Colony-Founding Among Ants

WITH AN ACCOUNT OF SOME PRIMITIVE AUSTRALIAN SPECIES

BY

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TO

P. J. DARLINGTON AND W. E. SCHEVILL

IN GRATEFUL ACKNOWLEDGMENT
OF THEIR COMPANIONSHIP AND ASSISTANCE
AS MEMBERS OF THE

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TO AUSTRALIA, 1931–1932

PREFACE

IN THE following pages I have recorded a number of field observations which reveal a new and hitherto unexpected mode of colony-founding behavior in certain ancient and very primitive (Ponerine) ants. These observations, which were made during 1931 and mainly in Western Australia, while I was in charge of the Harvard Australian Expedition for the Museum of Comparative Zoölogy, are supplemented by unpublished material from my notebooks of 1914, when I spent several months in New South Wales and Queensland. Because of our meager taxonomic knowledge of the ants in question, I could not, unfortunately, avoid revising several of the more common species and therefore introducing a considerable amount of purely classificatory data. In this portion of the work, which the general reader will gladly omit, I have been greatly assisted by Mr. John Clark of the National Museum at Melbourne, who has most generously given me a number of authentic specimens and the benefit of his conscientious, still unpublished study of the Australian Myrmecias. The long discussion with which the book concludes is, perhaps, too condensed and at the same time covers too much ground. It has seemed necessary because the Ponerine method of colony-founding not only proves to be a significant link connecting the behavior of the ants with that of the solitary and social wasps, but also

shows that the queen ant has far more initiative than she has been credited with in the past. Her behavior therefore is a valuable confirmation of the importance of the mother-family concept in the study of social insects.

The list of friends to whom the members of our expedition and myself in particular are greatly indebted for many kindnesses is a long one. I mention only those we remember with particular affection, because they were such congenial and helpful companions in the field: Dr. C. Anderson, Dr. G. A. Waterhouse, Professor W. J. Dakin, Mr. E. L. G. Troughton, Mr. F. H. Taylor and Mr. W. W. Froggatt of Sydney; Mr. John Clark, Mr. A. N. Burns and Mr. Charles Barrett of Melbourne; Dr. R. J. Tillyard, Dr. H. A. Nicholson and Mr. A. L. Tonnoir of Canberra; the late Mr. A. M. Lea of Adelaide; Mr. L. Glauert, Professor G. S. Nicholls, Mr. L. J. W. Newman, Mr. H. Womersley and Col. E. A. LeSoeuf of Perth and Mr. A. Patterson of Wiluna. For much assistance in the preparation of the large amount of ant material collected in Australia I am indebted to Mrs. C. M. Bartlett, for very carefully typing my manuscript to Miss Elsa Thorud, and for making a number of the illustrations to Messrs. E. A. Schmitz, F. P. Orchard and George Nelson.

W. M. W.

CAMBRIDGE, MASS.
  July 15, 1932

LIST OF ILLUSTRATIONS

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COLONY-FOUNDING AMONG ANTS

COLONY–FOUNDING AMONG ANTS

ENTOMOLOGISTS have been greatly interested, especially during the past thirty years, in the colony-founding behavior of ants. Investigation has shown this behavior to be much more diverse than the early writers had suspected, and to be clearly correlated with the peculiar structural and physiological endowment of the fecundated female ant, or queen, which as a rule establishes the new colony and may be said, therefore, to be its epitome or initial embodiment. It is customary to distinguish an independent and a dependent type of colony-founding behavior, according as the young queen establishes her colony and brings up her first brood of workers entirely by herself, or behaves as a parasite and is therefore compelled to resort to the workers of an alien colony and species capable of acting as a host for aid in accomplishing her task. The same two types of colony formation are also exhibited among the social wasps (Vespinæ) and bumble bees (Bombinæ). In a third type, that of swarming, or 'hesmosis,' as it may be called, a portion of the worker population emigrates with one or more fertile females to form a new colony. Obviously only polygynous, or pleometrotic ant-colonies, that is those containing more than a single fecundated female, are of this type, which bears much the same relation to the independent and dependent types that proliferation by budding bears to sexual

reproduction in the colonies of polyps, Bryozoans, Tunicates, etc.[1]

Hesmosis is therefore a secondary or derived type of behavior adopted by large colonies which, except in cases like that of the honey-bees, were originally founded either by the independent or by the dependent method. We must suppose that in the honey-bees (Apinæ) the independent method has been completely suppressed during phylogeny, leaving swarming as the sole method of establishing new colonies. In the following pages I shall consider in detail only the independent type of nest-founding behavior as it is developed in the ants, because I wish to call attention to certain field observations that reveal the existence of an unexpected and very primitive variant of this type. These observations were made on certain Ponerinæ while I was a member of the Harvard Australian Expedition (July 1931 to January 1932). I have introduced a number of more general notes, some of which have, perhaps, an added interest because they were made in Western and Southwestern Australia, portions of the continent that have been little explored by the entomologist and are zoögeographically more ancient and more isolated than Tasmania, Victoria, New South Wales and Queensland.

The methods of colony-formation adopted by three of the eight subfamilies of Formicidæ (the Dorylinæ, Cerapachyinæ and Leptanillinæ) are quite unknown.

[1] For definitions of the terms 'polygynous,' 'pleometrotic,' etc., see p. 114.

The method adopted by the Ponerinæ will be discussed at length in the sequel. In the four remaining subfamilies (the Pseudomyrminæ, Myrmicinæ, Dolichoderinæ and Formicinæ) the data abundantly show that the prevailing, if not the only, method of establishing new communities, except in the parasitic species, is of the independent type. The following is a list, compiled from the literature and my notebooks, of the genera in which it has been observed:

PALEARCTIC AND NEARCTIC GENERA

Formicinæ

Camponotus: Réaumur 1743; Potts (McCook 1883); Blochmann 1885; Adlerz 1886; Forel 1902; Janet 1904; Emery 1904; Pricer 1908; Viehmeyer 1908; Wheeler 1910; Schmitz 1911; Brun 1912; Eidmann 1925, 1926. *Lasius:* Gilbert White 1788; Adlerz 1886; W. F. White 1895; Janet 1904, 1907; Ernst 1905; von Buttel-Reepen 1905; Mrázek 1906; Southcombe 1907; Wheeler 1908; Wasmann 1910; Tanquary 1913; Crawley and Donisthorpe 1913; Donisthorpe 1927; Meyer 1927; Eidmann 1928, 1931. *Formica:* Gould 1747; Wasmann 1905, 1909; Crawley and Donisthorpe 1913; Donisthorpe 1917; Emery 1922; Meyer 1927; Eidmann 1929; Wheeler, several species. *Myrmecocystus:* Wheeler 1917. *Prenolepis:* Wheeler. *Nylanderia:* Wheeler.

Dolichoderinæ

Liometopum: Emery 1904; Wheeler.

Myrmicinæ

Messor: Meyer 1926. *Aphœnogaster:* Crawley 1910; Wheeler. *Myrmica:* Forel 1873; Lubbock 1879; Adlerz 1886; Crawley 1910; Emery 1911; Meyer 1926; Eidmann 1928. *Manica:* Eidmann 1926. *Pogonomyrmex:* Lincecum 1874; Wheeler 1908, 1910. *Pheidole:* Emery 1911; Wheeler. *Solenopsis:* Meyer 1927. *Myrmecina:* Donisthorpe 1917. *Crematogaster:* Emery 1904; Wheeler. *Leptothorax:* Forel 1874; Adlerz 1886; Emery 1904; Crawley 1910, 1912; Donisthorpe 1917; Wheeler. *Tetramorium:* Emery 1911; Donisthorpe 1917; Meyer 1927.

NEOTROPICAL, PALEOTROPICAL AND AUSTRALIAN GENERA

Formicinæ

Camponotus: Bruch 1921; Docters van Leeuwen 1929; Wheeler, many species. *Oecophylla:* Dodd 1902; Maxwell-Lefroy 1909. *Polyrhachis:* Karawaiew 1928, Wheeler. *Melophorus:* Wheeler. *Notoncus:* Wheeler. *Dendromyrmex:* Wheeler. *Calomyrmex:* Wheeler. *Acropyga:* Bünzli 1932.

Dolichoderinæ

Dolichoderus: Emery 1904. *Monacis:* Wheeler. *Hypoclinea:* Wheeler. *Azteca:* F. Müller 1880; Schimper 1888; H. von Ihering 1907; Fiebrig 1909; Wheeler 1929.

Myrmicinæ

Crematogaster: Paoli 1930; Wheeler. *Allomerus:* Wheeler 1929. *Pheidole:* Wheeler, several species. *Meranoplus:* Wheeler. *Solenopsis:* Wheeler. *Monomorium:* Wheeler. *Podomyrma:* Wheeler. *Xenomyrmex:* Wheeler. *Atta:* H. von Ihering 1898; Goeldi 1905; J. Huber 1905; Escherich 1926, 1929; Eidmann 1932; Wheeler. *Acromyrmex:* Gallardo 1907; Bruch 1919, 1921, 1922; Wille 1929. *Mœllerius:* Bruch 1921, 1922. *Trachymyrmex:* Wheeler. *Apterostigma:* Wheeler, two species.

Pseudomyrminæ

Pseudomyrma; Pachysima: Wheeler 1912, 1921.

The earliest recorded observations on independent colony formation are those of Réaumur (*Camponotus ligniperda* 1743) which I published in 1926, but these and the similar observations of Gould (*Formica* 1747), Gilbert White (*Lasius* sp. 1788),[1] Pierre Huber (*Lasius* sp. 1810), Forel (*Myrmica scabrinodis* 1874) and Lincecum (*Pogonomyrmex molefaciens* 1874) were inadequately controlled, or, in Forel's

[1] Myrmecologists seem to have overlooked the following historically interesting note in *The Natural History of Selbourne*: "August 23rd — Every ant-hill about this time is a strange hurry and confusion; and all the winged ants, agitated by some violent impulse, are leaving their homes, and, bent on emigration, swarm by myriads in the air, to the great emolument of the hirundines. Those that escape the swallows return no more to their nests, but looking out for fresh settlements, lay a foundation for future colonies. All the females at this time are pregnant; the males that escape being eaten, wander away and die." The species observed was probably *Lasius (Chthonolasius) flavus* Fabr.

case, misinterpreted. The earliest complete observa-
tions are those of Lubbock (*Myrmica ruginodis* 1879),
Fritz Müller (*Azteca mülleri* 1880) and Potts (*Camponotus pennsylvanicus*, edited by McCook, 1883).
Fritz Müller's figure, the first to be published of a
colony-forming ant queen in the hollow internode of
a Cecropia tree, is here reproduced (Fig. 1). The
most recent and most detailed researches are those of
Eidmann on species of Camponotus, Lasius and
Formica (1925, 1926, 1928, 1931) and E. Meyer on
Messor structor (1927). My own observations during
the past thirty-five years on colony-founding females
of the subfamilies Formicinæ, Dolichoderinæ, Myrmi-
cinæ and Pseudomyrminæ merely confirm the results
of the investigators last mentioned.

The fundamental behavior pattern or cycle of the
colony-founding female in all the ant genera listed
above is very uniform. After fecundation during the
nuptial flight she descends to the earth, discards her
wings and either seeks some small cavity under a
stone, log or piece of bark or digs into the soil and
forms a small cell which she closes off completely
from the outside world. Her large wing-muscles,
which now degenerate, and the abdominal fat-body,
acquired by her as a larva in the maternal nest, repre-
sent a supply of nourishment which enables her to
mature her ovarian eggs and to survive for several
months as an isolated, imprisoned organism.[1] Even-

[1] The fasting of a colony-founding queen may be of extraordinary
duration. Eidmann (1926) kept a queen of *Camponotus ligniperda* with-
out food for 373 days and one of *Lasius niger* (1928) for 382 days. Both
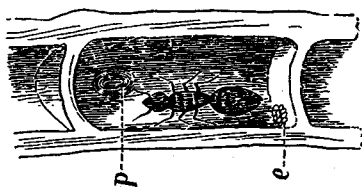of these insects succeeded in establishing incipient colonies. Meyer

FIGURE 1

Female of *Azteca mülleri* Emery with eggs
(*e*) in internode of Cecropia. *p*, prostomium
through which the insect enters the cavity.
This is the earliest figure of a colony-found-
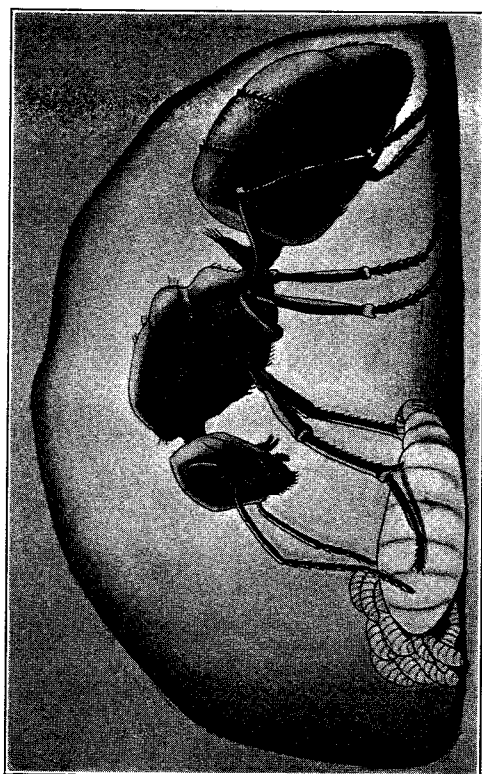ing ant female. After Fritz Müller.

FIGURE 2

Colony-founding queen of *Camponotus ligniperda* Latr. with the
larvæ of her first brood. After H. Eidmann.

tually she lays a batch of eggs, and feeds and cares for the resulting larvæ till they pupate and emerge as small workers Figs. 2 and 3 . These leave the cell and secure food for themselves and the queen. thus enabling her to produce further broods and insure the growth of the colony and the enlargement of the nest.

The recent careful observations of Eidmann (1926, 1928, 1929, 1931) on *Formica fusca, Lasius niger* and *flavus* and *Camponotus ligniperda,* and particularly those of Meyer (1927) on *Messor structor, Cremato-gaster scutellaris* and *Lasius flavus,* have emphasized the fact that the colony-founding female exhibits a singular penchant for eating her eggs and feeding them to the young larvæ. She may even devour the larvæ and pupæ or distribute them as food among the surviving brood. Furthermore, the larvæ may attack and devour one another till only a few of the more vigorous survive. J. Huber (1905) and Bruch (1919) had previously seen the colony-founding queens of the South American fungus-growing *Atta sexdens* and *Acromyrmex lundi* devouring their eggs or feeding them to the larvæ, and Tanquary (1913), in a paper which has been overlooked by European investigators, had not only observed this behavior in *Lasius americanus,* but believed it to be a normal occurrence. He says:

"In all my nests containing single queens, the queen was more or less given to eating her own eggs.

(1927) kept a female *Messor structor* without food for 396 days and Vieh-meyer (1908) one of *C. ligniperda* for more than 486 days, but neither of these queens was able to found a colony.

Some ate only a few, while others ate nearly all. This was not due to lack of food, as I had provided food for them. The fact that all the queens ate their eggs to some extent, and the fact that the number of young produced under natural conditions is so much less than the number of eggs laid, lead me to believe that the queen under normal conditions eats a certain proportion of her eggs. Possibly this habit enables her to get the proper kind of food for her larvæ."

In fact, this devouring of eggs, larvæ and pupæ is easily observed in our common North American species of Camponotus and Lasius kept in small artificial nests. Such behavior may seem, at first sight, to be pathological, but Tanquary, Meyer and Eidmann are probably right in regarding it as the rule and therefore as quite normal. It enables the starving queen to prolong her life and, by sacrificing a considerable portion of her initial brood, to bring to maturity at least a few very small but viable workers.

In certain genera there are modifications or elaborations of the basic pattern of the queen behavior briefly outlined above, owing in some cases to environmental factors, in others to ethological specializations or adaptations. The following may serve as examples:

(1) Occasionally two or even more fecundated sisters may, immediately after their nuptial flight, unite to start a colony in a single cell. Though they combine their eggs in a single packet and show a common interest in the mass of resulting larvæ, they may begin to attack one another as soon as the first workers emerge, and continue this behavior till only a

single queen survives (von Buttel-Reepen 1905, Mrázek 1906, Wheeler 1908, Wasmann 1910, Schmitz 1911, etc.). In some cases the workers are said to take the part of the more vigorous queen and to aid her in eliminating her rival. In other cases the hostility between the mothers may arise even earlier. Thus Meyer (1927) found that the young queens of *Messor structor* would oviposit together but soon separated, each appropriating a portion of the common egg-packet and excavating a cell for herself.[1]

(2) The colony-founding female of this same ant, according to Meyer, exhibits a peculiarity in the excavation of her initial nest, since it is not a simple cell, like that excavated by other ants, but consists of

[1] On the other hand, it is not improbable that in certain species the females starting a colony together may develop little or no mutual animosity and therefore become the mothers of a single colony. I believe this to be the case in *Myrmecocystus mimicus* Wheeler, which I observed (1917) near Phoenix, Arizona, immediately after a severe rainstorm on July 29: "The large reddish queens had evidently celebrated their nuptial flight immediately after the storm and were now busily digging into the wet adobe soil, making small craters about two inches in diameter with eccentric opening. The wall of the craters consisted of small pellets about one-eighth of an inch in diameter, evidently carried up in the psammophore, or crate of peculiar stiff hairs with which the gular surface of the head is furnished in these ants. On seizing a queen just as she was carrying out and dropping a pellet on the wall of the crater I was surprised to see another queen leave the entrance with a similar burden. This led me to examine some twenty nests — all, in fact, that I had time to excavate before I was obliged to proceed with the party. My rather hurried observations showed that about half of the craters had been established by single queens but that the others were each the work of two coöperating queens. One crater actually contained five queens, four deälated and one with intact wings! It appears, therefore, that about 50 percent of the colonies of *mimicus* are pleometrotic in origin. That they probably remain so is indicated by the fact that on former excursions in Arizona I have on several occasions taken more than one deälated queen from a single adult colony of this ant."

a series of two or even three cells, or chambers connected by galleries. A similar condition will be noticed below in the Australian genus Myrmecia.

(3) There is considerable discrepancy in the literature concerning the time of oviposition of the fecundated female. The variation has been shown by Eidmann (1925, 1926) to be correlated with the period of the nuptial flight. Thus when the nuptial flight occurs in the spring, oviposition may begin immediately after the excavation of the initial cell, and the first brood of workers appears before winter. When the nuptial flight occurs in summer the colony may be started at once, but the larvæ are carried through the winter and do not yield the first brood of workers till the next spring; and when the nuptial flight is autumnal, even oviposition may be delayed till the following year.

(4) According to Maxwell-Lefroy (1909), whose figure (Fig. 4) is here reproduced, the female of the Indian *Oecophylla smaragdina*, which is an exquisitely arboreal species, founds her colony quite openly on a leaf, probably because a closed cell cannot be obtained till the larvæ are old enough to be employed in spinning the leaves together with silk.

(5) The nest-founding queen of the fungus-growing ants (Attini) of tropical America, as H. von Ihering (1898), Goeldi (1905) and J. Huber (1905) first demonstrated, and as Gallardo (1907) and Bruch have since observed, not only brings up her first brood of workers in the same independent manner as the non-fungus-growing species, but is also able to de-
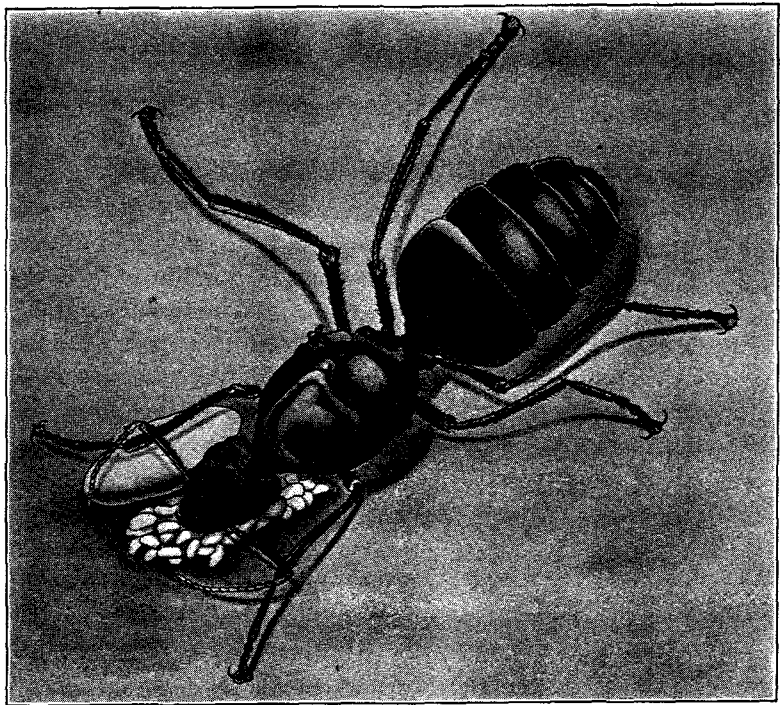
FIGURE 3

Colony-founding queen of *Lasius niger* L. with her incipient brood consisting of numerous just-hatched larvæ and a single pupa in its cocoon. After H. Eidmann.
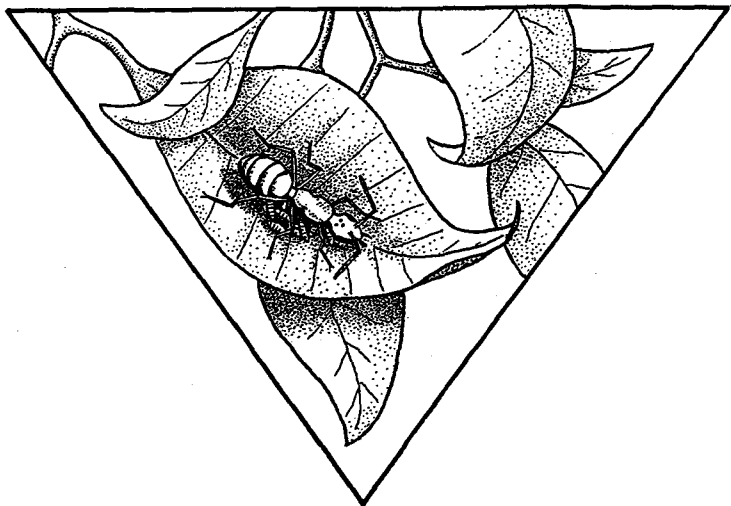

FIGURE 4

Female of *Oecophylla smaragdina* Fabr. with her first brood of larvæ on the surface of a leaf. After Maxwell-Lefroy.

velop at the same time a fungus-garden from the hypha-containing infra-buccal pellet which she has carried over from the maternal nest. I am able to confirm these observations from studies of queens of *Atta cephalotes* in Panama (Fig. 5) and of two species of Apterostigma in British Guiana.

(6) Another variant and elaboration of colony-founding behavior is exhibited by the huge females of certain African species of the genus Carebara. Here the difference in size between the female and the workers is so enormous that the former cannot nurse and feed the extremely minute larvæ of her first brood, though she is adequately provided with fat and wing-muscles and should be able to endure very prolonged fasting. When she sets out from the maternal nest on her nuptial flight she therefore carries a few of the minute workers attached to her tarsal hairs to aid her in bringing up her first brood (Arnold 1916, Wheeler 1928). Hence the Carebara queen cannot be said to establish a colony independently like the ants of the list on pp. 5–7. The new colony is really initiated by a peculiar form of hesmosis, because the queen, together with the transported workers, actually constitutes a very diminutive swarm. Carebara, therefore, seems to resemble certain pleometrotic, neotropical, social wasps in always forming new colonies by hesmosis. It might also be compared with the honey-bee, but the swarms of this insect are accompanied not by the younger but by the older queens.[1]

[1] The behavior of Carebara suggests that colony-founding ant queens

(7) The females of certain inquiline ants (*Formicoxenus nitidulus, Leptothorax emersoni*, etc.) and thief ants (Solenopsis, Pædalgus, etc.) establish their colonies in small cells after the usual independent manner, but in or very near the nests of other ants which serve as protectors and later also as sources of food for both adult ants and brood.

The Ponerinæ

In the preceding paragraphs I have given a very brief summary of our knowledge of colony formation in all the subfamilies of ants, except the Ponerinæ. This subfamily is represented in Europe and North America by so few species and they are so rare and sporadic that little has been learned about their behavior. In two papers published in 1900 on five of our

may act as vectors, or carriers of parasitic or pathogenic organisms. According to Bolívar (1901), the queens of the fungus-growing *Acromyrmex lundi* of Argentina do, in fact, transport the small myrmecophilous cockroach *Attaphila bergi* to new nests. He found this insect "sitting on the back, neck or even on the head of the sexual individuals (never on the neuters), and when these swarm forth during the spring and summer, it is carried out of the nest, still attached to the host." Much greater interest attaches to a recent important discovery of Dr. G. H. Bünzli in Surinam. He writes me that he has succeeded in demonstrating that "the queens of the subterranean *Acropyga pickelii* Borgmeier, during their nuptial flight distribute the root-coccids, *Rhizococcus coffeæ* L., of the coffee-plant on a great scale and thus cause the infectious phloem-necrosis which Professor Stahel has been investigating since 1917." In 1930 Professor Stahel discovered that the organism which directly causes the disease and is transmitted by the coccid, according to Bünzli, is a flagellate Protozoan (Phytomonas). Probably, therefore, the queens of Lasius, Brachymyrmex and other ant genera that are regularly associated with root-aphids and root-coccids transport the diminutive young of these plant parasites to new hosts and may thus act as indispensable agents in spreading various plant-diseases.
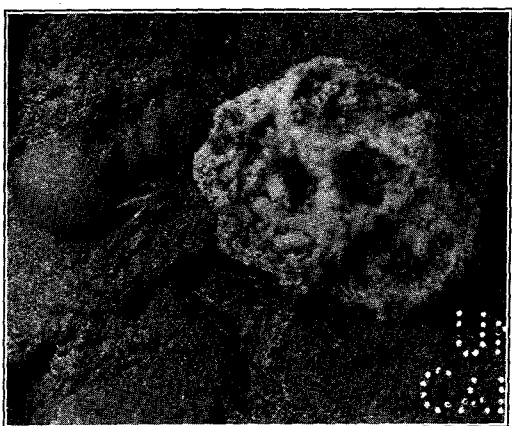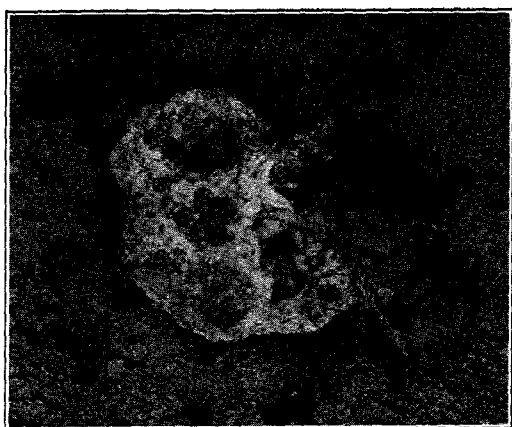
FIGURE 5

Two views of an incipient *Atta cephalotes* colony showing
the deälated female and her fungus-garden containing her
first brood of larvæ. $\times 1\frac{1}{2}$.

North American species, representing as many genera
(*Ponera pennsylvanica, Stigmatomma pallipes, Pachy-
condyla montezumia, Leptogenys (Lobopelta) elongata*
and *Odontomachus clarus*), I was able to demonstrate
that the larvæ are fed on pieces of insects captured
by the workers, instead of with regurgitated liquid
food. The same behavior has also been observed
in some Formicine and Myrmecine ants. Janet (1897)
recorded it for *Lasius mixtus*, and I have seen it in
Acanthomyops claviger, Pogonomyrmex imberbiculus
and *Aphœnogaster fulva*. Since 1900 I have found
so many Ponerine ant-larvæ feeding on pieces of in-
sects that Father Borgmeier's (1920) negative obser-
vations on the Brazilian *Odontomachus affinis* are
somewhat surprising. Though he fed his colonies on
termites as well as honey and sugar-water, he was
unable to detect any other method of feeding the
larvæ than by regurgitation. Moreover, contrary to
what I had claimed for Stigmatomma, he found that
the callows of *O. affinis* had to be assisted by the work-
ers to escape from their cocoons.

In my papers of 1900 I adopted what I am now
convinced was an erroneous hypothesis in regard to
the Ponerine method of colony-formation. At that
time I surmised that new colonies could be estab-
lished only by proliferation or splitting of the original
colony, that is, by hesmosis, instead of by the inde-
pendent method described above for the Formicinæ,
Dolichoderinæ, Pseudomyrminæ and Myrmicinæ.
Since 1900, however, I have observed in tropical
America not only the nuptial flights of species of

Ponera but also independent colony-formation by queens of Odontomachus, Anochetus, and especially of the smaller species of *Neoponera* (*N. crenata, unidentata* and *stipitum*), which nest in the myrmecodomatia of certain plants (Cecropia, Cordia). Nevertheless, incipient colonies of Ponerinæ are very far from common in tropical America. I found it advisable, therefore, to turn my attention to Australia, which, of all the continents, possesses the most magnificent Ponerine fauna. During my visit to New South Wales and Queensland in 1914, I found only a few incipient colonies of these ants, but was much more successful in Western Australia and Victoria in 1931, as will be seen from the following notes, which have been expanded to include a more general ethological and taxonomic account of the observed species, together with data gleaned from the Australian myrmecological literature.

Myrmecia

The confused taxonomy of the superb, large-eyed, aggressive and severely stinging ants of this genus, usually called 'bull-dog,' 'bull' or 'sergeant ants' by the Australians, has been recently revised, after many years of conscientious investigation, by my friend Mr. John Clark, of the National Museum, Melbourne. He recognizes more than 90 species, subspecies and varieties, confined to and generally distributed over the Australian continent, except, perhaps, its northwestern corner. They all nest in the ground, under stones or logs or in mound nests,

with the single exception of the formidable *M. mjö-bergi* Forel of Queensland, which is said to inhabit the large epiphytic ferns of the genus Platycerium. Emery divided the genus into three subgenera, Myrmecia *sens. str.*, Promyrmecia and Pristomyrmecia, on the structure of the mandibles, and I added a fourth, Halmamyrmecia, for the jumping species included by Emery in Myrmecia *sens. str.* Clark now recognizes only two groups, the Gressoria (subgen. Myrmecia *sens. str.*) and the Saltatoria (subgen. Promyrmecia), including Pristomyrmecia and Halmamyrmecia.[1] The colonies of Myrmecia *sens. str.*, which comprises the larger species, are larger than those of Promyrmecia, though numbering fewer than 200 and usually less than 100 individuals. The ground nest of these large species, as Clark says (1925–27), "usually goes down two feet, almost vertically. There is a series of three or four pockets on the ground level, just under the mound. Similar pockets occur at intervals down the shaft, which terminates in a large chamber. During the summer months the brood, more particularly the pupæ, generally is in the surface pockets. At the first alarm the brood is carried to the bottom chamber."

I have been unable, unfortunately, to witness the spectacular nuptial flights of these ants, because they

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[1] I adopt Clark's interpretation in this book, though I am inclined to believe that Promyrmecia, for the reasons given below (p. 54), may have to be retained as defined by Emery, for the single species (*M. aberrans*) possessing short, broad, subtriangular mandibles. If this is done, the other species of Clark's Promyrmecia will have to be assigned to Pristomyrmecia Emery.

occur during the late summer and I had to return from both of my trips to Australia in late December. The earliest account of one of these flights is that of Tepper (1882). The species observed was the "black bull-dog ant," probably *M. pyriformis* F. Smith. He describes the occurrence as "a rather formidable affair, owing to many hundreds of the large creatures (the females above an inch in length while alive) flitting about one's head, all armed with a sting about a quarter of an inch in length, while the shrubs near the nest were covered with scores of pairs and single ones. This took place on April 7, 1880 between ten and eleven o'clock A.M., and I learned here for the first time that the males differ so much in form from the more formidable and aggressive sex that till then they had been looked upon as belonging to a genus of wasps."

