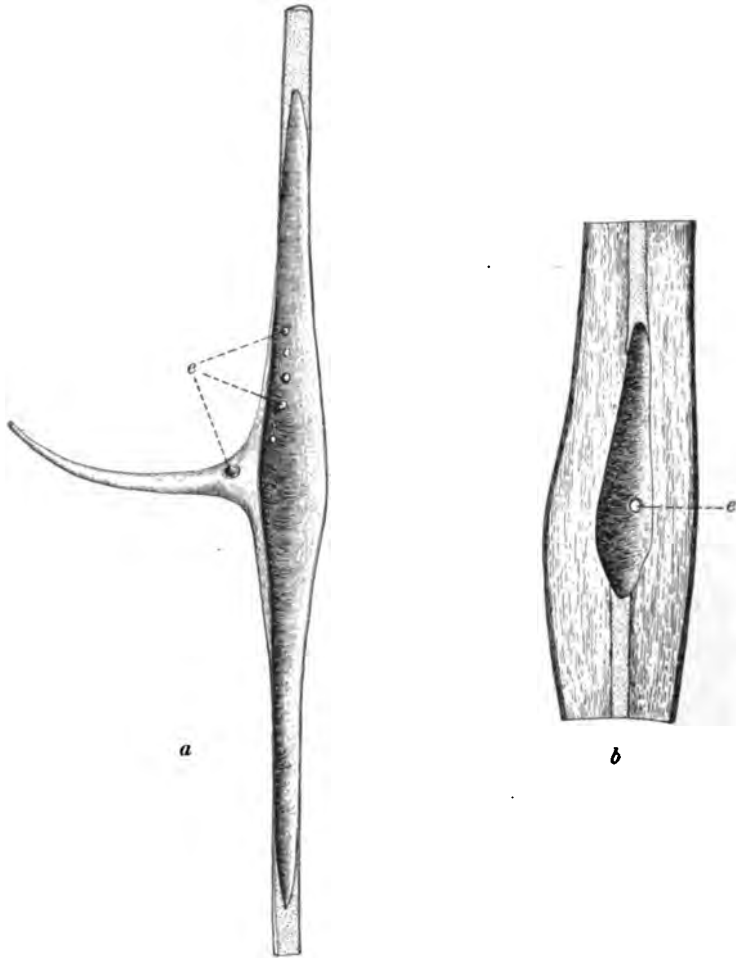


Fig. 97. *Plectronia* species B; a, portion of younger branch in longitudinal section, showing myrmecodomatium at the node which also extends into the base of the lateral ramification; b, portion of main stalk, showing shape of domatium in older parts of plant; e, apertures leading into the cavity. Drawn from life at Avakubi, January, 1914; natural size.

the woody cylinder, are but slightly or not at all swollen and their inner cavity is much reduced (3 to 4 cm. long, 5 to 7 mm. wide); they usually present two openings placed on a crateriform elevation, one above each of the nodal thorns. Frequently there are scars of other perforations which have been closed by callus growth.

The ants found inside this *Plectronia* belonged in both localities to a small, unidentified species of *Crematogaster* which can hardly give pro-

tection to its host. Even though most of the domatia were inhabited, the leaves had been eaten by caterpillars and both young branches and leaves bore numerous insect galls—elongate, pear-shaped swellings ending in a recurved tail-like apex and on one side of the tail with a small exit hole leading into a central chamber; their outer surface covered with many erect, brownish-red hairs; all the galls seen were empty.

*Plectronia* species C.—In the Semliki Forest, near Lesse (June 15, 1914; Coll. No. 4753), I came across a creeper whose many hanging branches had covered the bushes at the edge of a clearing. It is perhaps specifically identical with the preceding form (species B), possessing most of its general characters. Yet the domatia are sufficiently different in shape to deserve separate description.

The ant-swellings (Fig. 98) are short and broadly spindle-shaped, and occupy the lower part of the internodes of most of the branches. The inner cavity is very spacious, 6 to 8 cm. long and 15 to 20 mm. wide, continues a little below the node, and extends also into the slightly swollen bases of the side branches. A peculiarity of this *Plectronia* is that the domatia lack circular apertures, but communicate with the outside by means of two long slits, placed opposite each other in the upper part of the swelling, above each of the side branches. Often these openings are partly closed by callus growth. The plant at Lesse was inhabited by populous colonies of a small *Crematogaster* with a queen, numerous workers, and brood at various stages; also coccids which were fixed on the callosity tissue near the inner margin of the slits.

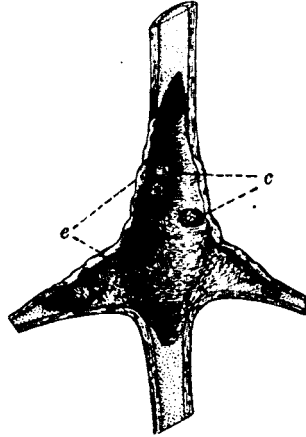


Fig. 98. *Plectronia* species C. Longitudinal section of swollen node inhabited by ants: e, callus growth bordering the slit which leads into the cavity; c, coccids attached to inner walls. Drawn from life at Lesse, June 1914; natural size.

#### CUVIERA de Candolle

*Cuviera* A. DE CANDOLLE, 1807, Ann. Mus. Paris, IX, p. 222; 1830, 'Prodromus Regn. Veget.', IV, p. 468. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 156. K. SCHUMANN, 1891, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' IV, pt. 4, p. 94.

Glabrous shrubs or small trees, rarely with puberulent young branches. Leaves usually large, broadly ovate, entire, opposite, coriaceous or leathery; stipules apiculate, united into a short sheath between the bases of the petioles. Flowers polyga-

mous, with large foliaceous bracteoles, in many-flowered, axillary panicles. Sepals 3 to 5, almost free or shortly united at the base, foliaceous, spreading, often unequal, persistent, much longer than the petals. Corolla hypocrateriform, with a short, straight tube furnished inside with a ring of deflexed hairs, and large, fleshy lobes. Stamens 5, exserted, placed on the mouth of the corollar tube. Ovary 3- or 5-celled, each cell with one ovule. Ovule suspended, with upper micropyle and flattened funiculus. Style with a semiglobose, cap-shaped or mushroom-shaped, sulcate stigma. Fruit an obovate drupe, often oblique or falcate, distinctly ribbed, with 3 to 5 seeds.



Map 46. Distribution of *Cuviera*, a genus of myrmecophytic plants.

*Cuviera* is a strictly African genus, of which fourteen species have been described. Its general distribution is shown on Map 46. The genotype, *C. acutiflora* de Candolle, is found in Upper Guinea. Only one form, *C. australis* K. Schumann, has been described from South Africa. All the others occur within the limits of Engler's Western Forest Province, either in the Rain Forest proper or on the forested river banks of the adjoining Savannah, below 3000 feet. With the possible exception of *C. australis*, all the members of the genus may be myrmecophytes

and their descriptions have, therefore, been reproduced here. Some of these so-called species are perhaps mere synonyms.

### *Cuviera acutiflora* de Candolle

*Cuviera acutiflora* A. DE CANDOLLE, 1807, Ann. Mus. Paris, IX, p. 222; 1830, 'Prodromus Regn. Veget.', IV, p. 468. BENTHAM AND HOOKER, 1849, 'Niger Flora,' p. 407. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 156.

*Cuviera africana* SPRENGEL, 1825, 'Syst. Veget.', I, p. 760.

"A glabrous shrub, 15 to 20 ft. high. Branches terete, divaricate, supra-axillary. Leaves oval-oblong, acuminate, subequal and rounded or somewhat narrowed at the base, coriaceous, glossy, rather or scarcely paler beneath, 4 to 10 by  $1\frac{3}{4}$  to 4 in.; some 4 to 6 in. wide (Bentham); lateral veins about 6 to 10 pairs, not conspicuous; petiole  $\frac{1}{8}$  to  $\frac{1}{4}$  in.; stipules ovate, apiculate,  $\frac{1}{3}$  in. long, connate and sheathing below, keeled, hairy within. Flowers greenish,  $\frac{3}{8}$  to  $\frac{1}{2}$  in. long in bud, on short, slender pedicels, very numerous, in ample, divaricately branched, rather lax, axillary and terminal, shortly pedunculate, dichotomous panicles of 2 to 6 in. diameter; bracteoles elliptic-linear,  $\frac{3}{8}$  to 1 in. long, accrescent. Calyx green; segments  $\frac{3}{8}$  to  $\frac{1}{2}$  in. long, linear-oblong, spreading, persistent. Corolla green and orange; segments lanceolate, caudate-acute,  $\frac{3}{8}$  in. long, spreading. Ovary 5-celled; style glabrous. Fruit obliquely egg-shaped,  $\frac{3}{4}$  to  $\frac{1}{2}$  in. long, obtusely 5-sided; pyrenes 5 or fewer" (Hiern, 1877).

Sierra Leone, type locality (Smeathman).

Ivory Coast: Grand Bassam (Th. Vogel).

Cameroon: Ambas Bay (Mann).

### *Cuviera angolensis* Hiern

*Cuviera angolensis* HIERN, 1898, 'Catalogue Afr. Plants Welwitsch,' II, p. 483. É. DE WILDEMAN AND TH. DURAND, 1901, Bull. Herbarium Boissier, (2) I, p. 826; 1901, 'Reliquiæ Dewevreanæ,' p. 124. É. DE WILDEMAN, 1904, 'Études Flore Bas-et-Moyen-Congo,' I, p. 205; 1907, *ibid.*, II, pp. 78 and 173; 1908, *ibid.*, II, 3, p. 348; 1910, *ibid.*, III, 2, p. 295; 1912, *ibid.*, III, 3, p. 489; 1906, 'Mission Émile Laurent,' III, pp. 296-299, Pl. CVI. H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 163-166. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 271. (K. Schumann, in Engler and Prantl, 1891, 'Die Natürl. Pflanzenfam.,' IV, pt. 4, p. 94, fig. 33J, without description; also mentioned without description by K. Schumann, 1890, Verh. Bot. Ver. Brandenburg, XXXI, 2, p. 121, and 1891, Ber. Deutsch. Bot. Ges., IX, p. 56).

"A small glabrous pyramidal tree, 12 to 20 ft. high, or in cultivated fields (*arimos*) usually only 8 to 12 ft. Sap milky. Trunk slender, straight, destitute of branches below, but densely armed with opposite, decussate, strong, very acute, quite patent spines of 1 to 2 in. in length. Branches and branchlets green, the latter swelled at the nodes. Leaves long, opposite, usually cuspidate at the apex, oblique and rounded at the base, papery, smooth, 4 to 9 in. long by  $1\frac{1}{2}$  to 4 in. broad, dull-green above, paler beneath, those on the older branches pendulous; petiole  $\frac{1}{2}$  to  $\frac{3}{8}$  in. long; lateral veins about 8 on each side of the midrib, rather slender and beneath conspicuous. Stipules sheathing, keeled, acuminate, about  $\frac{3}{8}$  to  $\frac{1}{2}$  in. long. Inflorescence axillary, branched, 2 to 4 in. long, pale yellow-greenish outside throughout except a bright rosy stellate patch about the naked throat of the corolla; pedicels very short;

common peduncle  $\frac{1}{4}$  to 1 in. long; bracteoles sub-linear, ranging up to 1 in. in length. Calyx including and adnate to the ovary; tube short, campanulate-ventricose, obtusely 3- to 4-angular, deeply 3- to 5-lobed; the segments elongate-lanceolate, unequal in length, bract-like, exceeding the corolla, herbaceous-green,  $\frac{1}{2}$  to 2 or 3 in. long. Corolla shortly salver-shaped, fleshy-coriaceous, deep herbaceous-green outside; tube short, bright-red inside, at the base inside with a ring of shiny silvery hairs directed downward; limb 5-cleft, shortly rotate; segments lanceolate or ovate-acuminate, rigid, green, expanded in a stellate manner in full flower, valvate at the base in estivation; the tips long, acuminate or subulate, contorted in the bud. Stamens 5, inserted in the sinuses of the corolla-lobes around the ring of hairs; rigid, exerted; filaments compressed-cylindrical, fleshy, curved-patent at the time of flowering; anthers ovate, cordate, introrse, 2-celled, obtuse at the apex, basifixed; cells separate at the base, cohering at the apex longitudinally, yellow. Ovary adnate to the calyx-tube, 5-celled; cells 1-ovuled; disk a little elevated, flat; style thick, columnar, rosy, densely pilose; stigma mitriform, large, obtuse, stigmatose and cleft at the apex. Fruit oblique, deeply furrowed, about 1 in. long, crowned with the more or less persistent calyx-limb or with its remains" (Hiern, 1898).

