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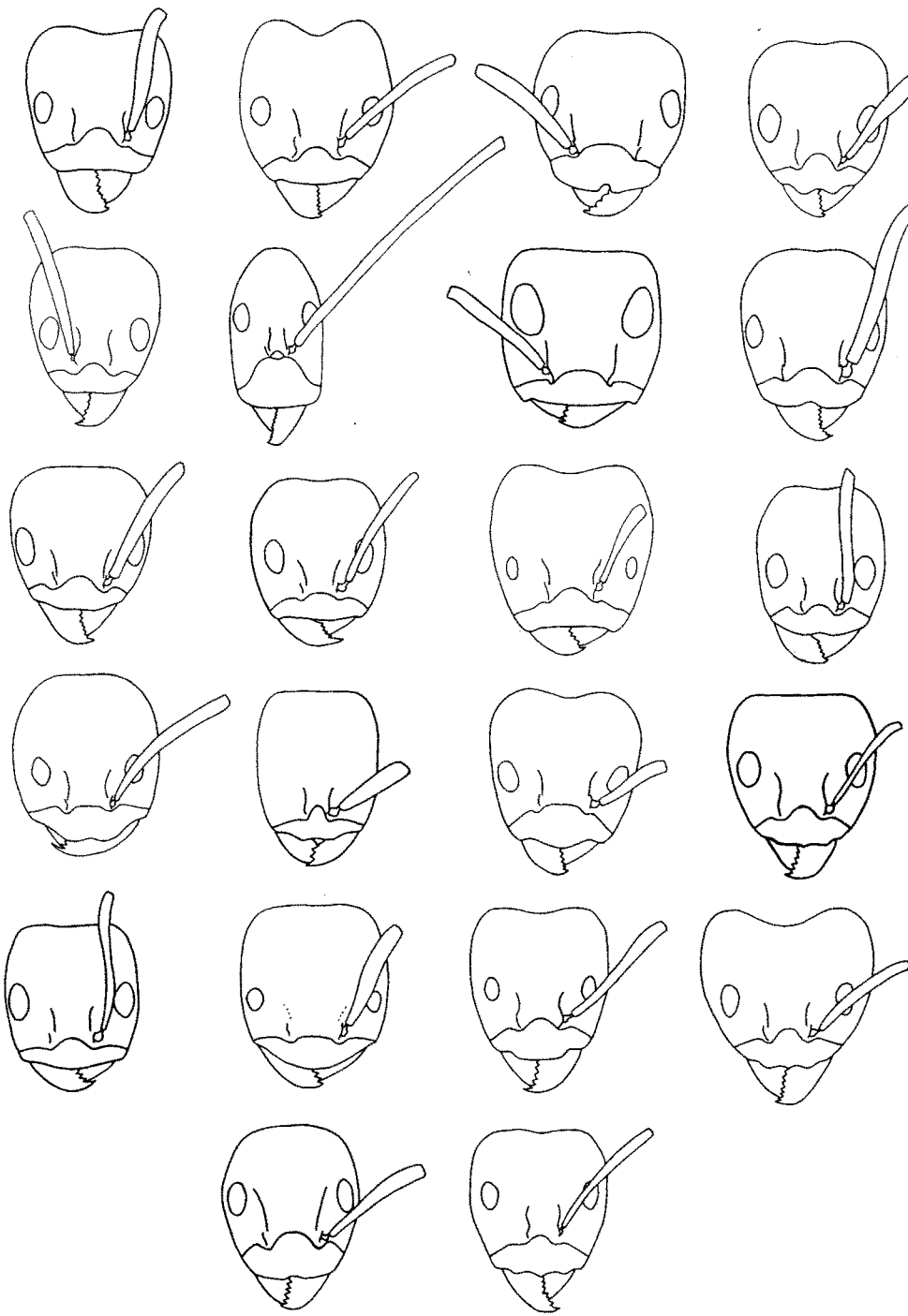

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Generic Revision of the Ant Subfamily Dolichoderinae (Hymenoptera: Formicidae by Steven O. Shattuck

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ABOUT THE COVER

Full face views of the workers of the genera of the Dolichoderinae. Most genera can be diagnosed from the overall habitus of the frontal view. For further explanation see the text. The editor of SOCIOBIOLOGY thinks these views are so useful that he is presenting uninterrupted reproductions of the outside cover on the insides of both front and rear covers. Interested users of the text can label them with their generic names.

Generic Revision of the Ant Subfamily Dolichoderinae (Hymenoptera: Formicidae)

by

Steven O. Shattuck[1]

ABSTRACT

In this study, the ant subfamily Dolichoderinae is revised at the generic level. Material from all geographic regions and representing all described genera (except fossils) is examined. Genera are diagnosed and described utilizing approximately 180 internal and external morphological characters drawn from workers, queens, males and larvae. Keys are presented for workers, queens and males, and distribution data is summarized for all genera. A total of 22 extant genera are recognized as valid. Proposed changes include the description of one new genus and the synonymy of seven previously valid names. The proposed generic-level classification of the Dolichoderinae is as follows: *Anillidris* Santschi, *Anonychomyrma* Donisthorpe, *Axinidris* Weber, *Azteca* Forel, *Bothriomyrmex* Emery [=*Chronoxenus* Santschi (syn. nov.)], *Doleromyrma* Forel, *Dolichoderus* Lund, (=*Acanthoclinea* Wheeler, =*Diceratoclinea* Wheeler, =*Hypoclinea* Mayr, =*Karawajewella* Donisthorpe, =*Monacis* Roger, =*Monoceratoclinea* Wheeler), *Dorymyrmex* Mayr [=*Ammomyrma* Santschi, =*Araucomyrmex* Gallardo, =*Biconomyrma* Kusnezov, =*Conomyrma* Forel (syn. nov.), =*Psammomyrma* Forel, =*Spinomyrma* Kusnezov], *Ecphorella* Forel, *Forelius* Emery [=*Amyrmex* Kusnezov (syn. nov.), =*Neoforelius* Kusnezov (syn. nov)], *Froggattella* Forel, *Iridomyrmex* Mayr, *Leptomyrmex* Mayr, *Linepithema* Mayr, *Liometopum* Mayr [=*Ctenobethylus* Brues (syn. nov.)], *Loweriella* (gen. nov.), *Ochetellus* Shattuck, *Papyrius* Shattuck, *Philidris* Shattuck, *Tapinoma* Förster [=*Micromyrma* Dufour, =*Neoclystopsenella* Kurian, =*Semonius* Forel (syn. nov.), =*Tapinoptera* Santschi, =*Zatapinoma* Wheeler (syn. nov.)], *Technomyrmex* Mayr [=*Engramma* Forel (syn. nov.), =*Aphantolepis* Wheeler], *Turneria* Forel.