In 1915 Mr. W. W. Froggatt sent me the following account of a nuptial flight of the red bull-dog, *M. gulosa* F. Smith, which I published in 1916:

"On January 30th, after some very hot, stormy weather, while I was at Chevy Chase, near Armadale, N. S. W., I crossed the paddock and climbed to the top of Mt. Roul, an isolated, flat-topped, basaltic hill, which rises about 300 feet above the surrounding open, cleared country. The summit, about half an acre in extent, is covered with low 'black-thorn' bushes (*Busaria spinifera*). I saw no signs of bull-dog ant nests till I reached the summit. Then I was enveloped in a regular cloud of the great winged ants. They were out in thousands and thousands, resting

on the rocks and grass. The air was full of them, but
they were chiefly flying in great numbers about the
bushes where the males were copulating with the
females. As soon as a male (and there were appar-
ently hundreds of males to every female) captured a
female on a bush, other males surrounded the couple
till there was a struggling mass of ants forming a ball
as big as one's fist. Then something seemed to give
way, the ball would fall to the ground and the ants
would scatter. As many as half a dozen of these balls
would keep forming on every little bush and this went
on throughout the morning. I was a bit frightened at
first but the ants took no notice of me, as the males
were all so eager in their endeavors to seize the
females."

After quoting Tepper's and Froggatt's observa-
tions, I added the following comments in my paper of
1916:

"The observations of Tepper and Froggatt prove
conclusively that the species of the Ponerine genus
Myrmecia celebrate a regular marriage flight like the
ants of the other taxonomic subfamilies, except the
species with wingless males or females, and that these
flights occur during January in northern New South
Wales or a few months later in the more southern and
colder portions of Australia. This season corresponds,
of course, to our autumn months, which are likewise
the nuptial season of some of our species of Lasius
(*L. claviger* Roger, *brevicornis* Emery, etc.). We may
also infer from the accounts of the two Australian
observers that each female *Myrmecia*, after fecunda-

tion, loses her wings in the same manner as other ants, except certain parasitic species, enters the ground and establishes a small colony without the assistance of workers of her own species. I am able to show that this is actually the case. On September 19th, 1914, I found under a stone in one of the deep sandstone canyons near Katoomba, in the Blue Mts. of New South Wales, a fine deälated female of *Myrmecia tricolor* Mayr occupying a little cavity in the soil and engaged in caring for about a dozen small larvæ. This little incipient colony was very similar to those just established by our common carpenter ants (*Camponotus pennsylvanicus* DeGeer and *noveboracensis* Fitch) under the bark of old logs. That the most primitive of existing ants should found their colonies in precisely the same manner as the most highly specialized species, is not without interest."

Clark (1925–26), who has also observed the nuptial flights of Myrmecia, has confirmed my observation on the independent founding of their colonies and has added considerably to this and other forms of behavior in these ants. "The winged males and females are found in the nests during the summer. Usually the nuptial flights take place during the afternoon, in the period from February to April. After the flight the male dies, but the female, using her legs, breaks off her wings. She constructs a cell under a log or stone, in which she deposits her eggs. Sometimes three or four females, with their eggs, are discovered in one cell, under a stone. When the eggs hatch these females fight with each other until but one remains

alive to found the new colony." He gives a more de-
tailed account of *M. nigriscapa:*

"The deälated females may be found during May
to July, in cells under stones with their eggs. The
eggs are small, slightly under 2 mm. in length and 1
mm. in width; they are yellowish white. From five to
seven eggs are laid at a time. The eggs hatch in from
six to nine days, but six to seven months elapse before
the first ants appear. These are always small ex-
amples, owing no doubt to the scarcity of food. The
first brood are raised entirely by the female. While
rearing this small family the queen devotes much time
to excavating a nest. By the time the first ants ap-
pear she generally has a small nest, about 6 inches
under ground, where the larvæ and pupæ are stored.
On the arrival of the small family the female stops all
work and devotes her energy entirely to egg-laying.
The new workers at once enlarge the nest and attend
to all future eggs, larvæ and pupæ. The second and
subsequent broods usually are normal size, as the
workers procure the food. Sometimes a few small
workers may be found, particularly in spring. These
are regarded by some naturalists as minor workers,
but I consider that they are merely the result of a
scarcity of food during the winter months."

The following observations are unusually interest-
ing, because they show that the bull-dog ants, which
are so very wasp-like in their general behavior, also
resemble the social wasps in being nectarivorous as
adults and insectivorous as larvæ.

"From my own observations, these ants carry

home every insect they capture; but the victims, as a rule, are honey-bees, and other soft-bodied insects, taken to feed the larvæ in the nest. I have never known adult Bull-ants to eat animal food; they always prefer the nectar of blossoms and the exudations of trees, shrubs, etc. In my artificial nests the food supplied is honey, sugar in various forms, and cake of all sorts, with plenty of water each day, also a quantity of insects and caterpillars for the larvæ. Although the adult Bull-ant is really a honey-eater, the larvæ must have an insect diet, or they will eat one another when close together. On more than one occasion, when the food supply was overlooked, I found that one larva had apparently been supplied as food to other two by the ants; and several times weak, or injured, ants have been served to the larvæ. When the larvæ have finished their feeding on the insect body, its remains are carried outside the nest to the rubbish heap, where, in the bush, they are promptly removed by other ants. Thus a Bull-ant's nest very rarely shows signs of food remains, either inside or out."

It would seem, therefore, that the Myrmecia queen, apart from feeding her larvæ on insect food, founds her colony in precisely the same manner as the young queens of the higher ants. This is not the case, however, since a significant idiosyncrasy of her behavior has been overlooked, as will appear in my account of *Myrmecia regularis* and several other species.

True myrmecophiles seem to be rare in the nests of the Myrmecias, probably because, unlike the higher

ants, they are unable to feed one another or other insects by regurgitation. Adult bull-dog ants, as I shall show in a future paper, are sometimes infested with Nematodes (Mermis), and the larvæ are often attacked by large hymenopterous parasites of the Chalcidid genus Eucharis. It is surprising therefore to find such apparently defenceless creatures as small amphibians living in the nests. Dr. T. Barbour calls my attention to a note (1929) in which he and Loveridge published some observations on the association of a small toad, *Pseudophryne nichollsi* Harrison with bull-dog ants. This toad, which is only 13 to 22 mm. long, was found by Mr. W. S. Brooks at Manjimup, Pemberton and Augusta, that is in the same forested region of Southwestern Australia in which Dr. P. J. Darlington, Mr. W. E. Schevill and I collected in 1931. Its habits are described by Brooks as follows:

"Here [at Manjimup, Feb. 7] under one log, a very large one, I found several dozens of these small frogs associated with the fearful 'bull' or 'sergeant' ants, the most vicious, poisonous and thoroughly terrifying insects which I have had the misfortune to meet. Apparently the best of relations were established between the ants and the frogs, as the latter were in and about the galleries, and it was with considerable fear and agility that I obtained my series with long steel forceps. Again, at Augusta, on the extreme southwest tip of Australia, I found on March 6, a colony of fifty-two associated with 'bull' ants, and using their galleries, or, at least the entrances thereof."

Brooks' description applies to *Myrmecia regularis* Crawley, and that it was really this ant with which he found the toads is attested by the series of specimens he brought back to the Museum of Comparative Zoölogy. On November 12 Mr. W. E. Schevill and I took 44 *Pseudophryne nichollsi,* singly or in pairs, under logs in a piece of moist, primeval karri forest about seven miles from Pemberton, but in no instance were they associated with bull-dog or other ants. Since, however, our collection was made during November, the association may be temporary or confined to the breeding season. Colonies of *M. regularis,* I would add, occurred under other logs in the same few acres of forest in which we found the toads. Brooks discovered the eggs of Pseudophryne under a log on March 17, but does not mention the presence of ants. The eggs, which are large and develop directly, without a tadpole stage, "had been rolled in the dust to retard evaporation, giving them the appearance of pills covered with powdered cinnamon." The Myrmecia nests would certainly afford a highly protective environment for the toads and their eggs, but even if the association observed by Brooks is only occasional, or facultative, we must assume that the toads are protected from the stings and mandibles of their extremely irritable protectors by some repulsive odor or secretion. This is obviously a problem to be solved by the resident Australian naturalist.

Myrmecia regularis Crawley

Crawley described this ant (Fig. 6) as a distinct species in 1925 from specimens taken at Albany, Western Australia, but Clark is inclined to regard it as synonymous with *M. lucida*, originally described from Hobart, Tasmania. I am convinced, however, from comparison of many specimens collected by myself in Southwestern Australia and a series taken by W. S. Brooks at Augusta in the same region, with typical specimens of *lucida* from Hobart and Georgetown, Tasmania (G. H. Hardy and F. M. Littler) and Ballarat, Victoria (Davey), that *regularis* is a valid species.[1] It is the dominant ant in the superb forests of karri, jarrah and tuart (*Eucalyptus diversicolor, marginata* and *gomphocephala*) at Pemberton and especially at Margaret River, in the southwestern corner of Western Australia. It does not build mounds but nests in the rather damp, black earth under logs or large stones in colonies of as many as 100 to 200 workers. These are distinctly smaller than the workers of *M. forficata* and more shining, owing to the more sharply rugose sculpture of the head and thorax. When moving about in the full sunlight *regularis* is a beautiful insect. It is very lithe and graceful; its head, thorax, pedicel and appendages are deep red,

[1] In the *regularis* worker the mandibles are distinctly narrower through their broadest basal portion than in *lucida*, the posterior corners of the head are more rounded, the petiolar peduncle is distinctly longer, its node more sharply truncated anteriorly and posteriorly, the rugosity of the head even sharper and more regular, the mandibles deeper red, and the posterior borders of the gastric segments broadly golden brown, as in *M. analis* Mayr.

distinctly flushed with purple, and its glistening black, golden-tipped gaster has blue and violet reflections. These vital tints are lost in dried specimens. The workers are very alert and when disturbed rush out of the nest without the slightest hesitation and pursue the intruder with their terrible stings to a distance of two or three yards. Dr. P. J. Darlington and I found them to be both nocturnal and diurnal foragers, climbing the great trunks of the eucalypts in search of sap and nectar and ruthlessly seizing any small insects encountered on their path.

The larger colonies investigated at Margaret River and Pemberton contained many eggs and larvæ. The former, unlike the eggs of the higher ants, are broadly ellipsoidal, almost spherical, in fact, and not kept together in packets with a glutinous salivary secretion, but scattered singly over the floor of the nest chambers. The same is true also of the eggs of all the other species of Myrmecia which I have observed. The slender, small-headed and long-necked larvæ are fed on pieces of insects or even on entire or nearly entire insects. Some of the larvæ had spun their cocoons before the middle of November. As these could not produce adult workers, males and females before January, the nuptial flight very probably does not occur before February at the earliest.

Diligent search enabled me to find more than twenty nest-founding females of *regularis*. Since these must have been fecundated sometime between February and April 1931, and since in the genus Myrmecia as in other Ponerinæ the females and work-
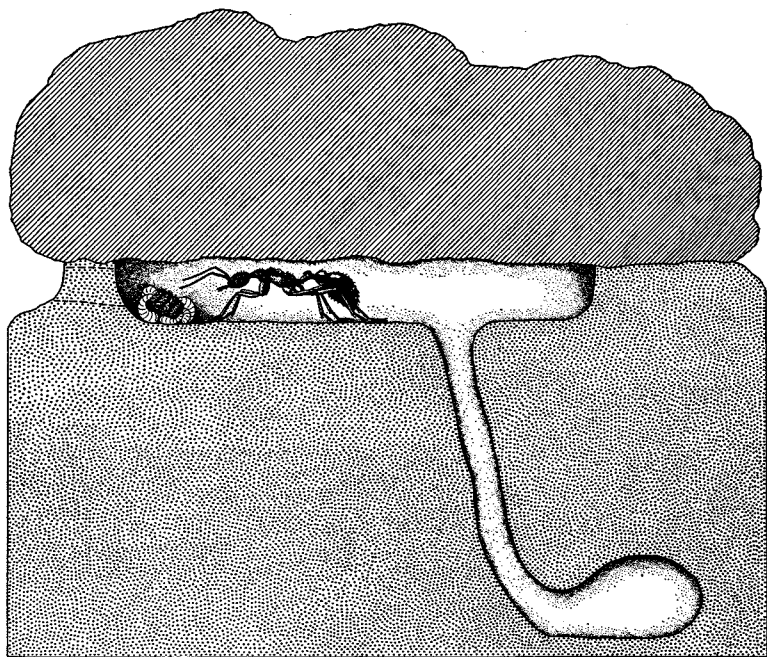
FIGURE 6

Subdiagrammatic section through the incipient nest of *Myrmecia regularis* Crawley under a stone; showing the flat surface chamber, the retreat leading off from it, the queen and her young larvæ feeding on a piece of caterpillar. The queen removes the portion of earth between the two broken lines when she leaves the chamber to forage.
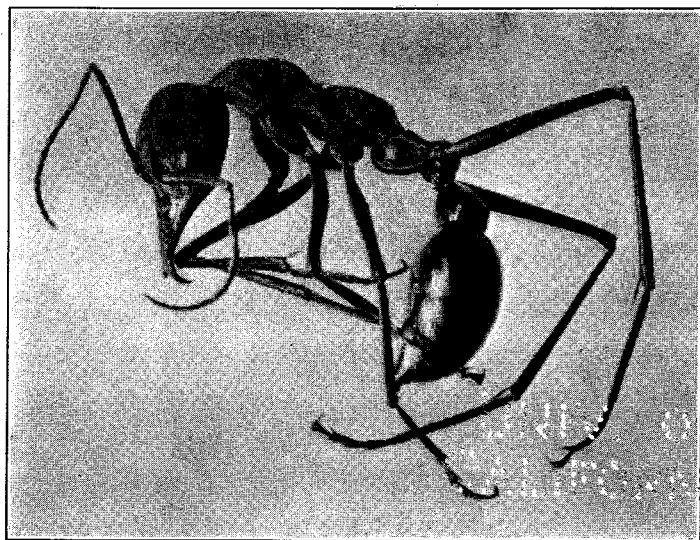

FIGURE 7

Myrmecia gulosa Fabr., worker. New South Wales. × 4.

ers differ so little in size, and especially in the relative volumes of the thorax and gaster, as contrasted with the queens and workers of the higher ants, it seemed to me improbable that the *regularis* queen could fast and survive on her small amount of fat and wing-musculature for a period as long as seven or eight months. That we are not compelled to make such a supposition was demonstrated by the following observations.

I found that each of the females occupied a large flat cell (Fig. 6) varying from $2\frac{1}{2}$ to 4 inches in diameter under a large stone or log rather deeply embedded in the soil. The lower surface of the stone or log formed the roof of the cell; its earthen floor was quite flat and its walls continuous on all sides. It was always situated nearer the periphery of the stone or log than the center, so that the outer wall of the cell was quite thin. In most cases a large gallery descended into the soil from the floor of the chamber perpendicularly or obliquely for a distance of about six inches and terminated in a second smaller and more irregular chamber. When the stone or log was turned over the queen fled precipitately into this second chamber, which is therefore used as a retreat in case of danger. It was sometimes difficult to capture the escaped queen because the gallery was often excavated between immovable stones or roots. Usually there was only one female under a stone, but on one occasion I found three, each in a separate cell and separated by nearly a foot of earth from the others. Some of the females were quite alone, but others had a number of eggs scattered on the floor of the upper

cell or a small cluster of young or nearly half-grown
larvæ. The latter were sometimes found feeding on
fresh pieces of insects, such as caterpillars and the
gasters of deälated ant females of the genera Cam-
ponotus and Orthocrema. This food, of course, must
be obtained outside the nest, and since the superficial
cell is closed off on all sides, we must assume that the
regularis female does not remain rigidly confined like
the females of the higher ants during her whole
colony-founding period, but leaves her nest from time
to time to secure insect food for her brood and also,
in all probability, nectar and sap for herself. This is
indicated also by the following observations and in-
ferences. First, I have taken a few *regularis* females
wandering about in the open. They could not have
been recently fecundated individuals because the
regularis nests contain no young sexual forms during
October and November and it was far too early for
any nuptial flight of the species. Second, I found two
incipient nests, each containing a cluster of sound and
active larvæ but no females. I could only suppose
that they happened to be out foraging at the time
when I uncovered their cells. Third, the outermost
earthen wall of the cell in several instances looked as
if it had been broken open and restored repeatedly.
In the case of *Myrmecia analis* mentioned on p. 44 I
actually found an opening in this wall! And fourth,
the cells inhabited by the females and larvæ were al-
ways exquisitely clean, indicating that the former
must carry all refuse insect food to the outside, as
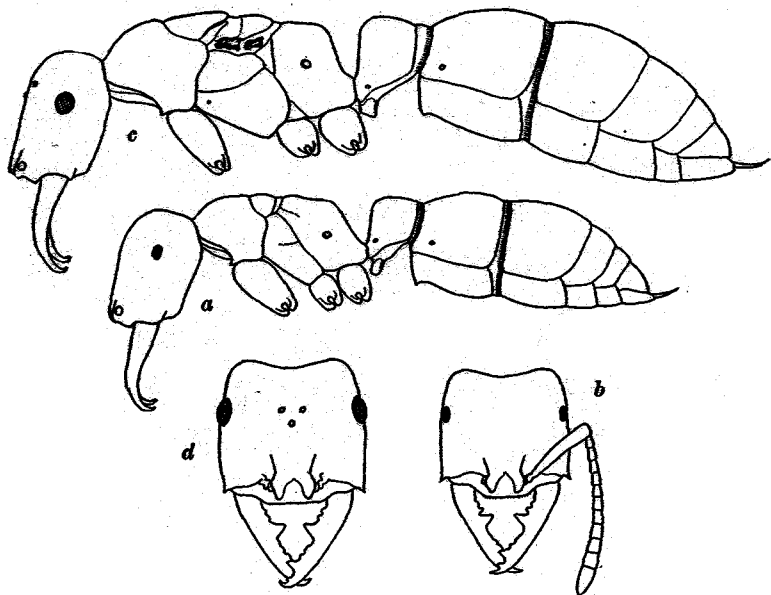Clark has described (see p. 22) for the adult colonies.

FIGURE 25

Amblyopone australis Erich. subsp. *foveolata* Wheeler. *a.* worker in profile; *b.* head of same, dorsal view; *c.* deälated female in profile; *d.* head of same, dorsal view.
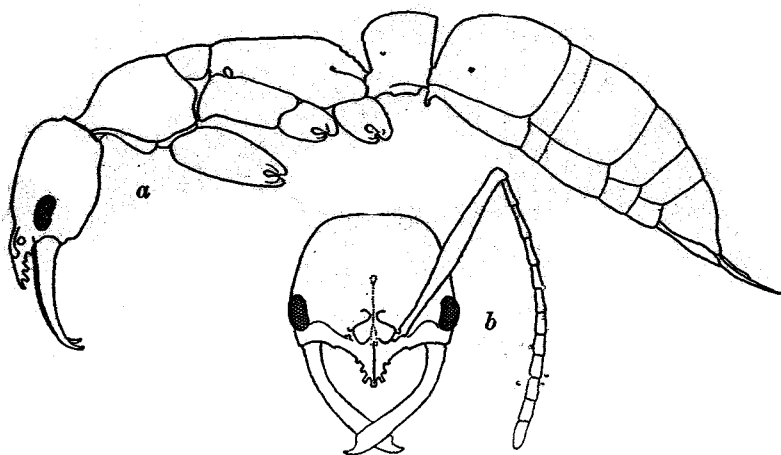

FIGURE 26

Leptogenys clarki sp. nov. Worker. *a.* lateral view; *b.* head, dorsal view.

I believe, therefore, that the *regularis* female makes her cells soon after her nuptial flight and then leads the life of a recluse till October or November, occasionally breaking through the outer wall and foraging for food. With the return of spring in October the more abundant food-supply enables her to lay a number of eggs and to rear a few larvæ with insect food which she captures on similar excursions. Additional evidence of this behavior is given in connection with several of the following species of Myrmecia.

Myrmecia gulosa Fabricius

Emery made this handsome and well-known species (Fig. 7) the type of the genus. The worker measures 12–25 mm. in length and is bright yellowish red, with yellow mandibles and the three apical segments of the gaster jet black. Though rare in Victoria, it is one of the most conspicuous species of Myrmecia in the sandy coastal portions of New South Wales and Queensland. In the neighborhood of Sydney, New South Wales, and on Bribie Island, Queensland, I have frequently found *gulosa* nesting in sandy woods (Fig. 8) or in pure sand on the beaches in mounds which may measure two to three feet in diameter and nearly a foot in height. At the slightest disturbance and without any signs of hesitation the workers sally out of the nest and pursue the intruder to a distance of fully twenty or thirty feet.

Myrmecia nigriscapa Roger

This fine species, originally described from an unknown Australian locality, resembles *gulosa* and is of the same size (worker 17–26 mm.; female 26–29 mm.; male 15–18 mm.). In color the worker and female are bright yellowish red, of a slightly darker tint than *gulosa*, with yellow mandibles, black antennal scapes and the gaster black, except the greater basal portion of the first segment and the tip, which are yellowish red. Clark (1925–27) describes the male as red, with the sides and occiput of the head, the pronotum and scutellum black, tinged with red, the remainder of the thorax, the pedicel, legs and antennæ yellowish red, the mandibles yellow, the wings hyaline.

Forel remarks that *nigriscapa* is very widely distributed in Australia. Clark repeats this statement and defines its range as "extending from Bunbury, Western Australia, round the Southern Coast to Rockhampton, Queensland." It must be rare or local in New South Wales, because I have never taken it in the field. The only specimens in my collection are from Western Australia (Waroona (H. Womersley)) and South Australia (Adelaide, Mt. Lofty, Mt. Pleasant and Kangaroo Island (J. G. O. Tepper), Lucindale (A. M. Lea) and Meningie (L. H. Minchin)). Clark records it from a number of localities in Victoria and gives an account of its nests, which apparently resemble those of *gulosa*, and its method of colony formation. In this account, quoted on p. 21, he says nothing about the feeding of the first larval
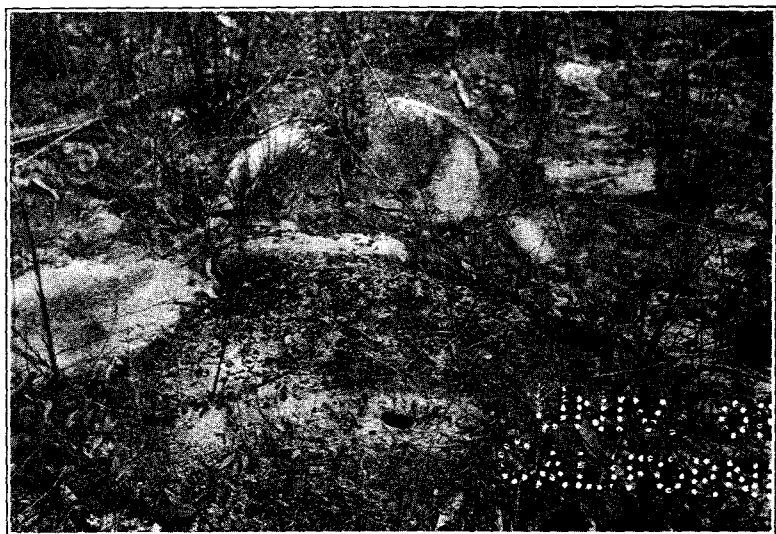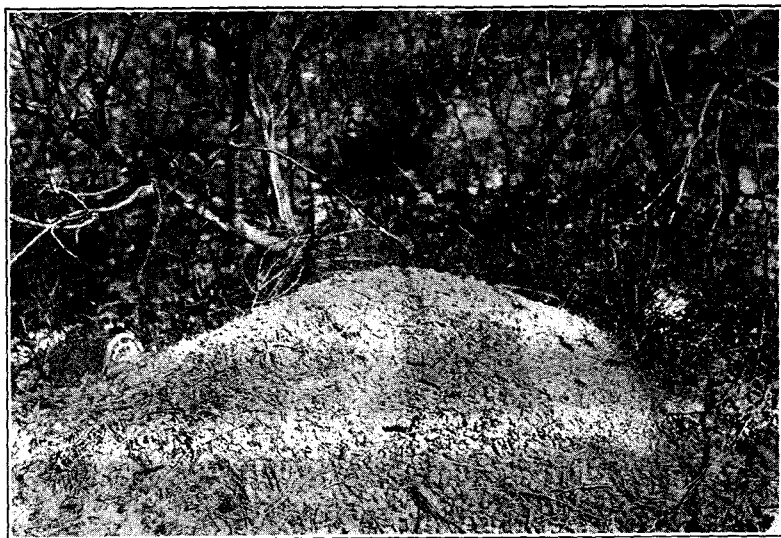
FIGURE 8

Two mound nests of *Myrmecia gulosa* Fabr. Southerland, New South Wales.

brood with fresh insects, but this detail in the be-havior of the queen is, in all probability, the same as in *M. regularis*.

Myrmecia forficata Fabricius

M. forficata, simillima and certain other large Myrmecias are so closely related and were so imper-fectly described by their authors that even after all the attention they have received at the hands of Roger, Mayr, Forel, Crawley and Clark their iden-tification is by no means easy. The typical *forficata* (Fig. 9) was described by Fabricius as early as 1787 from specimens taken in Tasmania by Sir Joseph Banks. According to Clark, it is the commonest Myrmecia in Southeastern Australia, that is in South Australia, Victoria and southern New South Wales. My observations indicate that it is really a mountain ant, most abundant above 3000 ft. The largest work-ers measure nearly an inch (20–22 mm.) and are red-dish brown, with a black gaster. The rather slender, externally concave mandibles are of the same color as the head or but slightly paler. The head and thorax are very feebly shining, the gaster very smooth and shining, with undeveloped pubescence. The sculp-ture is sharp and on the pronotum transverse and arcuate.

Forel described three varieties of *forficata*, namely *brevinoda*, a rather small form with broad postpetiole from New South Wales and Victoria, *rubra*, a form with more blood-red head, thorax and pedicel from Victoria, and *eudoxia*, a larger and paler red form

from Queensland and northern New South Wales. He regards *simillima* F. Smith, which differs in having the pronotal rugæ longitudinal and diverging behind, and a more pubescent gaster, as a subspecies of *forficata*, and has assigned to it a var. *violacea*, which he described from Healesville, Victoria.

After studying the considerable amount of material which I collected in 1914 and 1931 I believe that at least three different species are included in Forel's *forficata sens. lat. Brevinoda* and *rubra* seem to be valid varieties, but I am inclined, with Clark, to regard *simillima* as an independent species. *Eudoxia*, too, I believe to be specifically distinct, for reasons given below.

The var. *violacea*, which has the gaster metallic blue instead of black, presents a peculiar problem. The coloration is vivid in living and even in alcoholic specimens, but disappears when they are dried and mounted, so that it is impossible to determine whether cabinet specimens belong to this variety or to the typical *simillima*. Forel clearly states that his type specimens had the rugæ on the pronotum longitudinal and posteriorly diverging, and he therefore attached *violacea* to *simillima*. In 1931 I took numerous specimens of what I supposed to be this variety at Saw Pit Creek (4000 ft.) on Mt. Kosciusko, New South Wales, and in the mountains of Victoria (Sherwood Forest, Mt. Dandenong and Dee Creek, in the Warburton Range, not far from Healesville, the type locality of *violacea*), but all of them on examination proved to have the transverse and arcuate pronotal
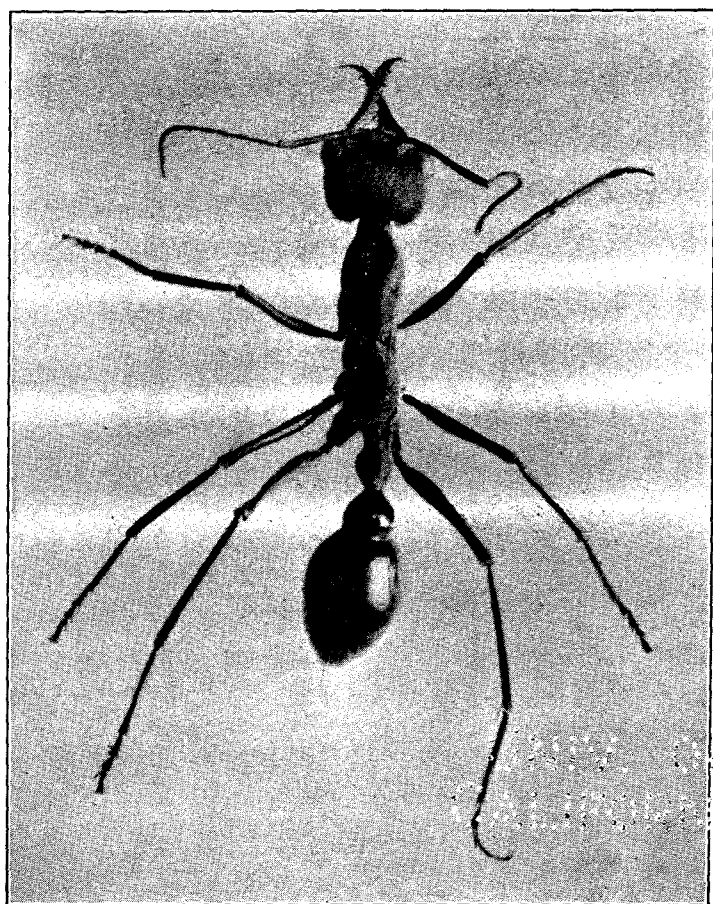
FIGURE 9

Myrmecia forficata Fabr., worker. Victoria. × 4.

sculpture of the typical *forficata*! We must conclude then that both *forficata* and *simillima* have varieties characterized only by blue reflections of the gaster. Since these varieties occur in the same ecological environment as the typical *forficata* and *simillima*, and since they are clearly recognizable only when living or preserved in alcohol, it is doubtful whether they deserve special names.

On Mt. Kosciusko *forficata* occurs at an altitude of 5500 ft., where even in early December, as at the time of our visit, the ground may be covered with snow. But colonies are rare and contain few workers at this elevation. At Saw Pit Creek (4000 ft.) they were much more numerous and more populous, but were not seen at the Creel, which is a thousand feet lower and where *simillima* was common. *Forficata* nests under large stones, under or in logs, or at times in mounds (Fig. 10.) That it establishes its colonies in precisely the same manner as *M. regularis* was shown by my finding on December 4 on the top of Mt. Dandenong, near Melbourne, a fine queen, with a number of eggs, occupying a large flat cell in the soil under a boulder. As soon as the boulder was rolled over, the insect promptly escaped through a gallery which led from the floor of the cell to an underground chamber like the one above described for *regularis*. Crawley (1922) records a deälated queen of *forficata* as having been taken by R. Kelly near Healesville, Victoria, under a log, and three queens as having been taken by Professor E. B. Poulton under a stone near Black Spur, Victoria, on August 15, 1914.