Angola: Golungo Alto: "among the mountainous forests of Alto Queta," type locality (Welwitsch).

Belgian Congo: Kisantu (Gillet). Kwango: Kikwit (Lescrauwaet). Middle and Upper Congo: Lukolela (Dewèvre); Likimi (Malchair); on the left bank of the Congo below Bolombo; Malema; Lie (Ém. Laurent); Irebu (Pynaert); Eala (M. Laurent). Northeastern Congo forest: Isangi; Tshopo River near Stanleyville (Ém. Laurent); Romée (H. Kohl); Nala; Lifungula (Soret); Manyema (Berger).

### ***Cuviera australis* K. Schumann**

*Cuviera australis* K. SCHUMANN, 1899, Engler's Bot. Jahrb., XXVIII, 1, p. 78.

"Shrubby, with rigid, divaricate, terete, glabrous branches; the young branches flattened and puberulent. Leaves with short petioles, oblong, ovate, or oblong-lanceolate, obtuse, rounded or acute at the base, glabrous above; on the under side softly puberulent on the primary veins, otherwise glabrescent; discolored, herbaceous. Stipules subulate or filiform from a broad base, not setose inside. Cyme twice, more rarely three times trichotomous, axillary, appearing below the leaves, pedunculate, minutely puberulent, with very slender branches. Flowers pentamerous, pedicellate. Ovary sub-semiglobose, slightly hairy, 5-celled. Calyx divided to near the base into foliaceous, subspatulate, elongate lobes. Corolla divided beyond its middle into five lobes, which are lengthened subtriangular and hirsute externally; tube glabrous on the outer side. Style exerted for twice the length of the tube, with 5-toothed stigma.

"The flowering branch at hand is 30 cm. long and 2 to 2.5 mm. thick at the base where it is covered with gray bark. The petiole is 3 to 6 cm. long and very finely pilose; the blade is 3 to 5 cm. long, 1.1 to 2.7 cm. broad in the middle, traversed on each side of the midrib by 5 or 6 stronger veins which are slightly prominent on both sides, black above, gray below. The stipules are 2 to 3 mm. long. The flowers are borne on finely pilose pedicels, 5 to 9 mm. long. The ovary is 2 mm. long, the calyx 7 to 8 mm.; its lobes are very obtuse and reach a width of 2 mm. above. The corolla-tube is 3 to 4 mm. long; its lobes are 6 to 7 mm. long and are very finely pilose outside. The anthers are a little over 1 mm. long and inserted on a filament of 0.5 mm. The style is exerted for 6 to 7 mm. out of the corollar tube.

"Different from all the other species, which occur in tropical West Africa only, by the much smaller flowers and leaves. I believe I should have distinguished two forms, one of the specimens is more hairy and has much smaller flowers. Schlechter thinks, however, that both specimens come from one and the same bush" (K. Schumann, 1899).

Portuguese East Africa: Delagoa Bay, at 30 m. (Schlechter).

### ***Cuviera calycosa* Wernham**

*Cuviera calycosa* WERNHAM, 1914, Journ. of Botany, London, LII, p. 7.

"Tree 90 feet high, glabrous, nigrescent in dried condition, with terete branches later on covered with grayish bark. Leaves parchment-like, elliptic or oblong, small for the genus, shortly and narrowly acuminate, obtuse, acute at the base, glabrous; petiole very short. Stipules small, lanceolate, acuminate, caducous except for the broad base. Inflorescences having few flowers, dichotomous, rather loose; bracts oblong-lanceolate, obtuse. Calyx large, much exceeding the corolla; with uneven, ovate-lanceolate, acuminate and very acute lobes. Corolla with a broadly funnel-shaped to cylindric, rather short tube; its 5 lobes acuminate with long appendages and a few scattered, rather long hairs. Drupe very glabrous, crowned by the persistent limb of the calyx.

"A remarkable species, the nearest affinity being clearly *C. nigrescens* (Scott-Elliot); the present species is distinct, especially in the very large calyx and small corolla. The leaves measure 10 to 11 cm.  $\times$  4 to 4.5 cm., with petiole about 1 cm. long; secondary veins 5 to 6 pairs; stipules 6 to 8 cm. long. Peduncle 3 cm.; cyme 11 to 12 cm. wide, 5 to 6 cm. long. Pedicel 5 mm.; calyx-tube minute, lobes 3 to 3.5 cm.  $\times$  4 to 7 mm. Corolla-tube barely 5 mm. long, and nearly as much in average breadth; lobes, flat part 4 to 5 mm., setæ over twice that length. Berry 1.4 cm.  $\times$  1.1 cm." (Wernham, 1914).

"Youngest flowers white, older ones cream, oldest thin orange. Centre of flower greenish. Calyx-lobes bright green, with margin and setæ white. Setæ of corolla-lobes white; anthers dark-purplish brown; style white, stigma pale green" (Mrs. Talbot).

Southern Nigeria: near Esuk Ekkpo Abassi in the Eket District (Mr. and Mrs. P. A. Talbot).

### ***Cuviera latior* Wernham**

*Cuviera latior* WERNHAM, 1918, Journ. of Botany, London, LVI, p. 311.

"A very glabrous shrub, with very smooth, subterete, moderately robust, striate branches, swollen and excavated at the nodes (apparently with a myrmecodomatium). Leaves large, parchment-like, broad, oblong, but little acuminate, cordate and very unevenly oblique at the base; petiole short, though distinct; primary veins conspicuous, 10 to 12 on each side. Stipules connate into a broad sheath, which is very short, arcuate above, and obscurely spiculate between the petioles. Flowers large for the genus, placed in loose, few-flowered, forked cymes; common peduncle much flattened; pedicels very short. Calyx with 3 lobes which are full of veins, broadly lanceolate, long acuminate, large and leaf-like. Tube of the corolla broad and very short, its 5 lobes oblong, very acuminate, subsetaceous and cucullate at the apex. Ovary deeply sulcate; style thick, densely and finely hispid.

"Notable for the broad calyx-lobes and the large flowers. Leaves 20 to 26 cm.  $\times$  8 to 9 cm., with petiole 6 to 8 mm. at longest; stipule-sheath 2.5 mm. deep. Peduncle 2 cm. long, forking at the tip into two floriferous branches about 10 cm. long. Calyx-lobes 3 to 3.5 cm. long, and 1 cm. or more broad. Corolla-tube barely 4 mm. long; lobes 1.6 cm.  $\times$  4 mm. Anthers 2 mm. long. Style 1 cm. long" (Wernham, 1918).

Belgian Congo: north of Boyeka (Nannan).

### **Cuviera Ledermannii Krause**

*Cuviera Ledermannii* KRAUSE, 1912, Engler's Bot. Jahrb., XLVIII, p. 418.

"Erect shrub or small tree, with slender, strong, glabrous branches and branchlets, which are swollen, a little flattened and hollow at the nodes; bark smooth, dark brown or almost black in spots. Leaves large, short-petiolate; stipules broadly ovate, minutely acuminate at the apex, soon dropping, connate at their base into a short sheath which persists longer; petiole short, strong, grooved above to near its base; blade thick, coriaceous, very glabrous on both sides, oblong or elliptic-oblong, rather long acuminate at the apex, obtuse at the base or even shortly decurrent along the petiole; primary veins 9 to 12, slightly prominent above, more distinctly so below, running in an obtuse angle from the costa. Inflorescence axillary, short, with few flowers; bracts large, narrowly oblong, obtuse. Ovary semiglobose; lobes of the calyx large, narrowly oblong, acute, 2 to 3 times longer than the ovary; tube of the corolla cylindrical, scarcely broadened above, the lobes lanceolate-oblong, acute, as long as or longer than the tube; stamens with very short filaments, the anthers small, oval-oblong; style rather highly exserted above the tube of the corolla, crowned with a rather large, mitriform stigma.

"The plant is a shrub or small tree; the branches which I have before me are covered with dark brown or almost black bark; they are 2 to 3 dm. long and 5 mm. thick at their base; the thickened, hollow swellings, above the nodes, are 7 to 9 mm. in diameter; they undoubtedly are inhabited by ants. The stipules are 8 to 10 mm. long, the petioles 1.2 to 1.6 cm. The blades in a dried state are brownish-green to gray-green and, including their apex of 1.2 to 1.6 cm., are 1.8 to 2.5 dm. long, 7 to 11 cm. broad. The inflorescences attain a length of 7 cm. The large bracts, which may reach a length of 1.8 cm., in drying take on a leather-brown color, as do also the sepals. The ovary has a diameter of 2.5 mm. The sepals are 7 to 8 mm. long. The corolla, white in life, turns dark brown in drying; its tube is 4 to 5 mm. long, its lobes 5 to 6 mm. The filaments are about 0.8 mm. long, the anthers 1.2 mm. The style, including a stigma of about 1.5 mm., measures 8 mm." (Krause, 1912).

Cameroon: near Nkolebunde on the Nanga-slopes in a rather sparsely wooded place, at about 200 m.; also near Malende in the vicinity of Nkolebunde in dense high forest with little underwood, at 150 m. (Ledermann; in flower during October).

The species agrees in most respects with *C. physinodes* K. Schumann, from which it is said to differ in "the branches, which are less strongly flattened and broadened at the nodes, and also in the darker, partly almost black bark."



corolla 4 mm. long, inside near the base with a ring of hairs bent downward. Lobes of the corolla triangular, acuminate-caudate, 1 cm. long, pilose externally, yellowish. Stamens 5, inserted between the lobes of the corolla; anthers sagittate, twice as long as the filaments. Ovary 5-celled, each with one ovule. Style 8 mm. long; stigma flask-shaped" (C. H. Wright, 1906).

Gold Coast: Kimaha (Johnson).

### ***Cuviera nigrescens* (Scott-Elliot)**

*Cuviera nigrescens* (Scott-Elliot) WERNHAM, 1911, Journ. of Botany, London, XLIX, p. 321.

*Vangueria nigrescens* SCOTT-ELLIOT, 1894, Journ. Linn. Soc. London, Botany, XXX, No. 206, p. 81. OLIVER, 1894, in Hooker's 'Icones Plantarum,' XXIII, pt. 4, Pl. MMCCCLXXXIII.

*Cuviera trichostephana* K. SCHUMANN, 1897, Engler's Bot. Jahrb., XXIII, 4, p. 461.

"A shrub with terete, grayish, glaucous branches, in youth black and covered with lenticels. Leaves becoming black by drying, very glabrous (except in the axils of the veins where they are hirsute), oblong-ovate or obovate, obtusely acuminate, subcuspidate, with coriaceous margin, narrowed at the base; 5 to 8 cm. long and 2 to 3 cm. broad; 5 or 6 pairs of lateral veins; petiole 6 to 8 mm. long. Stipules hirsute inside, rounded at the base, elongate-acuminate along the back, 3 to 5 mm. long. Peduncles faintly pilose, 5- to 10-flowered, 8 mm. long. Pedicels about 6 mm. long. Bracts ovate, obtuse, with reticulate venation, 8 to 9 mm. long and 4 mm. broad. Calyx with 5 large lobes, which are lanceolate, subacute, 8 to 9 mm. long and 2 mm. broad. Lobes of the corolla caudate-acuminate, 15 to 17 mm. long (the acumen 3 to 4 mm.), sparsely hirsute on the outside with white hairs 1 mm. long, internally with a ring of reflexed pile. Filaments 2 mm., anthers 1 to 2 mm. long. Stigma cylindrical, large, 1 to 2 mm. long and 1 mm. broad. Ovary 5-celled" (Scott-Elliot, 1894).

Sierra Leone: in the forest between 1000 and 3600 feet; near Kafogo in Limba and near Falaba (C. F. Scott-Elliot).