In addition to the generic-level changes, numerous species-level changes are also made within the subfamily. These include the transfer of *Bothriomyrmex pallidus* to *Acropyga*; 61 new or revised combinations in *Dolichoderus* involving taxa previously placed in *Hypoclinea*, *Iridomyrmex* and *Monacis*; the

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replacement of the preoccupied name *Dolichoderus gibbosus* (F. Smith) with *D. quadridenticulatus* (Roger); 42 new or revised combinations in *Dorymyrmex* involving taxa previously placed in *Araucomyrmex* and *Conomyrma*; 3 new combinations in *Forelius* involving taxa previously placed in *Amyrmex*, *Neoforelius* and *Iridomyrmex*; the transfer of *Camponotus flavitarsus* (F. Smith) to *Leptomyrmex*; the transfer of *Ctenobethylus succinalis* Brues to *Liometopum*; the original description of *Loweriella boltoni*; 5 new combinations in *Tapinoma* involving species previously placed in *Semonius* and *Zatapinoma*; the objective synonymy of *Tapinoma canalis* Wheeler under *T. panamense* Wheeler, together with lectotype designations for both; the synonymy of *Tapinoma dimmocki* (Wheeler) under *Tapinoma sessile* (Say) and a lectotype designation for the former; and finally, 24 new or revised combinations in *Technomyrmex* involving taxa previously placed in *Engramma*, *Iridomyrmex* and *Tapinoma*.

INTRODUCTION

The Dolichoderinae form one of the larger subfamilies of ants, with about 1000 described species and 42 generic or subgeneric names. They occur throughout the world, with the greatest diversity in the New and Old World tropics and Australia (Table 1). Unfortunately, generic limits within the subfamily have been poorly defined. Over 30 years ago Brown (1958) speculated that *Iridomyrmex*, then the largest genus in the subfamily, was a composite of unrelated species. Later authors have expanded these concerns, questioning both generic limits and species placements for numerous groups.

Generic-level research within the Dolichoderinae has been hindered by at least three factors: (i) an apparent lack of morphological diversity, (ii) reliance on a limited set of morphological characters, and (iii) a large number of described taxa placed in ill-defined genera. The first of these involves the misconception that members of the Dolichoderinae are morphologically similar and not particularly interesting. Many species within the Dolichoderinae appear superficially similar, with most species lacking spines, tubercles or elaborately developed sculpturing. This apparent uniformity led many taxonomists to direct their attentions to the morphologically more diverse myrmicines and ponerines.

Secondly, reliance on a limited set of morphological characters has compounded generic level confusion within the subfamily. From its inception in 1878, proventricular structure has been used extensively in the classification of the Dolichoderinae. The proventriculus is a structure located at the junction of the crop and midgut and dissection is required to determine its condition. The dissection procedure extends considerably the handling time for specimens, and discourages all but the most dedicated researchers from examining this structure.

Table 1. Approximate number of extant, described dolichoderine species and subspecies by geographic region. Geographically widespread species are recorded for more than one region. Numbers in parentheses indicate introduced species occurring outside their normal, native range. Regions follow Brown (1973) and are abbreviated as follows: Ne = Nearctic, No = Neotropic, Pa = Palearctic, Et = Ethiopian, Ma = Malagasy, Or = Oriental, Au = Australian.

Genus	Ne	No	Pa	Et	Ma	Or	Au	Total
Anillidris	-	1	-	-	-	-	-	1
Anonychomyrma	-	-	-	-	-	3	27	30
Axinidris	-	-	-	13	-	-	-	13
Azteca	-	130	-	-	-	-	-	130
Bothriomyrmex	-	-	32	-	-	7	6	45
Doleromyrma	-	-	-	-	-	-	3	3
Dolichoderus	4	63	3	-	-	56	27	154
Dorymyrmex	7	71	-	-	-	-	-	78
Ecphorella	-	-	-	1	-	-	-	1
Forelius	4	27	-	-	-	-	-	30
Froggattella	-	-	-	-	-	-	7	7
Iridomyrmex	-	-	-	-	-	6	56	62
Leptomyrmex	-	-	-	-	-	-	40	40
Linepithema	(2)	28	(1)	(1)	-	-	(1)	28
Liometopum	3	-	2	-	-	3	-	8
Loweriella	-	-	-	-	-	1	-	1
Ochetellus	(1)	-	-	-	1	1	8	10
Papyrius	-	-	-	-	-	-	6	6
Philidris	-	-	-	-	-	5	9	14
Tapinoma	3	21	23	22	1	20	7	95
Technomyrmex	(1)	2	6(1)	37(1)	8(1)	26	9(1)	88
Turneria	-	-	-	-	-	-	6	6

Both Forel (1878b) and Emery (1912) encouraged the use of the proventriculus, with Emery stating that "la dessection des organes internes a beaucoup contribué à éclaircir la classification des Dolichoderinae." Reliance on proventricular structure continued through much of the first half of the 20th century. It reached such an extent that Creighton (1950) concluded that "it seems impossible to secure clear-cut external characters to separate *Iridomyrmex*, *Forelius* and *Tapinoma*." He was reduced to separating North American *Iridomyrmex* (now *Linepithema*) and *Forelius* based on minor differences in setal patterns combined with subtle variation in the shape of the first gastral segment. In fact, Creighton's confidence in the proventriculus prevented him from recognizing the value of other character systems which clearly diagnose these groups (e.g. mandibular, clypeal and petiolar morphologies).

Finally, the Dolichoderinae have been plagued by the lack of clearly stated, concise generic concepts. Confusion has dominated genera such as *Dolichoderus* (treated as a single genus or as many as seven separate genera) and *Iridomyrmex* (previously a single genus, here treated as seven separate genera). Additionally, there are over 1000 named taxa within the Dolichoderinae placed, at various times, in 41 genera and subgenera. This large number of

taxa combined with weak generic concepts has hampered revisionary work within the subfamily.

The above three factors, apparent lack of morphological diversity, emphasis on a single character system, and ill-defined generic concepts, have combined to delay the understanding of the higher-level classification of the subfamily, even in the face of documented irregularities. The present study has been undertaken to resolve these problems. The entire subfamily is examined, and all generic names represented by extant species, including those previously considered invalid, are reevaluated. Material from all geographic regions is utilized, including representatives of all known extant genera. (Fossil-based species are not considered in detail.) Morphological characters are drawn from both internal and external structures, and from all adult castes (workers, queens, and males) as well as larvae. This information is used to develop new generic concepts for the subfamily. Each genus is separated from all others, and extended descriptions listing all characters examined are included. Keys for all adult castes are presented to aid in identification. Finally, distribution maps are given based on the material examined supplemented with selected literature records.