Myrmecia simillima F. Smith

This species resembles *forficata* in size and coloration, but the head and thorax are distinctly more opaque and, as previously remarked, the pronotal rugæ of the worker, except just behind the neck, are longitudinal and posteriorly diverging. The pubescence, especially on the gaster, is distinctly more abundant. The range of the species resembles that of *forficata*, but in mountainous regions it is most abundant at lower elevations. I have taken it in several localities in South Australia, Victoria and southern New South Wales; it often inhabits rather irregular mound nests one to two feet in diameter, in sunny, forested situations. It is common on Mt. Kosciusko at elevations between 3000 and 4000 feet, especially along the Threadbo River, near the Creel. In these localities it nests in populous and exceedingly ferocious colonies under large stones and Eucalyptus logs. On December 11, two colony-founding females were discovered at Saw Pit Creek under stones in isolated cells very much like those of *M. regularis* and *forficata*. In both cells there were subspherical eggs scattered on the earthen floor. Near the Creel, on December 15, a third female was found in a cell under a large stone with a compact cluster of young larvæ which were devouring a fresh saw-fly larva (*Perga* sp.). Since this larva feeds on the leaves of eucalypts, it could only have been secured by the queen on one of her foraging excursions.
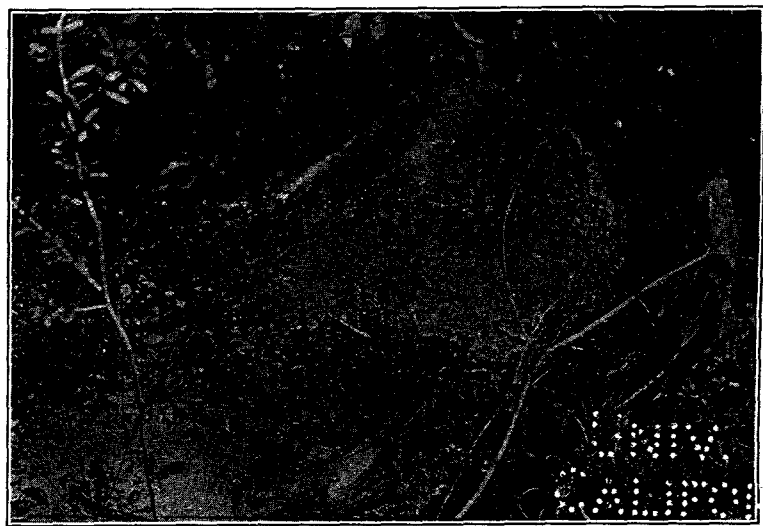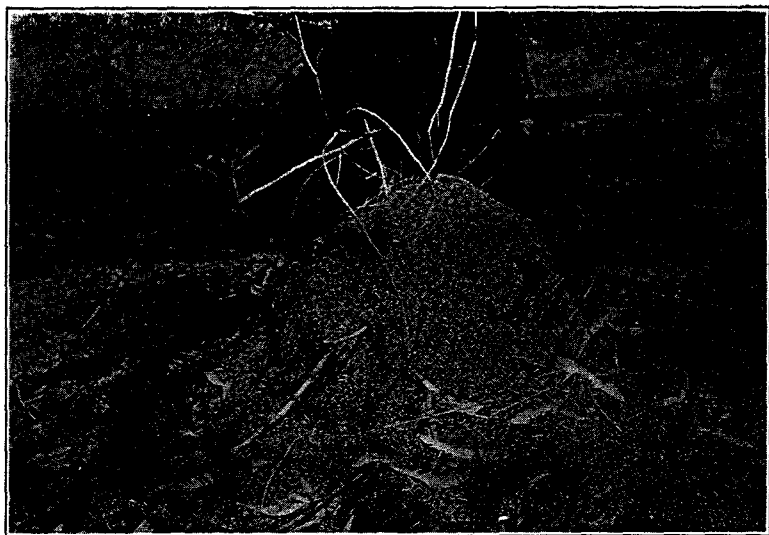
FIGURE 10

Two mound nests of *Myrmecia forficata* Fabr. Southerland, New South Wales.

Myrmecia eudoxia Forel

As previously stated, this form was described by Forel (1915) as a variety of *forficata*. It differs from both *forficata* and *simillima* in the greater, constant differences in size of the workers, which range from 12 to 25 mm. in each colony, the largest being decidedly larger than the largest workers of the two species mentioned. The head of the worker is distinctly broader than long, the pronotal rugosity like that of *simillima*, the color paler and brighter red than in this species or in the var. *rubra* of *forficata*. Though the gaster is black, it is not very shining, owing to its investment of white pubescence, which is even longer and more conspicuous than in *simillima*.

The types of *eudoxia* were taken by Mjöberg at Atherton, Queensland. I have specimens from the following localities, which indicate that the range of the species is Queensland and northern New South Wales:

Queensland: Toowoomba (W. R. Barnard); Mt. Tambourine (A. M. Lea); Roma District (F. H. Taylor).

New South Wales: Uralla, Gosford and Hornsby (Wheeler); Dorrigo (W. Heron); Jenolan Caves (J. C. Wiburd).

Eudoxia is rare as far south as the latitude of Sydney. I found only one colony at Gosford, and only a single worker at Hornsby, and though Wiburd found specimens at Jenolan Caves, I have never taken it on any of my numerous excursions in the Blue Mts. In

late November 1914, however, I found it to be the dominant and most formidable ant in the peppermint gum forests about Uralla, New South Wales. The nests (Fig. 11) were imposing structures, being distinctly conical mounds three to five feet in diameter at the base, covered with a layer of pebbles or bits of charred wood, and with a single, rather small, eccentric opening. Each mound contained about 100 to 150 ants, which varied greatly in size. The smallest workers stood on guard in a circle just within the mound entrance and were the first to sally forth when the colony was disturbed. They were soon followed by the large workers, which are quite as aggressive and belligerent as the workers of *M. gulosa*.

Myrmecia vindex F. Smith

The typical form of this species was originally described from Western Australia, but, according to Clark, is "wide-spread through Southern Australia." He records it from Sea Lake and Mallee, Victoria, and I have specimens from Kurrajong (W. W. Froggatt) and Sydney (A. M. Lea), New South Wales. In Western Australia I have taken it only in a few localities in the Darling Range, near Perth (Mundaring Weir, Rolleystone and National Park), but it was collected by the Hamburg Expedition at several other places (Guildford, Freemantle, Serpentine, Bridgetown and Torbay), and there are two females in my collection from Beverley (F. H. du Boulay). The workers and females are brownish red, with slightly paler legs, yellow mandibles and clypeus and black
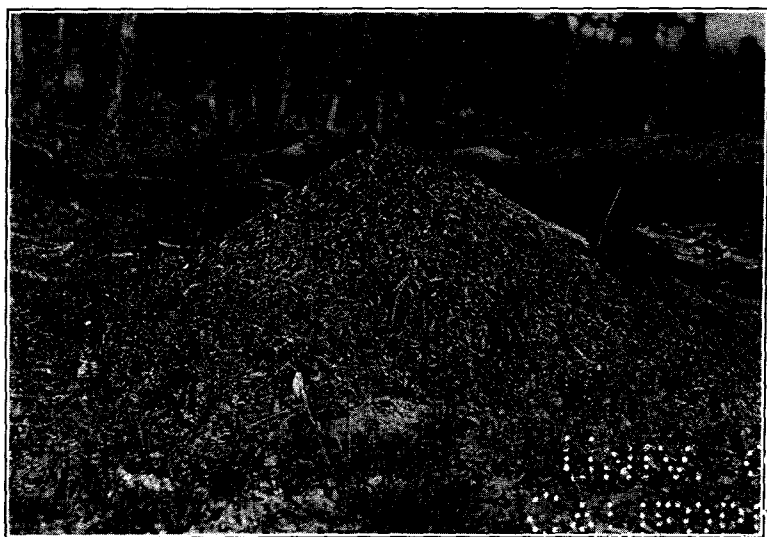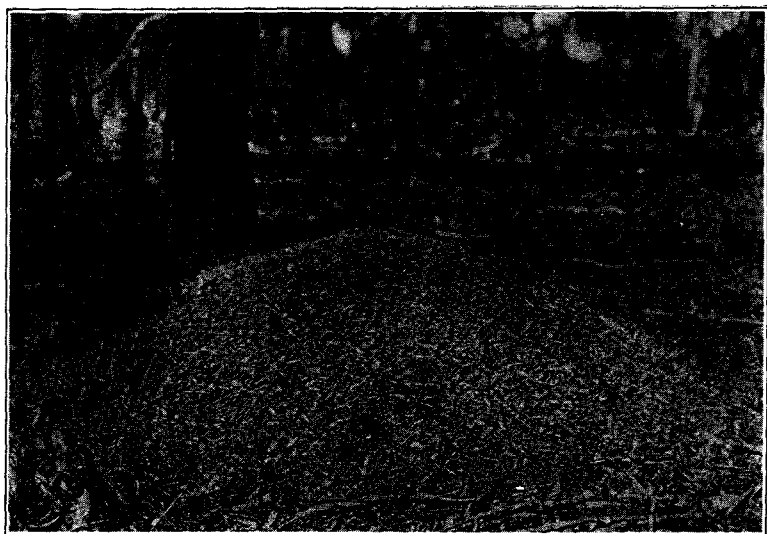
FIGURE 11

Two mound nests of *Myrmecia eudoxia* Forel. Near Uralla, New South Wales.

abdomen. The body is rather slender and the rugosity of the head, thorax and petiole rather fine but sharp, undulating on the head, transverse and arcuate on the pronotum.

M. vindex prefers dry, open woodlands, and makes clay or gravel mounds one to two feet in diameter, with a single large or several small openings. The colonies comprise only about 25 to 100 workers. When the nest is disturbed a few workers emerge and assume a threatening air, with wide-open mandibles, though they do not, as a rule, stray far from the mound, but soon withdraw into its interior. Rapping on the mound will again cause a sortie followed by withdrawal, and these tactics may be repeated again and again. This is a very different kind of behavior from that of such species as *M. regularis* and *gulosa.* Unusually large colonies of *vindex,* however, may be much bolder and more belligerent. According to Clark, "they drop off trees and plants on to the passer-by more readily than do most other species."

That *vindex* founds its colonies in the same manner as other Myrmecias is shown by my finding on September 7, 1931, a fine deälated female occupying a large cell under a flat stone in the National Park, Darling Range, Western Australia. The insect had deposited about a dozen large subspherical eggs on the earthen floor of the cell.

Forel's var. *basirufa,* originally described from Subiaco, a suburb of Perth, differs from the typical *vindex* in having the base of the first gastric segment red. This character is not as strongly marked in a

cotype in my possession as it is in four topotypes received from Mr. Clark. These show that the amount of red may vary greatly in workers from the same nest; in some it covers only the basal fifth, in others the basal half or three-fourths, of the segment. Moreover, the head may be either concolorous with the thorax, or distinctly darker and brownish, either anteriorly or throughout.

Myrmecia nigriceps Mayr

Mayr described this ant (Fig. 12) in 1862 as a distinct species, but more recently Forel (1907) and other myrmecologists have regarded it as a variety of *vindex*. I believe, however, that Mayr's interpretation is preferable, because it is clearly characterized and quite constant, though widely distributed as shown by the following list of localities which extend its known range to the whole Australian continent, except its central, extreme northern and northwestern portions.

Western Australia: Geraldton, Perth, Mundaring Weir, Kalagunda, National Park, Bridgetown, Margaret River (Wheeler); Wallcliffe (Schevill and Dixson); Warren River (W. D. Dodd); Augusta (W. S. Brooks); Murchison, Jarradale, Boyanup, Gooseberry Hill, Broome Hill and Albany (Hamburg Expedition); Kalgoorlie.

South Australia: Moorooloo, Flinders Range (W. J. Kimber); Pandappa (S. W. Pearse); Killalpaninna.

Victoria: Ferntree Gully (F. P. Spry, F. E. Wilson);

Cumberwell (C. F. Rawsay); Cheltenham (C. Barrett); Portland (H. W. Davey).

New South Wales: National Park, Epping, Heathcote and Bathurst (Wheeler); Como and Oatley (W. M. Mann); Murray Anabranch (J. G. Myers); Bourke and Sydney (A. M. Lea); Paramatta.

Queensland: Cunnamulla (H. Hardcastle).

The *M. nigriceps* worker differs from that of *vindex* in its greater average size, in having a black or dark brown head, distinctly darker and more brownish red thorax and pedicel, coarser and sharper rugosity and more abundant and more conspicuous white pubescence, especially on the gaster, which in most specimens is therefore far less shining than in *vindex*. The head of the larger workers is also broader and more rectangular behind. The nests and behavior, however, are very similar to those of *vindex*. Large colonies may rival *M. gulosa* in fierceness and pugnacity.

November 2, 1931, I found a very interesting incipient colony of *nigriceps* under a large log at Margaret River, Western Australia. It consisted of the mother, eight small workers, three worker cocoons and several larvæ of various sizes. The larvæ were feeding on small clusters of recently killed Camponotus workers, which had been cut in two at the petiole. Several entire males, apparently of the same species of Camponotus, were also present, but had not been attacked by the larvæ. Myrmecia workers seem to be quite ruthless in preying on other ants. On turning over another log covering a large colony of *M. regularis* I saw a worker seize and carry away a dea-

lated female Camponotus (Myrmophyma), which was founding a colony in a cell at the other end of the log.

Myrmecia desertorum Wheeler

I described this ant (Fig. 13) in 1915 as a variety of *vindex* from specimens taken by Captain L. A. White at Todmorden, South Australia, but I now agree with Clark in regarding it as a valid species. It was seen as long ago as 1896 by Kirby, who identified specimens taken by the Horn Expedition to Central Australia as *M. nigriceps*. Precisely the same identification was made by Forel (1910) of specimens from Tennant's Creek, Central Australia, as I find from examination of a portion of the series which he studied. The following list of localities shows that *desertorum* is confined to the arid portions of Australia where the annual rainfall is less than 20 or even less than 10 inches.

Western Australia: Geraldton and Yandil, near Wiluna (Wheeler); Beverley (F. H. de Boulay); Fortescue River, Hammersley Range (W. D. Dodd); Jigalong (J. Hickmer).

South Australia: Todmorden, type-locality (Captain L. A. White); Mallee, Renmark (J. G. Myers); Mt. Patawarta, Flinders Range (A. R. Riddle); Hargutt Spring (Blackburn); Opaline Spring, Musgrave Range (Winnecke); Lake Callabuna (A. Zietz); Yeelanna.

Central Australia: Reedy Hole, Bagot Creek, Alice Springs, Ayers Rock and Illamurta (Horn Expedition); Tennant's Creek (J. F. Field); Macdonnel Range (Captain L. A. White).
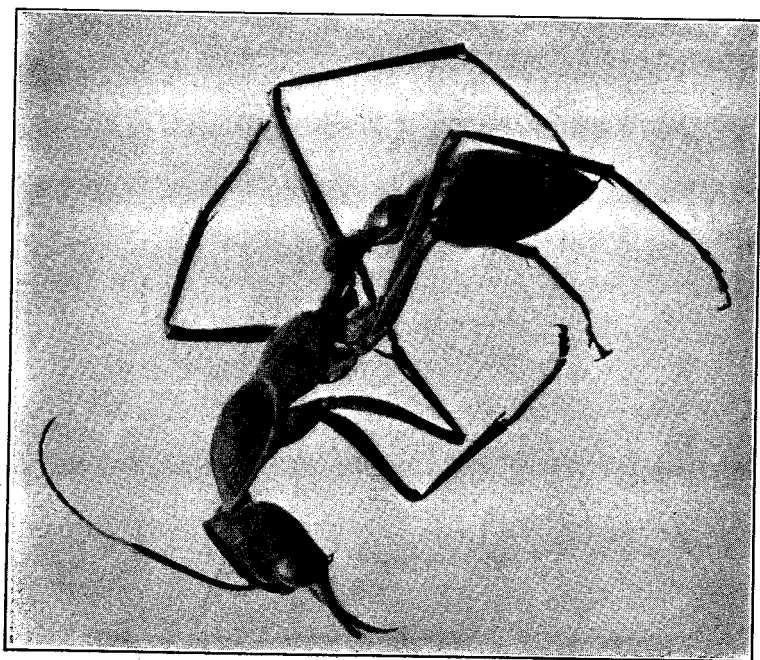
FIGURE 14

Workers of *Myrmecia tarsata* F. Smith   × 1¼

FIGURE 12

Myrmecia nigriceps Mayr, worker. New South Wales.   × 4.

Victoria and *New South Wales* (interior, according to Clark).

The worker and female of *M. desertorum* resemble those of *nigriceps* in size and in having a black or dark brown head, but the thorax, pedicel and appendages are of a decidedly paler, sordid yellowish brown color, the hairs on the body are longer and much more abundant, the rugosity of the head is more irregular and reticulate and that of the thorax and petiole coarser but less sharply defined. Clark describes the male as much like the male of *vindex*, but as having a black instead of a reddish first abdominal segment. He states that *desertorum* generally nests in the roots of trees in Central Australia, and adds that it is called "toon-jee" by the natives, who treat it with great respect. Field's label on my specimens from Tennant's Creek gives the native name as "injabadii."

In 1931 I found this ant only at Geraldton and at Yandil, about 30 miles from Wiluna. At Geraldton I saw only a single colony, but in parts of the much drier country about Yandil its nests were numerous. They were earthen mounds varying from one to three feet in diameter and from eight inches to more than a foot in height, with one or several large entrances, and were usually situated at the bases of the large white-trunked York gums growing along the edges of water holes. The behavior of the ants when disturbed was much like that of *nigriceps*, but the colonies were much more populous (some of them must have comprised fully 200 workers) and even more aggressive. Dr. P. J. Darlington, who was with me at

Yandil, secured an isolated colony-founding female that was occupying a cell in a Eucalyptus log.

Myrmecia analis Mayr

This species has been recorded by few of the writers on Australian ants. Mayr described it as long ago as 1862, but cited merely "New Holland" as the type-locality, so that its distribution has been very doubtful. Crawley, in 1925, redescribed it from Albany, W. A., as *M. atriscapa*. I found it to be rather common at Margaret River and Pemberton, and have specimens from Warren River (W. D. Dodd), in the same region. Mr. Clark, who has given me some specimens from Portland, Victoria (H. W. Davey), cites it as ranging from Bunbury, W. A., to Brisbane, Queensland. All the material examined is very constant in structure, sculpture, pilosity and coloration. The head, thorax and petiole of the worker and female are bright red, the postpetiole, legs, antennæ and mandibles more reddish yellow, the basal half or two-thirds of the scapes black or dark brown, the gaster black, with the two terminal segments and the posterior borders of the second and third yellow and covered with conspicuous, appressed, golden yellow pubescence. The hairs on the body and legs are whitish, short and not very abundant. The head, thorax and petiole are subopaque and rather finely and undulately rugose, the rugæ on the anterior portion of the pronotum, mesonotum, epinotum and petiole transverse, on the posterior portion of the pronotum longitudinal and posteriorly strongly diverg-
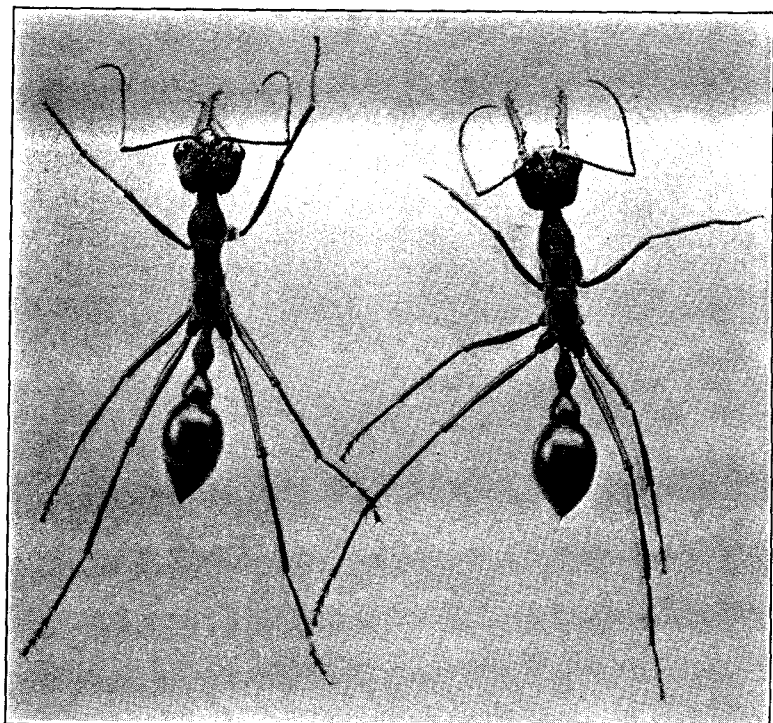
FIGURE 13

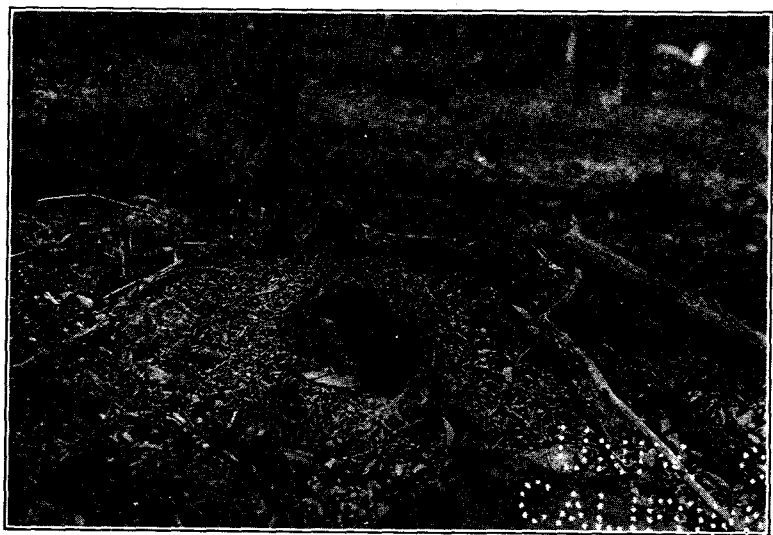*Myrmecia desertorum* Wheeler, workers. Western Australia. × 2.

FIGURE 15

Mound nest of *Myrmecia tarsata* F. Smith. Northern New South Wales.

ing. The postpetiole and gaster are very smooth and shining, the mandibles slender, with four large and nine or ten small teeth on their inner borders. Their surfaces are shining, rather minutely punctate-striate, with a row of large, spaced punctures along their inner borders. At first sight *M. analis* seems to be a hybrid between *M. vindex* and *regularis*, but its black antennal scapes and the absence of the typical *vindex* in the regions where it occurs show that it is a distinct species.

M. analis makes small mound nests 8 to 12 inches in diameter, usually with only a single large entrance at the top, but occasionally with two or even three smaller entrances instead. The workers, of which there are rarely more than 30 to 50 in a colony, behave very much like those of *vindex* and *nigriceps*. They sally forth in small numbers when disturbed, but do not pursue the intruder, and if no longer interfered with, promptly return into the nest. Clark has encountered much larger and much more aggressive colonies of this ant. He says: "I have frequently found this species nesting in decayed logs and grass-trees (Xanthorrhoea). The colonies usually contain about 200 individuals. They are pugnacious and will generally follow an intruder for some distance. They readily drop from trees on to a person passing close by."

Three of my observations prove that the colonies of *analis* are founded in the same manner as those of *regularis*. At Pemberton I found two queens, each immured in a large earthen cell. One was under a log

and possessed no eggs, the other was under a stone. The cell of this queen was very interesting, because it had a distinct opening, about one-third of an inch in diameter, to the outside! This insect had no eggs. A third queen found at Margaret River had an incipient colony comprising four diminutive workers and a few nearly mature larvæ.

Myrmecia tricolor Mayr

The worker of this species is nearly as large (11–23 mm.) as that of *forficata* and *simillima*, but has shorter, broader, reddish yellow mandibles, with straight external borders and only four large teeth on the internal borders. The sculpture is coarse, on the head and pronotum longitudinally rugose and posteriorly diverging. The typical form of the species is black, with brownish red antennæ and tarsi and the petiole, postpetiole, and in some specimens also the epinotal declivity, rather vivid red. Two varieties have been described, *nigriventris* Mayr, with the head, thorax and pedicel reddish brown, and *rogeri* Emery, with these parts black like the gaster. There are intermediates connecting the varieties with each other and with the typical form, and there is also considerable color-variation among workers of the same nest.

I have taken *tricolor* and its varieties only in New South Wales, although it has been cited as occurring also in South Australia, Victoria and Queensland. All three forms are not uncommon in the neighborhood of Sydney and in the Blue Mts. They nest in

colonies of about 50–100 individuals under large
stones or logs or in low mound nests, and are much
less aggressive than *forficata, gulosa* and *eudoxia*.
That the female of *tricolor* founds her colony in the
same manner as that of *regularis, analis* and *forficata*
is proved by the observation previously recorded
(p. 20).

Myrmecia tarsata F. Smith

During November and December 1914 I observed
several colonies of the typical form of this superb ant
(Fig. 14) at Hornsby and Uralla, New South Wales.
Clark mentions it as rare in Victoria. I have speci-
mens from Mallacoola, South Australia (Hosking).
Frederick Smith, Froggatt, Crawley and, more re-
cently, Clark describe the worker as black or dark
brown, but the color of all the specimens I have seen
was very different, being a magnificent cyan blue,
with the tip of the gaster orange, the mandibles yel-
low, the antennæ and tarsi pale ferruginous and the
tibiæ brown. The blue tint, however, is pronounced
only in the living insect. It disappears almost com-
pletely in alcoholic or dried specimens, like the very
similar color of some other Ponerinæ, e. g. certain
Bornean species of Trapeziopelta. The colonies
which I observed were nesting in rather large mounds
of the usual construction (Fig. 15) and were not very
aggressive. Froggatt had previously noticed the
timidity of this Myrmecia, since he remarks that "if
one or two are captured the other ants retreat into the
nest and do not show fight."

Forel has recognized two subspecies of *tarsata* from Queensland, namely *malandensis* and *rowlandi*. The former differs from the type in its smaller size (13.5 mm.), in having the tip of the gaster brownish and more pubescent, the mesoëpinotal impression shallower and longer, the petiolar peduncle longer, the node shorter and the antennal scapes longer. The subspecies *rowlandi* is only slightly smaller than the type (17–19 mm.), but more hairy and pubescent, with shorter scapes and the petiolar node irregularly and transversely, instead of longitudinally and concentrically, rugose. Both subspecies lack the blue color of the typical *tarsata*. I possess also specimens representing a few undescribed forms of this species.

Myrmecia auriventris Mayr

This beautiful species, originally described from Mackay, Queensland, is dull black, with the mandibles, antennæ, mesoëpinotum and petiole ferruginous red and the gaster covered with long, appressed, pale golden yellow pubescence. I found its nests occasionally in the forested region (1200 to 1300 ft.) in the neighborhood of Kuranda and Koah, in Queensland. The nests are compact earthen mounds less than a foot in diameter, with eccentric entrance and therefore somewhat oven-shaped. Not more than a dozen workers were found in a colony, and they were very timid compared with many species of the genus. When disturbed they usually retreated into the entrance and remained concealed. They

were sometimes found foraging on the trunks and branches of eucalypts.

Myrmecia forceps Roger

This species (Fig. 16), originally described from an unknown Australian locality, resembles *M. eudoxia* at first sight, but is very easily distinguished by its extraordinary mandibles, which are outwardly bowed, so that their external borders are convex, with long points and on their inner borders with only three, widely spaced teeth and several interspersed denticles. The head, thorax and petiole are rather bright red, the antennæ and legs somewhat paler and more yellowish red, the mandibles yellow with brown teeth, the gaster black tinged with red along the posterior borders of the segments and at the tip. The sculpture is not very pronounced, the head being finely and reticulately rugulose, the thorax transversely and on the pronotum arcuately rugose, the petiolar node reticulately rugulose. The surface of these parts is somewhat more shining than in *eudoxia*, the postpetiole and gaster very smooth and shining, with white pubescence mainly on the sides and posterior borders of the segments.

M. forceps seems to be a rare species. Clark does not record it from Victoria, and I found it only once, on December 7, 1914, at Heathcote, near Sydney. The nest, an ordinary mound, about a foot in diameter, was inhabited by less than 40 workers.

Myrmecia nigrocincta F. Smith

M. nigrocincta (Fig. 17) is one of the most beauti-
ful and most easily identified of all the species of
Myrmecia because of its striking and variegated
coloration. Though both worker and female are of
about the same size as the corresponding castes of
pilosula (worker 12–14, queen 16–17 mm.), they are
much more slender and graceful and have much
longer legs and antennæ. They are black, with brown-
ish yellow mandibles, tarsi and fore tibiæ; the coxæ,
femora, middle and hind tibiæ are brown; the an-
tennæ, pronotum, epinotum, petiole, two spots at the
base of the postpetiole, and in some specimens a small
elliptical spot on the mesosternum, are yellowish red.
The gaster is covered with rather long, dense, ap-
pressed golden pubescence, which converges in the
middorsal line at the posterior borders of the separate
segments.

In his original description of *nigrocincta* (1858),
Frederick Smith cited merely "Australia" as the
type-locality. The actual range of the species is indi-
cated in the following list of localities, from most of
which I have seen specimens:

Queensland: Peak Downs (Museum Godeffroy);
Kuranda and Brisbane (Wheeler); Brisbane (F. H.
Taylor); Gayndah, Bundaberg and Mt. Tambourine
(A. M. Lea); Mackay (G. Turner); Blackal Range,
Mt. Tambourine and Atherton (E. Mjöberg).

New South Wales: Sydney (Museum Godeffroy);
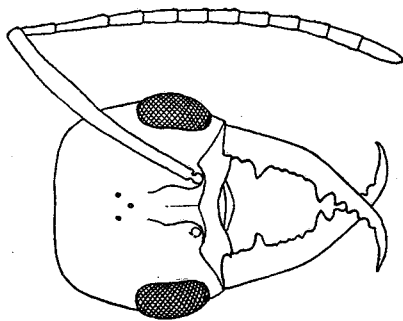Wallsend and Nurabeen (W. W. Froggatt); Souther-

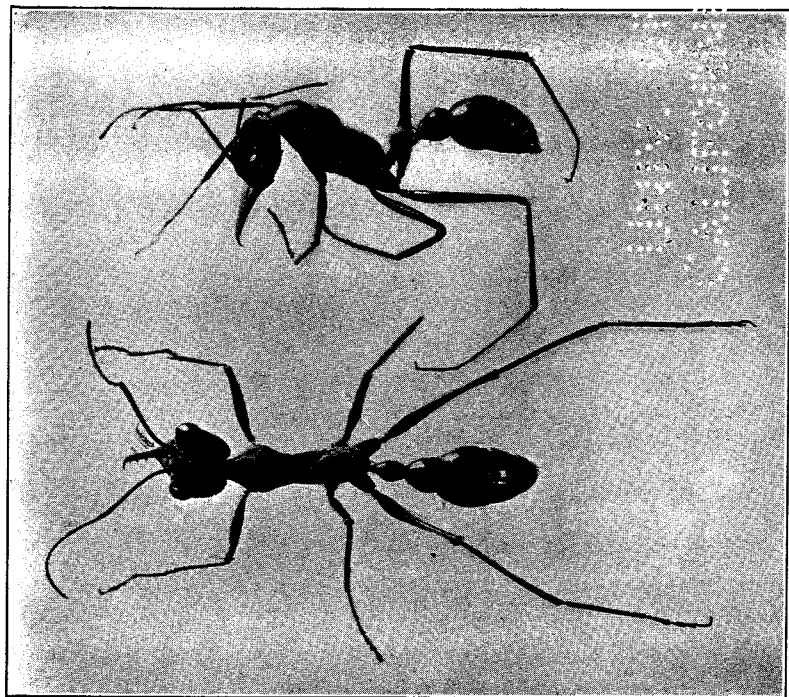FIGURE 17

Myrmecia nigrocincta F. Smith, workers, dorsal and lateral view. New South Wales. × 4.

FIGURE 16

Myrmecia forceps Roger. Head of worker, dorsal view.

land, Hornsby and Epping (Wheeler); Dorrigo (W. Heron).