Liberia: Golah Forest (Bunting).

The Liberia specimens differ from those of Sierra Leone only in the length of the caudæ of the corolla-lobes, which in the former appear to be longer and more setaceous in character (Wernham).

Both Scott-Elliot and Oliver compare this species with the two other *Vangueriæ* with caudate corolla-lobes: *V. velutina* Hiern, which has densely tomentose leaves and inflorescences; and *V. pauciflora* Schweinfurth, with solitary or geminate flowers and truncate calyx.

This species was evidently redescribed by K. Schumann, in 1897, as *Cuviera trichostephana*, on part of the material collected in Sierra Leone by Scott-Elliot. For the sake of completeness, Schumann's description of *C. trichostephana* is translated here:

A woody plant with slender, terete or subtetragonal branches, very glabrous even in youth. Leaves on the specimen examined not completely developed, petiolate, oblong, shortly and obtusely acuminate, acute at the base and often suboblique,

glabrous on both sides, but the axils of the veins with minute hairy domatia; stipules lineate-subulate, with triangular base. Axillary cyme with few flowers, glabrous; ovary 5-celled, glabrous; calyx with foliaceous or membranaceous, oblong, sharp lobes. Corolla divided to beyond its middle, with a corona of decumbent hairs inside, pilose at the outer side, with very long, caudate, linear-lanceolate lobes.

The branch at hand is 15 cm. long and at most 2 mm. thick at the base. The petiole reaches a length of 1 cm. and is slightly excavated above. The blade is 4 to 9 cm. long and 2 to 4 cm. broad in the middle; traversed by 5 stronger veins on each side of the midrib; black when dried; herbaceous in the specimen studied, but the leaves are apparently not yet fully developed. The stipules reach a length of 7 to 8 mm. The entire inflorescence is about 3 cm. long. The pedicels of the flowers reach a length of 5 mm. The ovary is semiglobose and 1.5 mm. long. The lobes of the calyx reach 10 mm. in length and 3 mm. in width. The corolla is 2.2 to 2.5 cm. long, of which the tube takes 9 to 10 mm. only. The anthers are 2 mm. long, placed on filaments 3 to 4 mm. long, exerted from the tube and curved. The style is 1.7 cm. long.

This species is easily separated from all others by the corolla covered with hairs, the smaller leaves, and the short inflorescences. It has more the appearance of the genus *Vangueria*, so that it makes the generic limits less distinct.

Sierra Leone (C. F. Scott-Elliot).

#### ***Cuviera physinodes* K. Schumann**

*Cuviera physinodes* K. SCHUMANN, 1891, Pringsheim's Jahrb. Wiss. Bot., XIX, pp. 55-56; 1891, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' IV, pt. 4, p. 12, fig. 5A.

*Cuviera physinodes* H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 162-163.

"Leaves large, 20 to 30 cm. long, 7.5 to 11 cm. broad, with thick petiole, ovate-oblong or oblong, shortly and obtusely acuminate, equilateral at the base, coriaceous, glabrous on both sides. Ovary 5-celled; stigma glabrous. Drupe oblong, 3 cm. long, about 1 cm. in diameter, acute at the apex, acuminate at the base, without ribs.

"It is a tree-like shrub about 3 m. high, with large, leathery leaves. The cymes are axillary, with many flowers, short, ramified; only a few of the greenish white flowers produce fruit, though all seem to possess well-developed ovaries. The cylindrical internodes, covered with gray bark, are regularly thickened in their upper part, but do not develop swellings there. The swellings are situated rather above, and close to the nodes" (K. Schumann, 1888).

Gaboon: Sibange farm, type locality (Soyaux).

The myrmecodomatia of this species have been briefly described by K. Schumann from dried specimens. One of the hollow, nodal swellings had a length of 3.5 cm. and greatest diameter of about 1 cm., the wall being about 1.5 mm. thick. The inner cavity was nearly spindle-shaped and ended slightly below the node; three openings led into the cavity; one of these, 2 mm. long and 1.5 mm. broad, was probably alone used as entrance, while the two others were reduced to mere slits, 1 mm. long and hardly 0.5 mm. wide. Traces of former holes, evidently closed by callus growth, could be seen on two other spots. A few remains of ants were found inside the swellings.

**Cuviera plagiophylla** K. Schumann

*Cuviera plagiophylla* K. SCHUMANN, 1903, Engler's Bot. Jahrb., XXXIII, p. 353.

"A shrub with thick, fistulose-inflated branches, which, even when young, are glabrous. Leaves strictly sessile, linear-oblong, short acuminate, rounded at the base, strongly inequilateral, glabrous on both surfaces. Stipules tubular, villose internally. Flower panicle axillary, with many flowers. Bracts very long, linear, acuminate. Ovary 5-celled. Sepals free almost to their base, linear, acute. Corolla with very short tube; the lobes acuminate, moderately appendiculate, cristate dorsally. Style glabrous.

"The bush reaches a height of 5 m. The leaves are 28 to 30 cm. long and 8 to 9 cm. broad; they are crossed on each side of the midrib by about 16 stronger veins, which are more prominent on the under side, as are also the reticulate veins; they are black when dry. The stipules are 9 mm. long. The lobes of the calyx are 11 mm. long and somewhat obtuse. The corolla is greenish-white, 15 mm. long, of which 2 mm. is to be allowed for the tube; the appendages measure 5 mm.; the keels on the dorsal face of the lobes make the bud sharply 5-ribbed.

"The species is very distinct by the strictly sessile, very oblique leaves and the acutely keeled corolla-lobes" (K. Schumann, 1903).

Cameroon: Bipindi, near Lokundje (Zenker).

**Cuviera subuliflora** Bentham

*Cuviera subuliflora* BENTHAM, 1849, in Bentham and Hooker, 'Niger Flora,' p. 407.

HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 157.

"An arborescent shrub or small tree of 15 feet, glabrous. Branches subterete, smooth, opposite. Leaves oblong, shortly acuminate, oblique and hollowed or rounded or somewhat narrowed at the base, chartaceous, rather paler beneath, 6 to 15 by 2 to 4 $\frac{3}{4}$  in.; lateral veins about 12 to 14 pairs, slender; petiole  $\frac{1}{4}$  in. long; stipules deltoid, connate at the base, keeled near the apiculate apex,  $\frac{1}{4}$  to  $\frac{1}{2}$  in. long, hairy within. Flowers numerous, on short pedicels, in divaricately branched axillary and lateral, subsessile, dichotomous panicles of 2 to 3 in. diameter; bracteoles linear, narrowed at both ends,  $\frac{1}{2}$  to 1 $\frac{1}{2}$  in. long, accrescent as well as the calyx-segments. Calyx whitish; segments narrowly or at length broadly linear, ranging up to 1 in. long. Corolla green; segments about  $\frac{1}{2}$  in. long, lanceolate, caudate-acuminate. Style glabrous. Ovary 5-celled. Fruit 1 in. long, obliquely egg-shaped" (Hiern, 1877).

Fernando Po; on the sea shore (Vogel).

Southern Nigeria: Abo (Vogel).

**Cuviera trilocularis** Hiern

*Cuviera trilocularis* HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 157.

"A small glabrous tree. Branches subterete, smooth. Leaves ovate-oval, acuminate, rounded and suboblique at the base, thinly coriaceous, glossy, of nearly the same color on both sides, 4 to 5 by 1 $\frac{3}{4}$  to 2 in.; lateral veins about 8 to 10 pairs; petiole  $\frac{1}{4}$  to  $\frac{1}{2}$  in.; stipules apiculate, ovate, keeled,  $\frac{1}{2}$  in. Flowers on short pedicels, several together, in the terminal or subterminal axils; panicles 1 $\frac{1}{2}$  to 2 in. diameter; common peduncle about  $\frac{1}{2}$  in., bracteoles lanceolate,  $\frac{1}{2}$  to  $\frac{3}{8}$  in. long. Calyx-segments greenish white,  $\frac{1}{2}$  in. long or rather more, linear-elliptical, acute, narrowed toward the base. Corolla shorter than the calyx; lobes lanceolate, caudate-acute. Style glabrous; stigma 10-sulcate. Ovary 3-celled" (Hiern, 1877).

Southern Nigeria: Old Calabar (W. C. Thomson).

ECOLOGY OF *Cuviera* IN THE BELGIAN CONGO

The representatives of this genus observed by me mostly occurred in low-lying or moist places, though not in those apt to be frequently flooded; raised river banks are favorite sites. Usually growing as shrubs or bushes, 2 to 4 meters high, under favorable conditions they may become small, pyramidal, bushy trees of 5 to 7 meters. The trunk is slender, erect, and destitute of branches below where it often, but not always, bears opposite, decussate, very sharp spines, 2 to 5 cm. long. The long, slender branches spread more or less horizontally and their tips hang down somewhat. In accordance with the decussation of the leaves, they are placed opposite each other in four regular rows. As a rule the upper part of the plant is unarmed, though in some specimens one finds in the axils of the leaves heavy, straight spines, evidently modified, aborted branches.<sup>1</sup> The leaves are very large, 10 to 25 cm. long, 5 to 11 cm. broad, borne on a short petiole (of about 1 cm.), entire and simple, thinly coriaceous, smooth and glabrous on both sides, dull green above, paler below; usually cuspidate or more or less acuminate at the apex, oblique and rounded or slightly heart-shaped at the base. The lateral nervures are rather thin, more conspicuous on the under side of the leaf, and number 8 to 10 on each side of the midrib. The stipules are connate into a short, loose sheath, which is keeled, acuminate, and about 0.5 to 1.5 cm. long. The base of this stipular sheath persists on older branches.

The plant is not often seen blossoming. Welwitsch, in Angola, found flowers in April and May and fruits in August; while in the Belgian Congo, flowering specimens were seen by Dewèvre in March (Lukolela) and by me in February (Penge), July (Kunga), and December (between Masisi and Walikale); fruits were found in January, 1915, between Walikale and Lubutu on a plant not in flower. From these very incomplete data, which may relate to different species, it would appear that *Cuviera* blossoms from December to July, yet it is quite possible that there is no definite flowering season, as is so often the case with bushes and trees of tropical rain forests.

Dewèvre in his field-notes accurately describes the flowers of *C. angolensis*. They are large, conspicuously colored, and placed as many as a dozen together in axillary, polygamous panicles, toward the upper end of the younger branches. The common peduncle is 0.5 to 4 cm. long, while the pedicels are very short, the flowers being sessile in the axils

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<sup>1</sup>Kohl (1909, p. 104) and De Wildeman (1906, p. 297) also note that the branches of certain specimens of *Cuviera angolensis* are unarmed, whereas in others they are spinose. There is a possibility that these differences are of specific value.

of slender and narrow bracteoles of about 2.5 cm. The calyx is pale green, deeply cut into 3 to 5 elongate-lanceolate lobes, extending far over the corolla, and 1.5 to 7.5 cm. long. The corolla is short salver-shaped (hypocrateriform), fleshy coriaceous, mostly deep green; the tube is short, bright carmine red, which color extends as a median acuminate line or triangular spot over the upper side of each of the five lobes. These five corollar lobes are lanceolate or oval-acuminate, rigid, and spread into a star when in full blossom. The tube of the corolla bears inside a ring of silvery, shiny hairs directed downward. The five stamens are exserted, placed in the sinuses of the corollar lobes, around the ring of hairs; their filaments are slightly flattened, fleshy, carmine red; their anthers are yellow. The style is thick, columnar, carmine red, densely white pilose, and ends in a large, obtuse, cap-shaped, pale green stigma. Frequently the fruit is oblique or even curved and falcate; but this is due to the aborting of one or more of the ovules; when the fruit is normally developed it is an obovate, dirty yellow drupe, about 23 to 32 mm. long and 18 to 25 mm. thick; its surface is deeply furrowed, there being 5 heavily developed ribs with less prominent ones between them; the ripe fruit is crowned with the remains of the withered calyx. It is noteworthy that very few of the flowers produce fruit.