Taxonomic History of the Subfamily Dolichoderinae

The subfamily Dolichoderinae was established by Forel (1878a) (as Dolichoderidae) for the genera *Bothriomyrmex*, *Hypoclinea*, *Liometopum* and *Tapinoma*. This followed the suggestions of Mayr (1868) and Forel (1874) that the subfamily Formicinae was composed of two groups, those in which (among other characters) the gaster terminates in a slit-like opening (Dolichoderinae), and those in which the gaster terminates in a circular orifice (Formicinae). Shortly after its establishment, Forel (1878b) gave the first synopsis of the subfamily, and included the genera *Azteca*, *Bothriomyrmex*, *Dolichoderus* (including *Hypoclinea*), *Dorymyrmex*, *Iridomyrmex*, *Leptomyrmex*, *Linepithema*, *Liometopum*, *Tapinoma*, and *Technomyrmex*. This system was followed, with minor additions, by Emery (1888) and Dalla Torre (1893). Subsequent authors have followed this same subfamily concept, and have added genera and subgenera to bring the total to 42.

Diagnosis and Monophyly of the Subfamily Dolichoderinae

Workers and queens of Dolichoderinae may be separated from those of other subfamilies by the presence of a single-segmented petiole, the gaster without a constriction between the first and second segments, and a slit- like opening (cloacal orifice) near the terminus of the gaster. Males may be separated from all other subfamilies except Formicinae by the presence of a single-segmented petiole with a short anterior peduncle, the gaster without a constriction between the first and second segments, and the subgenital plate without teeth. Separation of Dolichoderinae and Formicinae males is problem-

atical. This difficulty is due to the nature of the differences between these subfamilies. In the workers and queens, the most reliable differences are located at the terminus of the gaster (the shape of the terminal sclerites and the configuration of the furcula). In males, this region is modified for reproduction rather than the egg-laying and defensive functions of the worker and queen. Thus these worker and queen characters cannot be used in the male. Even the gross morphology of the proventriculus is similar between Dolichoderinae and Formicinae (Eisner 1957), reducing its usefulness in diagnosing these groups.

The monophyly of Dolichoderinae has recently been examined elsewhere (Shattuck 1992b). In that study, seven characters were found which suggest the subfamily is monophyletic. These are (1) loss of pupal cocoons, (2) reduction of the larval neck, (3) reduced number of larval hairs, (4) lightly sclerotized larval mandibles, (5) larval maxillary palp and galea reduced to sensilla, (6) small larval sericteries, and (7) cyclopentanoid monoterpene production. These seven unique characters support the subfamily status of Dolichoderinae.

The placement of the Dolichoderinae relative to other closely related subfamilies was also examined by Shattuck (1992b). Evidence was presented which indicates that Dolichoderinae are most closely related to Formicinae, rather than to Aneuretinae as most other authors have suggested.

Tribal History of the Subfamily Dolichoderinae

Emery (1912) was the first to develop a tribal classification for the subfamily. He proposed that the Dolichoderinae were composed of four tribes: Aneuretini (*Aneuretus*, transferred from Ponerinae to Dolichoderinae by Forel (1895b)), Dolichoderini (*Dolichoderus*, *Linepithema*), Leptomyrmicini [sic] (*Leptomyrmex*), and Tapinomini (*Azteca*, *Bothriomyrmex*, *Dorymyrmex*, *Engramma*, *Forelius*, *Froggattella*, *Iridomyrmex*, *Liometopum*, *Semonius*, *Tapinoma*, *Technomyrmex*, and *Turneria*). Shortly thereafter, Forel (1917) modified this classification by placing Emery's tribes Aneuretini, Dolichoderini and Leptomyrmicini [sic] in the "Prodolichoderinae" and the tribe Tapinomini in the "Eudolichoderinae". Neither of Forel's names are based on genus-group names and therefore both are invalid. Wheeler (1922), in his world key, did not follow Forel (1917), and appropriately reverted to Emery's (1912) system.

After a series of transfers the tribe Aneuretini was removed from the Dolichoderinae and is now given subfamily status. The tribe remained in Dolichoderinae between its transfer from Ponerinae by Forel (1895b) and its elevation to subfamily Aneuretinae by Wilson *et al.* (1956). It was then returned to Dolichoderinae by Brown (1973), reelevated to subfamily status by Snelling (1981), placed again in Dolichoderinae by Baroni Urbani (1989), and finally removed to its own subfamily by Bolton (1990) and Hölldobler and Wilson

(1990). A recent subfamily classification study by Shattuck (1992b) has reconfirmed the status of Aneuretinae as a separate subfamily and it is treated as such here.

Two additional tribes, Axinidrini (for *Axinidris*) and Anonychomyrmini (for *Anonychomyrma*) were added to the subfamily Dolichoderinae by Weber (1941) and Donisthorpe (1947), respectively. These tribes were poorly known and have received little attention by subsequent workers (*Axinidris* was known only from the two type workers, and *Anonychomyrma* from the single type male), with the exception of Brown (1973), who placed *Anonychomyrma*, without comment, in conditional synonymy with *Iridomyrmex*, effectively removing tribal status. Snelling (1981) and Wheeler and Wheeler (1985) recognized Axinidrini but accepted Brown's synonymy of *Anonychomyrma*.

In 1988, Dlussky and Fedoseeva examined the tribes of Dolichoderinae. They recognized the earlier tribes Axinidrini, Dolichoderini, Leptomyrmecini and Tapinomini, and added the tribes Liometopini (*Asymphylomyrmex* (fossil only) and *Liometopum*), Pityomyrmecini (*Pityomyrmex* (fossil only)) and Zherichiniini (*Zherichinius* (fossil only)). In the most recent treatment, Hölldobler and Wilson (1990) recognized only three tribes, Dolichoderini, Leptomyrmecini and Tapinomini. No consideration was given to the new tribes proposed by Dlussky and Fedoseeva (1988) and *Axinidris* was transferred to Tapinomini (removing the tribal status of Axinidrini).

While the tribal history of the subfamily is complex, the recognition of tribes has not proven particularly useful in classifying these ants. Most of the previously proposed systems have placed nearly all genera in a single tribe (Tapinomini), with only a small number of genera removed to individual, monotypic tribes (i.e. Anonychomyrmini, Axinidrini, Leptomyrmecini). Only the tribe Dolichoderini has contained more than a few genera, but even this tribe is rendered monotypic in this study. Additionally, no new assemblages of genera became apparent during this revision. The phenetic gaps among genera are fairly uniformly distributed throughout the subfamily. This reduces the utility of tribes, and they are therefore not recognized in this study.