Smith's types probably came from Sydney, but I believe that the species is really more common in Queensland and northern New South Wales. It prefers rocky ridges or in southern New South Wales the sandstone walls of canyons, where it constructs among the stones low mound nests about a foot in diameter, with a central opening. Sometimes the nest is partially or even entirely concealed beneath a stone and one may fail to notice it till suddenly apprised of its proximity by a very painful sting administered by some vigilant worker. A single colony contains about 40 to 50 workers, which when disturbed sally forth with short graceful leaps like *mediorubra*, but are much more pugnacious and will often pursue the intruder to a distance of a yard or more from the nest. The fully developed wings of a queen in my collection from Dorrigo, New South Wales, measure only 9 mm., and are therefore so short as to suggest that flight may be almost or quite impossible. A single deälated specimen which I found running over the ground at Southerland, New South Wales, on November 21, 1914, may give a clue to the time of mating, unless she happened to be a foraging nest-founding queen.

Myrmecia (Promyrmecia) aberrans Forel and froggatti Forel

These ants, which are exceptional among the species of Myrmecia in possessing short, broad mandibles, together constitute the subgenus Promvrmecia

as defined by Emery in 1911. Both are very rare, and nothing has been published on their habits. Clark says of *aberrans* that "so far only odd specimens have been obtained." No female of either species has ever been taken. During November and December 1914 I found in New South Wales the nests of three forms which have since been standing in my collection with a query on their labels, because they differ too much from Forel's original descriptions to be assigned to either of his species. Mr. Clark, while I was visiting him in Melbourne in 1931, generously presented me with a topotype of *froggatti* and two workers and a male of *aberrans*. I also possess some odd specimens of other forms received from Australian collectors. A study of all this material convinces me that there is really only one valid species, *aberrans*, and that the others are merely so many races, or subspecies, since they exhibit a considerable range of intergrading differences in color, sculpture and the proportions of the head and petiole, which are the characters on which Forel based his two species. The various forms are distributed over a considerable area, from South Australia and Victoria to New South Wales and Queensland. They are not mere nest-varieties, since all the workers of a colony are very similar. Before recording my field notes, it will be advisable to introduce brief taxonomic descriptions of the distinguishable forms (workers).

M. aberrans Forel (typical, Fig. 18). Length 10–13 mm. Mandibles brownish yellow, with darker brown teeth and tips; head, mesosterna, lower portions of metasterna, postpetiole,

gaster, femora, tibiæ and basitarsi black; trochanters and terminal tarsal joints brown; antennæ, pronotum, petiole and dorsum of epinotum red. Head not broader in front than behind; petiolar node rounded-subcuboidal, as broad as long, slightly narrower in front than behind; postpetiole about one and two-thirds broader than long. Shining; mandibles coarsely striate; head and pronotum longitudinally rugose, the rugæ on the former somewhat diverging and fading out on the occiput and posterior corners which are smooth and shining. Mesonotum smooth and shining, or in some specimens sparsely and feebly punctate, with fine longitudinal striæ on the sides. Epinotum and petiole less shining, the former rather coarsely and transversely, the latter more finely, irregularly and sometimes rather concentrically, rugose. Postpetiole, gaster and legs moderately shining, the former very finely punctate; the latter more punctate-striolate or shagreened. Pilosity yellowish, short, erect, most abundant on the epinotum and petiolar node, longer on the mandibles and tip of gaster, delicate and oblique on the legs. Gaster and postpetiole also with an investment of short, delicate, pale pubescence.

The type locality is Gawlertown, South Australia. My description is drawn from a worker from Baldumole, South Australia (A. Zietz), one from Coburg, Victoria (C. Oke), and two from Altona, Victoria (J. Clark).

Subsp. *maura* subsp. nov. Length 11–14 mm. Black; mandibles, antennæ and terminal tarsal joints reddish yellow. Mandibular teeth, clypeus, femora, tibiæ and basitarsi brown, trochanters more reddish. Petiolar node as broad as long, semicircularly rounded in front; postpetiole only one and one-half times as broad as long. More shining than the typical *aberrans*; sculpture more pronounced, the cephalic rugæ fewer and sharper. Mesonotum sharply longitudinally rugose; petiole rugose-punctate, as coarsely sculptured as the epinotum. Postpetiole, gaster and legs more shining and more minutely punctate than in the typical form. Pilosity noticeably less abundant, especially on the dorsal surface of the body, and the pubescence on the postpetiole and gaster more dilute.

Described from fifteen specimens from Bathurst, New South Wales (Wheeler).

Subsp. *hæmatosticta* subsp. nov. Length 10–13 mm. Colored like *maura*, but with a large spot behind each eye, one on the disk

of the pronotum and the upper surface of the petiolar node, except for a median longitudinal black streak, blood-red. Femora black; mandibles and antennæ distinctly darker than in *maura* and more reddish. Mesonotal rugæ less pronounced and in two specimens oblique, or asymmetrical. Petiole smoother, varying from coarsely punctate, without distinct rugæ, to loosely rugose-punctate. Postpetiole fully one and two-thirds times as broad as long.

Described from three specimens taken at Uralla, New South Wales (Wheeler).

Subsp. *formosa* subsp. nov. (Fig. 19). Length 10–13 mm. Head, thorax and petiole blood red, with the following black markings: a large chevron, extending across the front between the inner orbits, with its point extending backward and covering the ocellar triangle, but leaving the clypeus and the space between the frontal carinæ red, posterior portion of gula, neck, pleuræ, posterior borders of pronotum and epinotum, peduncle of petiole and in some specimens a median spot on the mesonotum. Mandibles and antennæ reddish yellow; gaster and legs black, sting and four apical joints of tarsi reddish brown. Posterior corners and sides of head very smooth and shining, sparsely and coarsely punctate. Mesonotum coarsely punctate, longitudinally or obliquely, in some specimens more feebly or more concentrically, rugose. Epinotum and petiole sculptured as in the typical *aberrans*. Postpetiole and gaster very smooth and shining, with fine grayish pubescence only on the sides and posterior borders of the segments. Legs less shining and very finely pubescent.

Described from thirteen specimens taken at Uralla, New South Wales (Wheeler).

Subsp. *froggatti* Forel. Length 11–13 mm. Head, thorax, petiole, coxæ and legs duller and somewhat more brownish red than in the preceding subspecies; a black spot on the ocellar triangle; femora somewhat infuscated in the middle; postpetiole and gaster black; mandibles and antennæ sordid yellow. Mesonotum strongly, transversely and arcuately rugose; petiole coarsely reticulate-rugose, more narrowed anteriorly than in the preceding subspecies. Postpetiole only one and one-half times as broad as long and like the abdomen less shining.

Redescribed from a cotype from Manilla, New South Wales (W. W. Froggatt), received from Mr. John Clark.
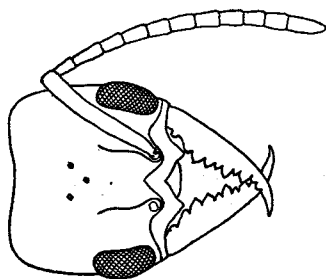
FIGURE 19

Myrmecia (Promyrmecia) aberrans Forel subsp. *formosa* subsp. nov.
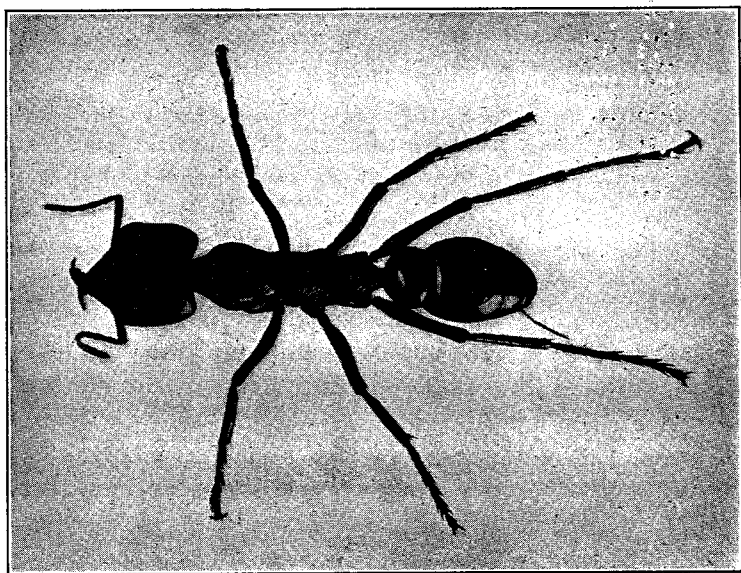Worker. New South Wales. × 5.

FIGURE 18

Myrmecia (Promyrmecia) aberrans Forel.
Head of worker, dorsal view.

Subsp. *taylori* subsp. nov. Length 15 mm. Larger than *froggatti* but similarly colored; body somewhat more opaque; the rugæ strong on the head and thorax but less sharp than in the preceding forms, arcuate and transverse on the mesonotum, reticulate on the epinotum and petiole. Node of the latter more sharply cuboidal than in *froggatti*, postpetiole nearly twice as broad as long, like the gaster subopaque and finely punctate, with longer and denser, yellowish pubescence. Pilosity on the body longer and more abundant than in the preceding forms.

Described from a single specimen taken by Mr. Frank H. Taylor in the Roma District, Queensland.

Subsp. *sericata* subsp. nov. Length 14 mm. Like *taylori* in coloration. Sculpture less pronounced, the rugæ on the head and pronotum coarse but rounded and interspersed with large, elongate punctures. Mesonotum coarsely punctate, with only indistinct traces of fine transverse rugules. Epinotum anteriorly indistinctly rugose, petiole more coarsely and distinctly, the node of the latter broader than long, the postpetiole nearly as broad as in *taylori*, and the pilosity, which is whitish, as long and abundant. Appressed pubescence on the gaster and postpetiole golden yellow, decidedly longer and converging from each side to the middle line at the posterior border of each segment.

Described from a single specimen taken by Mr. W. W. Froggatt at Wagga, New South Wales. Another specimen, perhaps to be regarded as representing a distinct variety of *sericata*, from Meningie, South Australia (L. H. Minchin), measures only 12 mm. and has the mesonotum coarsely, transversely and arcuately rugose with large interspersed punctures and the petiolar node longer and more coarsely rugose.

The nests of three of the above described subspecies, *formosa*, *hæmatosticta* and *maura* are practically identical. Those of the first and second subspecies were found November 26 and 27 near Uralla in open sheep pastures on volcanic soil at an altitude of about 3000 ft. only by patiently following the rare, single workers which were returning home with insect prey. No mound marks the site of the nest, which is a

mere hole (Fig. 20) a quarter of an inch in diameter, leading into a perpendicular gallery terminating at a depth of somewhat more than a foot in a small chamber. Usually only three or four workers and no female were found with a small number of cocoons in this chamber. Even including foraging workers a colony can scarcely comprise more than a dozen individuals. They were by no means aggressive. While foraging they crawled about rather slowly and were never seen to climb the vegetation nor to jump like other small species of Myrmecia.

The black subsp. *maura* was found December 16 and 17 at Bathurst, New South Wales (2300 ft.), which is on a disintegrated granite soil. The ants, encountered in dry, open pastures and on the cricket field of the experimental farm, were followed to their nests, which were precisely like those of *formosa* and *hæmatosticta* at Uralla. Only a few workers without a differentiated female could be extracted from each nest, and foraging workers were by no means frequently seen.

These meager notes indicate, perhaps, that the subgenus Promyrmecia should be retained as defined by Emery, since *aberrans* differs not only morphologically but also ethologically from all the other smaller Myrmecias which Clark has included in the group.

The absence of any winged or deälated females of the usual type either among the specimens of *aberrans* and its subspecies hitherto collected or in any of the nests which I excavated, raises the question as to the existence of such forms. That these ants may re-

semble the species with highly ergatomorphic females described below (p. 79) is suggested by an abnormal specimen of the subspecies *sericata* from Wagga, New South Wales (W. W. Froggatt), found in my collection by one of my students, Mr. G. S. Tulloch, and described in a recent number of *Psyche* (1932). This specimen he calls a 'gynergate,' because the right half of its body is female, the left worker. Of the former he says: "The structure of the right (female) side indicates that this specimen once bore two vestigial wings. The anterior one has been broken off but the hind one is still retained in the specimen. The structures which accompany wings are present, but reduced. The parascutal ridge and the transcutal suture are present in their usual positions. The plate covering the metathoracic spiracle may be noted as well as the upper plate of the metapleuron. The left side of the thorax is distinctly that of a worker." The wing vestiges figured by Tulloch are extremely minute and easily overlooked. If the right half of this specimen is that of the normal *aberrans* female, we should have to regard its wing development as very degenerate. In other respects *aberrans* reveals itself as the most primitive of all the Myrmecias and therefore of all existing ants, a veritable living fossil, which, judging by its rarity, may be far advanced on the road to extinction. I know of no other ant in which, the colony is reduced to so few individuals. Its careful study in artificial nests might throw some light on the phylogeny of the whole family Formicidæ.

Myrmecia (Promyrmecia) pilosula F. Smith

I have not taken this jumping Myrmecia in Western Australia, nor have I seen any record of its occurrence in that state. Forel has, indeed, described a subspecies *mediorubra* from Albany (King George's Sound), but this is really a distinct species, as shown by its habits which are described below. The range of *M. pilosula* is indicated by the following localities of specimens in my collection:

South Australia: Lucindale (A. M. Lea); Mt. Lofty (J. G. O. Tepper, Lee, Wheeler); Adelaide and Kangaroo Island (Tepper).

Tasmania: Hobart (Lea); Launceston (F. M. Littler). Forel cites several other Tasmanian records.

Victoria: Mt. Dandenong, Sherwood Forest and Dee Creek, 3000–4000 ft., in the Warburton Range (Wheeler); Sea Lake (J. C. Goudie); Mt. Donna Buang (P. J. Darlington).

New South Wales: Jenolan Caves (J. C. Wiburd); Leura (W. M. Mann); Wentworth Falls and Katoomba (Wheeler); Blundell's Creek, near Canberra, F. C. T. and Mt. Kosciusko, 3000–6000 ft. (Wheeler); Dorrigo (W. Heron); Uralla (Wheeler).

Mayr records this ant also from Cape York, Queensland, but I did not find it in that state in 1914.

The worker *pilosula* measures 8–13 mm. in length, the female 12–16 mm. Both are dull black, but when alive and exposed to bright sunlight, with a distinct bluish tinge, probably due to a fugitive pigment like
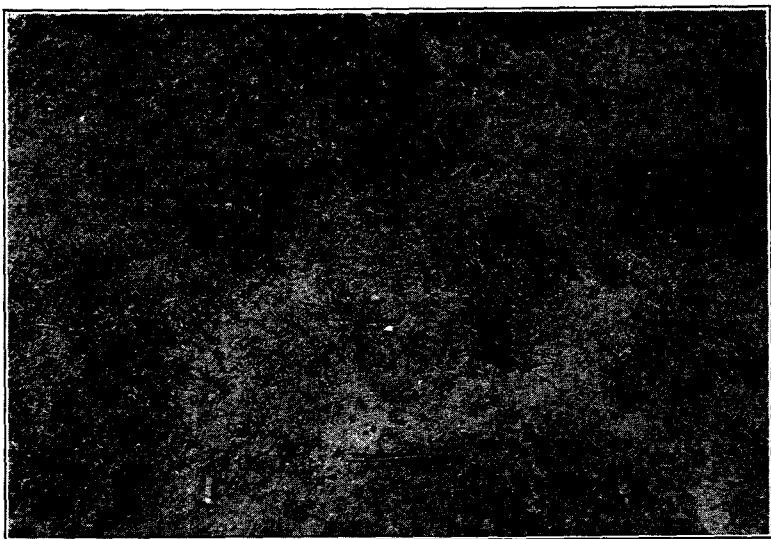
FIGURE 20

Nest entrance (just above tweezers) of *Myrmecia (Promyrmecia) aberrans* Forel subsp. *formosa* Wheeler in sheep-pasture at Uralla, New South Wales.

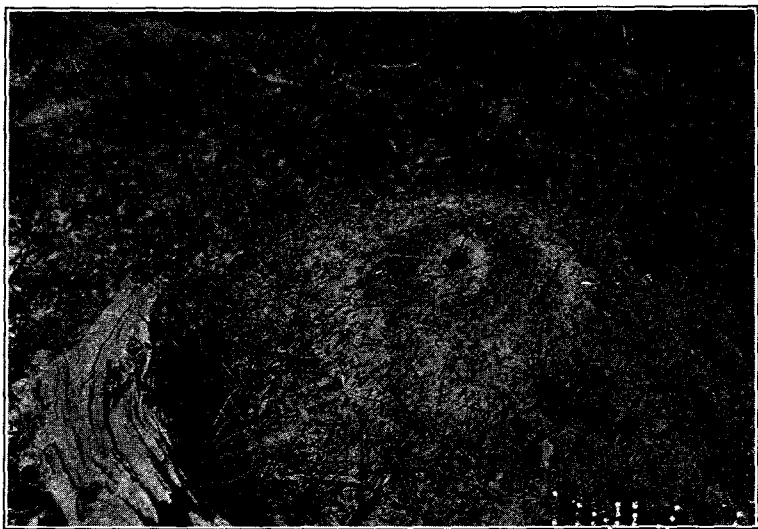FIGURE 21

Nest crater of *Myrmecia (Promyrmecia) pilosula* F. Smith. New South Wales.

that of *M. tarsata.* The mandibles, antennæ, knees
and fore tibiæ are reddish yellow, the middle and hind
tibiæ brown or even yellowish in the worker, the post-
petiole and gaster covered with rather abundant
grayish or rusty pubescence, not very shining. This
ant seems to be most common at elevations above
2000 ft. I found it to be very abundant on Mt.
Kosciusko, the dominant species in fact, at eleva-
tions from 4000 to 6000 ft., where it was everywhere
foraging on the trunks and foliage of the snow-gums
(*Eucalyptus coriacea*). At these higher levels it
usually nests under large stones, but at lower levels it
most frequently occupies flat craters or mounds (Fig.
21), varying from about a foot to three feet in di-
ameter, with central entrance and often covered with
particles of charred wood or rabbit droppings. The
workers are by no means aggressive, though their
sting is almost as severe as that of the larger species of
Myrmecia, nor do they follow the intruder any dis-
tance from their nest. Unless startled, they will walk
over one's skin without attempting to bite or sting.
When the nest is disturbed, *pilosula* sallies out in
short leaps from one to two inches in length, though
it can cover greater distances when leaping from a
height. A colony usually contains about 50 to 150
individuals. The species is peculiar in being pleome-
trotic, the nests sometimes containing as many as
four deälated mother queens. The eggs are rather
large, subspherical as in other Myrmecias, and scat-
tered on the floor of the nest chambers; the larvæ are
fed on pieces of various insects. On several occasions

I have found single colony-forming females or incip-
ient colonies comprising a queen and a few small
workers. The pleometrotic condition probably arises
from the permanent association of several queens in
the same earthen cell. Mr. John Clark called my at-
tention to the fact that colonies of a minute thief-ant,
Solenopsis froggatti Forel, are frequently associated
with *pilosula*. I found this to be the case in several
instances on Mt. Lofty, near Adelaide, and in the
Sherwood Forest, near Melbourne.

Myrmecia (Promyrmecia) mediorubra Forel

This exquisite ant, which is confined to Western
Australia, is somewhat larger than *pilosula*, with the
thorax and petiole bright red, and the remainder of
the body black, except the mandibles which are yel-
low, with brown teeth and tips. The sculpture and
pilosity are like those of *pilosula*, but the petiole and
postpetiole are broader. I saw only two colonies, one
at Bridgetown, the other at Mundaring Weir, in the
Darling Range. In both cases the ants were nesting in
hard clay near a railroad track, and the nest was dis-
covered only after carefully following foraging work-
ers carrying spiders and insects. It was a mere hole
about half an inch in diameter, without any traces of
a crater or mound. *Mediorubra* is a very agile jumper,
able to make leaps of two to four inches in rapid suc-
cession. When pursued on the surface of the soil, it
leaps straight ahead, but when closely pressed with
the tweezers it jumps in short frenzied zigzags in all
directions and when cornered seizes the tweezers and

attempts to sting them. Dr. P. J. Darlington discovered a single colony-founding queen under a log at Margaret River, but I failed to find any other specimens of the species in that locality.

The *mediorubra* worker may be readily mistaken for that of another West Australian form, *M. chasei* Forel, but the mandibles of the latter are darker and the petiole and postpetiole are even broader. The females of the two forms are surprisingly different, that of *mediorufa* being only 13–14 mm. long, whereas the female of *chasei*, of which Mr. John Clark generously gave me one of the very few known specimens, measures fully 22 mm. and is therefore much larger compared with its worker (13 mm.) than any other Myrmecia female. The female *chasei* is also much stouter than the female *mediorubra*, has a broader head, petiole and postpetiole and a very different sculpture.

I did not succeed in finding colonies of *chasei*. The nest is probably quite unlike that of *mediorubra*, since Crawley (1922) states that his variety *ludlowi* of the former species, from Ludlow, Western Australia, "builds a cone-shaped earth-mound about a foot in height, with an entrance on the top about two inches in diameter, but there are also other entrances in the ground beyond the mound. It is an active and fierce insect."

Myrmecia (Promyrmecia) michaelseni Forel

The worker (Fig. 22a) of this beautiful ant measures 11–13 mm. and resembles *pilosula*, but is jet-

black and more shining, with white pilosity, stouter, black mandibles and a dense pelisse of orange red pubescence on the dorsal surfaces of the gastric segments. In shape and dentition the mandibles resemble those of *pilosula* and the larger species of Myrmecia *sens. str.* The queen measures about 14.5 mm. and is therefore only slightly larger than the worker. The typical *michaelseni* is a rather rare ant and seems to be confined to Southwestern Australia. Forel's original description (1907) is based on specimens taken by the Hamburg Expedition at Albany. I possess a couple of cotypes and a series of workers collected more recently by W. S. Brooks at Augusta. In 1931 I found it only in two of the localities which I visited, namely Margaret River and Bridgetown. Crawley has described a var. *perthensis* from Perth, Forel a subsp. *queenslandica* from Queensland and Viehmeyer a subsp. *overbecki* from New South Wales. Mr. Clark informs me that he regards *perthensis* as a synonym of the typical *michaelseni* and *overbecki* as a synonym of *queenslandica*. This form, of which I have taken specimens at Darra, Queensland, has a narrower head, more irregularly rugose sculpture of the head, thorax and petiole, deep red mandibles and legs and a more grayish yellow pelisse on the gaster. Mr. Clark has given me specimens of a subsp. *rugosa* Clark (MS) from Ludlow, Western Australia, which has a very broad, rugose postpetiole and the pelisse on the gaster gray, with a golden yellow center on the first segment.

The colonies of the typical *michaelseni* which I

found at Margaret River and Bridgetown consisted of only 15–20 workers and a single female. They were nesting in rather moist soil under logs or more rarely under stones. All the colonies had eggs and larvæ, the former, as in other Myrmecias, rather large, sub-spherical and scattered loosely on the floor of the superficial nest chamber. When disturbed the workers escaped quickly into the surrounding vegetation and, unless seized, made no attempt to attack. They were not seen to jump.

Myrmecia (Promyrmecia) clarki Crawley

The worker (Fig. 23) of this species resembles that of *M. pilosula* in color and sculpture and averages about the same length (12–13.5 mm.), but its mandibles are very different, being very slender, long and straight, curved only at the tip. The proximal half of their inner border bears an even series of low, serrate, backwardly directed teeth, whereas the teeth on the distal half are unequal and set at right angles to the mandibular blade. Since, therefore, the bases of the mandibles are those of a Pristomyrmecia, as defined by Emery, and apically those of the small forms assigned by him to Myrmecia, to Halmamyrmecia by myself and to Promyrmecia by Clark, we can see why the author last mentioned declines to recognize Pristomyrmecia as a valid subgenus.

Crawley (1922) described *M. clarki* from workers taken by Clark at Mundaring Weir, Western Australia. The undescribed female, of which he has given me a specimen taken in the type-locality, measures

16 mm. and is proportionally longer and stouter than the female *pilosula*. I find in the Museum of Comparative Zoölogy a good series of workers taken some years ago by Mr. W. S. Brooks at Albany, Western Australia. I encountered the species only at Margaret River. The nests, of which I found five and Dr. Darlington one, were all under flat stones in sunny clearings in the forest. None of the colonies comprised more than one to two dozen workers. They jump with the same graceful agility as *pilosula*, but are even more timid.

Myrmecia (Promyrmecia) infima Forel

There are four small species of Promyrmecia, *picta* F. Smith, *urens* Lowne, *pumilio* Mayr and *varians* Mayr, which are more or less confused in the literature, owing to their similarity in structure and sculpture and the great variability, often among individuals of the same colony, in the red and black coloration of the thorax, petiole, postpetiole, legs and antennæ. Mayr, as early as 1876, actually lumped *picta, urens* and *pumilio* together as a single species, and Forel's interpretation of the forms which he observed leaves much to be desired. From a study of types and other authentic material Mr. J. Clark has been able to recognize all of the forms above mentioned and will, no doubt, present his conclusions in his forthcoming Myrmecia monograph. The only form with which I am here concerned is *infima*, which Forel described from Perth (1900) as a variety of *picta*. Clark has shown, however, that *infima* will
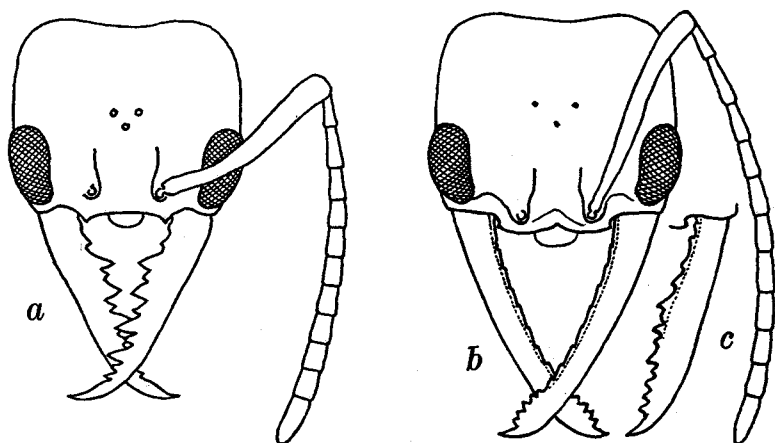
FIGURE 22

a. Head of *Myrmecia* (*Promyrmecia*) *michaelseni* Forel, worker, dorsal view; b. head of M. (P.). *mandibularis* F. Smith, worker, dorsal view; c. mandible of female.
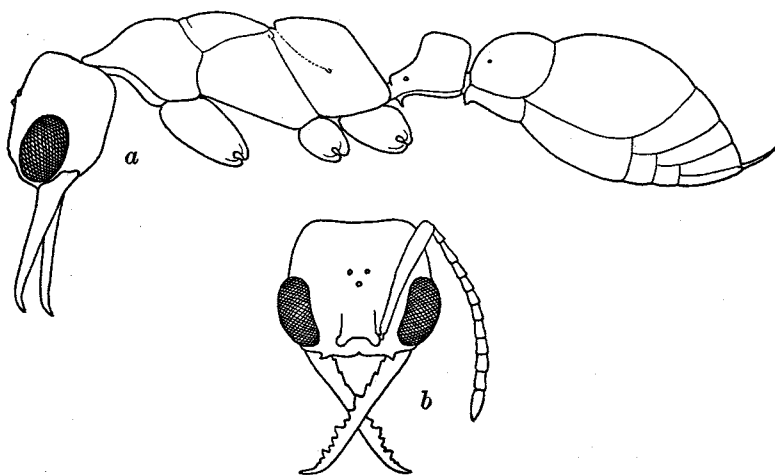

FIGURE 23

Myrmecia (*Promyrmecia*) *clarki* Crawley. a. worker, in profile; b. head of same, dorsal view.

have to be regarded as a distinct species. The var. *nigra*, which Forel attached to *picta*, should, therefore, be assigned to *infima*.

M. pumilio and *M. infima* are the smallest of all the Myrmecias, their workers measuring only 5–8 mm., their females 8–9 mm. Dr. Darlington and I frequently encountered the latter species on various flowers rich in nectar, such as those of Xanthorrhoea, Leptospermum and allied genera, in various localities in Western Australia (Geraldton, Perth, Mundaring Weir, Rottnest Island, Margaret River and Pemberton). Mr. Clark has also taken *infima* at Albany. A study of all this material with additional series from various localities in South Australia (Port Lincoln, Murray Bridge, Adelaide and Gawler) shows a considerable range in color variation. The typical form from Geraldton, Perth and neighboring localities, to which most of the specimens collected by Darlington and myself belong, is black, with honey-yellow mandibles, red epinotum and petiole and more or less reddish brown antennæ, knees, tibiæ and tarsi. The rugosity of the head, thorax and petiole is strong, their surfaces subopaque, as are also the postpetiole and gaster, which are rather densely covered with short grayish or yellowish pubescence. The erect hairs on the body and extensor surfaces of the legs are white. At Margaret River this variety is rarer than three other varieties, namely, first, the var. *nigra* Forel, which is black, without red markings on the body, with the antennæ more or less fuscous, the mandibles brown apically and the knees, tibiæ and

tarsi yellowish brown; second, a variety differing
from the latter only in having the epinotum and
petiolar node red, and therefore intermediate between
nigra and the typical *infima*; and third, a variety
with more extensive rufescence of the thorax, the
pronotum being in part or entirely red, as are also the
mesonotum and legs in many specimens. I doubt
whether any of these forms should be named, because
they are probably merely nest variations. Unfortu-
nately, I was unable, despite careful search, to find
the nests of this ant and thus determine the range of
variation in the single colony. Probably, as Mr.
Clark suggests, the entrance to the nest is merely a
minute, concealed hole in the soil leading into a per-
pendicularly descending gallery, like that of *M. aber-
rans*.

M. infima, as would be expected from its small size,
is a very timid ant. When pursued it leaps with con-
siderable agility and to distances almost as great as
those covered by some of the larger species of Pro-
myrmecia. On several occasions Dr. Darlington and
I swept deälated females as well as workers from the
flowers. The females, in all probability, had already
established their nests and were sustaining them-
selves with nectar till they could bring up their first
brood of larvæ.

Myrmecia (Promyrmecia) mandibularis F. Smith

At first sight this species (Fig. 24) may be readily
mistaken for *michaelseni*, since it has the same sculp-
ture, deep black coloration, pilosity and orange red

pubescence on the gaster. The mandibles of the
worker (Fig. 22b), however, have a very different
structure, being linear, much longer, with a series of
low, serrate, backwardly directed denticles, except at
their obliquely truncated tips, which are armed with
several erect teeth. The mandibles of the female
are quite unlike those of the worker (Fig. 22c).
Emery (1911) selected *mandibularis* as the type of his
subgenus Pristomyrmecia. It was described as long
ago as 1858 by Frederick Smith from Adelaide, South
Australia. I have examined specimens from the fol-
lowing localities:

Western Australia: Swan River (J. Clark); Mar-
garet River, Pemberton and Bridgetown (Wheeler).

South Australia: Ludindale, Murray River and
Kangaroo Island (A. M. Lea); Ardrossan (Tepper).

Victoria: Dimboola (Tepper).

Forel (1910) described a subspecies of *mandibularis*
from an unknown Australian locality as *aureorufa*,
distinguished mainly by the sculpture of the post-
petiole, which has "on its anterior three-quarters very
large, elongate punctures, partly transformed into
short, coarse rugæ." There are in my collection sev-
eral specimens which also have a sculptured post-
petiole but differ sufficiently from the type and the
form described by Forel to be regarded as a distinct
subspecies. They are here described.

M. mandibularis subsp. *postpetiolaris* subsp. nov.

Worker. Differing from the typical *mandibularis* in having the
rugæ of the head, thorax and petiole, and especially of the epino-
tum and petiole, distinctly coarser and somewhat more irregular.

eggs and larvæ in various stages of development. The eggs were of the usual subspherical shape and scattered on the floors of the superficial chambers of the nest. The larvæ are fed on insects. In one nest I found a cluster of them devouring a decapitated cricket. *M. mandibularis* is by no means aggressive; it jumps, but more awkwardly and more reluctantly than *M. pilosula* or *mediorubra*.