*Cuviera angolensis* was recognized as a myrmecophyte by K. Schumann (1890, p. 121), who found unidentified ants in the domatia of Welwitsch's herbarium specimens. The first field-notes on this plant were made by Dewèvre in 1896 (De Wildeman and Durand, 1900, p. 124) and these were completed by Ém. Laurent (De Wildeman, 1916, pp. 296-299) and H. Kohl (1909, pp. 163-166). Their accounts agree in almost every detail with my own observations on Congo *Cuvieræ* as reported below. The following ants are known from *C. angolensis*.

*Crematogaster africana* (Mayr). Romée (H. Kohl, 1909, p. 164; Forel, 1909b, p. 69).

*C. africana* subspecies *laurenti* (Forel). Romée (H. Kohl, 1909, p. 164; Forel, 1909b, p. 69). In that locality the coccid *Stictococcus formicarius* Newstead was living inside swellings of *C. angolensis* also occupied by this ant (Newstead, 1910, p. 19).

*C. africana* subspecies *winkleri* (Forel). Eala (Ém. Laurent; see Forel, 1909b, p. 69).

*Cuviera angolensis* Hiern was the only member of the genus recorded from the Belgian Congo, where it is far from rare. I had opportunity to examine in several localities a number of *Cuvieræ*, all

of which at the time I regarded as belonging to this species, since they agreed with its description. While studying the anatomy of *Cuviera*, Prof. Bailey discovered certain histological dissimilarities between specimens collected at different places, yet it is possible that these discrepancies are due either to the difference in the age of the various branches or to their mode of preservation. In view of the fact that the number of African species has been so increased recently, the *Cuvieræ* of the Congo Basin will need considerably more field study before their identity can be safely discussed. Meanwhile, my notes are presented separately for each of the specimens I examined.

1.—At Avakubi (January 6, 1914; Coll. No. 1796) a *Cuviera* was found growing on the banks of the Ituri River. It was a low bush (4 to 5 meters high), well answering the general description given above, but without flowers or fruit; flower buds were, however, noticed a few days later on another specimen in the same locality. The trunk was cylindrical, and neither swollen nor hollow. Most of the branches showed at each node a spindle-shaped swelling which extended over the lower two-thirds to three-quarters of the internode, and was about 8 to 10 mm. thick and 6 to 7 cm. long. Notwithstanding the fact that expanded portions were almost completely hollow, their solid, woody walls made them very resistant to pressure. They were present even on young limbs and early became hollow, through the drying of the medullary tissue, before being attacked by ants.

On some of the branches the swellings contained a beetle larva feeding on the remains of dried pith, but there was always an orifice by which the insect had entered the stem. Some of these beetle larvæ were accompanied by coccids, though no ants were associated with them in the cavity. This is of great interest because it shows that the coccids enter the domatia of their own accord as soon as an aperture is pierced.<sup>1</sup>

The majority of the swellings of older limbs were inhabited by ants of different species, the most common being an unidentified *Crematogaster*. I further collected in other domatia of the same plant *Cataulacus pilosus* Santschi and *Technomyrmex hypoclinoides* Santschi. All of them had established in the cavities regular formicaries with larvæ and pupæ. In the case of the swellings tenanted by *Crematogaster*, each sheltered a separate colony, with its own queen, a number of workers, and abundant brood. Furthermore, the younger swollen internodes on the upper end of the branches were often occupied by a solitary queen, some-

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<sup>1</sup>Kohl (1909, p. 165) also mentions the presence of an insect larva, together with scale insects, in some of the swellings of *Cuviera angolensis*.

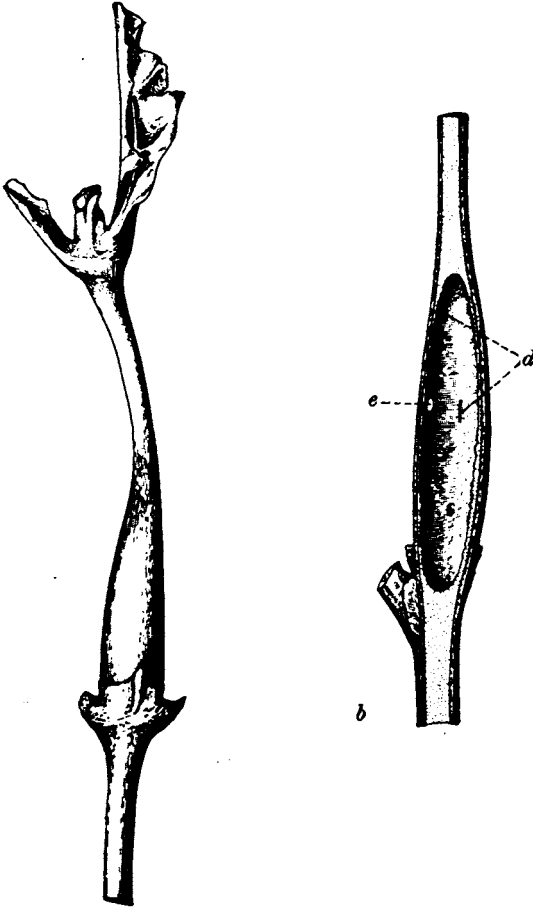


Fig. 99. *Cuviera angolensis* Hiern: a, upper portion of branch with one of the caulinary myrmecodomatia above the node; b, longitudinal section of one of the swellings; e, aperture gnawed by the ants and leading into the cavity; d, pits often occupied by coccids. Drawn from alcoholic specimens collected at the Tshopo River, near Stanleyville; natural size.

times in company with a few coccids, the exit hole being partly closed by callus growth. Working down the branch, one frequently met with all stages in the development of the colony, ending with the appearance of the winged, sexual phases. It thus appears that the various colonies in a single *Cuviera* do not fuse into one great community as is the case with the *Pachysimæ* of *Barteria* and the *Viticolæ* of *Vitex Staudtii*, yet they manage to live peacefully side by side.

pith cells containing it are aggregated in the center of the more deeply lobed medulla (Bailey). The plant from this locality is referred to as "unidentified *Cuviera*" in Prof. Bailey's contribution (Part V, p. 593).

### 3. SYNOPSIS OF RECORDED MYRMECOPHYTES

The study of ant-inhabited plants is in such an incomplete state that no adequate or standard definition of the term "myrmecophyte" has so far been formulated. The student must therefore be prepared, in reading the present synopsis, to meet with cases of very unequal value. Warburg (1892, p. 130) has proposed to classify plants according to the nature of their relations with ants into the following three groups:

a. MYRMECOTROPHIC plants provide only food to the ants, either in the form of sugary exudates (nectaries,) special food-bodies (bromatia of the fungi), seeds or fruits of the myrmecochores, and the like.

b. MYRMECODOMIC plants furnish only shelter to the ants' nests, either in normal cavities, such as hollow stalks, or in special swellings or myrmecodomatia.

c. MYRMECOXENIC plants act as true hosts, offering to their ant guests both shelter and food. Typical cases of the kind are *Cecropia adenopus* (with the Müllerian bodies) and *Acacia cornigera* (with the Beltian bodies).

The term "myrmecophyte" is here used to include Warburg's "myrmecodomitic" and "myrmecoxenic" plants. A further distinction of these two categories seems very unwise at present, because we are, it appears, just beginning to understand the true relations existing between ants and the plants they inhabit. My definition of "myrmecophytes" is based on practical considerations and is thus merely provisional. In the main, however, I agree with Ule (1906b, p. 335), who proposes to designate as ant-plants all plants which are steadily inhabited by certain species of ants, excluding only cases where the ants occasionally settle in normal leaf-sheaths, slits in the bark, dead branches, etc. Schumann's (1888) definition, on the other hand, is quite teleological and therefore of little use under present circumstances, since he wishes to restrict the term "myrmecophyte" to those plants "that are not merely visited by ants, but are purposely inhabited by them, and that therefore have probably entered with them into a true symbiotic relation."

The exquisite manner in which many ants have come "to know plants" (Michael Gehlerus, 1619) must indeed astonish the botanist who is but little acquainted with the psychic activities of these tiny insects. In his search for a much-needed explanation he naturally turns to the magic action of "Natural Selection," following in this the general trend of present ecological botany. Various theories of myrmecophytism are fully exposed and critically discussed by Prof. Bailey in part V of this



the common *Camponotus caryæ* (Fitch), several forms of which occur throughout the Palearctic and Nearctic Regions (Wheeler, 1910c, pp. 219-220). Many species of *Crematogaster* and *Leptothorax* remove the pith from dead twigs of trees, briar and rose bushes, etc., to make homes for themselves (Forel, 1903b; Stäger, 1917 and 1919).<sup>1</sup> A peculiar cœnobiotic association was described by Wheeler (1912a) in the case of a mistletoe, *Phoradendron flavescens* variety *villosum* Nuttall, which grows on live oaks (*Quercus emoryi* Porter and Coulter) in the Huachuca Mts., Arizona. The branches of this mistletoe are very frequently hollowed out for some distance by a curculionid larva; the beetle makes its exit through a round hole at the side of the twig and the deserted gallery is then usually occupied by a colony of *Crematogaster arizonensis* Wheeler. Furthermore, the walls of these formicaries are invariably covered with reddish coccids, *Pseudococcus phoradendri* Cockerell. In the tropics of both hemispheres, many species of *Cataulacus* (Paleotropical) and *Cryptocerus* (Neotropical) are true wood-boring ants. Similarity in habits has gradually resulted in a remarkable resemblance in the shape of the head and the flattened body of these two genera, though they are not closely related to each other.

The keenest carpenter ants, such as the holarctic *Camponotus herculeanus* (Linnæus), with its various races and varieties, and the European *C. vagus* (Scopoli), frequently extend their burrows into the live, healthy wood of standing timber. It is, however, among the tropical and subtropical Pseudomyrminae that we find all transitional stages between the common wood-boring habit and the more specialized behavior of nesting inside living, normal organs of plants and myrmecodomatia. The impulse to gnaw through living vegetable tissues not only presupposes a greater inquisitiveness on the part of the ants, but it is undoubtedly also influenced by the anatomical structure and chemical composition of the plant, as is clearly shown by Prof. Bailey's histological study of myrmecophytes (See Part V, p. 585-621).<sup>2</sup> From the habit of boring into normally existing cavities of plants it is only a step to the excavating

<sup>1</sup>In January, 1910, I found several nests, with queens and workers, of *Leptothorax angustulus* (Nylander) variety *brunneus* Santschi inside dead, hollowed stalks of wild roses near Algiers. The common North American *L. curvispinosus* Mayr usually nests in hollow twigs or stalks.

<sup>2</sup>The larvae of many Hymenoptera, such as the Tenthredinidae and Siricidae, most Cynipidae, and certain Chalcididae, are phytophagous, feeding on the living tissues of healthy, growing plants. It may not be so commonly known that as adults, too, some of them attack living parts of plants. Certain of the larger saw-flies are known to injure twigs of bushes by girdling them with their mandibles. The large hornet, *Vespa crabro*, gnaws the new bark of trees in order to get building material for its paper nests. A number of tropical and subtropical bees and fossorial wasps are known to excavate nesting galleries in the green, juicy pith of living plants. According to Brauns, this is one of the peculiarities in the behavior of certain South African *Xylocopa*, *Ceratina*, and *Dasyproctus*. I have observed similar habits in species of *Allodape* and *Dasyproctus* in the Belgian Congo. Bertoni, in Paraguay, found *Xylocopa umbrosus* Schrottky nesting in the green stalks of radish which ripens its seed about the time the young wasps are hatching.

A species of *Polypodium* (?*P. megalophyllum* Desvaux = *P. Schomburgkianum* Kuntze) of South America (Rio Negro; Rio Napo) is said to have rhizomes similarly swollen and occupied by ants. A Costa Rican species, *Polypodium Brunei* Werckle, possesses small bulbs, about 2 to 2.5 cm. in diameter, fixed by short peduncles at the sides of the rhizome; these bulbs are hollow, provided with an orifice, and divided by partitions into four or five spacious chambers. G. Senn (1910) regards them as water reservoirs; whether they are occasionally inhabited by ants is not known. *Polypodium bifrons* Hooker, of Brazil, has similar swellings which, according to Ule (1906b), act also as water reservoirs and are not occupied by ants.

**Lecanopteris** Blume. Malay Region. Represented by four or five closely allied species, all epiphytes, with swollen, tuberiform rhizomes, traversed by a system of galleries inhabited by ants. The genus is doubtfully distinct from *Polypodium*.