History of the Genera of Dolichoderinae

The generic-level classification within the Dolichoderinae has been in a state of confusion for some time. Species and genera have been added with little effort to evaluate the overall effects these additions have on other genera. This almost haphazard activity has resulted in numerous taxonomically undesirable effects. These include the accumulation of unrelated species in the genus *Iridomyrmex*, the formation of paraphyletic and monotypic genera, and instability in generic and subgeneric concepts. These factors have combined to obscure even the distinct and well defined genera within the subfamily.

One of the first to suspect problems with the prevailing dolichoderine generic-level classification system was Brown (1958). He speculated that the New World species placed in *Iridomyrmex* were likely distinct from the Old World species. He expanded these concerns in 1977, stating differences between the Old and New World groups and hypothesizing that the Old World species may be further divided into groups based on internal and external structures. However, detailed changes were not proposed by Brown.

In the present study, the genus *Iridomyrmex* was found to be one of the most ill-defined in the subfamily. The 152 species previously placed in the genus are here considered to belong to seven separate genera. The majority of taxa (62) remain in *Iridomyrmex* (strict sense); 30 are transferred to the previously monotypic genus *Anonychomyrma;* the New World species, some 28 described species and subspecies, are transferred to *Linepithema*; three taxa are placed in the newly resurrected genus *Doleromyrma*, and the remaining taxa are placed in the recently described (Shattuck 1992a) genera *Ochetellus* (10 taxa), *Papyrius* (6 taxa) and *Philidris* (14 taxa). For a more complete discussion of all these groups see the Taxonomic Discussion section below.

A second problem within the generic-level classification system is that several genera have become paraphyletic due to the establishment of different genera for morphologically divergent taxa. For example, *Semonius* was diagnosed as those species with 11 antennal segments. (Almost all species in the subfamily have 12 segmented antennae.) Unfortunately, all other major character systems in *Semonius* are shared with *Tapinoma*, including the characters used to diagnose the latter. Thus it appears that "*Semonius*" represents several species of *Tapinoma* which have undergone a reduction in antennal segment number, but little else. Additionally, the recognition of *Semonius* removes those unique characters used to diagnose *Tapinoma*, leaving the latter without a clear definition.

Several other sections of the subfamily have suffered from the recognition of specialized subgroups as well. These include *Dolichoderus* and *Dorymyrmex*. Both of these groups contain a morphologically diverse assemblage of species and have accumulated numerous genus-group names. For example, *Dolichoderus* (broad sense) included seven genus-group names, all of which have been treated as valid genera or subgenera in various combinations by various authors (Fig. 61). Similarly, *Dorymyrmex* (broad sense) contains seven genus-group names. However, only three names have been proposed as full genera, the remaining four being considered as subgenera only.

The recognition of these numerous subgroups has had several undesirable side-effects. These include a general instability in classification which often seemed based as much on personal preference as on morphological characters; the obscuring of the phylogenetic relationships among groups caused by the recognition of subgroups based on a few obvious characters without regard

for other character systems; and the lack of consideration for the species remaining after the recognition of specialized subgroups. This last consequence results in artificial assemblages of species which lack defining features.

Another cause for generic-level confusion within the subfamily is the misinterpretation of characters caused by the lack of material. The African genus *Engramma* is typical of the problem. *Engramma* was defined as having a palp formula of 4:3. However, upon closer examination the only species which actually has this palp formula is the type species. All others, although morphologically similar and seemingly closely related, have palp formulas of 5:3 or 6:4, the latter being typical of the subfamily in general. Examination of African *Technomyrmex* species led to the discovery of morphological variation connecting typical *Technomyrmex* with the type of *Engramma*, and leaving *Engramma* without a clear and distinct characterization. Further, the species placed in *Engramma* possess the characters used to diagnose *Technomyrmex,* and the recognition of *Engramma* leaves *Technomyrmex* without a clear diagnosis.

Of the 39 generic or subgeneric names previously available in the Dolichoderinae, most recent authors have considered about 23 to represent valid genera (22 genera by Brown (1973), 24 by Snelling (1981), 22 by Wheeler and Wheeler (1985)) (Table 2). In this study 22 genera are considered to be valid, including three recently described elsewhere (Shattuck 1992a) and one described herein. Of the previously available generic names, 15 are retained as valid, one is removed from synonymy, two are greatly expanded and redefined, seven are newly placed in synonymy, and the synonymies of 16 others are confirmed.

Biology

Although detailed biologies are few, most species of Dolichoderinae seem to have monogynous colonies with fully winged queens and males. Queens of *Iridomyrmex purpureus* have been shown to mate only once (Page 1986) and to found colonies singly (independent founding, primary monogyny - Hölldobler and Carlin 1985). However, data on polyandry are unavailable for other species of Dolichoderinae, and significant variation in this pattern is known to occur in several groups. For example, most species of *Leptomyrmex* have ergatoid queens (Wheeler 1934), while ergatoid males are known to occur in several *Technomyrmex* species (Terron 1972). Some species of *Linepithema* are highly polygynous and form new colonies by budding from established nests (swarming, secondary polygyny). Worker reproduction has been recorded in *Dolichoderus quadripunctatus* (Torossian 1968, 1974), *Linepithema humile* (Torossian 1974), *Iridomyrmex purpureus* (Hölldobler and Wilson 1990), and *Technomyrmex albipes* (Terron 1972). Temporary social parasites

Table 2. Previous and present generic classification of the extant Dolichoderinae.