The similarity, except in the structure of the mandibles, between *mandibularis* and *michaelseni*, and the occurrence in both of subspecies (*postpetiolaris* and *rugosa*) with a similarly sculptured postpetiole, are the more striking because none of the other species of Myrmecia exhibit the same combination of size, form, color, sculpture and pilosity. Mimicry cannot be invoked as an explanation of this likeness, because both forms are equally cowardly and equally able to sting severely when seized. They apparently represent an interesting case of convergent or parallel development. The peculiar disparity in the structure of the mandibles of the workers may point to differences in food and therefore to the occupation of different ecological niches, though both species live in the same forest environment. The truth of this supposition, however, can be proved only by careful studies of the colonies both in the field and in artificial nests by some resident entomologist.

Myrmecia (Promyrmecia) piliventris F. Smith

The type-locality of this handsome species was not recorded, but was probably somewhere in New South

Wales. All my specimens of the typical form of the species are from that state (Sydney (A. M. Lea), Como (W. M. Mann), Heathcote, Manly, Uralla (Wheeler)); Mayr's record "Rockhampton, Queensland," probably refers to *M. gilberti* Forel (*vide infra*).

The worker *piliventris* measures 9–15 mm. and is distinctly shining, black, with reddish tarsi. The mandibles are long, linear, furnished with 5 or 6 large, erect apical teeth and low, serrate, retrorse denticles along the inner borders. The rugosity of the head, thorax and petiole is strong and regular. The postpetiole and gaster are covered with a pelisse of appressed dull golden pubescence, which converges from each side to the mid-dorsal line.

Each of several colonies which I observed in 1914 was nesting under a stone and comprised about 50 to 60 workers, which jumped quite readily, like the workers of *M. pilosula*, and were rather timid.

The subspecies *rectidens* described by Forel as a variety from Kingston, South Australia, measures only 8 to 9 mm. and therefore averages decidedly smaller than the typical form. It differs also in having the legs, antennæ and mandibles deep reddish brown instead of black, the retrorse denticles on the mandibles less distinct, the postpetiole narrower and with less developed golden pubescence. I have taken this subspecies at Bathurst and Uralla, New South Wales, and have received specimens from Lucindale, South Australia (Feuerherdt).

Myrmecia (Promyrmecia) fulvipes Roger

The geographical range of this species, described as long ago as 1861, without precise locality, embraces South Australia, Victoria, New South Wales and Queensland. Among my material, I recognize in addition to the typical form a variety (*femorata* Santschi) and three subspecies, *fulviculis* Forel (originally described as a variety) and two undescribed. I have seen the male only of *fulviculis* and the female only of *barbata* subsp. nov. The following brief descriptions will serve for the identification of the five forms:

M. fulvipes (typical) *Worker.* Length 9–12 mm. Head distinctly broader than long; mandibles straight, linear, not subtruncate at the tips, which are long and curved, with several erect subapical teeth followed basally by a serration of small, low, retrorse denticles along the inner border. Petiolar node as broad as long or somewhat broader; postpetiole one and one-half times as broad as long. Distinctly shining, the rugosity of the head, thorax and petiole sharp, longitudinal on the head and thorax, transverse at the anterior end of the pronotum and declivity of epinotum; more reticulate on the petiole. Mandibles smooth and shining, with small, scattered, elongate punctures. Pilosity pale, very delicate, erect, of uneven length and not conspicuously abundant. Pubescence abundant and appressed on the gaster where it forms a dull, greenish golden pelisse, convergent at the mid-dorsal line, less abundant on the postpetiole. Black; mandibles and antennæ castaneous; legs, including coxæ, and sting yellowish red.

New South Wales: Uralla (Wheeler); Wentworth Falls and Leura (W. M. Mann).

Victoria: Ferntree Gully (C. Barrett); Mt. Dandenong (Wheeler).

Tasmania (A. M. Lea).

I have found this form nesting under stones in colonies of about 50 individuals. They progress in short jumps and are not aggressive.

Var. femorata Santschi. *Worker.* Of the same size as the typical form and differing from it in having the mandibles distinctly broader toward their tips, with large and small teeth alternating in the subapical series. The mandibles, antennæ, tibiæ, tarsi and knees are black or dark brown.

Victoria: Franktown, type-locality (C. Barrett).

New South Wales: Mt. Kosciusko, 3000–4000 ft. (Wheeler).

This form was attached by Santschi to *M. piliventris*, but it is clearly little more than a color variety of *fulvipes*. The colonies found on Mt. Kosciusko were all nesting under stones. They were of the same size and exhibited the same timid behavior as those of the typical *fulvipes*.

Subsp. fulviculis Forel. *Worker.* Length 12–14.5 mm. Much larger than the two preceding forms. Mandibles straight but narrower and longer, gradually narrowed towards the tip, with an even row of erect, subapical teeth and very low basal denticles. Head broader. Petiole as broad as long or very slightly longer than broad, not very sharply truncated anteriorly; postpetiole variable but usually fully one and one-half times broader than long. Somewhat less shining than the typical *fulvipes*, with less regular rugosity; mandibles distinctly striate. Pilosity more abundant; pubescence of the abdomen almost as abundant on the postpetiole as on the gaster, longer, coarser and of a deeper, more brilliant golden yellow tint. Antennæ and mandibles castaneous; head, thorax and petiole blue black; legs reddish yellow, coxæ often slightly brownish; postpetiole and gaster brown, posterior border of first segment and whole of remaining segments reddish yellow.

Tasmania, type-locality (A. M. Lea).

New South Wales: Como (Wheeler, W. M. Mann).

Queensland: Brisbane and Bribie Island (Wheeler);
Mt. Tambourine (A. M. Lea).

Mr. Clark (*in litteris*) doubts the occurrence of this subspecies in Tasmania. A colony which I found at Como, near Sydney, was nesting under a stone and comprised about 50 workers. They leaped quite readily but stood their ground, though rather cautiously. A colony observed at Brisbane was nesting in a low, pebble-covered mound about 10 inches in diameter. When disturbed the workers leaped towards me with some hesitation but eventually pursued me to a distance of four feet from the mound.

Subsp. *barbata* subsp. nov. *Worker.* Length 12–14.5 mm. Head broader than in the preceding forms, especially behind and therefore more rectangular. Mandibles somewhat shorter, stouter and distinctly curved, the subapical teeth smaller. Petiole and postpetiole as in *fulviculis*, but the former more sharply truncated anteriorly. Surface of head, thorax and petiole somewhat more shining, with more regular rugosity. Pilosity more abundant, conspicuously long on the gula. Pubescence dense, present on the postpetiole and gaster as in the typical *fulvipes*, but fine and dull, greenish golden as in *M. piliventris*. Black, antennæ and mandibles red; legs reddish yellow as in *fulviculis*; sting black.

Female (deälated). Length 14.5 mm. Very similar to the worker. Mandibles broader and somewhat shorter, with subapical teeth larger and occupying fully one-half of the inner border. Thorax more robust, with larger mesonotum and scutellum and shorter epinotum. Petiole and postpetiole broader. Gular hairs shorter; pubescence on abdomen as in the worker and fully as dense on the postpetiole as on the gaster.

Described from 10 workers from Dorrigo, New

South Wales (W. Heron), and a worker and female from Belgrade.

Subsp. *cælatinoda* subsp. nov. *Worker*. Length about 13 mm. Mandibles as in *barbata*, but the subapical teeth worn away, the serrate basal denticles very minute and indistinct. Petiole as in *barbata*, postpetiole one and one half times as broad as long, semicircular anteriorly, its posterior border somewhat emarginate in the middle. Gaster slender, the first segment nearly as long as broad. Sculpture as in *barbata* but much more of the posterior portion of the epinotum transversely and the petiolar node more coarsely rugose. Unlike all the preceding forms of *fulvipes*, the postpetiole is sculptured, being sharply longitudinally rugulose, with elongate foveolæ between the rugules as in *M. mandibularis rugosa*. Pilosity somewhat less abundant than in *fulviculis*, the pubescence of the pelisse on the gaster of the same bright golden color, but coarser, longer and less distinctly converging at the mid-dorsal line. On the postpetiole there is only a minute patch of golden pubescence at the emargination of the posterior border. Mandibles, antennæ, legs and gaster red; head, thorax and petiole blackish red.

Described from a single specimen from Belair, South Australia (J. W. Haacke). This subspecies is readily distinguished from all the other forms of *fulvipes* by its color and its sculpture and posteriorly emarginate postpetiole.

Myrmecia (Promyrmecia) gilberti Forel

Forel described this beautiful ant in 1910 from Mackay, Queensland (Gilbert Turner), as a variety of *fulvipes*, but later (1913) raised it to subspecific rank. In 1928 Santschi redescribed it as a distinct species, *M. regina*, from specimens taken at Townsville, Queensland (F. P. Dodd). After he had sent me a cotype I discovered that I already possessed several

specimens belonging to the same series and that I had myself taken others both at Townsville and at Koah, near Kuranda, Queensland, in December 1914. I have also a few workers collected by Froggatt at Gin Gin in the same state. Although Forel's description is rather perfunctory, there can be little doubt that *gilberti* and *regina* are synonyms, but that Santschi is right in regarding this ant as an independent species.

My specimens vary from 9 to 15 mm. in length. The most striking structural differences, as compared with *piliventris* and *fulvipes*, are in the mandibles, which have stronger teeth, with the larger apical series occupying fully one-half of the internal border, and in the gaster, which is much shorter, the first segment being convex and decidedly broader than long, and the apical segments very short. The petiolar node is as broad or nearly as broad as long and somewhat less sharply truncated anteriorly, and the sculpture and pubescence are quite different. The head, thorax and petiole are more opaque and more finely and irregularly rugose. The postpetiole has only grayish pubescence; the pelisse, which is brilliantly golden on the gaster, as in *fulviculis*, is confined more to the mid-dorsal portions of the segments and fades into gray on the sides. The mandibles and antennæ are dark brown, the legs black or in some specimens dark brown, the terminal tarsal joints reddish.

The male (undescribed) measures about 11.5 mm. and is more opaque than the male of *piliventris*, with much more finely rugose head, thorax and petiole. The head is proportionally smaller than in *piliventris* or *fulviculis*, the thorax, petiole and postpetiole distinctly narrower and less robust, the postpetiole as long as broad and gradually narrowed anteriorly. The pubescence on the gaster is like that of the worker; the wings are slightly smoky as in the males of *piliventris* and *fulviculis*, with yellowish brown veins and darker brown pterostigma.

A fine colony of this ant, which I found at Koah, was inhabiting a low mound nest nearly a foot in di-

ameter and containing about 60 workers and two males. The workers had a tendency to jump, but were timid and did not venture to attack me.

Forel has described a variety of *gilberti* as *luteiforceps*, from Herberton, Queensland (E. Mjöberg). It measures 11–12 mm. and is therefore somewhat smaller than the typical form. It differs also in having yellow, smoother mandibles and paler, reddish tarsi.

Amblyopone australis Erichson

This is a very primitive, sluggish, deep red, subterranean, small-eyed Ponerine, widely distributed in the moister regions of Australia, from Tasmania to Queensland and from Victoria to Southwestern Australia. Several allied forms, which are scarcely more than subspecies, occur in New Zealand, New Caledonia, Lord Howe Island, Norfolk Island and New Guinea. Like Myrmecia the genus Amblyopone probably belongs to the ancient Eocene or Cretaceous antfauna. The various Australian forms of *A. australis* are described in my monograph of the group (1927). The habits of all of them are very similar. They live under and in rotten logs and in rather moist soil under stones. The nest is really a loose and ill-defined system of galleries which nowhere communicate with the outside. Clark observed that these ants "travel long distances under half-buried logs and stones, and have tunnels diverging in all directions." The colonies are often pleometrotic, or contain several deälated queens. That they are originally established by single or several queens is clear from my observations

on the subsp. *foveolata* (Fig. 25), which is very common in the forested areas of Southwestern Australia (Darling Range near Perth, Bridgetown, Nannup, Warren, Margaret River, Pemberton, Denmark, Albany, etc.). As a rule, each nest contains only a small number of individuals, one or two dozens or even less, but occasionally large colonies of 40 or 50 individuals may be encountered. The precise number, however, is difficult to estimate owing to the diffuse arrangement of the galleries. When exposed to the light the ants at once slink away into the nearest gallery leading into the soil. In one large colony of the typical *australis* found on Mt. Lofty near Adelaide, South Australia, I noticed that all the workers dropped on their sides and feigned death as soon as the stone was lifted. At Margaret River and Pemberton Dr. Darlington and I not infrequently found myrmecophiles in the galleries of *foveolata*, especially a small yellow Staphylinid, a Pselaphid and a Lepisma-like Thysanuran.

All the nests of *foveolata* examined during October and November contained larvæ, and during the middle of the latter month also brownish yellow cocoons, but as yet no winged females nor males. The larvæ are fed with bisected or entire insects, as the following observations show:

Margaret River, October 31. A fine colony of about 20 workers and numerous nearly mature larvæ under a large log. Some of the latter were devouring an Elaterid beetle nearly an inch long, which the workers had brought in and cut in two at the junction of

the prothorax and mesothorax. Two of the larvæ had thrust their small, narrow heads and slender necks deeply into the small opening at the anterior end of the mesothorax in order to reach the soft tissues at the only vulnerable point of the heavily armored prey.

The three following observations show that a single Amblyopone female can establish a colony:

Margaret River. November 3. An isolated female was found in a small earthen chamber under a deeply buried log with several partly grown larvæ, which were feeding on a large piece (about three-quarters of an inch long) of a Tenebrionid beetle larva. In this case also the larvæ were compactly clustered at one end of the piece with their heads and necks immersed in the soft tissues.

Margaret River. November 4. A small incipient colony under a log, comprising a single female with a few young larvæ which were devouring the decapitated body of an Amblyopone worker! This must have been either found dead or captured by the queen from some fully developed colony in the same log.

Margaret River. November 6. A fine incipient colony under a large log and comprising a female with a number of nearly mature larvæ and a few cocoons. There were no traces of food in the cell, which was perfectly clean, suggesting that the Amblyopone like the Myrmecia queen scrupulously removes all refuse from the nest. The considerable amount of brood with this queen could only have been reared on an abundance of food, but the large log was probably inhabited by an adequate supply of insects. Clark

says: "I have several times found (Amblyopone) nests in rotten logs in S. W. Australia. These logs always contained colonies of Termites and the larvæ of Lamellicorn beetles, upon both of which, no doubt, the Amblyopone depend for food."

That several fecundated females may occasionally combine and successfully bring up their brood in common is shown by the following observation:

Margaret River. October 30. Four large females were found under a log in a small earthen cell with a number of nearly mature larvæ and one of the yellow Staphylinid myrmecophiles. Many of the larvæ were devouring an entire Scarabaeid larva about two-thirds of an inch long. It would seem that the queens of these primitive ants exhibit none of the mutual hostility which has been noticed among the queens of the higher ants, when starting their colonies in the same cell. At any rate, we must suppose that the hostility, if hostility there be, can only develop much later in Amblyopone, because the larvæ in the instance observed were nearly ready to spin their cocoons.

In December 1931 I found a smaller, bright red variety resembling the var. *pallens* Wheeler, very common on Mt. Kosciusko. At 5000–6000 ft. it was nesting under large flat stones, not infrequently in colonies of at least 50 individuals. Most of the larvæ had spun their cocoons, but the mature sexual forms had not yet appeared. Here, too, a Pselaphid myrmecophile was found in some of the nests. Both at 5000 ft. and also near Saw Pit Creek (4000 ft.), where

the colonies were often under rather small stones. I found a few solitary females founding colonies in the same manner as those of *foveolata* at Margaret River.

Amblyopone, apart from its subterranean habits and tendency towards pleometrosis, thus closely resembles Myrmecia in the methods of founding its colonies and feeding its larvæ. We must suppose that the Amblyopone, like the Myrmecia, female leaves her cell from time to time to forage for herself and her larvæ. To be sure, her hunting grounds are restricted to the log and the subjacent soil in the immediate neighborhood of her nest, but, as we have seen, the supply of insect food must be adequate. The males and winged females probably emerge in late December or in January, and since both are winged and possess larger eyes and a deeper pigmentation than the workers, there is probably a true nuptial flight. We must also suppose that the fecundated females then lead a solitary existence till the ensuing October or November, since the founding of the colonies was actually observed at that season. The above-recorded observation on four colony-founding females in the same cell suggests that the pleometrosis so often observed in adult Amblyopone colonies may be a continuation of the primary and not a secondary polygyny, or permanent adoption of virgin or fecundated females by the workers of their own colony.

Genera with Ergatomorphic Females

Evidence which has been accumulating for many years shows that in quite a number of genera of Pone-

rine and Cerapachyine ants the female caste is erga-
tomorphic, that is externally very similar to or even
indistinguishable from the worker. Thus no female
appreciably different from the workers has ever been
seen in the East Indian and Papuan genus Diacamma,
the Australian Rhytidoponera, the tropicopolitan
Leptogenys *sens. str.*, the South African Streblo-
gnathus and the South American Dinoponera. Chap-
man actually found the male of a Philippine species of
Diacamma *in copulâ* with a form externally indis-
tinguishable from the worker (Wheeler and Chapman
1922), and neither Mr. John Clark nor I have ever
been able to detect a differentiated female in any of
the numerous species of Rhytidoponera which we
have collected. In 1931 as in 1914 I diligently sought
in nest after nest for an individual that might be re-
garded as the mother of the colony, but without suc-
cess; and all the species of Leptogenys *sens. str.* and
other genera mentioned above have yielded results
no more positive. Perhaps, as suggested on p. 55, the
Myrmecia aberrans female is either indistinguishable
from the worker or possesses very minute, deciduous
wings. In another series of forms, however, compris-
ing the large subgenus Lobopelta of the genus Lepto-
genys, the Australian genera Onychomyrmex, Par-
anomopone and Eusphinctus, the neotropical Acan-
thostichus and the Ethiopian *Megaponera fœtens* and
Plectroctena mandibularis the female, though wingless
and workerlike, may be distinguished, nevertheless,
by her larger size, her more voluminous gaster and in
some species by her somewhat differently shaped

thorax and petiole. In Lobopelta only a single species, *L. langi* Wheeler (1923) of British Guiana, is known to have a normal winged female, and in a single species, the African *L. ergatogyna* Wheeler (1921-22), this caste, though apterous, has well-developed ocelli and a thorax of the normal female structure. Among the other species of Lobopelta we can recognize an interesting series of increasing approximations to the completely ergatomorphic female of Leptogenys *sens. str.* Distinctly ergatomorphic females are, of course, known to exist as rather unusual occurrences with typical winged females in some other Ponerine and Cerapachyine genera, such as Ponera, Myrmecia, Odontomachus, Anochetus, Cerapachys and Phyracaces. It is very doubtful, however, whether these ergatomorphs are ever able to found colonies like their winged sisters. Yet conditions like those seen in all species of Lobopelta, except *langi* and *ergatogyna*, may be assumed to have originated by the phylogenetic suppression of the winged female and the transfer of her reproductive and colony-founding functions to a workerlike female. A further loss of all the external female characters in this ergatomorph would lead to the conditions which we find in Leptogenys *sens. str.*, Diacamma, Rhytidoponera, etc. That so many Australian Ponerinæ and Cerapachyinæ have been found to have ergatomorphic females is probably due to the fact that so many genera of those ancient subfamilies have survived on that continent. Of course, ergatomorphic females also occur as the only females in some other subfamilies of

ants. The peculiar queen, or "dichthadiigyne," of the Dorylinæ and Leptanillinæ is really a modified erga- tomorph, resembling that of Acanthostichus, as Emery observed. And in the Australian Dolicho- derine genus Leptomyrmex and the African Myrmi- cine genus Ocymyrmex, the conditions are clearly like those of Leptogenys *sens. str.*, since a female form externally distinguishable from the worker has never been detected in either genus.[1]

Leptogenys clarki sp. nov.

In the Ponerine section of the *Genera Insectorum*, published in 1911, Emery divided the genus Lepto- genys into four subgenera: Leptogenys *sens. str.*, Machærogenys, Odontopelta and Lobopelta. Three species from Madagascar were assigned to Ma- chærogenys, a single species from Queensland to Odontopelta, 26 species from the Neotropical, Paleo- tropical and Malagasy regions to Leptogenys *sens. str.* and 61 species from the same regions to Lobo- pelta. Emery called attention to the fact that no species of Leptogenys *sens. str.* was known from Aus- tralia. In 1915, however, Forel described a large species, *L. sjöstedti*, of this subgenus, taken by Mjö- berg at Malanda on the Lamington Plateau, Queens- land. October 9, 1931, I found at Geraldton, Western

[1] I have recently received from Mr. Herbert Lang several fine series of specimens of *Ocymyrmex weitzaeckeri* Emery var. *arnoldi* Forel and *O. picardi* Forel, which he collected in the Kalahari Desert, South Africa. There are males among them, but no female forms distinguishable from the workers, which vary perceptibly only in details of cephalic sculpture.

Australia, another large species, which is here described.

Leptogenys clarki sp. nov. (Fig. 26)

Worker. Length 12–13 mm.

Resembling *L. sjöstedti* Forel, but really very different. Black; mandibles, frontal lobes, tips and bases of scapes, funiculi, trochanters, tarsi, tip of gaster and posterior borders of its segments castaneous; tibial spurs paler, brownish yellow.

Head broader than long, distinctly broader in front than behind, with rounded posterior corners and straight, marginate occipital border. Eyes rather small, convex, near the anterior corners of the head, their inferior orbits straight. Mandibles longer than the head, narrow, linear, moderately and evenly curved, somewhat broader at the tips which have an acute apical and a blunter subapical tooth. Clypeus very short, sharply carinate in the middle with a narrow, projecting median lobe, which is beaklike in profile, but seen from above is tridentate, with larger median truncated tooth. At its base this lobe bears on each side one or two smaller teeth, and more laterally the anterior border of the clypeus bears on each side a distinct denticle. Frontal carinæ very closely approximated, expanding anteriorly into a pair of well-developed frontal lobes, laterally somewhat upturned. Frontal groove extending back to the middle of the head, but interrupted anteriorly. Antennæ slender; scapes reaching nearly one-third their length beyond the posterior corners of the head; first funicular joint three times as long as broad, about two-thirds as long as the second and slightly shorter than the third joint, penultimate joint only one and two-thirds times as long as broad. Thorax with rather straight dorsal outline; pronotum as broad as long, rather convex anteriorly; promesonotal suture pronounced but followed by only a slight incision in the dorsal profile; mesonotum broader than long, convex transversely, the mesoëpinotal suture indistinct; epinotum as long as the pro- and mesonotum together, its base straight and horizontal in profile, distinctly longer than the sloping declivity which is somewhat crenulate on each side, the crenulation terminating in a distinct tooth posteriorly. Petiole large, nodiform, subcuboidal; from above subtrapezoidal, as broad as the epinotum and as broad as long,

slightly narrower in front than behind, its posterior border straight, its lateral and anterior borders somewhat rounded. In profile the node is distinctly higher than long and thicker above than below, truncated anteriorly and posteriorly, the dorsal surface feebly convex, the posterior truncation with subcircular, marginate border. Ventrally the petiole bears near its middle a low, median, angular projection. Abdomen slightly constricted behind the postpetiole, which is somewhat broader than the petiole and nearly as broad as long. It bears a small, sharp, transverse projection at its anteroventral end. Sting long and well developed. Legs long and rather slender.

Head, thorax and petiole lustrous; mandibles, postpetiole, gaster and legs distinctly more shining Mandibles finely striate and obliquely punctate, especially along their inner borders. Clypeus and gula finely, longitudinally striate; head very finely striolate-foveolate posteriorly, anteriorly more reticulate-foveolate, with a few concentric rugæ around the antennal foveæ. Thorax finely striate, the striæ arcuate on the pronotum, laterally longitudinal; transverse and coarser on the mesonotum and epinotum, especially on the declivity of the latter, longitudinal on the pleuræ. The dorsal surface of the pro- and mesonotum is also indistinctly foveolate, the epinotum above with transverse punctures among the striæ. Petiole finely striate, transversely on the anterior surface, longitudinally on the sides and more irregularly or concentrically on the dorsal surface which is also indistinctly foveolate; the posterior surface, however, is very smooth and shining. Postpetiole somewhat coriaceous, covered with sharp, elongate foveolæ which are smaller and sparser than those on the head. Gastric segments smoother, finely and sparsely punctate, except the first which has a number of coarse punctures at the base on the dorsal side. Legs smooth, with sparse piligerous punctures, coxæ regularly and transversely striate.

Hairs grayish yellow, erect, moderately abundant, of unequal length, somewhat shorter and more oblique on the scapes and legs, conspicuously long on the clypeus and gula.

I take great pleasure in dedicating this interesting species to Mr. John Clark, who has done such excellent work on the Australian ants. It can be readily

distinguished from *sjöstedti* Forel, by its larger and broader head, different clypeus, longer mandibles, more anteriorly placed eyes, more robust thorax and abdomen, longer sting, very different petiole, sculpture, etc. The Papuan *L. triloba* Emery differs from *clarki* in having a longer head, trilobed clypeus, longer and laterally compressed petiole, deep mesoepinotal incision, very different sculpture, pilosity and coloration.

Four colonies of *clarki* were found on a sandy area sparsely covered with low wattles, eucalypts and other shrubs just back of the beach, near the Geraldton lighthouse. In each case the nest was a rather high crater 8 to 10 inches across, with central entrance about half an inch in diameter, built around the stems of sedges. The galleries, which extended down into the sand to a depth of about a foot, were carefully excavated and all the ants secured. This was not difficult, because they moved very slowly compared with most species of Lobopelta. One colony, apparently on the verge of extinction, comprised only 6 ants, the others 20, 24 and 25 respectively. There were some brown cocoons and full-grown larvæ in two of the nests. The ants were extremely timid, sometimes leaving the nest reluctantly, when it was disturbed, at others sneaking away, occasionally with a cocoon or larva in their long, slender mandibles. On careful examination all the specimens proved to be workers, or, at any rate, if a fecund female was present among them she could not be distinguished by any external characters.

Nor, as previously stated, has it been possible to detect a differentiated female or queen in any of the described species of Leptogenys *sens. str.* We may therefore conclude that such a form does not exist. The same, in all probability, is true of the species which have been assigned to the subgenera Machærogenys and Odontopelta. In 1914 I took near Kuranda, Queensland, a colony of *O. turneri* nesting under a log and numbering perhaps 50 individuals with a quantity of brood. No differentiated female could be detected among the considerable portion of the colony collected. The three subgenera mentioned are therefore quite different from Lobopelta (*vide infra*), since the colonies of this subgenus contain a distinctly recognizable ergatomorphic, or in very rare cases like *L. langi*, even a winged queen. It may be advisable, therefore, to raise Lobopelta to generic rank, just as it seemed proper to Emery to separate Chalcoponera, which possesses winged queens, from the closely allied Rhytidoponera, which, like Leptogenys *sens. str.*, completely lacks such a caste.

Leptogenys (Lobopelta) neutralis Forel

Forel originally described this ant in 1907 from worker specimens taken by the Hamburg Expedition to Southwestern Australia at Pickering Brook. It has since been recorded only from Western Australia. More recently (1922) Crawley has described the female from a specimen collected by Mr. John Clark at Mundaring Weir, in the Darling Range. The species seems to be rare and local in the vicinity of Perth,

since I observed it only twice, once on Rottnest Island, where it was nesting in moist soil under a log at the edge of a small pond, and once at Kalagunda, in the Darling Range, where it was nesting under a log on the bank of a stream. I was therefore surprised to find it one of the commonest ants in Southwestern Australia in the great forests of karri, jarrah and tuart about Margaret River and Pemberton. In the latter locality I not infrequently encountered as many as forty or fifty colonies in a single day. This is the more extraordinary because all the other numerous species of Lobopelta, whether in Australia, India, Indonesia, Africa or tropical America, are rare and sporadic. Judging from my observations, there are few other Ponerine ants that seem to be really common, namely the Australian *Brachyponera lutea* Mayr (*vide infra*) and *Mesoponera castanea* F. Smith of the North Island of New Zealand.

L. neutralis is a very active, timid, shining, jet-black ant, with castaneous mandibles, antennæ, legs and anal segments. The worker (Fig. 27a, b) measures 6–7.5 mm. The colony comprises only 30 to 40 workers and a single queen, which so closely resembles the workers that she is difficult to detect when the colony is disturbed and its members scurrying away in all directions. Since Crawley's description of this interesting insect is drawn from a single specimen and omits certain structural peculiarities, I here redescribe it and insert outline figures (Fig. 27c, d):

Head shorter and proportionally broader than in the worker, though distinctly longer than broad; usually slightly broader

anteriorly than posteriorly, with somewhat shorter and stouter antennal scapes and in most specimens with a pair of small posterior ocelli. Thorax somewhat broader and stouter than in the worker, with distinctly more convex dorsal outline in profile, the mesonotum much larger, the mesoëpinotal impression longer and less pronounced. Minute scutellar and metanotal sclerites, which are absent in the worker, can be distinguished. Epinotum proportionally shorter and more rounded in profile, the base much more convex and less clearly marked off from the declivity. Petiole much shorter, nodiform, scarcely longer than broad when seen from above, in profile distinctly higher than long and nearly as high in front as behind, convex dorsally, with distinct, flattened, perpendicular anterior and posterior surfaces. Postpetiole and gaster much more voluminous than in the worker, the former fully one and one-half times as broad as long (in the worker distinctly longer than broad). Sting shorter and stouter. Sculpture and color as in the worker, but the scapes, femora and tibiæ darker and more blackish, except at their bases and tips. Grayish pilosity on the body, and especially on the gaster, distinctly longer and more abundant than in the worker. Length 7–7.5 mm.

At Margaret River and Pemberton the *neutralis* colonies were nesting under logs or, less frequently, under stones, in rather moist soil. That this is the optimum environment is shown by the fact that they were much less abundant in the sandy and less heavily forested tracts in the vicinity. The nest consisted of a surface chamber with a gallery leading down into the soil to a few smaller chambers at depths of about five to seven inches. When under old logs the nest was often continued up into the wood if it happened to contain crevices or abandoned insect burrows. As soon as the log or stone was rolled over the ants fled in all directions, neglecting their brood, which during the latter half of October consisted of slender, long-necked, tuberculate larvæ and in early

November of pupæ in slender brownish-yellow co-
coons. When the disturbance had subsided some of
the workers, which had taken refuge in the depths of
the nest or in cavities of the log, would very stealthily
return and salvage the brood.

In many of the nests Dr. Darlington and I found
entire or dismembered insects. In most cases the
neutralis larvæ were feeding on them, but sometimes
the insects had been placed in a small chamber apart
from the brood and were therefore a store from which
food could be taken when required. Some of the en-
tire insects seemed to be paralyzed, like the prey of
solitary wasps, and moved their legs or antennæ when
stimulated. The prey consisted of the following in-
sects, which are listed in order of decreasing fre-
quency:

(1) *Crematogaster (Orthocrema) dispar* Forel var.
Deälated females of this small yellow ant were most
often encountered in the *neutralis* nests. They had
been cut in two at the petiole and only the succulent
gasters given to the larvæ, which inserted their slen-
der necks into the opening at the anterior end.

(2) Deälated females of three small species of
Iridomyrmex, one of which was *I. conifer* Forel.
These had been treated in the same manner.

(3) The abdomens of deälated females of two small
species of Camponotus.