*L. deparioides* (Cesati). Borneo (Shelford, 1916).

*L. carnosus* Blume (= *Polypodium patelliferum* Burck). Perak, Borneo, the Moluccas, Philippines, Celebes, Java (Yapp, 1902; Ridley, 1910; Shelford, 1916). Inhabited by *Crematogaster yappii* (Forel) and *C. difformis* F. Smith. Hooker believed that *L. carnosus* represented a teratological condition of *Polypodium lomarioides*, but this view has been discarded following Burck's (1884a) observations of this plant.

*L. Curtisii* Baker. Sumatra.

*L. Macleayii* Baker. Java.

Some of the Old World epiphytic ferns of the genus *Drynaria* Bory have been improperly included among the myrmecophytes. They are remarkable in having, in addition to the normal, fern-like leaves, others which are sessile, broad, superficially divided, and pressed against the support and the rhizome. Humus accumulates underneath the cover of these appressed leaves and is soon invaded by roots. Frequently ants nest in this humus, but their presence there is merely accidental and I agree with Gœbel (1888) that these cover-leaves ("Nischenblätter") can by no means be considered as myrmecodomatia. *Drynaria Laurentii* Christ is one of the commonest epiphytic ferns of the Congo Basin and shows all the peculiarities of the genus beautifully. *D. quercifolia* (Linnaeus) is abundant in the Oriental Region, from India to Polynesia.

*Pheidole javana* Mayr subspecies *jacobsoni* Forel variety *taipingensis* Forel was found by v. Buttell-Reepen forming small colonies in the cavities of the irregularly thickened root of an epiphytic fern in Malacca

*K. angustifolia* Blume. Malay Region. In Sumatra, Beccari found the ocreæ pierced with a hole and inhabited by *Camponotus korthalsiæ* Emery (Beccari, 1884).

*K. horrida* Beccari, *K. Scortechinii* Beccari, and *K. cheb* Beccari, all from the Malay Region, have a similarly constructed ocrea, with an orifice undoubtedly pierced by ants which have not been identified (Beccari, 1884).

**Calamus** Linnæus. About 150 species in the Oriental Region from India to tropical Australia and Polynesia; one species in tropical Africa.

*C. amplexans* Beccari. Borneo. The two lower segments of the leaves are folded back and embrace the stem so as to enclose it, the resulting cavity being inhabited by ants (Beccari, 1884; Shelford, 1916).

**Dæmonorops** Blume. Oriental Region. Represented by seventy species, all rattans. In several of them ants habitually make nests in the large, stiff flower-spathes, which often quite cover the flower-panicles. The genus is closely allied to *Calamus*.

*D. Jenkinsianus* Martius. Malay Region. Flower-spathes inhabited by a *Camponotus* allied to *C. mitis* (F. Smith) (Ridley, 1910).

### Orchidaceæ

One of the largest families of plants, containing 500 genera and over 15,000 species. Cosmopolitan, but chiefly in warm and humid regions. The following cases of myrmecophytism are still doubtful and need closer investigation.

**Diacrium** Lindley. Epiphytes of the Neotropical Region; four species.

*D. bicornutum* (Hooker), of Trinidad and Guiana, has a swollen, spindle-shaped stem, which is normally hollow and perhaps regularly inhabited by ants (Rodway, 1911, p. 111). Schlechter<sup>1</sup> claims that even under cultivation the pseudobulbs form at their base a slit through which the ants gain access into the cavity.

**Schomburgkia** Lindley. Epiphytes of the Neotropical Region. Represented by thirteen or fourteen species, from Mexico to Guiana and Peru, several of which have hollow pseudobulbs.

*S. tibicinis* (Bateman), in Central America (from Mexico to Venezuela), has voluminous, elongated pseudobulbs, which are hollow, with a smooth inner lining and usually inhabited by ants; these go and come through a small opening pierced at the base of the pseudobulb (Ross,

<sup>1</sup>'Die Orchideen,' (Berlin), 1915, p. 214.

nest" in a spindle-shaped swelling of the bole were inhabited exclusively by *A. muelleri* Emery; he believes that this is a case of dimorphism between the younger and older generations of workers in the same colony. He has, however, not given any conclusive evidence that such is the case, since he has not observed transitional colonies of these two forms.<sup>1</sup> H. v. Ihering also found *A. lanuginosa* Emery in *Cecropia adenopus*; he mentions the frequent occurrence of coccids (*Lachnodiella cecropiæ* H. v. Ihering) in the nests. In his opinion, the main food of the adult ants consists in the soft pith-parenchyma of the upper, still growing internodes, also in the Müllerian bodies. He was unable to find how the larvæ are fed.

Fiebrig's (1909) observations were made in Paraguay on what he calls "*Cecropia peltata* L.," but what is evidently not the Central American *C. peltata* but *C. adenopus* of Brazil.<sup>2</sup> The internodes were practically always inhabited by *Azteca alfaroi* variety *mixta* Forel. The ants go only short distances from their exit holes, unless disturbed, when they become very aggressive. Fiebrig thinks that the main food of the ants is the Müllerian bodies, on which the larvæ are probably fed exclusively, while the workers may also eat soft pith tissues and feed on the sweet fruits of the tree. There is little doubt that *A. alfaroi* is wholly vegetarian, while most other species of *Azteca* are carnivorous. In Paraguay the internodes of *Cecropia* are very often invaded by caterpillars (*Heliothis* species). The very young larvæ of this moth were repeatedly observed in internodes where a queen ant had just started a new colony; later on the caterpillars crowd the ants out and finally occupy the entire branch and destroy even the septa.

Wheeler has called attention to the occurrence in Cuba and Porto Rico of species of *Cecropia* fully equipped with prostoma and Müllerian bodies, though never tenanted by *Azteca*, since this genus of ants is lacking on all the larger Antilles.

*Cecropia lyratiloba* Miquel. Under this name a swamp *Cecropia* of southern Brazil was studied by H. v. Ihering (1907). It possesses the same so-called myrmecophilous structures as *C. adenopus* and is also inhabited by a species of *Azteca*.

*Cecropia sciadophylla* Martius. Brazil. Inhabited by *Azteca emeryi* Forel (Ule).

<sup>1</sup>Emery (1912, 'Gen. Insect., Dolichoderinæ,' p. 34) still regards *nigella* as a distinct variety of *A. muelleri*.

<sup>2</sup>Chodat and Vischer (1920, p. 235) assert that *A. adenopus* is the only species of the genus found in Paraguay.

without any exit hole. After long, unsuccessful investigation of all the branches, I inspected the lower portion of the trunk and finally discovered there the remains of an early branchlet, dried and broken off, but with a pith cavity communicating with the central cavity of the very trunk. It is by this old branch that the *Pseudomyrma* came and went.

Warming (1894) has published some interesting information on a *Triplaris* of Venezuela, which he doubtfully identifies as *T. americana*. The ants found in this plant belonged to a species of *Pseudomyrma* which he calls "*P. mordax* Meinert," a name not backed by any description in the literature.

*T. americana* Linnæus. South America. The earliest accurate account of myrmecophilism in the genus *Triplaris* was published, it appears, by Robert Schomburgk (1838, pp. 264-267) for the species under discussion. After a description of this tree, which he found common on the sandy banks of the inland rivers in Guiana, and often over-towering the other vegetation, he continues:

The uncautious botanist, who, allured by the deceptive appearance, should approach the tree to pluck the blossoms, would bitterly rue his attempt. The trunk and branches of the tree are hollow, like those of the trumpet tree (*Cecropia*), and provided with partitions, which answer to the position of the leaves on the outside. These hollows are inhabited by a light brownish ant, about two- to three-tenths of an inch long, which inflicts the most painful bites. Its antennæ are placed near the middle of the anterior portion of the head; mandibles triangular; peduncle of the abdomen with two rings; the anus hairy and provided with a sting or piercer. They fall upon their prey with the greatest virulence, and insert their mandibles almost instantly, as soon as they come in contact with any soft substance, emitting a whitish fluid; their bite causes swelling and itching for several days. If they find themselves captured, they attack and kill one another like the scorpions. The Arawak Indians call the tree *Jacuna*, and the ant *Jacuna sae*; the Warrows *Epouahari*, the literal translation being ant tree; the Caribis *Itassi*; the colonists, from its growth, "long John."

Richard Schomburgk (1848, II, pp. 449-450) also records his painful experience with the same tree, which he found growing on the banks of the Barima and Barama Rivers, British Guiana.

Penzig found the caulinary cavities of *T. americana*, cultivated at Buitenzorg, Java, occupied by *Dolichoderus bituberculatus* (Morteo, 1904).

*T. Cumingiana* Fischer and Meyer. Central America. Wheeler (1913) observed this species in Panama and writes about it as follows:

These trees were 15 to 20 ft. high, with very slender trunk, smooth, light gray bark, and long, narrow, lanceolate leaves. When the trunk was cut down and split longitudinally, it was seen to have a very slender cavity in the centre and extending its full length, and communicating with a similar slender cavity in the centre of each branch. This continuous system of cavities communicated with the surface by numerous slender galleries, excavated by the ants, and terminating in small round orifices, which served as exits and entrances.

Each tree was occupied by a single large colony of *Pseudomyrma arboris-sanctæ* Emery. Wheeler adds: "as the *Triplaris* trees were isolated and as their bases must stand in the water during the rainy season, it is difficult to understand how the ants manage to exist, unless they remain rather dormant this season or find some hitherto unknown food supply on the foliage." Recent, unpublished observations of Prof. I. W. Bailey on *T. surinamensis*, in British Guiana, however, show that the cavities of *Triplaris* contain great numbers of coccids from which the *Pseudomyrmæ* obtain at least much of their food.

*T. caracasana* Chamisso and Schlechtendal. Venezuela. Trunk inhabited by ants (Karsten in Huth, 1887). Schimper (1888) examined branches sent to him by Ernst and curiously enough states that they presented no adaptations to ants: "the branches possess an inner cavity which is only 5-8 mm. wide and interrupted by diaphragms; round apertures, pierced by the ants, lead into the cavity." He does not believe that there is any true symbiosis in this case.

*T. nolitangere* Weddell. Brazil. Stem inhabited by ants (Huth, 1887).

*T. surinamensis* Chamisso and Schlechtendal. Brazil, Guiana. Myrmecophytic (Spruce, 1908).

*T. Macombii* Don. Smith. Guatemala. Wheeler (1913) says:

This is a larger tree (than *T. Cumingiana*), often attaining a height of 30 to 40 ft., with more diffuse branches and large, coarse, ovate leaves. Early in January it began to put forth bunches of long, yellowish flower-spikes, which were covered with a deciduous sheath. The branches have much larger cavities than in *T. Cumingiana* and the septa at the nodes are not broken through. On examining the surfaces of the branches, each internode is seen to be surrounded near its distal end by a circle of lenticels, and one of these, for some unknown reason, often becomes considerably enlarged and bears a long slit-shaped impression. It is in this impression that the queen ant makes the circular perforation that permits her to enter and take possession of the internodal cavity.

The same observer found the cavities of this species occupied by several species of ants belonging to the genera *Crematogaster*, *Pheidole*, *Tapinoma*, and *Iridomyrmex*, but two species were especially common, a small, black, narrow-headed *Azteca* and the black *Pseudomyrma sericea* Mayr. None of these, however, are obligatory plant ants.

*T. Schomburgkiana* Benthham. Brazil. Inhabited by ants (Spruce, 1908). Ule (1917) found in this species *Pseudomyrma dendroica* Forel and *P. triplaris* Forel.

*Pseudomyrma dendroica* was originally described from specimens found by A. Gøeldi in the pith channel of young, unidentified *Triplaris* on the Rio Purus, Brazil. Some of these plants having been introduced

into the Botanical Garden at Pará, Gœldi observed that this ant soon invaded one the *Triplaris* of the Garden which thus far had not been inhabited (Forel, 1904, p. 41).

**Ruprechtia** C. A. Meyer. Tropical and subtropical South America. There are twenty species, most of which are said to possess solid branches; the following is perhaps an exception.