Previous classification	Proposed classification
Tribe Anonychomyrmini	*Anillidris* Santschi
Anonychomyrma Donisthorpe	*Anonychomyrma* Donisthorpe
	Axinidris Weber
Tribe Axinidrini	*Azteca* Forel
Axinidris Weber	*Bothriomyrmex* Emery
	= *Chronoxenus* Santschi (syn. nov.)
Tribe Dolichoderini	*Doleromyrma* Forel
Dolichoderus Lund	*Dolichoderus* Lund
Hypoclinea Mayr	= *Acanthoclinea* Wheeler
= *Acanthoclinea* Wheeler	= *Diceratoclinea* Wheeler
= *Diceratoclinea* Wheeler	= *Hypoclinea* Mayr
= *Karawajewella* Donisthorpe	= *Karawajewella* Donisthorpe
Monacis Roger	= *Monacis* Roger
Monoceratoclinea Wheeler	= *Monoceratoclinea* Wheeler
	Dorymyrmex Mayr
Tribe Leptomyrmecini	= *Ammomyrma* Santschi
Leptomyrmex Mayr	= *Araucomyrmex* Gallardo
	= *Biconomyrma* Kusnezov
Tribe Tapinomini	= *Conomyrma* Forel (syn. nov.)
Amyrmex Kusnezov	= *Psammomyrma* Forel
Anillidris Santschi	= *Spinomyrma* Kusnezov
Azteca Forel	*Ecphorella* Forel
Bothriomyrmex Emery	*Forelius* Emery
= *Chronoxenus* Santschi	= *Amyrmex* Kusnezov (syn. nov.)
Conomyrma Forel	= *Neoforelius* Kusnezov (syn. nov)
= *Ammomyrma* Santschi	*Froggattella* Forel
= *Araucomyrmex* Gallardo	*Iridomyrmex* Mayr
= *Biconomyrma* Kusnezov	*Leptomyrmex* Mayr
Dorymyrmex Mayr	*Linepithema* Mayr
= *Psammomyrma* Forel	*Liometopum* Mayr
= *Spinomyrma* Kusnezov	= *Ctenobethylus* Brues
Ecphorella Forel	*Loweriella* (gen. nov.)
Engramma Forel	*Ochetellus* Shattuck
Forelius Emery	*Papyrius* Shattuck
Froggattella Forel	*Philidris* Shattuck
Iridomyrmex Mayr	*Tapinoma* Förster
= *Doleromyrma* Forel	= *Micromyrma* Dufour
= *Ctenobethylus* Brues	= *Neoclystopsenella* Kurian
Linepithema Mayr	= *Semonius* Forel (syn. nov.)
Liometopum Mayr	= *Tapinoptera* Santschi
Neoforelius Kusnezov	= *Zatapinoma* Wheeler (syn. nov.)
Semonius Forel	*Technomyrmex* Mayr
Tapinoma Förster	= *Engramma* Forel (syn. nov.)
= *Micromyrma* Dufour	= *Aphantolepis* Wheeler
= *Neoclystopsenella* Kurian	*Turneria* Forel
= *Tapinoptera* Santschi	
Technomyrmex Mayr	
= *Aphantolepis* Wheeler	
Turneria Forel	
Zatapinoma Wheeler	

are known in *Bothriomyrmex*, and *Anillidris* is thought to be a cryptoparasite.

Dolichoderines show a variety of nest site preferences. These include soil with or without covering, and living and dead wood. Some species (some *Azteca* and *Technomyrmex, Papyrius*) utilize carton in nest construction. Several groups, including *Azteca*, some *Dolichoderus*, *Liometopum*, *Philidris*, some *Tapinoma* and *Technomyrmex*, and *Turneria*, exhibit arboreal habits. This habit is especially well developed in *Azteca* and *Philidris*, which are often associated with myrmecophytes. Additionally, several species of *Tapinoma* have developed a phragmotic worker caste, an adaptation found only in highly arboreal groups.

Colonies can be of moderate size, containing a few hundred individuals (*Leptomyrmex fragilis*, 350 (Wilson 1959); *Turneria bidentata*, about 430 (Shattuck 1990)), to very large and containing tens or hundreds of thousands of individuals (*Iridomyrmex purpureus*, 11,000-64,000 (Greaves and Hughes 1974); *Iridomyrmex purpureus*, 300,000 (Ettershank 1971)). Polydomy occurs in several groups, and worker exchange between nests has been recorded for distances of up to 650 meters (Greenslade and Halliday 1983).

Most species of Dolichoderinae are omnivorous scavengers, foraging on the ground surface. (Even arboreally nesting groups, such as *Liometopum*, forage epigeically.) Food consists of live and dead arthropods, as well as honeydew and plant exudates. Replete workers occur in *Leptomyrmex*. Foraging trail formation is prevalent in some groups (*Anonychomyrma*, *Forelius*, *Iridomyrmex*, *Linepithema*, *Liometopum*, *Tapinoma*) and active recruitment has been observed in *Leptomyrmex* (P. S. Ward, pers. comm.).

Chemical communication and defense are highly developed in dolichoderines (Billen 1986, Blum and Hermann 1978). The pygidial gland is enlarged and serves as the primary source of defensive and alarm secretions (Hölldobler and Engel 1979), while the Pavan's gland produces recruitment substances (Wilson and Pavan 1959, Robertson *et al.* 1980). The poison and Dufour's glands are reduced, probably as a result of the non-functional sting. The defensive and alarm substances are primarily cyclopentanoid monoterpenes, but also include nonterpenoid methyl ketones, cyclopentyl ketones, alcohols and other compounds (Blum and Hermann 1978), while trail pheromones are primarily aldehydes (Cavill *et al.* 1979). In total, about 29 compounds have been identified from the pygidial gland alone (Blum and Hermann 1978).

While most dolichoderines are relatively inconspicuous, several groups are ecologically dominant, or are notable pests. Species of *Iridomyrmex* in Australia form the dominant ground foraging component in most habitats. They may be represented by as many as 10 to 15 species at some sites, with very high population densities (P. J. M. Greenslade, pers. comm.). Several other dolichoderine groups have become widespread through commerce. The most significant of these, the "Argentine ant" *Linepithema humile*, is an

important pest species in North America, Europe, southern Africa, parts of Australia, and Hawaii. This species has had a negative impact on plant and animal communities with which it has come into contact (Bond and Slingsby 1984, Ward 1987).

MATERIALS AND METHODS

This study examined as much dolichoderine material as possible from all geographic regions, and utilized a wide range of internal and external morphological characters drawn from workers, queens, males and larvae. These characters were given equal weight while examining generic concepts, without giving any single character or character system undue emphasis. The results confirmed the concerns about generic limits expressed by earlier authors, but also demonstrated an unexpectedly diverse external morphology within the subfamily. This diversity is sufficient to allow generic definitions and diagnoses without the use of internal characters. Additionally, numerous generic-level changes are proposed, and character systems which have previously received little attention are shown to be very useful in these ants.

An attempt was made to examine as wide a selection of morphological traits as possible. By examining workers, queens, males and larvae approximately 180 characters were found which vary among taxa. These characters are distributed across all body regions and are explained in detail below. The proventriculus was examined with varied success. A few genera (*Azteca*, *Philidris*, *Technomyrmex*) can be readily separated from all others based solely on proventricular structure. However, others (*Froggattella*, *Iridomyrmex*, *Ochetellus*, *Papyrius*, *Turneria*) have nearly identical proventricular morphologies. Thus this structure is similar to other complex morphological systems, such as mandibular dentition, configuration of the anterior clypeal border, and clypeal setal patterns, which are of value in separating some groups but of little value for others.