(4) The abdomens of deälated females of *Bra-
chyponera lutea.*

(5) Entire deälated males and females of ter-
mites.
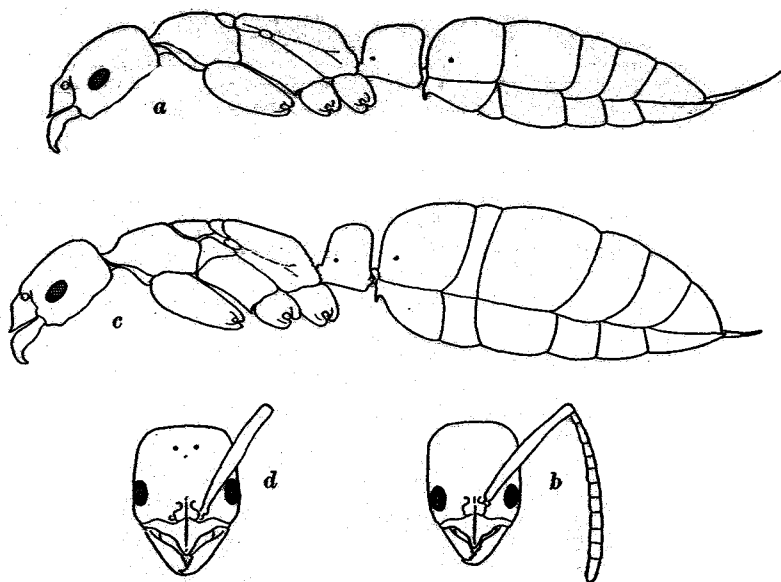
FIGURE 27

Leptogenys (Lobopelta) neutralis Forel. *a.* worker, lateral view; *b.* head of same, dorsal view; *c.* female, lateral view; *d.* head of same, dorsal view.
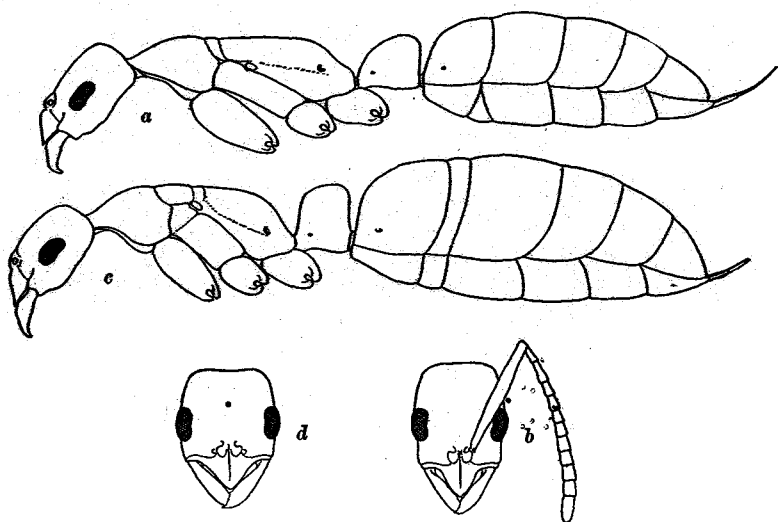
FIGURE 28

Leptogenys (Lobopelta) darlingtoni sp. nov. *a.* worker, lateral view; *b.* head of same, dorsal view; *c.* female, lateral view; *d.* head of same, dorsal view.

(6) Entire small Carabid, Staphylinid and Scarabaeid beetles (2 species).

(7) A single small entire female Thynnid wasp.

Several of these insects were sometimes found in the same nest. It will be seen that the favorite prey consisted of the queens of some seven species of ants, especially of *Orthocrema dispar* var., which is one of the most abundant ants in Southwestern Australia. It occurs so frequently in the logs covering *neutralis* colonies that it is difficult to avoid the conclusion that the Ponerine excavates its nests by preference near or in actual contact with the Orthocrema nests. This ant is subterranean and at the time of our visit was rearing great numbers of queen larvæ. In most nests, in fact, I could find no worker brood but only female larvæ, which were nearly spherical and resembled pearls. They were always kept separate from one another in the galleries. Since none of these larvæ had pupated, I inferred that the dismembered Orthocrema females in the *neutralis* nests were either the mothers of colonies or single nest-founding individuals which had been extracted from their chambers in the soil or rotten wood. The same is probably true of the Iridomyrmex, Camponotus and Brachyponera females, which are frequently found in or under the same logs. The *neutralis* workers forage singly and, I believe, mostly at night, or, if in the daytime, only under and in the large logs covering their nests. The termites and beetles belonged mostly to species which live in the same situations. It is easy to see why *neutralis* prefers female ants and male and female ter-

mites, because these castes contain a greater amount of nutritious food than the workers or beetles.

A single observation showed that the *neutralis* queen founds her colony in the same manner as the queens of Myrmecia and Amblyopone. After much search and just before leaving Pemberton, I found on November 14 an isolated female guarding a few nearly mature larvæ in a small earthen cell under a log. Though no insect prey was present, there can be no doubt that the larvæ had been reared by the female on such food, obtained by occasional excursions either under the log or in its crevices. Since the female is apterous, she cannot, of course, engage in a true nuptial flight, but must be fecundated either in the maternal nest or while wandering about in the open. Owing to the unusual abundance of this ant at Pemberton and Margaret River, some Australian entomologist might readily fill this gap in our knowledge of the behavior of *L. neutralis* by visiting these or neighboring localities during the latter half of November or the first half of December. Since nearly all the other numerous but much rarer species of Lobopelta have similar ergatomorphic queens, whatever is learned about the mating behavior of *neutralis* would in all probability apply to them also.

Leptogenys (Lobopelta) darlingtoni sp. nov.

A single colony of this ant (Fig. 28) was found September 12, 1931, under a large stone in the shade of some jam wattle trees near Mullewa, Western Australia. The less than 40 individuals in the colony

were so agile and escaped so quickly into the sur-
rounding grass that I secured only eight. Fortunately
one of them proved to be the mother queen of the
colony. This species, of which I possess also two
workers taken many years ago at Cue, Western
Australia, by H. W. Brown, is dedicated to Dr. P. J.
Darlington, who, as junior entomologist of the Har-
vard Australian Expedition, was my companion on
many delightful excursions.

Worker (Fig. 28a, b). Length 7.5–8.5 mm.

Black; mandibles, bases and tips of antennal scapes, funiculi,
trochanters and tarsi brownish red; femora and tibiæ darker,
brownish black or dark brown; tibial spurs, tip of gaster and sting
paler, yellowish brown; posterior edges of postpetiolar and gastric
segments yellowish.

Body slender; head rather small, about a fifth longer than
broad, subrectangular, slightly broader at the anterior than at
the posterior corners, with marginate broadly concave posterior
border and nearly straight sides. Eyes rather large, convex, as
long as their distance from the corners of the head. Mandibles
broad and convex, leaving when closed no space between their
inner borders and the clypeus, with distinct subequal basal and
apical borders meeting at a rounded angle, the latter finely den-
ticulate, with a few larger acute teeth at the tip. Clypeus sharply
carinate, produced anteriorly as a bluntly pointed triangular
lobe. Frontal lobes small, closely approximated and produced
backward as short, subparallel carinæ, separated by a narrow
groove. Antennal scapes rather stout, surpassing the posterior
border of the head by nearly one-third their length. First funic-
ular joint two-thirds as long as the second, which is two and one-
half times as long as broad and longer than any of the succeeding
joints, except the last. Thorax, and especially the epinotum, long,
somewhat compressed laterally, as broad behind as through the
pronotum. In profile the dorsal outline is very feebly convex and
not interrupted at the posterior mesonotal suture. Pronotum as
broad as long, rounded on the sides and anteriorly, about half as
long as the rather high mesoëpinotum. Mesonotum very short

and transverse; epinotum passing posteriorly without an angle into the very short, rounded declivity. Petiole shaped as in *L. conigera* and *chinensis* Mayr, from above more than twice as long as broad posteriorly, much narrowed anteriorly, with straight sides and distinct posterior angles, strongly compressed laterally; in profile high and perpendicularly truncated behind, the anterior surface slightly perpendicular in front, then rising in an even curve to the apex of the posterior truncation. Abdomen slender, somewhat constricted behind the postpetiolar segment. Legs rather long and slender. Sting well developed.

Shining; mandibles very sparsely punctate; clypeus very finely, longitudinally striolate; head, thorax, abdomen and legs with sparse, scattered piligerous punctures, somewhat larger on the head; antennal scapes, femora and tibiæ subopaque, very finely and densely punctulate.

Pilosity pale yellow, coarse, of uneven length, erect and rather abundant, especially on the head, gaster and dorsal surface of thorax and petiole, short and more oblique on the scapes and legs. Pubescence distinct and rather dense only on the antennæ and coxæ.

Female (Fig. 28c, d). Length 8.25 mm.

Differing from the worker as follows: The red coloration of the mandibles and antennæ paler and extending even to the coxæ, tibiæ and femora. Head slightly broader in proportion to its length; scapes somewhat shorter. There is a well-developed median ocellus. Thorax distinctly shorter than in the worker, owing to the shorter epinotum; the mesonotum much larger, nearly as long as broad; metanotum indicated but without distinct posterior suture. Petiole much shorter, distinctly nodiform, from above not more than one and one-third times as long as broad and much less narrowed anteriorly, in profile higher than long, truncated anteriorly as well as posteriorly, where it is somewhat higher, the dorsal surface nearly straight, sloping upward and backward. Gaster longer and much more voluminous than in the worker. Punctuation coarser and pilosity decidedly more abundant.

This species is closely related to *neutralis*, but is distinctly larger and the petiole of the worker is much longer and anteriorly of a different shape, the head is

broader, with more concave posterior border, the eyes larger, the antennal scapes distinctly shorter, there is no notch in the thorax at the posterior mesonotal suture and the pilosity is longer, coarser and more abundant. *L. centralis* Wheeler of South Australia differs from *darlingtoni* in having smaller and less convex eyes, distinctly shorter antennal scapes, a somewhat shorter first funicular joint, a sharper angle at the junction of the basal and apical borders of the mandibles, longer mesonotum and a different anterodorsal petiolar surface, which in profile is less convex and not truncated in front. The pilosity is also much finer and sparser. *L. conigera* Mayr, which is known only from Queensland and North Australia, is also very similar to *darlingtoni*, but the typical form of the species and its subspecies *mutans* Forel are much larger (10–12 mm.), its subspecies *adlerzi* Forel and *exigua* Crawley distinctly smaller (6.4–7.5 mm. and 7 mm. respectively). Judging from the descriptions, these various forms also differ in the proportions of the petiole, length of the antennal scapes, pilosity and coloration, so that one is inclined to regard them all as distinct species.

Brachyponera lutea Mayr

Mayr, in his report of the Formicidæ of the Novara Expedition, published 70 years ago (1862), carefully described all three castes of this interesting ant. At the time he was not certain that the female was really cospecific with the worker, but in his paper (1876) on the Australian ants of the Museum Godeffroy he

mentioned receiving from Sydney and two localities (Rockhampton and Gayndah) in Queensland a large number of workers, females and males, which evidently convinced him that his original allocation of the female was correct. As will be seen from the figures (Fig. 29 *a-i*) and the following brief taxonomic descriptions, doubt might easily arise, because of the striking difference in size and coloration between the worker and the two sexual castes.

B. lutea Mayr (Fig. 29a, b, c). *Worker.* Length 4–5 mm. Usually pale brownish yellow but varying to darker brown or more rarely to brownish black, especially on the head and thorax; mandibles and antennæ deep red; legs pale yellow. Eyes small, flat, situated a distance equal to their greatest diameter from the anterior corners of the head, which is nearly as long as broad, sub-rectangular, with convex sides and straight posterior border. Pronotum broader than long, with rounded humeri; mesonotum transversely elliptical; mesoëpinotal impression rather pronounced; epinotum with subequal base and declivity, the former narrow, horizontal or feebly convex, the latter sloping, submarginate on the sides. Petiolar node thick, narrower than the postpetiole, only about one and one-half times as high as long; subcircular from behind, its anterior surface transversely convex, its posterior surface flat or even somewhat concave; its superior border blunt and rounded. Ventrally the petiole bears a large, laterally compressed, plowshare-shaped projection. Postpetiole sharply, perpendicularly or even concavely truncated anteriorly. Sting long and well developed. Shining; head more opaque, finely and densely punctate; pronotum with more superficial and less crowded punctures. Pilosity and pubescence yellowish, the former erect, moderately abundant; short on the head, almost absent on the appendages; the pubescence rather dense, appressed, most distinct on the head, postpetiole and gaster.

Female (Fig. 29d, e, f). Length 10–11.5 mm. Brownish black; antennæ, mandibles, trochanters, tibiæ, tarsi and bases and tips of femora dull brownish red; tip of abdomen yellowish

red; wings distinctly infuscated, with brownish yellow veins and pterostigma. Head decidedly broader than long; eyes moderately large but flattened, as broad as their distance from the anterior corners of the head. Thorax short and robust; epinotum with short base and long, flattened nearly perpendicular declivity. Petiolar scale broad, subcircular from behind, in profile more than twice as high as long, much compressed anteroposteriorly, with rather sharp, entire, superior border, broadly, transversely convex anterior and flattened posterior surface. Ventrally, as in the worker, the petiole bears a large, plowshare-shaped projection terminating behind in a blunt point. Postpetiole and gaster voluminous, the former truncated and flattened anteriorly. Somewhat shining, finely punctate; head more opaque, with denser punctures. Pilosity and pubescence much as in the worker but longer.

Male (Fig. 29*g, h, i*). Length 7–8 mm. Black; antennæ, mandibles, posterior borders of postpetiolar and gastric segments, genitalia, trochanters, tarsi, and bases and tips of femora and tibiæ, brown; palpi pale yellow; wings as in the female but pterostigma dark brown. Head very small, broader than long, eyes moderately large, convex; ocelli small. Mandibles vestigial, indistinctly denticulate. Antennæ long; scapes nearly twice as long as broad; first funicular joint slightly broader than long; remaining joints fully twice as long as broad, the second and terminal joints longer. Thorax robust, with swollen mesosterna. Petiolar scale narrow, cuneate in profile, broader above than below, its upper border sharp, angularly excised in the middle; ventral surface with a projection like that of the female and worker but terminating in a more acute point posteriorly. Postpetiole plus the gaster subelliptical, robust, the former truncated and flattened anteriorly but less sharply than in the worker and female. Genitalia large, exserted; pygidium spiniform, deflected at the tip; cerci very distinct; hypopygium transverse, its posterior border sinuate in the middle. Legs slender, rather short. Shining; head subopaque and indistinctly punctate anteriorly. Pilosity less developed than in the female and worker, confined almost entirely to the venter and tip of gaster; pubescence finer and more dilute.

Since Mayr's time, *B. lutea* must have been taken by every collector of ants in Australia, because it is not only one of the commonest species, but excels all others in the extent of its range, which seems to cover the whole continent. It is ubiquitous on the Hawkesbury sandstone of New South Wales and is almost equally at home in Queensland and Western Australia. I have taken it near Wiluna, on the arid shores of Lake Violet, in the white sand-dunes of Geraldton, and in the damp black soil of the Eucalyptus forests of the Darling Range and Southwestern Australia. It is probably able to inhabit such diverse ecological situations because its colonies are subterranean, like those of Amblyopone, a peculiarity which may, indeed, be inferred from its small, yellow, myopic workers and large, deeply-colored, euopic males and females. It prefers pure sand or very sandy soil and most frequently excavates its long, irregular galleries under stones or logs. The galleries, which must descend to some depth, are sometimes excavated where they do not reach to or continue along the under sides of stones or logs, but terminate in small, free craters, thrown up, presumably during the night, on the exposed surface of the soil. I have so often found this ant in or near termitaria that I have come to suspect that termites must be an important constituent of its diet. At Koah, in Queensland, I found *B. lutea* to be one of ten species of ants regularly inhabiting the lowermost galleries and chambers of the numerous conical termitaria which stud the landscape in that locality. Another observation made at

Margaret River, in Southwestern Australia, shows that *lutea* also feeds on adult male and female termites. At about 6 P.M., November 2, 1931, I witnessed a great dissemination flight of the sexual forms of a small species of termite. On the following morning I noticed that *lutea* and a few other ants (*Lobopelta neutralis* and *Camponotus consobrinus* var.) had stored the galleries of their nests with deälated male and female termites, which they had captured during the night, probably under the stones and logs.

After observing many dozens of *lutea* colonies and finding in them males and females agreeing in all respects with Mayr's description, I was surprised to find Crawley, in a paper published in 1918, casting doubt on Mayr's conclusions and describing as the true female of *lutea* a very different insect measuring only 7 mm. The specimen was taken by Professor E. B. Poulton in August 1914 under a stone with workers of *lutea* at Picton Junction, near Perth. Crawley concluded that "either Mayr's female (an ant ordinarily occurring in collections without accompanying workers), should be referred to another species, or the new female (taken with the workers in the same nest) must be considered as a B form." By 1922 Crawley had obtained females of the form described by Mayr accompanied by *lutea* workers, but he did not abandon his earlier interpretation of his small specimen, though he suggested that it might belong to some other species. The possibility that it might be a microgyne was not considered. While examining *lutea* nests during 1931 I therefore devoted special atten-

tion to the sexual castes. The season was again propitious, because males and females were abundant in the nests, as in 1914, from the middle of September to the end of October in nearly all the localities which I visited. *Large black females and males of the form described by Mayr and showing extremely little individual variation were the only males and females encountered.* Hence Crawley's small female must be either an anomalous female *lutea* (microgyne) or belong to some different species of Brachyponera. The latter is the more probable supposition. I may add that Mr. John Clark, who is intimately acquainted with *B. lutea*, informs me that females of the form described by Mayr are the only ones he has ever been able to find in the nests.

Such differences in size, coloration and eye-development as are exhibited by *B. lutea* between its worker and sexual forms are unusual among the Ponerinæ, but not uncommon in certain thief-ants among the Myrmicinæ (Carebara, Tranopelta, Pædalgus, Aëromyrma, Solenopsis, etc.). One other species of Brachyponera, *sennaarensis* Mayr, which also has a very wide range, including southern Arabia and the whole of tropical Africa, exhibits similar but less pronounced differences (worker 4–5 mm.; female 8 mm.; male 5.5–6 mm.). The female *lutea* is therefore fully ten times as voluminous as its worker, whereas the female *sennaarensis* is only five or six times as voluminous. In all the other known species of Brachyponera the female is only slightly larger than the worker, as in the genus Ponera. The habits

of *B. sennaarensis* are also similar to those of *lutea*.
Arnold says that "the economic value of this little
species (*sennaarensis*) can hardly be over-estimated,
since it is exceedingly plentiful and preys unceasingly
on termites." It is also known to collect and store
grass seeds, a kind of behavior unique among the
Ponerinæ. Perhaps both species attend root-coccids.
The workers of *lutea* and *sennaarensis*, like the work-
ers of Carebara, Pædalgus, etc., are probably able to
rear unusually large females and males because the
termites furnish such an abundant, nutritious and
easily accessible supply of food.

I have not seen the larvæ of *lutea* devouring insect
food and am therefore inclined to believe that they
may be fed with liquids by regurgitation. This is
suggested also by the numerous myrmecophiles
sometimes found in the nests. I find in my notebooks
records of five of these, three beetles, including the
singular Brenthid, *Chordes hospes*, which usually
lives with species of Iridomyrmex, a small Diapriid
Hymenopteron and a large mite. The nuptial flight
of *lutea* was not witnessed, but on two occasions in
late September I found males and deälated females
running over the ground immediately after mating.
In 1914 and 1931 fecundated females were found
during November and December in small individual
cells under logs and stones in many different localities
in New South Wales, Queensland and Southwestern
Australia. None of these females, however, had pro-
duced any eggs by the end of December. Although I
am unable, therefore, to describe the actual founding

of the *lutea* colony, I am convinced that it must be of the perfectly claustral type of the higher ants, for first, the females are so well provided with wing-muscles and fat that they should be able to bring up a brood of minima workers without foraging for food, and second, their cells are usually so far from the edges of the stones and logs as to suggest that the females would have to make long tunnels to reach the exterior, and I have never seen traces of such excavations leading away from any of the many cells which I have examined. The females, furthermore, were always very lethargic and behaved as if they were merely estivating. They probably do not begin to oviposit till several months have elapsed.[1]

E. lutea is of unusual interest for three reasons: first, on account of its method of colony formation, which has just been discussed; second, because its termitophagous habits may prove to be of some economic importance, and third, on account of the great age of the particular Ponerine group to which it belongs. Emery, in the *Genera Insectorum* (1911), made Brachyponera a subgenus of Euponera (which has only a single species, *sikorœ*, from Madagascar), and included in it also two other subgenera, Meso-

[1] After writing this paragraph, I received from Dr. Eidmann an interesting paper (1931) on the founding of *Lasius flavus* colonies, which, perhaps, throws light on the conditions in *B. lutea*. He finds that the females of *L. flavus*, *L. niger* and *Formica fusca*, all of which require several months to ripen the eggs in their ovaries, excavate a cell for hibernation, but later leave it and make another in which to oviposit and bring up their first brood. Perhaps, therefore, the cells in which I found the *lutea* females were merely estivacula. This possibility could be easily tested by the resident Australian entomologist.

ponera and Trachymesopus. Now Euponera *sens. lat.* contains some of the commonest Ponerine ants and as a whole has an unusually wide distribution, since it extends not only over the whole pantropical but also into the subtropical zone, both in the northern and the southern hemisphere. This distribution, which includes New Zealand and Madagascar, is an indication of the great antiquity and stability of the group. There is also paleontological evidence in favor of this statement, since a typical Trachymesopus (*succineus* Mayr) is known from the Baltic Amber (Lower Oligocene) and a Mesoponera (*crawleyi* Donisthorpe) occurs in the somewhat later Oligocene of Gurnet Bay, England. These fossils indicate that Euponera *sens. lat.* had in all probability a cosmopolitan distribution even as early as the beginning of the Tertiary and must, therefore, have had a previous history extending back into the Cretaceous at least. And since the group of subgenera included under Euponera is much less archaic than Myrmecia and Amblyopone, we must suppose that the subfamily Ponerinæ had undergone considerable radiational evolution as early as Mesozoic times.

General Considerations

The foregoing accounts show that the queens of the Ponerinæ establish their colonies independently, though, with the probable exception of *Brachyponera lutea*, in a decidedly more primitive manner than the higher ants. Five of the eight subfamilies of Formicidæ, therefore, have essentially the same method of

colony formation excepting, of course, the sporadic parasitic species, which, so far as known, all belong to the three highest subfamilies, the Myrmicinæ, Dolichoderinæ and Formicinæ. Unfortunately nothing is known about the establishment of the colony among the Cerapachyinæ, Dorylinæ and Leptanillinæ. Since the Cerapachyinæ are closely related to the Ponerinæ and since some of them (Cerapachys, Phyracaces) have winged as well as ergatomorphic females, their colonies are very probably founded in the same manner. The highly predatory and nomadic Dorylinæ, which have very populous colonies and huge, blind, apterous females (dichthadiigynes), probably establish new colonies, as I suggested in a former paper (1921 *a*), only by hesmosis, or splitting of the original colony, and may be supposed, therefore, to have lost the original independent method during their phylogeny. This may be true also of the Leptanillinæ, a small, obscure group of subterranean ants, with blind, ergatomorphic females not unlike those of the Dorylinæ.

There seems to be no doubt that the method of founding colonies adopted by the higher ants — Camponotus, Lasius, Formica, Azteca, Myrmica, etc. — represents a specialized condition, which might be called the *claustral* type of colony formation. The ability of the recently fecundated female to immure herself in a cell and to fast, or remain asitotic, for a considerable and often astonishingly long period while rearing her initial brood must depend on her voluminous wing-musculature and ab-

dominal fat-body. And these nitrogenous and lipoid reserves must, of course, be merely the unusually abundant metabolized food with which she was provided during her larval life. For recently fecundated ant females possessing such reserves in insufficient amounts there are only two available resources when it comes to establishing colonies: they must either become parasites in the colonies of other ants willing to rear the incipient larval brood or be capable of foraging for themselves and later for this brood. The first alternative is adopted by the slave-making and temporarily parasitic species of Formica, Lasius, Aphænogaster and Bothriomyrmex, and the workerless, permanent parasites, of which a number of genera have been discovered in all the continents except Australia. The small size of the females as compared with the cospecific workers in the slave-makers and temporary parasites as contrasted with the relatively large size of the females in the independently colony-forming species of Formica and Lasius has been graphically illustrated by Eidmann (1926) and had, indeed, been previously emphasized in some of my early papers. The second alternative is adopted, as I have shown in this volume, by the species of Myrmecia, by *Amblyopone australis* and *Lobopelta neutralis*. In these forms the thorax and abdomen of the female are but slightly larger than in the worker. No one seems to have considered the possibility that some female ants, poorly endowed with fat and wing-musculature, might establish their colonies by leaving their cells from time to time and

foraging for themselves and their first brood. Yet, if I am not greatly mistaken, this is the normal behavior in the Ponerinæ, with the exception of such forms as *Brachyponera lutea*, in which the difference in volume between the female and worker is much the same as in the higher ants. In this case we are, perhaps, justified in assuming that colony formation is also of the perfectly claustral type. There may be a few other species with similar behavior among the Ponerinæ, but I know of none.

Morphologically Myrmecia and Amblyopone are so primitive that they have always been assigned to the lowest taxonomic rank among existing Formicidæ. It is reasonable, therefore, to regard their colony-founding behavior as equally primitive, or archaic. This is indicated also by the striking resemblance between this behavior and that of colony-founding Vespinæ, and the resemblance, in the case of Myrmecia especially, is the greater if, as Clark asserts, the adult ants of this genus, which feed their young on insect food, are themselves nectarivorous. Perhaps such resemblances might be expected, because the Formicidæ are really a family of Vespoids. They constitute, however, such a sharply defined group that there is no consensus of opinion as to their closest allies among the various groups of Vespoids. The Mutillidæ, Thynnidæ and Apterogynidæ have been suggested, but these all have apterous females. I proposed the Tiphiidæ or Scoliidæ, but Dr. J. C. Bradley, who has made a careful study of both groups, has stated in conversation that in his opinion

the Anthoboscidæ may be nearer to the ancestral Formicidæ. The Chilian *Anthobosca chilensis*, the only member of the family which I have examined except our North American *Sierolomorpha ambigua*, seems, in fact, to be a very generalized form, with the habitus of a Scoliid and a wing-venation very similar to that of Myrmecia and other Ponerinæ. Unfortunately, the life-history of the Anthoboscidæ is unknown, but the structure of their legs, which seem to be admirably suited for digging in the soil, suggests that, like the Scoliidæ and Tiphiidæ, they are parasites, or rather parasitoids, of subterranean larvæ or nymphs.

A comparative study like that recently undertaken by Nielsen (1932) and myself (1928) enables us to recognize three different types of reproductive behavior among the females of the solitary Vespoids. The first of these (Type A) is essentially the same as the behavior of the parasitic Hymenoptera (Terebrantia) that seek out their prey, sting it till it is motionless and, after ovipositing on it, leave it *in situ*. In the second type (Type B) the prey, stung and immobilized in the same manner, is not left where it was discovered, but is transported to and stored ("mass provisioning") in some preëxisting cavity (Subtype *a*) or in a cell specially excavated or constructed (Subtype *b*). In the latter case the egg is either laid in the cell before the prey is secured or attached to it after it has been stored. In Type C, which is a further development of B*b*, the female survives the hatching of the larva and feeds it from day to day

("progressive provisioning"). Type A is the most prevalent and often the only type exhibited by the lower Vespoid families (Plumariidæ (?), Bethylidæ, Cleptidæ, Chrysididæ, Sapygidæ, Rhopalosomatidæ, Anthoboscidæ (?), Bradinobænidæ (?), Scoliidæ, Tiphiidæ, Methocidæ, Thynnidæ, Myrmosidæ and Mutillidæ). There are three families, however, the Bethylidæ, Scoliidæ and Psammocharidæ, in which behavior of Type B subtype *a* has been observed. Subtype *b* is the rule in the solitary Vespidæ (excepting, of course, the pollen- and nectar-storing Masaridinæ) and the prevalent type among the Psammocharidæ. Type C occurs in sporadic species of the Vespid genera Synagris, Eumenes, Odynerus and Zethus. This last type, in which a rudimentary family has come into existence automatically, has been further developed in the social Vespidæ and in the Formicidæ (Type D), in which the queen and her first brood as adults constitute a family or embryonic society. This will be considered in greater detail in the sequel. Even if we make due allowance for the independent or parallel development of Types B and C, we are bound, nevertheless, to regard them as representing two critical phylogenetic and ontogenetic developments which originated within the parasitoidism of Type A and culminated in the definitive society.

We can only speculate on the probable colony-founding behavior of the archetypal Formicid, or Proformicid on the basis of what we know of Myrmecia, which must be a very ancient form since it is

represented in the Baltic Amber, of Lower Oligocene age, by a rather closely allied genus, Prionomyrmex. The ancestral Proformicid was obviously a terrestrial form, with a winged female, which had a nuptial flight and had acquired the habit of deälation after fecundation, a form of behavior peculiar to the Formicidæ among the Vespoids. The primitive nest consisted of a cell that was excavated in the soil and served as a home for the alert, large-eyed female, which was furnished with formidable jaws and sting and, unlike the females of higher ants, was able to hunt and capture active insects of various kinds, including other species of Formicidæ. The eggs were not kept in a packet, but were strewn on the floor of the cell. Very probably the salivary glands were too poorly developed to furnish the glutinous coating that keeps the eggs of the higher ants together. The larvæ were brought freshly captured and only partially dismembered insects as food, a type of behavior intermediate between that of the solitary Vespidæ, which provision their larvæ with entire, paralyzed insects, and that of the social Vespidæ, which thoroughly malaxate the insect food before presenting it to their offspring. The adults of the first brood of the Proformicid female were probably very small, as in the higher ants, and though of the same sex as their mother and like her able to forage independently, apterous and with imperfect ovaries. With the appearance of these dwarfed but coöperative individuals, the mother definitively confined herself to the nest and to producing additional broods, like the females of the

higher ants. In the latter, however, the foraging be-
havior has completely disappeared, probably owing
to a greater development of the salivary glands,
which enabled the mother insect to feed her larvæ by
regurgitation.[1]

The Amblyopone female founds her colony in essen-
tially the same manner as the Myrmecia female from
which I have drawn the foregoing sketch of the hypo-
thetical Proformicid, but the genus has become sec-
ondarily hypogaeic, or subterranean. In Lobopelta
the female has become apterous and the great reduc-
tion of her thorax is compensated by an increase in
the size of her abdomen as compared with that of the
worker. She is able, nevertheless, to bring up her first
brood independently by leaving her cell from time to
time to hunt for insect provisions. We possess no
information, unfortunately, regarding colony found-
ing in the Ponerine genera with females indistinguish-
able, at least externally, from the workers, namely,
Leptogenys *sens. str.*, Rhytidoponera, Diacamma,
Dinoponera and Streblognathus. We know only that
the Diacamma female is fecundated in the nest either
by one of her brothers or by a male from another
colony. It is improbable that one of these females,
which has a fat reserve as meager as any of the work-

[1] In a footnote on p. 100 I called attention to Eidmann's recent dis-
covery (1931) that the fecundated female of some of the higher ants ·
(*Lasius flavus*, *L. niger* and *Formica fusca*) leaves her hibernaculum and
may be found wandering about in the open before excavating the defini-
tive cell, or nursery in which she brings up her first brood. He suggests
that the queen may secure food for herself during this interval. If this
suggestion proves to be correct, we have a partial or vestigial survival of
Ponerine behavior in some of the higher ants.

ers, can rear a brood independently unless, like Myrmecia and Amblyopone, she actually forages during the colony-founding period. Indeed, it would seem that the perfectly ergatomorphic female of these ants must establish her colony immediately after fecundation and during the early summer, when insect food is abundant. I have assumed that the extreme ergatomorphism of the female in all the genera above cited is secondary, or derivative, the original winged female after becoming apterous and passing through a stage like the female of Lobopelta having reached a stage of involution indistinguishable from the worker. These changes may have been due to ability to forage and oviposit soon after mating. But an alternative interpretation is equally probable, because, for aught we know to the contrary, the original female may have disappeared and any of the workers of the colony may be capable of mating and founding a colony. Which of these interpretations is correct might be readily determined by some Australian entomologist, since colonies of numerous species of Rhytidoponera are by no means rare in the warmer and drier portions of Australia and since one species of Diacamma (*D. australe* Mayr) is not uncommon in parts of Queensland.