*R. Jamesoni* Meisner. Brazil. The stem and branches are hollow and inhabited by ants (Spruce, 1908).

**Symmeria** Benth. This genus contains two species; one has been described from Senegambia; the other, *S. paniculata* Benth., according to Spruce (1908), is an ant plant; it occurs in Guiana, northern Brazil, and curiously enough also in Sierra Leone.

**Coccoloba** Jacquin (including *Campderia* Benth.). Tropical and subtropical America. A large genus, with about 125 species; only one of them has been mentioned as a myrmecophyte, but the others should also be studied in this respect. The common sea-side grape, *Coccoloba uvifera* Linnæus, in Porto Rico, sometimes has ants nesting in some of the internodes; but these are facultative forms, such as *Camponotus sexguttatus* (Fabricius), more common elsewhere. This species, at least, cannot be regarded as a myrmecophyte (Wheeler, 1908a, p. 157).

*C. parimensis* Benth. British Guiana, Brazil. The stem and branches are hollow, but not inflated, and are inhabited by ants (Spruce, 1908).

### Myristicaceæ

A small, exclusively tropical family, which, according to Warburg's monograph (1897), contains 15 genera with about 240 species.

**Myristica** Linnæus. Indomalayan Region; eighty species. In two related species from New Guinea, the internodes are in places swollen and hollow; these swellings are irregularly scattered along the branches, and their inner cavities do not communicate with one another; they are inhabited by ants, which pierce the entrances, often slit-like and placed on the side facing the leaf of the lower node. Warburg (1897), who has studied their histology, concludes that these swellings are probably not hereditary, but produced by the irritation of the ants; he considers them true ant galls, not myrmecodomatia. There is, however, no experimental proof that ants can produce such swellings.

*M. subalulata* Miquel (= *M. myrmecophila* Beccari). This species has been studied by Beccari (1884) and Warburg (1892; 1897); the latter figures (1897, Pl. xi) coccids on the inner walls of the swellings.

species the pouches are large pits with ciliolate orifices on the under side in the axils of the lowest one or two pairs of nerves, the pits corresponding to large hollow tubercles on the upper side. Whether these pouches are merely acarodomatia or occasionally settled by ants is not known.

### Nepenthaceæ

Oriental Region, the Seychelles, and Madagascar. Only one genus, *Nepenthes* Linnæus, with some 60 species, one of which has been recorded as myrmecophytic, but the case needs further investigation.

*N. bicalcarata* Hooker fil. Borneo. The petiole of the pitcher-shaped leaves is curled up and, in the curled part, swollen and hollow. According to Shelford (1916), there is no evidence that this cavity is inhabited by ants; while Beccari (1884) saw an opening leading inside and apparently found ants in the swelling.

### Rosaceæ

Cosmopolitan. Includes 1700 species, belonging to 102 genera.

*Hirtella* Linnæus. Tropical America, with forty species; one species occurs in Madagascar. Myrmecophytism seems to be exceptional in this genus, as is also the case in *Cola* and *Randia*.

*H. physophora* Martius. The cordate leaves have at the base of the blade a pair of compresso-globose sacs inhabited by ants (Spruce, 1908).

### Leguminosæ

Cosmopolitan, with 12,000 species and 530 genera. This and the Compositæ are the largest families of plants.

*Acacia* Willdenow. Tropical and subtropical regions of both hemispheres. There are over 600 species.

The so-called bull's-horn acacias of Mexico, Central America, and Cuba are apparently true myrmecophytes; their stipular thorns are much enlarged and flattened or inflated; they are usually hollowed out by ants, which pierce an entrance below the tip of the thorn, more rarely near its base, and establish their nests inside; furthermore, the young leaves bear at the tips of their pinnæ, minute, bright yellow food-bodies (Beltian bodies)<sup>1</sup> which are eagerly collected by the ants and carried inside the thorns. These plants all grow in dry or semi-desert regions under conditions very different from those of other myrmecophytes.

<sup>1</sup>Meneghini and Savi (1844), Fr. Darwin (1877), and A. F. W. Schimper (1888), who have studied the inner structure and development of these Beltian bodies, all agree that they are homologues of the glandular serrations which frequently occur on the margins of young leaves. Such glands often secrete mucus or resin and, as a rule, disappear at an early stage; while in the ant acacias they increase considerably, are filled with proteins and fats and, when not removed by the ants, finally drop off.



of the *Pseudomyrma* nests were placed not far from the tip, those of the other species pierced at various levels, often also several on one thorn." The only other observations on these interesting plants were made by Fiebrig (1909), who studied *Acacia cavenia* Hooker and Arnott in the Chaco of northern Paraguay; the thorns of this species are very large, 90 mm. long and 8 mm. wide, and usually inhabited by *Pseudomyrma fiebrigi* Forel; normal thorns are filled with pith; in those occupied by ants that substance is more or less removed and an opening is found below the tip. Frequently, however, the pith is destroyed by a caterpillar which pupates inside, the moth escaping through a hole near the point of the thorn. Fiebrig believes that the ants appropriate these excavated thorns, using apertures made by the moth. According to Chodat and Carisso (1920), the swelling of the thorns of *A. cavenia* is due to the sting of an insect, the gall thus produced being eventually settled by ants, after its maker has left it. I cannot agree with this explanation.

In a foregoing chapter (p. 372) I have discussed the so-called ant acacias of East and South Africa and have given my reason for not regarding them as true myrmecophytes. In their case, the swellings of the thorns are typical insect galls, probably produced by a lepidopterous larva. When the gall maker has left, the empty shelters may be invaded by various ants, even before they are completely dry, thus simulating myrmecodomatia.

**Sclerolobium** Vogel. Tropical South America. Containing twelve species.

Only one of the species, *S. odoratissimum* Spruce, of Brazil (Rio Negro), is said to be myrmecophilous; its leaves have a large sac, furrowed along the upper face and extending upward from the knee of the petiole to the base of the second pair of leaflets (Spruce, 1908). It is possible that this pouch is merely an insect gall which, when empty, becomes settled by ants.

**Humboldtia** Vahl (= *Batschia* Vahl). Ceylon and British India. Represented by four species, one of which is myrmecophilous.

*H. laurifolia* Vahl. India. The swollen internodes are occupied by ants (Bower, 1886 and 1887; Schimper, 1903; Morteo, 1904; Ridley, 1910). Figured by Taubert, 1894, in Engler and Prantl, 'Die Natürl. Pflanzenfam.', III, pt. 3, p. 143, fig. 80, and by A. F. W. Schimper, 1903, 'Plant Geography', p. 147, fig. 83; this figure is also copied by Escherich (1906b) and Wheeler (1910b).

Escherich (1911a, pp. 46-47) re-examined *H. laurifolia* in the Botanical Garden at Peradeniya, Ceylon. He found that only compara-

tively few of the swollen internodes (at most 20 per cent in the Garden, as contrasted with 50 per cent in the wild state, according to Green) contained a number of species of ants that are also found nesting in other locations (*Technomyrmex*, *Tapinoma*, *Monomorium*, *Crematogaster*, etc.). Since the ants are not in the least aggressive and, furthermore, often keep coccids inside the domatia, he concludes that they are decidedly noxious to the plant, the more so since they frequently attract woodpeckers which damage the branches in order to feed on them and their brood.

**Schotia** Jacquin (= *Theodora* Medikus). Tropical Africa. There are twelve species, one of them possibly myrmecophytic.

*S. africana* (Baillon) (= *S. humboldtioides* Oliver). Cameroon, Spanish Guinea, Gaboon. The young branches often have swollen and hollow internodes settled by ants. There is still a possibility that these enlargements are mere insect galls, which are invaded by ants after being left by their makers (see above, p. 409).

**Tachigalla** Aublet (= *Cubæa* Schreber; *Tachia* Persoon). South America. Includes six species, all of which have inflated petioles inhabited by ants. *Pseudomyrma picta* Stitz and *Azteca brevicornis* (Mayr) were found in *Tachigalia* by Ule in Brazil (Stitz, 1913a).

*T. caripes* Spruce. Brazil. The trigonous petioles are mostly dilated at the base into a fusiform sac tenanted by ants (Spruce, 1908).

*T. ptychophysca* Spruce. Brazil. Like the preceding (Spruce, 1908).

*T. formicarum* Harms. Eastern Peru. The petiole is swollen and inhabited by *Pseudomyrma* (Ule, 1908).

**Platymiscium** Vogel. South America. Contains fifteen species.

The stem is hollowed and inhabited by ants, and even sometimes dilated at the nodes (Spruce, 1908).

### Meliaceæ

Tropical and subtropical regions of the globe. Has 42 genera, with about 700 species.

**Chisocheton** Blume. Indomalayan Region. About thirty species.

*C. pachyrhachis* Harms. New Guinea. A tree with the nodes of the branches and the base of the petiole swollen and hollow; several apertures leading into the cavity (K. Schumann and K. Lauterbach, 1901, p. 382).

**Aphanamixis** Blume. Indomalayan Region. Includes eleven species.

*A. myrmecophila* (Warburg) (= *Amoora myrmecophila* Warburg). New Guinea. The branches are often swollen and excavated, even the younger upper portions, the growing extremity narrowing very abruptly;

several apertures lead inside the irregular cavities, which have smooth, brown walls; the swellings are inhabited by ants (Warburg, 1894, pp. 194-196).

### Euphorbiaceæ

A large, cosmopolitan family, with 4500 species, belonging to about 250 genera.

**Endospermum** Bentham. Indomalayan Region to New Guinea. Includes twelve species, two of which are to all appearances true myrmecophytes.

*E. moluccanum* (Teysmann and Binnendijk). Amboina, Moluccas, Celebes. There is a question whether this species is myrmecophytic. According to Beccari, this is the plant figured by Rumphius (1741, II, pp. 257-259, Pl. LXXXV) as "*Arbor Regis*".<sup>1</sup> In the latter's description, however, a confusion may have been made between several plants; so that it is by no means sure that the following remarks concerning the myrmecodomatia of his *Arbor Regis* apply to *E. moluccanum*:

Truncus, omnesque crassi rami nullo constant corde, sed excavati sunt, ejusque loco referti sunt plurimis magnis et nigricantibus formicis, quæ in una alterave parte truncum perforant, et fenestras quasi formant, perambulantes illum usque ad ramorum extremum tanquam murum concavum, ita ut hæc arbor solo ex cortice suum hauriat nutrimentum, tenuiores vero rami medullam gerunt, qualem *Sambucus* habet. Si quidam amputetur ramus, formicæ hæc magna vi ac celeritate excurrunt, mox circumstantes invadentes homines ac mordentes tanto impetu, ut periculosum valde sit huic accedere arbori, immo totum circa hanc solum mordentibus hisce animalibus repletur, quæ adpropinquantium etiam pedes infestant. Observavi autem Indos non ita horum morsus presentire per duram ipsorum cutim, ac nos, unde et intrepide ad illam accedunt arborem.

The relations of *E. moluccanum* to ants have apparently not been studied in the field since Rumphius' time.

*E. formicarum* Beccari. New Guinea, Bismarck Archipelago. In New Guinea, according to Beccari (1884), the branches are normally swollen and hollow toward their extremity; he found them inhabited by *Camponotus angulatus* Smith, which had apparently pierced the entrances to the cavities. Dahl (1901) describes this plant in the Bismarck Archipelago as having normal branches, filled with pith which is partly excavated by ants, *Camponotus (Colobopsis) quadriceps* (Smith).

**Macaranga** DuPetit-Thouars. Tropical and subtropical regions of the Old World. About 170 species, a number of which are myrmecophytic.

<sup>1</sup>Merrill (1917) admits the correctness of Beccari's reduction of Rumphius' "*Arbor Regis*" to *E. moluccanum*.

Donisthorpe (1917) described *Dolichoderus (Hypoclinea) crawleyi* from Singapore, "associated with species of *Lecanium* (coccids) in hollow stems of *Macaranga*." Wheeler (1919, p. 77) also mentions *Crematogaster (Decacrema) decamera* (Forel) "from *Macaranga* with slightly trifid leaves" at Kuching, Borneo.

*M. hypoleuca* (Reichenbach fil. and Zollinger). Malay Peninsula, Sumatra, Borneo. Inhabited by forms of *Crematogaster (Decacrema) borneensis* (Ern. André) (Viehmeyer, 1916).