Fortunately, with the greatly expanded set of characters used in this study all genera can be readily separated utilizing external characters alone. Thus, while the proventriculus does contain useful characters, the undue emphasis or reliance on it has caused confusion by obscuring relationships and groupings, and by discouraging the use of other, more informative character systems.

Distribution Data

The geographic range for each genus is based on specimens studied supplemented by published records and type locality information from original descriptions. Published information was included only if its accuracy could be determined. Every attempt has been made to determine the geographic limits for each genus. However, caution should be used in interpreting exact

distributions as the maps are of a large scale and rare or geographically isolated populations may not be included. Collection sites thought to represent range expansions caused by human introductions are noted separately from naturally occurring populations.

Criteria Used to Recognize Genera

Two general criteria are currently used to recognize higher groups of organisms: phenetic gaps (Mayr 1969) and monophyly (sensu Hennig 1966, Wiley 1981). The former method is based on the degree of phenetic divergence between groups, combined with the nature of the characters involved and the number of taxa in each group. Monophyly is based on the demonstration of uniquely derived characters (autapomorphies); only groups defined by autapomorphies are recognized. The latter method has two primary advantages over phenetic gaps. First, it eliminates the subjective decisions used to determine the width of gaps needed for group recognition, and second, it increases the heuristic information content of the recognized groups as the taxa contained within recognized groups are, at least in theory, most closely related to themselves.

Most previous studies of the higher classification of formicids have used phenetic gap criteria for group recognition. This has led to the formation of numerous genera or subgenera based on readily observable but often trivial characters, such as the number of antennal segments (e. g. *Semonius*) or the development of spines or processes (e. g. the subgenera of *Dolichoderus*). These groups are phenetically distinct but often exclude phylogenetically related taxa. The primary effect of a cladistic approach is to place these specialized subunits within the more general groups from which they diverged, thus representing more accurately the phylogenetic relationships among taxa within the groups. Therefore, the approach adopted in this study has been to recognize only those groups which show evidence of monophyly through the possession of apomorphic character states.

Initial generic characterizations were developed using material from throughout the known geographic range of each genus. These characterizations were then compared with the extensive holdings of the following museums: ANIC, BMNH, MCZC, PSWC and USNM. The number of specimens and species examined for each genus varied from the single known worker of *Ecphorella* to about 10,000 specimens and 75 species of *Iridomyrmex*. In all cases, as much material as possible was examined, including types.

Data for each genus is presented in the Taxonomic Discussion section, below. Each entry includes the following: 1) current genus name, 2) generic synonymy (if applicable), 3) diagnosis, 4) description, 5) separation from other genera, 6) taxonomic notes, 7) general habits, 8) distribution, and 9) species notes (if applicable). The genera are treated in alphabetical order.

Sources of Material

The following museums were visited and/or provided loans of material during this study:

AMNH - American Museum of Natural History, New York, New York, USA.

ANIC - Australian National Insect Collection, Canberra, ACT, Australia.

BMNH - The Natural History Museum, London, UK.

BPBC - B. P. Bishop Museum, Honolulu, Hawaii, USA.

CASC - California Academy of Sciences, San Francisco, California, USA.

IZAV - Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela.

LACM - Los Angeles County Museum of Natural History, Los Angeles, California, USA.

MCZC - Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.

MHNG - Muséum d'Histoire Naturelle, Geneva, Switzerland.

MVMA - Museum of Victoria, Abbotsford, Victoria, Australia.

OXUM - University Museum, Oxford, England, UK.

PSWC - P. S. Ward collection, University of California, Davis, California, USA.

SAMA - South Australian Museum, Adelaide, South Australia, Australia.

SOSC - S. O. Shattuck collection, Canberra, ACT, Australia.

UCDC - University of California, Davis, California, USA.

USNM - United States National Museum, Washington, D. C., USA.

List of Characters Studied: Worker, Queen, Male

Characters examined are morphological, both internal and external, and are recorded from workers, queens, males and larvae. Most characters are discrete although a few are continuous. Data were recorded and manipulated using the DELTA computer package (Dallwitz and Paine 1986).

Characters comparing relative body part positions assume the specimen is positioned with the head tilted anteriorly and the petiole and gaster parallel with the mesosoma. The caste applicable to each character is given in square brackets using the abbreviations W, Q, and M for worker, queen and male, respectively.

Head

The shape of the vertex (= posterior margin) [W, Q] in full-face (dorsal) view. The outline may be convex (Fig. 97), flat (Fig. 81), weakly concave (Fig. 64), or concave (Fig. 6).

The compound eyes [W, Q, M] in workers may be present and elongate (Fig. 157) or round (Fig. 6), or absent (Fig. 1). In workers and queens the placement may be relatively anterior (Fig. 6) or relatively posterior (Figs. 89, 95) on the head. In males, the inner margin may be flat (Fig. 5) or angularly concave (Fig.

53).

The presence or absence of dorsal ocelli [W]. Ocelli are always present in queens and males.

The number of antennal segments [W, Q], including scape, are 8, 11 or 12 in workers, and 11 or 12 in queens. All known males have 13 segmented antennae.

The scape length [W, Q, M] in workers and queens is relative to the posterior margin of the head in full face view when the scape is positioned longitudinal with the body and parallel with the dorsal surface of the head; in males, the length is relative to the length of the funicular segments.

The first funicular segment [M] may be similar in diameter to the second segment and cylindrical or cone-shaped (Fig. 5), or enlarged and barrel-shaped (Fig. 43).

The second funicular segment [M] may be straight (Fig. 5), or compressed medially and with a lateral bend (Fig. 69). It may also be uniformly cylindrical (Fig. 5) or swollen medially (barrel-shaped) (Fig. 28).

The relative lengths of funicular segments 2 and 3 [M].

The junction of funicular segments 3 and 4 [M] may be straight, or bent. If bent, the angle is formed either in the distal section of segment 3, or at the junction of segments 3 and 4.

The anterolateral clypeal margin profile in full face view [W, Q] may be posterior to (Fig. 89), even with (Fig. 39), or anterior to (Fig. 24) the mediolateral margin.

The anteromedial clypeal margin profile in full face view [W, Q, M] may be entire and without a central notch or concavity of any type (Fig. 6), with a broad, shallow concavity (Fig. 39), with a distinct, central notch separated from the general outline of the margin by distinct or indistinct corners (Fig. 16), or may have a central projection, either pointed or rounded (Fig. 89).

The (i) number, (ii) length and (iii) degree of curvature of the setae originating along the anterior margin of the clypeus, viewed laterally [W, Q, M]. The number varies from absent to about 28. The length varies from short, only slightly surpassing the anterior clypeal margin, to long and surpassing the distal edge of the closed mandibles. The degree of curvature varies from straight to moderately curved ventrally.