The differences to which I have alluded between the perfectly claustral type of colony formation in the higher ants and the imperfectly or intermittent claustral type of the Ponerine ants of the genera Myrmecia and Amblyopone lead to a consideration of the "cenobiotic instinct" to which Forel (1902) attrib-

uted the protracted abstention from food of his colony-founding *Camponotus ligniperda* queen. Brun (1912), who had a queen of the same species that fasted fully 11 months (from August 1, 1910, to the beginning of July 1911) while rearing a few eggs as far as the larval and one larva as far as the pupal stage, also has recourse to "an obligatory fasting instinct (cenobiosis), active during the entire period of colony formation and beginning to disappear only with the emergence of the first workers." Such an instinct is, of course, useless as an explanation of the queen's activities, since, like the many instincts postulated by the late Father Wasmann and others as causes of particular behavior patterns in insects, it is merely an abstruse descriptive name. This is apparent from an examination of the concept of fasting which implies simply an abstention from food; an abstention which may or may not be accompanied by hunger. Many fully fed insect larvæ fast for long periods and, since they will not eat, cannot be regarded as hungry. Their condition might be more properly designated by such a neutral, descriptive term as 'asitosis.' If the colony-founding ant-queen is in this state, no instinct is required to explain her behavior, because her condition is purely physiological. If, however, her fasting is accompanied by hunger, appeal to a special instinct is equally unnecessary, because she is manifesting a well-known appetite. That she is actually hungry while she is rearing her first brood is shown by the observations of Meyer (1927), who found that she will not only eat when given food in the artificial nest,

but normally devours a certain number of her eggs and larvæ. He therefore rejects the special instinct postulated by Forel and Brun, as will be seen from the following remarks: "When young, fecundated ant-females, like those of *Camponotus ligniperdus* and *Crematogaster scutellaris*, make their claustral nest in the fall and fast throughout the winter, there is no food at hand and no eggs are laid at that season. But as soon as oviposition commences in the spring, the eggs begin to disappear almost simultaneously, being devoured by the female, as Emery very cautiously claimed for Crematogaster and as I have directly observed in two females of *Lasius flavus* and one of *Solenopsis jugax*. The same is probably true also of *Camponotus ligniperdus*. That we are not here concerned with a peculiar 'instinct of cenobiosis,' is proved by the fact that in Brun's experiment one of the Camponotus females devoured the pupæ which she had robbed from the other female, so that there can really be no 'absolute abstention from food.' Furthermore, such isolated females by no means despise food when it is placed within their reach, but at once eagerly devour it. This I observed, for example, in a young, fecundated female of *Myrmica scabrinodis*, which I fed with honey and white of egg throughout the winter. Although she was later constantly provided with this food some of her eggs disappeared in the spring as soon as she began to lay. From this we may conclude that the devouring of her eggs by the cloistered female during the period of colony formation is an hereditarily fixed trait. The

assumed fasting is, therefore, not instinctive but compulsory, and endures only till food in some form is forthcoming, and this in the isolated brood-chamber can, as a rule, consist only of eggs laid by the female or of other brood stages."

Instead, therefore, of ascribing a special cenobiotic instinct to the nest-founding females of the higher ants, we must suppose that they have actually lost an "instinct," or form of behavior, namely foraging, which is still retained by the colony-founding females of the more primitive Ponerinæ. Moreover, it would seem that in the higher ant female the loss of this behavior is really due to a physiological specialization that has accompanied a greater development of stature, adipose tissue and wing-musculature and therefore a greater ability to use these accumulations in maturing the ova and as food-reserves for the protracted period of colony founding. The habit of devouring the young brood, which, as we have seen, is quite normal, according to Tanquary, Meyer and Eidmann, shows that the reserves may be inadequate and that the mother insect may have to consume portions of their metabolized products, namely, the eggs and young larvæ, in order to prolong her own life and to rear at least a small number of her potential progeny. The considerable mortality among the queens is proof sufficient of the precariousness of this method of establishing the colony. On the other hand, though Myrmecia, Amblyopone and other Ponerinæ have remained in a more primitive phylogenetic stage, they are apparently no less handicapped by their

more meager tissue-reserves, their less developed sali-
vary glands and the difficulty of securing insect prey
during the winter months. Indeed, if we may judge
by the greater rarity of their colonies, the Ponerine
method of colony formation would seem to be much
less successful than that of the higher ants. The same
is true also of the female hornets and bumble-bees,
which have adopted analogous methods of rearing
their incipient broods. It is well known that the suc-
cess of the overwintering females of these insects in
accomplishing this result depends, at least in the
north temperate zone, on favorable weather condi-
tions, and this may also be true of the Ponerinæ, not-
withstanding the fact that they are almost exclusively
tropical and subtropical insects. Of course, the fact
that adult colonies of these ants are much less popu-
lous than the colonies of many species of Myrmicinæ,
Dolichoderinæ and Formicinæ indicates that the
Ponerine female is less fecund, and this constitutional
deficiency may also, to some extent at least, account
for the comparative scarcity of colonies of Ponerinæ
in all parts of the world, except Australia, which is
faunistically still in the Mesozoic Age.[1]

Although my observations on the Ponerinæ

[1] The archaic character of the Australian ant-fauna is indicated by
the fact that at least 300, or 25 per cent, of the 1200 species, subspecies
and varieties of ants known from the island continent are Ponerinæ.
From the United States, which has about the same area, some 500
species, subspecies and varieties have been described, but only 24, or
less than 5 per cent, are Ponerinæ. In the Palearctic Region the per-
centage of Ponerinæ is certainly no larger, and even in the Neotropical
and Paleotropical Regions probably less than a tenth of the ant-fauna
belongs to this ancient subfamily.

strongly support the conclusion that the Formicidæ were originally and still are haplometrotic insects,[1] the question as to whether the same is true of the two other groups of social Aculeates, the social wasps and the social bees, is still unanswered. The Vespidæ would seem to be unusually favorable for a study of the phylogenetic and ontogenetic origin of the colony, because within this single family we have solitary, subsocial and social forms, and these last are represented by a series of subfamilies beginning with groups as primitive as the Stenogastrinæ, certain Polybiinæ (Belonogaster) and the Ropalidiinæ and ending with the more specialized Polistinæ and Vespinæ. We can trace in this series the very gradual development of a sterile or substerile worker as distinguishable from a fertile female caste, but this evolution is not clearly completed till we reach the Vespinæ (Vespa). In the subsocial forms of the subfamily Zethinæ (e. g. the East Indian *Zethus cyanopterus,* according to F. X. Williams, and *Zethusculus lobulatus,* according to Ducke), the mother wasp builds brood-cells of small leaf-fragments and feeds her larvæ with malaxated caterpillars. Several females of

[1] The terms 'haplometrosis' and 'pleometrosis' were proposed by Wasmann in 1910 to designate the founding of ant-colonies by single females or by several associated females respectively. These terms are not exact synonyms of O. M. Reuter's 'monogyny' and 'polygyny' introduced in 1913 to replace the rather inept 'monogamy' and 'polygamy' previously employed by students of the social wasps, because they merely denote the presence in a colony of one or several fertile females and do not necessarily apply to the method of its establishment. I prefer Wasmann's terms because they are more expressive, have priority and do not conflict with the terms 'monogyny' and 'polygyny' as employed by the anthropologists.

Zethusculus establish their cells in close proximity to one another, and these are later united to form a common nest by the addition of intermediate cells. In the larger nests females and males are found, and at least a part of the new generation remains in the nest, which is then enlarged by the young females. Our knowledge of the Stenogastrinæ is rather fragmentary. The mother wasp may bring up several larvæ simultaneously, in the same manner as was observed by Roubaud (1916) in the solitary wasp *Odynerus tropicalis,* and several females occupy the same nest, but each may care only for her own brood. In the African Belonogaster, the most primitive genus of Polybiinæ, Roubaud found that the simple paper nest is usually started by a single female, but that frequently several females coöperate in its construction and in caring for the brood. While immature the females of the new generation function as nurses, but there is no differentiated worker caste. In the paleotropical genus Ropalidia the colonies are often pleometrotic, as frequently happens in Belonogaster, but smaller individuals regarded as workers have been distinguished, though they are few in number compared with the females. In Polybia, which comprises many species of neotropical wasps, the colonies are perennial and often very populous. They contain numerous fecundated and unfecundated females, but the existence of true workers is doubtful. According to H. von Ihering (1896) and Ducke (1905, 1914) these wasps regularly form new colonies and nests by sending off swarms of workers with one or two dozen

females. Concerning the conditions in the Polistinæ
we are better informed because there are several com-
mon European and North American species. Here,
too, the existence of a distinct worker is difficult to
establish. Like the Polybiinæ, some of the neotropi-
cal Polistes are said to be pleometrotic and to have
perennial colonies. The northern species are normally
haplometrotic, but the colonies of some of them are
not infrequently started by several coöperating fe-
males. Bequaert reviewed the known cases of pleo-
metrosis in the European and North American
Polistes in 1918. More recently Rau (1931) has made
an interesting study of the same behavior in several
species (*P. annularis, rubiginosus* and *pallipes*) in the
Mississippi Valley and of two of the neotropical
species (*canadensis* and *versicolor*) in Panama. He
finds that though the females of our northern Polistes
hibernate, several of them, especially of *annularis,*
frequently unite in the spring to construct a single
nest and rear their brood in common. One nest care-
fully studied by Rau was originally started by 17 fe-
males (later reduced to 13). When it was accidentally
destroyed, 8 or 9 of the females built a new nest near
by. His study of this and other pleometrotic colonies
has led him to the following interesting conclusions:
"After viewing the occurrence of this habit in our
Polistes, I am inclined to believe that pleometrosis in
our northern species of Polistes had its origin in the
'swarming' habit of tropical Polistes. In a paper
now in the course of publication on *Polistes canadensis*
and *Polistes versicolor* of Barro Colorado Island in

Panama, I show that when the colony grows too large or a catastrophe occurs to the nests, swarming occurs much after the fashion of swarming of honey-bees, with this difference; whereas the honey-bee swarm seeks a new location in body, the swarm of Polistes wasps in the tropics breaks up into many smaller groups of few or many individuals, and these found the new homes. In the tropics where winter and hibernation do not occur, this is the method of dissemination. In the north, cold and hibernation interfere with this method, but we do see an adherence more or less complete (but in certain species no less complete) to the habit of pleometrosis, after assembling on the old home site which, after all, is very similar to swarming. This may or may not be vestigial in character, for it is difficult to tell whether pleometrosis is ascending to higher socialization, or is in a vestigial condition. Thus we see that the occasional condition (more or less frequent according to the different species of Polistes) of more than one mother founding a colony has an analogous counterpart in the swarming of a sister species in the tropics. There seems to be but little difference between the psychological reactions of members of a colony when activities are cut short by the violent destruction of the nest in the tropics, or the violent curtailment of their activities in the north by the cold. In both cases, members of the colony disband and found new colonies with one, two or more queens present; however, in the tropics the founding of new colonies occurs immediately after adverse conditions occur, while in the north the found-

ing of new colonies is interrupted by a period of hibernation in which the wasps are numb with cold. In any event, the long period of dormancy in the northern species apparently has not caused the wasps to forget how to behave like their tropical sisters when colonization occurs. Pleometrosis of Polistes in the tropics is due to the fact that with a twelve-month calendar, the colony splits up occasionally when it reaches great size, and one to many sister wasps go forth and found a new nest. But in the north where cold weather curtails the Polistes activities to only a fraction of a calendar year, pleometrosis undoubtedly has its origin in the queen's remembering the home location, going there in the spring and meeting sister queens, and founding their nests near by. This marked difference between the two populations exists, however: in the northern Polistes, only the queens survive the winter and are ready to scatter in the spring, whereas in the tropical species, some of those which found new colonies may be workers."

Caste differentiation in the Vespinæ is very much like that in bumble-bees. There are large females, or queens, smaller sterile or substerile forms known as workers and intermediate, or annectant forms. Only a single species, *Vespula squamosa* Drury (= *carolina* Lep.), exhibits a sharp differentiation of female and worker forms. According to Bequaert (1932), "*Vespula squamosa* is unique, not only in the subfamily Vespinæ, but among all social Diploptera, for the extraordinary dimorphism of the sexes. While worker and male are very similar, the queen is so different in

size and color pattern that for a long time its true identity was not even suspected. Intermediate examples, which in most social Diploptera connect the fertile queens with the sterile workers, are not known for *V. squamosa.*" We find as a result of their more incisive female dimorphism that the colonies of the Vespinæ are founded by single queens and remain haplometrotic like the colonies of bumble-bees and most ants.

Considerations like the preceding have convinced several investigators (H. von Ihering (1896), O. M. Reuter (1913), Ducke (1914), Roubaud (1916) and Bischoff (1927)) that in the social wasps the haplometrotic has developed out of a pleometrotic condition, contrary to the manifest course of development in the Formicidæ. We have seen that Rau, though offering a valuable theory of the origin of regular haplometrosis and occasional pleometrosis in northern Polistes, does not reach a definite conclusion as to which form of colony formation is the more primitive. Von Buttel-Reepen, however, in an important chapter of his *Leben und Wesen der Bienen* (1915), vigorously supported the thesis, "Der Weg zum Insektenstaat läuft sicherlich nur durch die Familie," and therefore held that the family consisting of a single mother and her daughters is the prototype of all insect societies. He was the first to clarify the problem by critically reviewing the literature and carefully distinguishing between primary and secondary polygyny (pleometrosis), or what he called 'Sippenpolygynie,' in the various groups of social insects.

Primary polygyny is the founding of a single colony by more than one fecundated female, secondary polygyny the subsequent development, either in an originally monogynous or in a primarily polygynous colony, of daughter females, which after fecundation remain in the nest as so many secondary queens.[1] After producing a large population, these colonies may divide by swarming (as in tropical bumble-bees and Polistes) and give rise to incipient colonies, which are either of the haplometrotic, or primary pleometrotic type, according to the number of nest-founding females. Bequaert (1918) expresses himself as "much in favor of H. von Ihering's and Roubaud's opinion that, among the Vespidæ at least, the evolution of solitary into social instincts did not proceed from the habit commonly observed in many solitary wasps of building their nests in close proximity [as e. g. in the Zethinæ], the isolated nests of different females thus tending to merge gradually, so to speak, into larger, common structures cared for by several females; but that it was rather the outcome of a tendency of the young wasps to stay with their mother upon emerging from the nest [see also Wheeler, 1922, p. 131]. These primitive polygynous societies upon becoming more populous tended to divide by pleometrosis, the haplometrotic or monogynous condition being much

[1] Bischoff (1927, pp. 443, 444) uses "primary and secondary polygyny" in an unusual, apparently phylogenetic sense. Thus he calls the monogynous (haplometrotic) Belonogaster colony "primarily polygynous," because its entire personnel is of the same fertilizable, female type. His "secondary polygyny" is what Wasmann called primary pleometrosis, namely the founding of a colony by several fertile females.

more specialized and of a later date." The last sentence of this quotation shows that the term 'monogyny' is not always used by students of wasps as an exact synonym of Wasmann's 'haplometrosis' because true workers as contrasted with females are scarcely distinguishable, at least without dissection, except in the Vespinæ. As Bequaert implies, a haplometrotic colony, consisting of a mother wasp and her morphologically indistinguishable daughters, such as we find in Belonogaster, would seem to represent the primitive condition out of which have developed along diverging lines both the primary and secondary pleometrosis of such forms as Polybia and the primary and accentuated haplometrosis of Vespa, without subsequent, secondary pleometrosis. Dr. Bequaert informs me that this is still his opinion. He believes that the one-mother-family was originally the universal form of the wasp society and that the pleometrosis and swarming of the type seen in Polybia are a more recent, tropical development, confined, with the possible exception of Polybioides, to the wasps of the New World.

Turning to the groups of social bees severally derived from diverse ancestors among the solitary bees and therefore originally from Sphecoid wasps, we find that opinions differ in regard to the importance of the independent, or haplometrotic, foundation of the colony. Von Buttel-Reepen (1915) was convinced that bee societies are essentially like ant societies in having arisen phylogenetically as a family consisting of a single fertile mother and her affiliated daughters.

Bumble-bee colonies have long been known to be of this type, and the Meliponinæ (stingless bees) and Apinæ (honey-bees) may obviously be interpreted as representing a more specialized, secondary, or derivative condition. It was assumed that the most primitive conditions, linking the solitary bees with such a society as that of the Bombinæ, might be found among some of the lower bees, notably the Halictinæ. At that time Brauns had not yet published his interesting studies (1926) on various small carpenter bees of the South African genus Allodape, which show that there are other primitive societal types among the Apoidea. Within the limits of the single genus Allodape he was able to recognize a series of hypothetical phylogenetic stages beginning with a mass provisioning of the larvæ with pollen and honey, comparable with Type B among the solitary wasps, and ending with a stage of progressive provisioning (Type C) which involves an acquaintance of the mother with her offspring and their temporary affiliation with her as adults. In Allodape, therefore, the colony has a haplometrotic origin as in Bombus.

Although European entomologists have studied the Halictine bees for more than a century, there is no consensus of opinion in regard to their behavior, probably because they are among the most difficult insects to investigate. They form a great complex (more than 1000 species) of often closely related species which even at the present time seem to be undergoing evolutionary changes and subtle adaptations to their ecological environment. The species

therefore present peculiar differences in the number of their annual generations, and these may differ in slight morphological characters. Fabre (1879–80), who studied mainly *Halictus calceatus* and to some extent *scabiosæ* and *fodiens*, maintained that the over-wintered fecundated females produce only female offspring and that these in turn produce parthenogenetically the fall generation consisting of both sexes. He therefore distinguished two annual generations, an autumnovernal, with fecundated females, and a parthenogenetic, or agamic, summer generation. Armbruster (1916), mainly interested in proving the parthenogenetic origin of the bisexual fall generation, undertook to determine the number and character of the annual generations by a statistical study of the flight records of German Halicti, and reached the conclusion that the males and females mate in the fall, but that the females, as well as the males, at least in northern Europe, die after provisioning their cells. Hence the brood alone passes the winter, and produces nothing but females the following spring. These give rise without fecundation to a summer generation of females which in turn become the parthenogenetic mothers of the fall generation of males and females. Thus, according to Armbruster, there are three annual generations, since the fall and spring females are not the same individuals, as Fabre and others have maintained, and there are two parthenogenetic generations, the first producing only females (thelytocous), the second both sexes (ampherotocous). In a later contribution (1925) he

records some remarks on *H. malachurus*, which add little to Legewie's observations. These appeared in a preliminary note in 1922 and in more elaborate form in 1925. In the meantime Stöckhert (1923) had published independently on the same species of Halictus. The great discrepancy between these authors, both in regard to the facts and in regard to their bearing on prevailing theories of the origin and meaning of insect societies, calls for more detailed consideration.

Legewie, whose account agrees in the main with Armbruster's, devoted two years to the study of a single large *H. malachurus* aggregation near Gottenheim, Baden. He found that the fertilized female, after hibernating in some unknown shelter (not the last year's nest!), digs in the spring a perpendicular tunnel in the earth to a depth of 20–25 cm. and constructs at right angles to it about half a dozen brood-cells. These she provisions with bee-bread and lays an egg in each, but does not close them. She dies in about six weeks, either before or soon after her brood emerges. This brood, which constitutes a distinct generation (first agamic, or summer generation) and develops from eggs fertilized during the preceding autumn, consists entirely of females of the form known to systematists as *H. longulus*. They remain in the old nest and coöperate with one another in deepening the tunnel and in constructing and provisioning a cluster of 19 to 20 brood-cells, which are also left open. The eggs laid in the cells by the larger individuals of this first agamic generation are unfertilized, but nevertheless give rise to a second agamic

summer generation of somewhat smaller *longulus* females. The latter repeat the behavior of the preceding generation, but their parthenogenetically produced offspring (60 to 65 in number; in one case 98!) consist of males and females in about equal numbers of the form *malachurus* and constitute the fall (first) generation. After mating in the nest the males die, while the females leave the old nest to pass the winter in unknown hibernacula and in the following spring become the mothers of the first agamic generation.

Stöckhert's observations were carried out during seven years in Upper Bavaria, for the most part on *Halictus malachurus, maculatus, sexcinctus, immaculatus* and *puncticollis*, which happen to represent most of the European groups of the genus. The observations relating to reproduction and parthenogenesis were carefully controlled by Zander, who dissected the female reproductive organs. It appears that the number of annual generations differs in different species of Halictus. Thus some northern forms, e. g. *H. lineolatus*, have only one generation, like many species of Andrena, and others (*H. (Lucasius) clavipes* and *H. soror*) have two, each consisting of both sexes, also like certain Andrenas. Moreover, some Halicti with long flying periods may have a third generation intercalated in the autumn, especially when the advent of winter is delayed (*H. morio, puncticollis, villosulus*). But whether there are one, two or three generations, the males die in the fall, though rarely in some South European species a few may survive and fly during the following spring, whereas the females

always hibernate in the nest where they were born. The overwintered *malachurus* females sometimes appear as early as the middle of March and begin to clean and varnish the burrows and to visit the flowers of willows and dandelions. Although several females have been hibernating peacefully in the same burrow, their number is now reduced to three, two or normally only one, owing to the struggles among them for possession of the burrow. The ousted individuals have to move to unoccupied nests or to dig new ones. The brood-cells are built directly off the main gallery, provisioned and provided with eggs. If more than one female remains in the nest, these daughters of the same mother nevertheless build separate cell-clusters. By the middle of June the brood emerges and consists almost exclusively of females. They are smaller than their mother, differently sculptured and belong to the form *longulus*. There are no *longulus* males. The mother *malachurus* still survives, and her *longulus* daughters remain with her and begin to construct brood-cells. The eggs for these cells are laid by the mother and not by the *longulus* daughters, which, however, collect the provisions consisting mainly of hawkweed and dandelion pollen. The old mother remains at home and guards the nest entrance in the manner described by Fabre and others. The *longulus* females forage till about the last of September, although each individual lives only four to six weeks. Their number increases till in August there are about a dozen in each nest. Fertile females of the *malachurus* form begin to appear about the beginning of

August, also from eggs laid by the old mother. They are very drowsy and lethargic, compared with the very active, bustling *longulus* females, and collect no pollen, though they visit the flowers for nectar. The males, which have been appearing and increasing in numbers in the meantime, and are also the offspring of the old mother *Halictus*, pay no attention to the *longulus* females, but eagerly pair on the surface of the nest with the young *malachurus* females when they leave the burrow for the first time on some sunny day. Dissection of the *longulus* females shows that they are never fecundated. The old mother, after surviving the preceding winter and producing the summer brood of *longulus* and the fall brood of *malachurus*, though much worn and with frayed wings, lives till the end of the season. Zander's dissections showed that her ovaries may contain ripe eggs and her spermatheca an abundance of sperm till the end of August. Somewhat later she loses her power of flight, crawls away and dies. The *longulus* females and the males then also perish, but the young fecundated *malachurus* females go into hibernation in their mother's nest.

It seems to be impossible to harmonize these diverse accounts of *H. malachurus*. According to Stöckhert, the overwintering female lives a full year, surviving as the mother of the colony throughout the spring and summer and producing all the *longulus* females as well as the fall, or *malachurus*, brood of both sexes. There is no infringement of the Dzierzon rule. The sterile *longulus* females are clearly analogous to

the workers of the bumble-bee, wasp and ant colonies. There is really no alternation of generations, but a single annual haplometrotic colony, with successive, more or less overlapping broods, only the last of which consists of sexual individuals, except for occasional males which may appear in the same broods as the *longulus* females. According to Armbruster and Legewie, on the contrary, *malachurus* has three discrete annual generations, namely two successive agamic summer generations alternating with single fall (overwintering) bisexual generations. The agamic generations consist entirely of females, which lead a coöperative social existence, though a mother queen is absent. We have, therefore, an extraordinary heterogony of two social alternating with single nonsocial generations, because the overwintering females behave exactly like solitary bees. In fact, Bischoff (1927), who adopts Legewie's account and says nothing about Stöckhert's in his admirable volume on the biology of the Hymenoptera, states that in northern Germany there is only one generation of *H. malachurus*, as in most other solitary bees, and that the conditions so differently interpreted by Legewie and Stöckhert have developed in more southern latitudes in response to the longer foraging season. If Armbruster's and Legewie's interpretation is correct, the Dzierzon rule has been "shot to pieces" by this climatic increase in the number of generations, for though the first *longulus* generation develops according to the rule from fertilized eggs, it produces fe-

males, and these in turn produce both sexes from unfertilized eggs.

In a postscript to his paper, Stöckhert takes exception to many of Legewie's assertions, affirming that the old females of the fall generation certainly survive throughout the following spring and summer, that the brood-cells are always closed after oviposition, that the number of individuals cited for the *longulus* and *malachurus* broods is much smaller (not more than 40 in the extremest cases), that the females of the fall generation hibernate in the maternal nest, that mating takes place on the surface of the nest, etc. And although he concedes that the *longulus* females probably coöperate in constructing and provisioning the brood-cells, he is at a loss to understand how Legewie was able to obtain this information. There is, indeed, nothing in his papers to prove that his conclusions were reached by any other process than observing, counting and measuring the bees at the nest entrance and the completed brood-cells and their contents after they had been excavated. It seems strange, moreover, that the small *longulus* individuals of the third generation, corresponding, according to Stöckhert, to the smallest and sexually least endowed workers of the Bombus colony, should produce the resistant, fertile females of the fall generation.

Both Armbruster (1923) and Legewie (1923) have criticized Stöckhert's paper, but in a rather loose and indefinite manner. Bischoff (1927), as previously stated, is silent on the subject and seems to accept

Legewie's interpretation of the facts as established. Perhaps the strongest confirmation of the latter's work comes from Alfken, a most competent student of the taxonomy and ecology of the Halicti.[1] Here, then, the matter rests till the behavior of these bees can be reinvestigated, and I should close the discussion at this point were it not that Legewie (1925, 1931) has advanced several generalizations which differ in certain respects from those of von Buttel-Reepen, myself and other writers on the social behavior of insects. In discussing these generalizations, which relate mainly to parthenogenesis, "matriarchy," the "brood-egotism" of the female, and the origin and social behavior of the worker caste, I accept provisionally Legewie's interpretation of the annual generations of *H. malachurus*.

(1) *Parthenogenesis.* Von Buttel-Reepen was of the opinion that "all society formation [in insects] is based on the existence of parthenogenetic reproduction." Legewie, however, concludes from his study of *H. malachurus* that the form of reproduction, whether gamic or agamic, has "as good as nothing to do with the social life of bees, wasps, ants and termites." I cannot assent to either of these assertions. Parthenogenesis, which has never been observed among the termites, is apparently in the social Aculeata an ancient idiosyncrasy, which they have inherited not only from their solitary, but even from

[1] Legewie says (1923, pp. 76, 77): "I know from many written and oral communications with Alfken, that his findings and those of his student Wagner have been correctly interpreted ("durchaus richtig gedeutet") by Armbruster."

their more remote, Terebrant ancestors. Far from having no bearing on social developments, it seems actually to have led to the adoption of a purely feminine type of society, since the unfertilized eggs of the females and workers develop, at least as a rule, into haploid males, which, though necessary agents of fecundation, nevertheless take no part in the social activities of the community. Such social participation was, in fact, precluded by the narrowly specialized, purely fecundative rôle which the male had already acquired among the solitary Aculeates long before the progressive feeding of the young by the mother laid the foundation for future social developments. Hence, in accordance with Dollo's well-known law of evolution, the Aculeate male could only become more specialized instead of reverting to a stage in which it might be capable of sharing equally with the female in caring for the young, as in the termites. The phylogenetic origin of the latter from such primitive and relatively unspecialized insects as the primitive cockroaches (Protoblattoids) may very well account for the bisexual structure of their societies.

(2) *Matriarchy.* Legewie believes that the "mother-family, or matriarchate does, indeed, characterize certain species [of social insects] but is at any rate unnecessary for social life." This statement is based on his conviction that the overwintered female of *H. malachurus* dies before or soon after the emergence of her progeny of the first agamic generation and that the latter nevertheless coöperate with one another and exhibit a social division of labor in build-

ing and provisioning the brood-cells that are to yield
the second agamic generation. In further support of
this contention he cites the development of fertile
gynaecoid workers and the rearing of substitution
queens in ant and termite colonies that have lost their
mother, the well-known fact that the young honey-bee
queen may not be the mother but a sister of the work-
ers, and the regular absence of queens in the hives of
the Cape honey-bee. Since in his opinion social be-
havior is manifested only "when an animal labors for
the progeny of other individuals and incidentally for
the adults themselves," an insect society is possible
without a nest-mother. I am willing to accept the
definition, though it is neither new nor altogether
satisfactory. Whether the coöperation of the workers
is completely explained by the genetic, mother-
daughter relationship, or whether it is only one of
several conditions of social life in the insects, will be
discussed in the sequel.

Limitations of space preclude an adequate defence
of the importance of the mother-family concept in the
comparative and phylogenetic study of social and
subsocial insects, but attention may be called to a few
matters which appear to have been overlooked by
Legewie. First, I would take exception to his inter-
pretation of the conditions in *H. malachurus*, because
it is not permissible to homologize the overwintered
female *plus* the first agamic generation with the
mother-daughter family of monogynic ants, Vespa,
Allodape and bumble-bees. According to Legewie's
own account, though the overwintered female is ob-

viously the mother of the first agamic, the grand-mother of the second agamic and the great-grand-mother of the solitary, or bisexual, generation, we are dealing with three discrete generations, and the agamic generations are really two different, self-contained, primary, pleometrotic societies, analogous to the small, recently founded, pleometrotic societies of Polistes and Polybia. The agamic females differ, to be sure, in remaining unfertilized, but since some of them at least are able to produce female, and in the second generation both male and female, offspring, there is, as Legewie admits, nothing to be gained by fecundation. However unusual among bees, the coöperation of females without a mother is not more remarkable than that several Amblyopone females should bring up their brood in common or several *Myrmecocystus mimicus* females should unite to excavate a single initial nest. What is exceptional among ants and northern Polistes appears to be the rule among certain European Halicti and tropical Polistes. It seems that the consociation of the agamic Halictus females is due to the strong attraction of the old nest, an attraction which is manifested also by the females of the fall, or hibernating, generation.[1]

[1] A similar but feebler attraction, also accompanied by pleometrosis, occurs in several American species of Polistes, as Rau (1928, 1930, 1931) has recently discovered (see p. 117). "Hibernating Polistes wasps, after spending the winter in shelter away from the nest, visit the home at intervals, whenever the temperature is favorable, and finally return in the spring to the old home site," to found their colonies in the immediate vicinity. Janet and Ferton have made similar observations on the European *Polistes gallicus*, and Hoffer, Frison and Plath have shown that over-wintered bumble-bee females also remember the site of the old nest in

The importance of the mother-family pattern, or *Gestalt*, among insect societies is indicated also by two further considerations. First, there is the previously mentioned substitution of a fertile, or gynaecoid, worker or of a new fertile female specially reared from an undifferentiated larva by the workers to replace a missing queen. Legewie interprets this as proving that the mother is an inessential social element in the colony, but it seems to me rather to imply the opposite. The lost reproductive center of the unitary colonial organism is restored by a process clearly analogous to the regeneration or restitution of a lost organ or tissue in the body of the individual organism. The damaged colonial pattern, or *Gestalt*, is repaired with a functional, or even morphological, equivalent of the original nest-mother, though of different genetic relationship, just as the lens of a salamander's eye may be regenerated from the iris instead of from the original integumentary ectoderm. Second, a similar tendency is manifested in the cases of what Wasmann (1910) has called 'allometrosis' among ants, that is, by a colony adopting a parasitic female of another species. Such adoption may occur either in colonies of workers that have lost their queens or in intact mother-daughter colonies. In the

which they were reared. Descy (1925) is so greatly impressed by the homing behavior, or attraction of the nest, that he regards it as the basic factor in the development of all insect societies. "In all its forms, even the most rudimentary, and in all its tendencies, even the most complex, social life is essentially the result of the return to the nest; this action of memory which unites the individuals into a group is reinforced by more or less important and exceedingly variable environmental factors which should be analyzed in each individual case."

former, which are apt to offer little resistance to the intrusion of the parasite, the haplometrotic pattern of the colony is at once reconstituted. When the parasite invades a colony of the host already possessing a queen, she may be eliminated and the parasite adopted in her place, or the mother-family, if very vigorous or strongly integrated, may expel or kill the intruder.