*M. caladifolia* Beccari. Borneo (Beccari, 1884).

*M. formicarum* Pax and O. Hoffmann. Borneo. A low tree with thick, hollow branches which are pierced with an entrance and inhabited by ants (Pax, 1914).

In these three species ants live within the hollow, slightly swollen stem and branches, and also underneath the lanceolate, erect, persistent bud-bracts in the axils of the leaves; food-bodies, white and globular, are scattered on the back of the young leaves between the raised veins. The food globules are most plentiful in plants not settled by ants, and have been seen carried about between the mandibles of these insects (Beccari, 1884; Ridley, 1910; Pax, 1914; Shelford, 1916).

*M. triloba* (Reinwardt). Malay Peninsula and Archipelago.

*M. Griffithiana* Mueller. Malay Peninsula.

*M. Hulletii* King. Malay Peninsula.

In these three species, the stems are also hollow and settled by ants; furthermore, the bud-bracts are reflexed into a ring-like pouch which almost completely surrounds the stem. The concave under side of the bracts bears abundant pear-shaped or globular, white food-bodies, which are much sought for by the ants and are conveyed to the nest in the hollow stem, where the larvæ are fed on them; the ants not only hide beneath the bracts but occasionally take their larvæ there. *M. Hosei* King possibly has similar myrmecodomatia. The ant of *M. triloba* is a *Crematogaster* near *C. daisyi* (Forel) (W. Smith, 1903; Ridley, 1910).

In an unidentified species of *Macaranga* of Sarawak, the bracts are very large, lanceolate, acuminate, deflexed, coriaceous, not appressed to the stem, but concave, thus providing a nidus or feeding ground for ants (Ridley, 1910).

*M. saccifera* Pax.

*M. Schweinfurthii* Pax (= *M. rosea* Pax).

The above two species are from Tropical Africa and have pouch-like stipules, which in *M. saccifera* are sometimes inhabited by ants of the genus *Crematogaster* (see above, p. 412).

**Mabea** Aublet. South America. Contains thirty species, some of which have long, hollow branches, often settled by ants (Spruce, 1908).

#### **Sterculiaceæ**

Tropical regions of both hemispheres. Represented by 820 species and 57 genera.

**Cola** Schott and Endlicher. Tropical Africa. With forty-five species. The following three closely allied forms have at the base of the leaf-blade a pair of pouches which are often inhabited by small species of *Engramma* (see above, p. 417).

*C. Dewevrei* de Wildeman and Durand.

*C. Laurentii* De Wildeman.

*C. marsupium* K. Schumann.

**Scaphopetalum** Masters. Tropical Africa. Includes eight species, two of which have an elongate pouch at the base of the leaf-blade often occupied by ants of the genus *Engramma* (see above, p. 422).

*S. Dewevrei* De Wildeman and Durand. Belgian Congo.

*S. Thonneri* De Wildeman and Durand. Belgian Congo, Cameroon.

#### **Flacourtiaceæ**

Tropical regions of both hemispheres. With 650 species and 84 genera.

**Barteria** J. D. Hooker. Tropical Africa. Includes four species, all of which probably have hollow or swollen internodes, normally inhabited by *Pachysima æthiops* (F. Smith) or *P. latifrons* (Emery); accidentally by other ants (see above p. 432).

*B. Dewevrei* De Wildeman and Durand. Belgian Congo.

*B. fistulosa* Masters. Fernando Po, Cameroon, Belgian Congo.

*B. nigritana* J. D. Hooker. Southern Nigeria, Cameroon, Spanish Guinea, Gaboon, (Belgian Congo?).

*B. Stuhlmannii* Engler and Gilg. German East Africa.

**Gertrudia** K. Schumann. New Guinea. With one species, *G. amplifolia* K. Schumann. It is a tree or shrub with branches "strongly swollen at the apex below the leaf-bud, hollow and with an aperture leading into the cavity (probably a myrmecodomatium)" (K. Schumann and K. Lauterbach, 1901, p. 455, Pl. xv). Perhaps this swelling is only an insect gall.

#### **Melastomataceæ**

Tropical and subtropical parts of both hemispheres; very abundant in America, where a few forms reach the Nearctic Region. Represented by 2800 species and 170 genera. With the exception of *Pachycentria*,

which is a doubtful myrmecophyte, all the myrmecophytic members of this family are restricted to the Neotropical Region.

**Tococa** Martius. South America. Includes forty species which, with one or two exceptions, have ant-pouches on the leaves. Either all the leaves or only one of each pair have a hollow sac or pair of sacs at the base of the blade, or in the upper part of the petiole; these pouches are usually inhabited by ants (species of *Azteca*<sup>1</sup>).

*T. disolenia* Spruce. Brazil (Spruce, 1908).

*T. bullifera* Spruce. Brazil (Spruce, 1908).

*T. macrophysca* Spruce. Brazil (Spruce, 1908).

*T. formicaria* Martius. Brazil (Spix and Martius, 1831).

*T. guianensis* Aublet. Guiana. Aublet (1775) describes the two pouches which in this species are placed along the upper part of the petiole, each with an opening beneath the base of the leaf-blade; ants are usually found in them and from the description it would seem that they also inhabit the stem of the plant.

**Microphysca** Naudin. Northern Brazil and Peru. Contains two species, *M. quadrialata* Naudin and *M. rotundifolia* (Spruce), with pouches on the leaves.

**Myrmidone** Martius. South America. There are two species, both with sacs on the leaves shaped much as in certain forms of *Tococa*.

*M. macrosperma* Martius. Brazil (Spruce, 1908).

*M. rotundifolia* Spruce. Brazil (Spruce, 1908).

**Majeta** Aublet (including *Calophysca* de Candolle). South America. Includes eight species, probably all with ascidia serving as abodes for ants.

*M. guianensis* Aublet (= *M. hypophysca* Martius). Guiana, Brazil. The branches are fistulose and swollen at the nodes; the leaves also bear pouches (Spruce, 1908).

To judge from his figure, this is the unidentified melastomataceous plant alluded to by Belt (1874, pp. 223-224) in the following passage:

In each leaf, at the base of the lamina, the petiole or stalk is furnished with a couple of pouches, divided from each other by the midrib, as shown in the figure. Into each of these pouches there is an entrance from the lower side of the leaf. I noticed them first in Northern Brazil, in the province of Maranhão; and afterwards at Pará. Every pouch was occupied by a nest of small black ants; and if the leaf was shaken ever so little, they would rush out and scour all over it in search of the aggressor. I must have tested some hundreds of leaves, and never shook one without the ants coming out, excepting one sickly-looking plant at Pará. In many of the

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<sup>1</sup>*Azteca trasilii* Emery was found in the ascidia of a melastomataceous plant by Schulz at Pará.

pouches I noticed the eggs and young ants, and in some I saw a few dark-colored coccidæ or aphides.

*M. tococoidea* (de Candolle). Brazil, Peru, Guatemala. A large bifid sac at the base of the petiole (Spruce, 1908).

**Pachycentria** Blume. Malay Archipelago. Includes twelve species. These are woody epiphytes, some of which have tuberous swellings on the roots, filled with a spongy tissue. Ridley did not find any ants inside these enlargements and doubts whether the plants are true myrmecophytes. It is probable that the swellings are merely tubers.

*P. macrorhiza* Beccari. Borneo. Tuberous and galleried roots inhabited by ants (Shelford, 1916).

*P. microstyla* Beccari. Borneo. Like the preceding (Shelford, 1916).

**Medinilla** Gaudichaud. India, Malay Archipelago, Oceania, Madagascar, tropical Africa. Contains over 100 species.

*M. loheri* Merrill. Luzon, Philippine Islands. Only one of the leaves in each pair is normal; the other is modified into a crop-shaped ascidium opening on the upper side with a slit. According to Loher's observations, this pouch is sometimes occupied by ants, the species of which is not stated (Solereeder, 1920).

*M. disparifolia* C. B. Robinson. Luzon, Philippine Islands. The leaves have a similar structure as in the foregoing, and are perhaps also used by ants.

#### Loganiaceæ

Tropical regions of both hemispheres. Represented by 400 species and 35 genera.

**Fagraea** Thunberg. Oriental Region. Contains twenty-five species. In the three forms enumerated below, the base of the petiole bears auriculate appendages, which are curved downward and more or less pressed against the stem. The cavities thus formed are occupied by ants, which cover the opening with a papery substance and keep their brood inside (Burck, 1891).

*F. borneensis* Scheffer. Borneo.

*F. imperialis* Miquel. Sumatra.

*F. auriculata* Jack. Oriental Region.

#### Gentianaceæ

Cosmopolitan. Represented by 71 genera, with 900 species.

**Tachia** Aublet (= *Myrmecia* Schreber). South America. There are four species. Bushes or small trees. The stem and the long, slender

branches are hollow. In the original description of *T. guianensis* Aublet, of Guiana, there is a note as follows: "Le tronc et les branches qui sont creux, servent de retraite aux fourmis; c'est pour cette raison que cet arbrisseau est nommé 'Tachi' par les Galibis, ce qui en leur langue signifie, suivant leur rapport, 'nid de fourmis'" (Huth, 1887; Spruce, 1908).

#### Apocynaceæ

Cosmopolitan, though chiefly in tropical regions. Represented by 165 genera containing 1300 species.

**Epitaberna** K. Schumann. One species, *E. myrmæcia* K. Schumann, in Cameroon: upper part of the internodes swollen, spindle-shaped, with a cavity inhabited by ants (see above p. 442).

#### Asclepladaceæ

Cosmopolitan; chiefly in tropical and subtropical regions, and abundant in Africa. Represented by 267 genera, with 2200 species.

**Dischidia** R. Brown (including *Conchophyllum* Blume). Oriental Region. Includes fifty species. They are all twining epiphytes; a few are associated with ants.

*D. Rafflesiana* Wallich. Malay Region.

*D. timorensis* Decne. Malay Region.

In these two species a certain number of leaves are converted into cone- or pitcher-shaped pouches with an opening at the base through which roots project into the cavity; this pouch also contains soil and sometimes ants, which make regular nests there, with brood (Treub, 1883a; Beccari, 1884; Groom, 1893; Ridley, 1910). The seeds are scattered by ants (see above, p. 357). Beccari found *D. Rafflesiana* in Java inhabited by *Dolichoderus bituberculatus* Mayr and *Crematogaster brevis* Emery.

*D. complex* Griffith. Malacca (Pearson, 1902).

*D. pectenoides* Pearson. Philippines (Pearson, 1902).

*D. Shelfordii* Pearson. Borneo (Pearson, 1903; Shelford, 1916).

In the above three species a certain number of leaves are double pitchers; a small pitcher is found inside each large pitcher; the inner surface of the former is thickly beset with glandular hairs; the larger, outer pitcher is filled with soil and numbers of rootlets, which spring from the petiole or stem and grow through the orifice; in the outer one are found also numbers of ants, *Crematogaster difformis* F. Smith. "Microscopic examination of the inner surface of the outer pitcher revealed the presence of a dense waft of superficial mycelium which was



*C. longituba* Chodat and Vischer. Chodat found in the swellings of this species in Paraguay nests of *Pseudomyrma chodati* Forel (Forel, 1920a).

*C. miranda* de Candolle and *C. hispidissima* de Candolle possess, according to Beccari (1884), similar myrmecodomatia; they form, together with *C. nodosa*, a special section of the genus (*Physoclada* A. de Candolle).

### Verbenaceæ

Cosmopolitan, but mostly in tropical and subtropical climes. Represented by 900 species, belonging to 80 genera.

**Clerodendron** Linnæus. Tropical regions of the Old World. About 200 species.

*C. myrmecophilum* Ridley. Malay Peninsula, Sumatra, Borneo.

*C. breviflos* Ridley. Malay Peninsula.

• *C. fistulosum* Beccari. Borneo.