The position of the posterior clypeal margin [W, Q, M] relative to a pair of imaginary horizontal lines connecting the anterior-most and posterior- most surfaces of the antennal socket cavities. The posterior clypeal margin may be anterior (Fig. 31), between (Fig. 6), or posterior (Fig. 47) to these lines.

The anterior tentorial pits [W, Q, M] may be located either nearer the antennal socket than the mandibular insertion, or near the lateral junction of the gena and clypeus (near the mandibular insertions).

The frontal carina [W] may be present, or reduced or absent.

The condition of the lateral and anterior corner of the hypostoma (ventral surface of the head near the insertion of the mandible) [W, Q, M]. The anterior hypostoma may be reduced to a thin sclerite (Fig. 166), or in the form of an expanded flange directed ventrally and anteriorly (Fig. 164).

The configuration of the hypostoma along the medial and posterior region of the oral cavity [W, Q, M]. The hypostoma may have either an entire (Fig. 169) or notched (Fig. 168) margin, or be reduced and nearly absent (Fig. 171).

The development of a psammophore [W, Q] (a non-randomly placed set of elongate, usually curved, hairs on the venter of the head and mandibles). Psammophores are unknown in males.

Mouthparts

The palp formula [W, Q, M] is the number of maxillary and labial palp segments separated by a colon. Known conditions include 6:4, 5:3, 4:3, 4:2, 3:4, 2:3 and 2:2.

The length of the third maxillary palp segment [W, Q, M] may be subequal in length to segment 4 , or elongate and subequal or longer than the combined lengths of segments 4+5+6 (Fig. 175).

The configuration of the attachment of the fifth maxillary segment to the fourth [W, Q, M]. The attachment is either at the apical extreme of segment 4, or subapical and with a finger-like extension distal of the attachment point.

Mandibular dentition [W, Q, M] in most dolichoderines occurs in two size classes. The larger are termed teeth, while the smaller are termed denticles. In some taxa teeth occur in either a continuous size series (from large to small), or a single size class, on the mandible. In these cases, regardless of size, all are termed teeth.

The length of the apical tooth of the mandible compared to the first subapical tooth [W, Q, M]. The apical tooth varies from subequal in length to the subapical tooth (Fig. 177) to elongate and much longer than the subapical tooth (Fig. 176).

The configuration of the basal angle (junction of the masticatory and basal margins) of the mandible [W, Q, M]. The basal angle may be distinct, with a well developed tooth or angle separating the masticatory and basal faces (Figs. 176, 177, 180), or indistinct, with a relatively uninterrupted curve between the two faces and without a distinct tooth or angle (Fig. 172).

The development of dentition on the basal margin of the mandible [W, Q, M]. The margin varies from smooth and without teeth or denticles (Fig. 176), to denticulate, with teeth or denticles present along the entire margin (Figs. 172, 181).

Mesosoma

The configuration of the posteroventral pronotal corner (the corner nearest

the mesocoxa) [W, Q, M]. The corner may be lateral and rounded or angled (Fig. 167), or elongate and expanded medially (Fig. 165).

The development of a longitudinal suture dividing the episternum [Q, M]. The suture varies from weakly developed and nearly absent (Fig. 68), to complete (Fig. 52).

The development of a spine-like or tooth-like projection on the anteroventral surface of the mesothoracic epimeron near the insertion of the fore coxa [W, Q]. The tooth or process may be present (Fig. 59) or absent (Fig. 7).

The degree of anterior expansion of the anteromedial margin of the mesosternum [W, Q, M]. The margin is either even across its entire width (Fig. 167), or the medial region is expanded anteriorly of the lateral regions (Fig. 165).

The shape of the medial regions of axilla (which may be parallel sided, constricted, or reduced and absent), and the development of a medial suture [Q, M].

The shape of the anterior axillar suture [Q, M] may be straight (Fig. 183) or angular (Fig. 182).

The shape (in lateral profile) of the declivitous face of the propodeum, dorsal of the petiolar insertion (which is almost always concave) [W, Q, M]. The face may be convex (Fig. 7), flat (Fig. 119), or concave (Fig. 48).

The shape (in lateral profile) of the dorsal face of the propodeum [W, Q, M]. The face may be convex (Fig. 7), flat (Fig. 17), or weakly concave (Fig. 99).

The relative length of the dorsal face of the propodeum compared to the declivitous face [W, Q, M]. The dorsal face may be longer than (Fig. 7), subequal in length to (Fig. 90), or shorter than (Fig. 32) the declivitous face.

The presence of a well defined angle between the dorsal and declivitous faces of the propodeum [W, Q, M]. The angle is distinct if there is a noticeable division between the two faces (Fig. 2). The angle is absent if there is a continuous, uninterrupted arch between the two faces (Fig. 7).

The development of spines or denticles on the pronotum [W, Q]. They may be present as distinct spines, reduced spines or protuberances, or be absent.

The (i) number and (ii) length of erect hairs on the dorsal surface of the pronotum [W]. Hairs may be short or elongate, and vary from none to over 100.

The (i) number and (ii) length of erect hairs on the dorsal surface of the mesoscutum [Q]. Hairs may be short or elongate, and vary from none to over 100.

The development of spines or denticles on the mesonotum [W, Q]. They may be present as distinct spines (Figs. 59, 60), reduced spines or protuberances (Figs. 55-58), or be absent (Fig. 7).

The development of spines or denticles on the propodeum [W, Q]. They may be present as distinct spines (Fig. 50), reduced spines or protuberances (Fig. 17), or be absent (Fig. 7).

The development of a single, medial tooth or projection at the propodeal angle [W, Q]. The tooth may be present (Fig. 65) or absent (Fig. 7).

The configuration of the junction of the pronotum and mesonotum viewed in lateral profile [W]. The mesonotum may be even with the pronotum (Fig. 40), slightly above the pronotum (Fig. 25), or below the pronotum (Fig. 7).

The configuration of the metanotal groove (area between the mesonotum and propodeum) [W]. The metanotal groove may (i) form a distinct, deep trough or notch depressed below the level of the adjacent mesosomal notum (Fig. 66), (ii) be even with the adjacent regions but with the mesonotum and propodeum forming a distinct angle at the metanotal groove (Fig. 48), (iii) be absent, with the mesonotum and propodeum forming a continuous, uninterrupted surface (Fig. 112), or (iv) be a narrow, distinct notch in the relatively flat dorsal mesosomal surface (Fig. 122).

The placement of the metathoracic spiracle [W]. The spiracle may be either dorsal and lying on the dorsal thoracic surface when viewed in lateral profile, or lateral and ventral of the dorsal surface.