In addition to these considerations attention may also be called to the fact that the mother-family arises naturally from the mother-brood relations in the solitary Aculeates and that it is the prevailing societal type in subsocial as well as social insects. Among the former we find it exhibited by such diverse groups as the Embidaria, Dermaptera, Gryllotalpa, Perga, etc., and among the latter in fully 95 per cent of the 8000 or more species of ants, in four of the five groups of social bees (Allodape, Bombinæ, Meliponinæ and Apinæ), and in nearly 70 per cent of the social wasps.[1] Termite colonies, too, apart from being biparental,

[1] Dr. Bequaert has given me some data on the prevalence of haplometrosis as compared with pleometrosis in the various subfamilies of Vespidæ. Omitting the Stenogastrinæ, in which the existence of true social conditions is still in doubt, we have the following approximate numerical distribution of the two forms of colony formation in the four other subfamilies:

> Polybiinæ: Belonogaster and Mischocyttarus (together about 50 sp.)
> haplometrotic; Polybia (about 100 sp.) pleometrotic; Polybioides
> (12 sp.) possibly pleometrotic.
> Ropalidiinæ (about 100 sp.) haplometrotic.
> Polistinæ (50–75 sp.) haplometrotic.
> Vespinæ (about 50 sp.) haplometrotic.

See also Ducke's table (1914), in which, however, the old terms 'monogamous' and 'polygamous' are used.

are substantially of a very similar type. Legewie's statement, therefore, that matriarchy "does, indeed, characterize certain species," is somewhat disingenuous, and the condition he describes in the very rudimentary and short-lived Halictus colonies, far from diminishing the theoretical significance of the mother-family, is rather an exception that proves the rule.

(3) '*Brood-egotism.*' This term, invented by Legewie to designate the intolerant behavior of the female of the social Aculeates towards other females of the same species, is synonymous with von Buttel-Reepen's 'monogynous instinct' (1915), which is, of course, open to the same objections as the 'cenobiotic instinct.' Legewie's term, though somewhat anthropomorphic, may be used for lack of a better. The phenomena designated by both terms are, however, by no means clearly defined or univocal, for whereas the females of the social insects often evince intense hostility to the very presence of other females of the same or other species, as in the classical example of the honey-bee queen, such predatory parasites as *Formica sanguinea*, Polyergus, Wheeleriella, *Bothriomyrmex decapitans* and *Labauchena daguerrei* [1] and

[1] Bruch (1930) has given us a most interesting account of this extraordinary, workerless Argentinian ant, which is a parasite of the fire ant, *Solenopsis saevissima* var. *richteri*. He found that from four to six of the small, dealated Labauchena females mount the back of the large Solenopsis nest-mother and coöperate with one another in gnawing off her head. As many as 45 days may be required to bring about this result! During all this time the parasites are protected from the Solenopsis workers by their contact with the host-queen's body and probably, therefore, by acquiring her individual odor. Perhaps the parasites drink the host-

many nonparasitic females while they are seeking to establish their colonies, numerous instances may be cited in which no such hostility is displayed. The above-mentioned colony-founding females of Amblyopone, Lasius, Myrmecocystus, Polistes, the agamic females of Halictus, and especially the secondary egg-laying queens in prosperous haplometrotic colonies of ants and wasps live most amicably not only with one another but also with the nest-mother. In all these cases the females are sisters, to be sure, and among the ants the amity of the females may subsequently yield to hostility, but brood-egotism is not definitely correlated with the reproductive maturity of the female, as is proved by the secondary queens in colonies of ants, wasps and tropical bumble-bees. These fertile individuals are sometimes very numerous in prosperous colonies. Von Buttel-Reepen (1915) found about 100 deälated queens in a single nest of *Tapinoma melanocephalum* var. *malesianum*, and Forel, Wasmann, Emmelius (1919) and I have observed similar cases. Legewie and Bischoff believe that these conditions are possible because ant-nests are such extensive systems of chambers and galleries that the females are able to avoid mutual contact. This supposition is unwarranted, because, as every experienced collector of ants knows, the numerous

queen's blood while they are leisurely beheading her. At any rate, they oviposit during their long period of attachment, and their eggs are carried away and reared by the Solenopsis workers. The parasites are definitively adopted by the latter only after decapitating the Solenopsis queen. Since the Labauchena females combine in their attack on the host queen, they may be said to exhibit both coöperation, or at any rate mutual toleration, and brood-egotism at the same time.

secondary queens and nest-mother are commonly found huddled together in one or a few chambers. They seem actually to crave one another's company. The same is true of the females in the cramped nests of the Meliponinæ, pleometrotic wasps and, to judge from Legewie's account, of the summer generations of *Halictus malachurus.* And even when the ant-nest is fragmented so that it forms a great number of disconnected chambers as happens in the cauline swellings of the South American ant-plant, *Cordia nodosa,* inhabited by *Allomerus octoarticulatus,* the small cavity of each swelling, as I have observed, not infrequently contains several crowded queens.

Brood-egotism, moreover, is not peculiar to the females of the social insects, but has been frequently noticed in those of the solitary wasps and bees. It is also exhibited, often to an exaggerated degree, by the workers of the social forms in their well-known hostility to workers and females from other colonies of the same species. Nor is this surprising since the workers are, of course, sterile or substerile females. Indeed this egotism, on further reflection, turns out to be fundamentally the same as all other animal 'self-assertion,' such as the mutual intolerance of the larvæ of Terebrants and parasitic Aculeates in general. It is well known that each of several larvae hatched in the body of the same host or in the same provisioned cell attacks the other till only one survives to appropriate the limited food-supply. This behavior has not been ascribed to a special 'larva-killing instinct,' because it is so obviously a manifes-

tation of the universal competition for food, mates, nesting sites and brood security, in short, of what has been so often called the 'instinct of self-preservation,' or in more behavioristic terms the 'struggle for existence.' It seems to me, therefore, that general statements concerning brood-egotism are not very illuminating and that more penetrating investigations undertaken to reveal the physiological and ecological bases of its variable and not infrequently contradictory manifestations might be more fruitful.

(4) *Origin and social behavior of the worker caste.* I agree, of course, with many of Legewie's comments (1925, Part II) on this topic, but he seems to me to attribute undue theoretical importance to the rudimentary and aberrant conditions in Halictus and to be insufficiently acquainted with the social wasps and ants, which, taken together, furnish such a consistent and interesting series of stages illustrating the progressive differentiation of the primitive monomorphic Aculeate female into female proper (queen) and worker. Notwithstanding his able criticism of traditional views based largely on the retrogressively specialized honey-bee and termite queens, he seems not to have freed himself altogether from the prevailing underestimation of the endowment, initiative and versatility of the more typical ant, wasp and bumblebee females. The behavior of these independent females is essentially that of the solitary wasp female, but they have increased their original endowment till it embraces also the progressive feeding of the brood and the adoption of the resulting adults. Since the

workers are merely smaller, modified replicas of their mother, we are justified in interpreting their structural, physiological and behavioristic peculiarities as being, to a considerable degree at least, so many phenotypic deviations from the original female genotype. Much of the following discussion, therefore, might have been included in the section on 'matriarchy.'

Legewie's contention is summed up in the following passage:

"We have seen that the auxiliary females, or workers, of all insect societies are little or not at all concerned with copulation and less given to oviposition than the normal females, or sexual individuals. To this we are unable to assign any other cause than the reduction of the sexual apparatus. The more feebly developed impulse to species-preservation through oviposition is, in my opinion, directly associated with the 'social instinct,' that is, with the carrying on of operations beneficial to the offspring of other individuals or to the latter themselves. The offspring help their mother, not because their oestrus has disappeared and therefore because only males can develop from their eggs, as von Buttel-Reepen and others believe, *but because the intimate bond which exists in the mother between her own brood and her nursing activities is severed, or at any rate loosened, in her [worker] offspring.*" There is here, and more especially in other passages in Legewie's paper, an interesting adumbration of the view which has been held by many priesthoods, namely that sexual repression is the path to

holiness and therefore to exalted thinking and ethical, social behavior.[1]

The biologist would regard this as a partial and distorted expression of the well-known incompatibility or antagonism in plants between sexual reproduction and vegetative growth or in animals between specialization in sexual activities, i. e. obedience to the interests of the species, and the activities which have to do with the development and maintenance of the individual. In non-social animals the antagonism is mitigated by such devices as periodic oestrus, barriers to inbreeding, preferential mating, combats among males, etc., but in social organisms even a partial solution of the conflict between reproduction and the welfare of the society is more difficult, owing to the close and precarious dependence of population-growth on the food-supply. In both human and insect societies starvation is obviously a controlling factor, more or less unregulated and often catastrophic in human, but exquisitely regulated and even exploited in the insect, society. This is possible because the latter is so highly integrated, owing to the close behavioristic interdependence of the nest-mother and the workers.

As previously remarked, the progressive differentiation of the worker from the female can be recon-

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[1] Hence the ancient priestly apophthegm, quoted by Schopenhauer: *seminis emissio est partis animæ jactura.* Perhaps the Freudians might inquire whether there is any significance in the fact that so many divines, from Gilbert White to Dzierzon, Langstroth, Mendel, McCook and Wasmann, have busied themselves with ants or honey-bees. Statesmen or ecclesiastical politicians rarely or never devote themselves to such avocations.

structed from the study of a long series of Vespidæ
and Formicidæ. The social wasp series, which de-
velops so very gradually out of that of the solitary
forms (Eumeninæ, Zethinæ), may be said to begin
with such a form as *Belonogaster juncea*, so adequately
described by Roubaud in 1916, and to terminate in
Vespula squamosa. In Belonogaster there is no worker
caste, since all the members of the colony, whether of
haplometrotic or pleometrotic origin, are monomor-
phic, fertile females. The haplometrotic colony con-
sists of the nest-mother and her daughters, the pleo-
metrotic of several sister wasps and eventually of
their daughters. In both cases the females are clearly
'social' in Legewie's meaning of that term, since they
coöperate in building the nest and in feeding one an-
other's larvæ. Even in this very primitive colony,
however, the recently emerged females act at first as
nurses and only later take to foraging and comb-
building. They are in all probability held together by
such chemical, trophallactic stimuli as the odor of the
nest and the secretions which they solicit and imbibe
from the mouths of the larvæ as a recompense for the
food administered. When the colony has grown too
large for the nest the older females leave it and either
singly or in small numbers establish new colonies.
Belonogaster thus represents a stage from which we
can derive on the one hand the haplometrotic, stelo-
cyttarous colonies of Polistes and Vespa and on the
other the very populous pleometrotic colonies of the
neotropical Polybias, with their elaborate phragmo-
cyttarous nests. Yet in all these forms, except Vespa,

the workers are so little differentiated from the females as to be indistinguishable externally, except in size, and internally only by their more rudimentary ovaries and the absence of a receptaculum seminis. Only in Vespa are the differences between the female and worker pronounced, and only in one species, *V. squamosa*, have the two castes been definitively established by suppression of intermediate, or annectant, worker forms. The morphological inferiorities of the worker as compared with the female were long ago shown by Paul Marchal (1896) to be due to insufficient feeding, or *alimentary castration* during the larval stage. In the adult workers the ovaries remain rudimentary except under unusually favorable conditions, because of their nursing activities which prevent the workers from appropriating sufficient nutriment to develop their oöcytes. There is, therefore, in the adult a physiological, *nutricial castration* (from *nutrix*, a nurse), which normally persists and reinforces the larval alimentary castration. This is enforced by the nest-founding mother on her first larval brood during the early spring months and is perpetuated in the larvæ of subsequent broods by the nutricial activities of the adult workers. But since the number of adult workers and therefore the food supply progressively increase as the season advances, both alimentary and nutricial castration gradually relax so that by the end of the summer larvæ can be reared as fertile females from the fertilized eggs of the nest-mother and males from her unfertilized eggs and those of the workers.

In the great family Formicidæ we are able to construct a more elaborate series to illustrate the further differentiation of the worker, beginning where the wasp series ends and leading up to extremely specialized conditions not unlike those encountered in the higher bees (Meliponinæ, Apinæ). In the lowest Ponerinæ (Myrmecia, Amblyopone) and in the Pseudomyrminæ, the difference between female and worker is of somewhat the same magnitude as in Vespa, but more striking, because of the complete absence of wings in the worker. Yet even these morphological differences are probably due to merely quantitative differences in larval feeding. The dimorphism increases in the Dorylinæ, many Myrmicinæ, Dolichoderinæ and Formicinæ, in which the workers may be diminutive, nearly or quite sterile and morphologically unlike the female. In some genera they may become polymorphic or dimorphic, separating into subcastes of maxima, media and minima workers or of soldiers and workers proper. The production of such diverse and extreme deviations from the primitive female type would seem to be due to qualitative as well as to quantitative differences in larval feeding.

The female ant shows a similar versatility or tendency to specialization in different directions. She, too, may become dimorphic, or exhibit alpha- and beta-forms as in the North American *Acanthomyops latipes* and the Japanese *Dendrolasius spathepus*, or much more frequently increase in volume and resign herself to being nothing but an egg-laying machine as

in Carebara, the Dorylinæ and numerous parasitic species. These females are much like the honey-bee queen in having completely lost the nest-constructing and brood-rearing behavior, which is still retained by most young female ants. Other females (Anergates, Anergatides, Bruchomyrma, etc.) have become such highly specialized parasites that they are no longer able to produce worker offspring, so that this caste has disappeared and the species has returned to the simple, original, sexually dimorphic condition. From one point of view these workerless parasites, which are also represented among the wasps (*Vespula austriaca, omissa* and *adulterina*) and bumble-bees (Psithyrus species), have ceased to be social organisms, since they no longer care for one another or their brood; from another, they have lost the worker caste because it could be most advantageously replaced by the worker personnel of the host colony. Finally, the female may herself disappear as a special caste and her reproductive rôle be usurped by the workers, as we have seen in the case of Diacamma, Rhytidoponera, Leptogenys *sens. str.*, Ocymyrmex, Leptomyrmex, etc. (see p. 79). This usurpation is the final stage of a process which had its phylogenetic inception among the haplometrotic wasps and lower ants, in which the first brood of workers, as soon as they are mature, take over the control of all the communal activities and by abundant feeding encourage their mother to devote herself exclusively to the single function of providing them with as many eggs as it is possible to rear. In the genera above mentioned, where

even this function is usurped by certain workers, outwardly at least indistinguishable from their sisters, the colony is very much like the colonies of the agamic generations of *Halictus malachurus*, and might have been cited by Legewie in support of some of his arguments. It is obvious from a consideration of Lobopelta, however, that the apparently queenless condition of the colony is a secondary development and at bottom merely a functional reëstablishment of the original mother-worker family.

The preceding is, of course, a crude and hasty sketch of what was undoubtedly a very long and complicated process, for the fossil ants of the Eocene and Lower Oligocene show that by the beginning of the Tertiary the worker had become as different from the female as it is at the present time. In the social wasps the differentiation is either still in progress or, more probably, has been arrested in its earliest phylogenetic stages. All our data, nevertheless, give a consistent picture of the worker as a comparatively short-lived hunger-form of the female, a product, in other words, of a persistent, social, trophic constraint, and a being capable under normal conditions of repeating only the earlier brood-rearing portion of the female's behavior cycle as it is exhibited by such forms as the Ponerinæ. The female of higher ants seems no longer to forage, but Eidmann's recent observations (1931) indicate that at least in some species she may perhaps retain a latent or rudimentary disposition to do so, just as she retains the ability to repeat the whole colony-founding portion of her be-

havior cycle if her first brood of workers is removed, though she never attempts this under normal conditions. The development of the gynaecoid worker, or substitution queen, from an ordinary adult worker indicates that the latter must inherit the sensory, visceral and cerebral basis of her mother's activities. There is in the normal worker, therefore, merely a physiological curtailment of the purely egg-laying stage of the old female, but neither a disruption nor even a loosening of the neural Anlage of her behavior cycle. Legewie postulates these conditions because he believes that the colony-founding female is capable of caring only for her own first brood whereas the workers alone rear all her subsequent broods and are therefore truly social. But, as we have seen, several females even of normally haplometrotic species of wasps and ants (Belonogaster, Polistes, Amblyopone, etc.) may start a colony together and on such occasions bring up their brood in common as if they were so many coöperating workers. There is, indeed, no reason to suppose that the females are aware of any such distinctions as those suggested by our words 'own' and 'other,' as applied to the brood. As soon as the nest-founding female has oviposited, her eggs become, of course, so many foreign objects and her care of them and the resulting larvæ is a mystery as great or as small, from our human point of view, as her care of objects of the same kind deposited by other associated females in her immediate neighborhood. Thomas (1929, p. 97), in his recent highly reactionary, anti-evolutionary volume on instinct, finds

the care of her young by the animal mother an in-
scrutable mystery. He says: "As soon as the egg is
laid or the young born, it constitutes a distinct in-
dividual, whose sensations and needs are entirely
foreign to the parent individuals. That the sensation
of its own hunger should be dynamogenic for the in-
dividual itself, is very natural, but I still ask, and we
shall probably forever ask, how the requirements of
the young, and particularly those of the egg, can im-
pose themselves on the parents." If pressed, Thomas
would, perhaps, appeal to something in the nature of
a clairvoyant 'maternal instinct' or 'sympathetic in-
sight,' even when confronted with facts like the occa-
sional adoption of the young of other animals by dogs
and cats that have lost their sucklings. Bonnet and
Giard would interpret such cases of perverted as well
as those of normal 'mother love' as due to the
mother's urge to relieve the pressure of milk in her
mammary glands. But what shall we say of the be-
havior of the solitary wasp or bee that not only builds
a cell but provisions it with just the right amount and
kind of food for the larva that is to issue from the
carefully deposited egg? All these apparently pur-
poseful arrangements are indeed wonderful, but so
are the intricate devices which insure the nourish-
ment and protection of the embryo in the seed of the
higher plant or of the foetus in the uterus of the mam-
mal, and yet neither the botanist nor the embryol-
ogist imagines that he is gaining any insight into such
physiological phenomena by attributing them to
'maternal instinct.' The term is quite as useless when

applied to the behavior of the mother wasp, bumble-bee or ant, which is acquainted with her eggs and larvæ. We may assume, at least till proof to the contrary is forthcoming, that the eggs and young larvæ "impose themselves on the parent," that is, act as stimuli which elicit the nursing responses, because they emit specific agreeable odors or secretions that make these responses irresistible. Since in all probability all the eggs and young larvæ have the same chemical properties, there is no reason for the female to distinguish the progeny of other females from her own. And since the worker inherits the neural basis of her nursing behavior from her mother, any egg deposited by the latter or by another worker will act as a stimulus to the same response. The equality of the eggs and larvæ, at this stage at least, is indicated by the way they are kept in packets by all the higher ants or strewn indiscriminately on the floor of the nest by the Ponerinæ. Subsequently, chemical, size and probably secretory differences appear among the progeny and lead to differential treatment both by the mother and by the workers. The brood behavior of these insects is therefore best described as motivated by a craving or appetite. That it is actually a modified appetite ('Reizhunger') for food or trophic stimuli is shown by the normal paedophagy, or devouring of the eggs and larvæ of the first brood by the female and of later broods by the workers even in opulent colonies.

Although the preceding considerations are opposed to some of Legewie's views, they do not militate against his contention that the workers of the social

insects are much more alert and display more versatile responses to their environment, or, as he expresses it, have a more expanded *Umwelt* (in von Uexküll's sense) than the females, because their brain is less powerfully influenced by their ovaries through the visceral, or sympathetic nervous system. That these differences in *Umwelt*, however, may occur during the lifetime of the individual worker as in the female of the Ponerine ants (e. g. Myrmecia) is shown by the gynaecoid, in which, as soon as it begins to oviposit, the Umwelt is narrowed like that of the old nest-mother, and the insect becomes, so to speak, little more than an egg-laying monomaniac, irresponsive to the multiform communal activities in which it participated before its oöcytes began to mature. Hence I believe that we are justified in assuming that there is no sharp constitutional neural difference between the female and worker and that the neural endowment of both castes is such as to permit a considerable range of adaptation to the coöperative social milieu in which they are immersed. That the neural endowment is really the same in female and worker and the differences in their behavior very largely phenotypic, or due to environmental influences, seems clearly to follow from the fact that both castes develop from eggs of the same genetic constitution and that the nervous system of the worker larva is very probably little if at all affected by the partial inanition or malnutrition to which it is subjected during its development. Jackson (1925) has shown that the nervous system and other ectodermal tissues of ani-

mals are more resistant to such influences than the entodermal, and much more so than the mesodermal tissues (fat-body, etc.). Be this as it may, however, the Aculeate insect-society, from its very inception, is a mother-daughter colony, consisting originally of like homodynamous individuals which, as a result of their interactions with one another and a peculiar ecological environment, undergo progressive differentiation and integration to form a social superorganism of considerable stability and capable of reproducing itself by processes analogous to sexual reproduction and budding in individual organisms.

Conclusion

The reader who has had the patience to wade through the preceding discussion must have been impressed by the plasticity and complexity of social reactions and adjustments among the Aculeate Hymenoptera. Our present knowledge, however, probably covers only a limited number of the existing types of insect societies. That it has taken so many years to bring to light the Vespine method of colony formation in the most primitive ants encourages the belief that field observations on other exotic forms will bridge many important gaps in our theories of the origin and development of insect communities. Before many of the problems to which von Buttel-Reepen, Legewie, myself and others have been devoting our attention can be adequately formulated we need much more detailed information concerning the behavior patterns of the Zethinæ, Stenogastrinæ and

higher Polybiinæ among the wasps, the Cerapa-
chyinæ, Dorylinæ and Leptanillinæ among the ants,
and the Meliponinæ, tropical Halictinæ, Ceratininæ,
Bombinæ, Apinæ, Euglossa, etc., among the bees.[1]
Here, as has happened in so many other fields of in-
vestigation, progress may have been slow because we
have not asked the right questions. The geneticists,
biochemists, biometricians and general physiologists
have been little interested in our ethological pursuits
and problems, and when they have endeavored to

[1] The large carpenter bees of the genus Xylocopa should be added to
this list. Mr. Phil Rau has generously permitted me to read the manu-
script of his forthcoming book, in which, after a very interesting account
of the wasps and bees of Panama, he devotes a chapter to his observations
on our common *X. virginica* in the vicinity of St. Louis, Missouri. He
shows that the young brood of this bee emerges in August but continues
to inhabit the long, cylindrical burrows made in the wood by the mother
till the following spring. "The juveniles are very gregarious, and huddle
so close together that they literally pile themselves one atop the other.
Early in life they get the feeling of living together as children." Before
hibernation some of the individuals collect pollen and nectar and store it
for common consumption. It "is stored by being banked firmly against
the far end of the tunnel. Here it is eaten from time to time in luxurious
ease and safety. In early and middle September I found a number of
these caches of pollen, but by October 10 it had practically all been con-
sumed; only a few grains adhered to the walls to tell the story." This food
is not of the same consistency as that prepared by the mother for her
larvæ. Even in the spring, when the overwintered females start their
broods in the same or freshly dug burrows, sisters may feed one another
with regurgitated honey, as Rau observed on one occasion. Because *X.
virginica* seems to have been gradually moving northward since glacial
times, "one wonders," he remarks, "if any precedent for this habit exists
among the immediate relatives and ancestors in the tropics, or if it is a new
acquisition among the pioneers in a new climate." These observations
are of considerable interest in connection with Legewie's account of the
agamic generations of Halictus. Mutual feeding is certainly more inti-
mately social than coöperation in building and provisioning brood-cells,
and yet the Xylocopas both before and after hibernation are best de-
scribed as gregarious, as Rau has perceived.

apply to them their own methods of investigation, have not been particularly helpful, partly, no doubt, because the taxonomic and morphological data with which they were supplied were insufficient. We know that the most fruitful experimentation in morphology, embryology and physiology was delayed till the comparative work in these sciences had reached an advanced stage. It has been recently claimed by German theoreticians, and especially by Adolf Meyer (1926), that comparative morphology, embryology and physiology, which he embraces under the term 'typology,' will retain their importance among the biological sciences till they can be completely converted by more searching, experimental analysis into biochemistry and biophysics. Granting that such a conversion may be the ultimate aim or fate of the sciences in question, there is certainly no immediate prospect of its realization, even if, as seems highly improbable, structural, developmental and functional biotypes as such should cease to arouse and sustain our interest. At the present time comparative typological procedure seems to be one of the most fruitful methods in the new and very complex biological sciences of ethology, behaviorism, psychology and sociology. This is evident from the recent developments of psychoanalysis and from the work of Jung (1924), Kretschmer (1927, 1931) and Jaensch (1926) on constitutional and psychological types in man. More attention to typological methods in human sociology has been warmly advocated by Oeser (1932). Certainly in comparative sociology in general

and in that of the insects in particular it seems advisable to continue with the description and comparison of typical behavior patterns, gleaning such hints and indications of the deeper processes as we can, till our data are of more interest and use to the experimentalists and statisticians in their minute analyses. From this point of view the preceding pages may be regarded, perhaps, as a slight contribution to the typology of social behavior in the Aculeate Hymenoptera. I have attempted to describe and discuss in detail only the independent method of colony formation among the ants. The two dependent methods, that of swarming and the parasitic, or allometrotic, have been given only incidental and cursory consideration. Much labor would be required to collate the scattered and rather fragmentary accounts of the former in the myrmecological literature and would hardly be worth publishing at the present time unless accompanied by fresh material. The data on allometrosis, on the other hand, owing to the greater interest which it has aroused since the beginning of the present century, would require another volume for their adequate presentation. The mutual relations of all the known types of colony-founding in the Formicidæ are summarized in the following table:

FORMICID METHODS OF FOUNDING COLONIES

I. *Independent Methods:*

    A. *Haplometrotic.*

        (1) *Myrmecia Type.* Female intermittently claustral, forages for self and brood during nest-founding period. Probably most Ponerinæ.

(2) *Camponotus Type.* Female completely claustral, rearing brood without leaving cell. Most Pseudomyrminæ, Myrmicinæ, Dolichoderinæ and Formicinæ; probably a few Ponerinæ (e. g. *Brachyponera lutea*).

(3) *Atta Type.* Female completely claustral, but starts and maintains a fungus-garden while rearing her initial brood. Attini among the Myrmicinæ.

(4) *Carebara Type.* Very large female founds colony in termite nests with aid of minute workers transported on her feet. This type may be regarded as a variant of I B (2).

(5) *Formicoxenus Type.* Inquilines. Female founds colony claustrally but in the nest of another species. *Formicoxenus nitidulus, Leptothorax emersoni, Symmyrmica chamberlini, Myrmoxena gordiagini, Chalepoxenus gribodoi,* among xenobiotic inquilines; many small species of Solenopsis, Pædalgus, Aëromyrma, etc., among thief-ants; and a peculiar inquiline (*Cepobroticus symmetochus*) living in the nests of the fungus-growing *Sericomyrmex amabilis.*

B. *Pleometrotic.*

(1) *Amblyopone Type (Primary Pleometrosis).* Colony founded by several coöperating females; usually an occasional and temporary method, and becoming haplometrotic by death or separation of females. Alternative method to I A (1) or (2); probably regular and permanent in some Formicidæ.

(2) *Iridomyrmex humilis Type (Secondary Pleometrosis).* Colony proliferates by swarming (hesmosis) of detachments of workers accompanying secondary queens (daughters of nest-mother). Alternative method to II B (2) in a number of Formica species; perhaps the only method of colony formation in the Dorylinæ.

II. *Dependent, Parasitic or Allometrotic Methods:*

   A. *Dulosis, or Slavery.*

   (1) *Formica sanguinea Type (Facultative Dulosis).*
   Female invades nest of host species (*Formica fusca*,
   etc.), kills resisting workers and secures worker
   brood which on maturing rears her progeny. The
   mixed colony thus arising and later increased by ·
   slave-making raids by the *sanguinea* workers on
   other colonies of the host species may eventually
   become a pure colony of the parasite. *F. sanguinea*
   and its subsp. *aserva*, etc.

   (2) *Polyergus Type (Chronic Dulosis).* Female invades
   nest of host species (*Formica fusca*, etc.), kills
   nest-mother and is adopted by workers. Worker
   offspring of parasite increase mixed colony by slave-
   raiding, but no pure colony of the parasite super-
   venes. *Polyergus rufescens* and its subspecies;
   Strongylognathus huberi, alpinus and *rehbinderi,
   Harpagoxenus sublaevis* and *americanus.*

   B. *Temporary, or Protelian, Social Parasitism.*

   (1) *Bothriomyrmex decapitans, or Aggressive Type.* Fe-
   male invades nest of host (*Tapinoma nigerrimum*),
   decapitates nest-mother and is adopted by her
   workers, which rear the successive broods of the
   parasite. Eventually the host species dies out and a
   pure colony of the parasite survives. Bothriomyr-
   mex species of the subgenus Chronoxenus; probably
   also the Formicas of the *exsecta* group.

   (2) *Formica consocians, or Conciliatory Type.* Female
   invades nest of host species (*Formica incerta*) and is
   adopted by the workers after acquiring the brood-
   and nest-odor. Host queen probably killed by her
   own workers. Brood reared and eventual history
   as in **II B** (1). Formicas of the *rufa* and *microgyna*
   groups; *Lasius (Chthonolasius) umbratus* and its
   subspecies; probably *L. (Acanthomyops) latipes;
   Aphænogaster tennesseensis* and *mariæ.*

(3) *Dendrolasius, or Hyperparasitic Type.* Exhibited by females of *Lasius (Dendrolasius) fuliginosus* and probably also by *L. (D.) spathepus*, temporary parasites of *L. (C.) umbratus* which starts its colony as a temporary parasite of *Lasius niger*.

C. *Permanent Social Parasitism.*

(1) *Strongylognathus testaceus Type.* Female invades nest of host (*Tetramorium cæspitum*), but the nest-mother is permitted to survive and the parasite's brood is reared by the host workers. The workers of the parasite are few in number and do not make slave-raids; a more regressive stage of II A (2).

(2) *Epimyrma gösswaldi Type.* Female invades nest of host (*Leptothorax unifasciata* or *nigriceps*) and kills the nest-mother. Host workers bring up parasite's brood which comprises a few workers. Possibly also *E. foreli* and *kraussei*. Transition to II D (1).

D. *Workerless Social Parasitism.*

(1) *Wheeleriella Type.* Males very similar to the females, with well-developed wings. Female invades nest of host species and at least in some cases kills the nest-mother. Species of Wheeleriella, Epoecus (*pergandei*), Labauchena (*daguerrei*), Pseudoatta (*argentina*), Anoplolepis (*nuptialis*), Crematogaster (*kennedyi*), Sympheidole (*elecebra*), Epipheidole (*inquilina*), Epimyrma (*vandeli*); probably also Sifolinia, Parapheidole, Epixenus and Hagioxenus.

(2) *Bruchomyrma Type.* Males subpupoidal and subapterous. Host queen killed by her own workers. *Bruchomyrma acutidens, Anergatides kohli* and perhaps *Gallardomyrma argentina*.

(3) *Anergates Type.* Males pupoidal and apterous. Host queen killed by her own workers. *Anergates atratulus.*

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