These three species have normally hollow branches, which are often inhabited by ants (Beccari, 1884; Ridley, 1910; Shelford, 1916). According to Beccari and Shelford, the ant of *C. fistulosum* is *Camponotus (Colobopsis) clerodendri* Emery; it gnaws entrances to the hollow stem always directly below the insertion of the leaves, either on one or on both sides of each node; on plants free from ants, these spots are marked by a little circular patch of a texture and structure different from that of the surrounding parts. Beccari also describes and figures the internodes as markedly swollen, and more so towards their upper extremity.

An unidentified species of *Clerodendron* in the Belgian Congo also shelters ants inside its hollow branches (see above, p. 443).

**Vitex** Linnæus. Tropical regions of both hemispheres. With 120 species. Two myrmecophytic species have been mentioned as occurring in Africa, and probably some others also shelter ants inside their stem.

*V. Staudtii* Guerke. Togo, Cameroon, Spanish Guinea, Belgian Congo. Creeper with hollow stems and branches, which are inhabited by *Viticicola tessmanni* (Stitz) (see above, p. 447).

*V. yaundensis* Guerke. Cameroon.

### Rubiaceæ

One of the largest families of plants: over 5000 species, classed under some 400 genera, have been described. They are cosmopolitan, though the majority are found between the tropics. About sixty-five species belonging to eleven genera present myrmecodomatia, this family thus containing by far the largest number of myrmecophytes.

**Myrmecodia** Jack.<sup>1</sup> Oriental Region, from Cochinchina and the Malay Peninsula to New Guinea, northern Queensland, the Solomon and Fiji Islands. There are eighteen species. All are epiphytic, low shrubs, with rhizomes swollen into basal pseudobulbs or tubers, occupied by anastomosing cavities which communicate with the exterior by means of numerous pores and are often inhabited by ants; the apertures seem to be formed naturally, without the intervention of the ants, at least in certain cases.

Beccari originally (1884) held that the galleries of the swollen rhizomes were the work of ants; that it was impossible for plants to reach maturity without the intervention of these insects; that the tunnelling by them caused the tuber to grow enormously, while its weight was not proportionally increased, the galleries thus enlarging the absorbent surface of the rhizomes.<sup>2</sup> Later he altered his views somewhat, as can be seen in the following quotation from his 'Wanderings in the Great Forests of Borneo' (1904, p. 405):

At first I thought that the ants by the irritation they produced on young budding plants of *Myrmecodia*, favored the swelling of the base of the stem, and were the direct cause of such an hypertrophy. Further investigations and researches and the observations of Dr. Treub have, however, convinced me that from the very beginning these swellings appear independently of any action of the ants, and that when the latter are absent the tubers develop much in the same manner. I do not, however, think it equally certain that ants have no part in the formation of the internal galleries. My observations tend to prove that in some cases, in non-Bornean species of *Myrmecodia* (*M. alata* and *bullosa*), ants take an active part in the formation of the galleries and especially in that of the apertures which lead to them. But be this as it may, the hospitating Rubiaceæ live on a footing of reciprocal utility or mutualism with their inhabitants, which act as a formidable army of defence, for no animal dares to meddle with a plant guarded by a host of biting ants, ready to assault the imprudent invader in myriads.

H. O. Forbes (1880 and 1885, pp. 79-82) and Treub (1883, 1888) raised young *Myrmecodiæ* from seed and found that the tuber is a normal production of the plant and that the galleried inner structure arises in the absence of ants. Treub's investigations are of such importance that they should be considered more in detail. He saw that soon after germination and before the first leaves are formed, the axis below the

<sup>1</sup>Rumphius (1750, VI, p. 119, Pl. LV) first discovered the remarkable East Indian Rubiaceæ with ant-tubers. He distinguished two kinds: "*Nidus formicarum niger*" (*Hydnophytum amboinense* Beccari) and "*Nidus formicarum ruber*" (*Myrmecodia Rumphii* Beccari). He believed that not only the swellings but also the entire plant were produced by the ants! Beccari (1884) has given a complete account of the earlier history of these plants; it contains very little of interest to the ecologist and entomologist.

<sup>2</sup>H. N. Moseley (1879, p. 389) had before expressed the opinion that in *Myrmecodia* and *Hydnophytum* "as soon as the young plants develop a stem, the ants gnaw at the base of this and the irritation produced causes the stem to swell; the ants continuing to irritate and excavate the swelling, it assumes a globular form, and may become larger than a man's head." He also believed that these plants cannot thrive without the ants.

cotyledons begins to enlarge and it is from this part of the plant that the whole tuber is produced. When the swelling is quite young the entire mass of cells, including the central bundle, is continuous; but when older, some of the central cells have dried up and thus form the first cavity whose inner walls are covered with a layer of suberose cells; later other galleries are formed, which at an early stage communicate with one another. Treub also apparently admits that the entrances to the cavities are produced by the *Myrmecodia* itself without any outside help. In his opinion, the tuber and inner labyrinth are normal ecological peculiarities of the plant, the latter being used for aërating purposes. The walls of the galleries are in some parts smooth and uniform, in others studded with little prominences, which Treub thinks are not, as originally supposed, glands secreting some fluid attractive to ants or absorbing organs for nutritive substances, but lenticels or rudimentary breathing organs. The ants he regards as mere opportunists who have taken advantage of the secure shelter afforded by the excavated tubers, but are of no visible utility to the plant.

G. Karsten (1895) also disclaims the supposed symbiotic relations between the *Myrmecodiæ* and ants. He believes, however, that the cavities have not only a respiratory function, but that their inner walls can also absorb transpiration water condensed inside the tubers during the cooler nights and at the same time assimilate certain dissolved nutritive elements introduced by the ants or found in the excrement of these insects.

Rettig (1904) agrees with Karsten and Treub in explaining the peculiarities of the *Myrmecodiæ* and allied genera on the ground of the physiological needs of the plant. He notes that these epiphytes are light-loving, thriving in nature on branches which are much exposed to intense sunshine or even on rocks; the galleries of the tubers are filled with air and act as aërating tubes, which isolate the inner tissues and prevent the plant from drying out. This author does not discard Treub's idea that the pimples on the inner walls may be for respiration; he even observes that there is undoubtedly a current of air through the apertures, since fresh air enters during the cooler nights and partly escapes during the day. He believes, however, that in many cases rain-water enters the cavities through the openings and is then absorbed by the tuber; he has shown experimentally that such absorption can actually take place.

Our knowledge of the *Myrmecodiæ* has been materially increased by Miebe's (1911b) researches. According to his findings, the inner walls of the cavities of *Myrmecodia tuberosa* are, as a rule, clean; those in

*Crematogaster difformis* F. Smith subspecies *sewardi* (Forel) was also described from a Bornean *Myrmecodia*.

*M. armata* de Candolle. Java. As Rettig remarks (1904, p. 12, footnote), this is evidently the plant so carefully investigated in Java by Treub, and originally called by him (1883) "*Myrmecodia echinata* Gaudichaud." Later (1888), Treub agreed with Beccari that his former identification was incorrect but claimed, apparently with reason, that his plant was not *M. tuberosa* Jack. It is the species used by Rettig (1904) for some of his experiments and the one studied by H. Miehe (1911) under the name "*M. tuberosa* Beccari." Miehe found most of his specimens inhabited by *Iridomyrmex myrmecodix* (Emery); in one locality, however, exclusively by *Camponotus maculatus* subspecies *pallidus* (Smith). Beccari (1884) also mentions the occurrence of *Iridomyrmex myrmecodix* in the tubers of Javanese "*M. tuberosa*" (= *M. echinata* de Candolle).

*M. tuberosa* Jack. Sumatra, Borneo, and probably elsewhere in the Malay Archipelago. Beccari (1884) found in Bornean specimens *Crematogaster difformis* Smith and Shelford (1916), also in Borneo, *C. difformis* and *Iridomyrmex myrmecodix* (Emery). Shelford mentions that both ants are by no means restricted to the tubers of epiphytic Rubiaceae, for they frequently nest in hollowed-out branches of various dead or living shrubs or trees.

*M. bullosa* Beccari. New Guinea, Amboina (G. Karsten, 1895). Inhabited by *Iridomyrmex cordata* (Smith) in New Guinea (Beccari, 1884).

*M. Menadensis* Beccari. Celebes. S. H. Koorders<sup>1</sup> gives the following interesting remark concerning this plant: "Especially common in the Minahasa in the lower plain to 1000 m. above sea-level in young forests, preferably in abandoned coffee-orchards. One sees there on most of the half-dead dadap trees (*Erythrina*) a number of these strange epiphytes. It is remarkable that as a rule I have found, on the same trees, one or more specimens of the following other curious myrmecophilous epiphytes with tuberous stem divided into chambers, viz., *Hydnophytum formicarum* Jack, *H. Selebicum* Beccari, *Polypodium sarcopus* DeVr. and Teysm. and *Polypodium carnosum* Christ, and of the most peculiar *Conchophyllum maximum* Karsten." Thus there seem to be regular "associations" of myrmecophytic epiphytes, in the sense plant ecologists use this term.

<sup>1</sup>1898, 'Verslag oener botanische dienstreis door de Minahasa.' (Batavia), p. 497.

Both from the Belgian Congo; internodes swollen into spindle-shaped myrmecodomatia (see above, p. 465).

*R. physophylla* K. Schumann. Cameroon, Belgian Congo. Rudimentary pouches with a nectary, attracting ants, at the base of the leaf-blade (see above, p. 467).

**Electronia** Linnæus. Tropical and subtropical parts of the Old World. Includes 200 species.

*P. glabriflora* (Hiern) of Tropical West Africa, *P. Laurentii* É. De Wildeman of the Belgian Congo, and some other species of Tropical Africa have swellings of the stems in which ants often nest (see above, p. 471).

**Cuviera** de Candolle. Tropical Africa. There are fourteen species, a number of which have swellings of the internodes inhabited by ants of the genus *Crematogaster* (see above, p. 488). Such myrmecodomatia are known with certainty for the following species:

*C. longiflora* Hiern. Cameroon.

*C. latior* Wernham. Belgian Congo.

*C. Ledermannii* Krause. Cameroon.

*C. angolensis* Hiern. Angola, Belgian Congo.

*C. physinodes* K. Schumann. Gaboon.

**Psychotria** Linnæus. A very large genus with over 400 described species and distributed throughout the tropics of the Old and New World.

*P. myrmecophila* Lauterbach and Schumann. New Guinea. A bush with pouch-like stipules; the margins are reflexed and the stipule itself much inflated; the cavity thus formed is divided into two by a median projecting carina; apertures are pierced through the wall and also through the inner partition. Remains of ants, together with coccids, have been found in these stipular pouches (K. Schumann and K. Lauterbach, 1901, p. 579, Pl. xxii).

#### 4. BIBLIOGRAPHY OF THE RELATIONS BETWEEN PLANTS AND ANTS

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PLATE XXVI

Fig. 1. Nest of a harvesting ant (*Messor* species) in the Athi Plains, British East Africa, July, 1906.

Fig. 2. Bushes of a species of *Acacia* with galls on the swollen thorns, often inhabited by ants. Athi Plains, British East Africa, July, 1906.

Fig. 3. Species of *Acacia* with galls on the thorns inhabited by ants. Near the Tana River, 25 miles below Fort Hall, British East Africa, September, 1910.

Photograph by Mr. Carl E. Akeley



PLATE XXVII

Fig. 1. *Scaphopetalum Thonneri* De Wildeman and Durand. Niapu, January 1, 1914. Extremity of a branch with ant inhabited pouches at the base of the leaf-blade. The five leaves still attached are seen from above; the two detached (lower part of photograph) show the under side with slit leading into the pouch; between them is a longitudinal section of one of the ascidia.

Fig. 2. *Cola Laurentii* De Wildeman. Stanleyville, March, 1915. Extremity of a branch with flowers and fruit. Many of the leaves show the pair of characteristic ant-pouches at the base of the blade.



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PLATE XXVIII

*Barteria fistulosa* Masters

Fig. 1. Tree growing in secondary forest near the Tshopo River, Stanleyville, April, 1915. The horizontal branches and the spreading leaves are well illustrated.

Fig. 2. Two lateral branches inhabited by *Pachysima aethiops* (F. Smith). The upper one demonstrates the spreading leaves and the sudden swelling at the base of the branch; the lower one, sectioned longitudinally, shows the cavity occupied by the ants. Medje, October, 1910.



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