The placement of the propodeal spiracle [W, Q]. It may be placed (i) laterally near the middle of the declivitous face length (Fig. 112), (ii) dorsal and medially along the dorsal face (Fig. 17), or (iii) dorsal and posteriorly, near the propodeal angle (Figs. 178, 179).

The development of barbules on the inner surface of the hind tibial spur [W, Q].

Wings

The configuration of the radial cell [Q, M]. The cell may be open or closed.

The number of closed cubital cells [Q, M] varies from none to two.

The number of closed discoidal cells [Q, M] varies from none to two.

The presence or absence of a finger-like structure ("pterostigmal appendage" (Wheeler 1934)) on the ventral, leading edge of the wing near the pterostigma [M].

The number of closed hind wing cells [Q, M] varies from none to three in queens and from none to two in males.

Petiole

The structure of the petiolar scale, including its presence, the shape of the dorsal surface (rounded, angular, spined), and the degree of anterior inclination [W, Q, M].

The development of a lobe on the ventral surface of the petiole [W, Q, M]. There may be a well developed lobe (Fig. 25), a slight or weakly developed lobe (Fig. 7), or no lobe (Fig. 75).

Gaster

The degree of anterior projection of the first gastral (third abdominal) tergite [W, Q, M]. The tergite may project anteriorly and sometimes hide the petiole in dorsal view, be vertical and not conceal the petiole in dorsal view, or be elongate posteriorly.

The configuration of the anterior region of the first gastral tergite immediately dorsal of the petiolar insertion [W, Q, M]. The tergite may have a groove or indentation for the reception of the entire height of the petiole, a partial groove for the reception of only the basal portion of the petiole, or be smooth and without a groove or indentation.

The configuration of the anterior tergosternal suture of the first gastral tergite immediately lateral of the petiolar insertion, viewed anteriorly [W, Q, M]. The suture may be present and vary from being horizontal near the helcium to arching dorsally and extending noticeably above the dorsal surface of the helcium; or the suture may be reduced (nearly absent) and arching dorsally to extend noticeably above the dorsal surface of the helcium; or the suture may be absent near the helcium. If the suture is absent near the helcium, the lateral gastral tergosternal suture may terminate immediately above the helcium, or extend dorsally and terminate near the dorsal surface of the gaster.

The configuration of the terminal segments of the gaster [W, Q]. The most widespread condition (in living, undamaged material) is for the fifth gastral (seventh abdominal) tergite to be ventral and anterior of the fourth gastral (sixth abdominal) tergite and thus with the terminus of the gaster formed by the junction of the fourth and fifth tergites (Fig. 173). In some species, the fifth gastral tergite is dorsal, and thus the terminus of the gaster is formed by the junction of fifth tergite and fifth sternite (Fig. 174). Occasionally the fifth gastral segment is more or less vertical and the terminus of the gaster is not well defined. The position of terminal sclerites can be determined in all but the most damaged specimens by counting the number of apparent tergites and sternites in the gaster. If the fifth tergite is dorsal, there will be five apparent tergites and five apparent sternites. If it is ventral, there will be four apparent tergites and five or six apparent sternites.

The orientation of compression of the medial region of the gaster [W, Q]. Compression can be lacking (gaster circular in cross section), dorsoventral, or lateral.

The configuration of the fourth gastral (sixth abdominal) sternite [W, Q]. The sternite may be either uniformly arched across its width, or keel- shaped medially.

The width of the attachment of the petiole to the gaster [M]. The attachment varies from wide relative to the maximum height of the petiole (Fig. 13), to narrow (Fig. 21).

Genitalia

The development of pygostyles [M]. They may be present, present but reduced in size, or be vestigial.

The configuration of the posterior margin of the subgenital plate [M]. The margin may be convex, even across its entire width, concave, or with a "V"-shaped notch medially.

The configuration of the parameres [M]. The parameres may be entire, divided, or rarely with the gonostylus elongated into a finger-like structure.

The degree of ventral curvature of the digitus [M].

The development and placement relative to the digitus of the cuspis [M].

The development of a ventral lobe on the volsella [M].

The development of teeth on the ventral margin of the aedeagus [M].

The configuration of the proventricular cupola [W, Q, M]. Important parameters include its diameter relative to the bulb, its shape, the development and length of pile, sculpturing, and the presence of phragma.

The degree of exposure of the proventricular bulb below the cupola [W, Q, M].

The presence or absence of the longitudinal muscles no. 1 of the proventriculus (see Eisner 1957) [W, Q, M].

The presence or absence of an occlusory tract (see Eisner 1957) [W, Q, M].

General Characters

Development of morphological castes [W, Q]. The worker caste may be monomorphic, dimorphic, or polymorphic. The queen caste may be either differentiated from the worker (fully winged and with an enlarged mesosoma) or worker-like (ergatoid, without wings or enlarged mesosoma).

The number of known chromosomes [W, Q, M] varies from n=5 to n=16.

The integument [W] may be thin, flexible and weakly sculptured, or thickened and often strongly sculptured.

List of Characters Studied: Larva

For detailed discussions and definitions of the following characters, see Wheeler and Wheeler (1976).

The body shape may be crematogastroid, dolichoderoid, leptomyrmecoid or pheidoloid.

The (i) development, (ii) number and (iii) placement of protuberances on the body.

The (i) abundance, (ii) shape and (iii) length of body hairs.

The number of spiracular pairs.

The size of the antennae.

KEYS TO GENERA OF DOLICHODERINAE

Key to dolichoderine genera based on workers

1a. Hypostoma with an anterolateral tooth-like expansion (sometimes weakly developed) (Fig. 164); mesosternum expanded anteromedially, convex (Fig. 165); integument thickened, often heavily sculptured; declivitous face of propodeum concave (rarely flat) (Figs. 48, 50, 55, 57, 59) (world wide) ..... *Dolichoderus*

1b. Anterolateral hypostoma a reduced, thin band (Fig. 166); anterior border of mesosternum flat across entire width (Fig. 167); integument thin and flexible, generally weakly sculptured; declivitous face of propodeum usually convex (Figs. 98, 129), less commonly flat or concave (Fig. 122) 2

2a. Hypostoma notched medially (Fig. 168); scapes surpassing the posterior margin of head by about one-half their length, or more (Fig. 97) (New Guinea, New Caledonia, Australia) ..... *Leptomyrmex*

2b. Hypostoma entire medially (Fig. 169) (rarely grooved (Fig. 170) or completely absent (Figs. 120, 171)); scapes surpassing the posterior margin of head by less than one-half (often less than one-third) their length (Fig. 142) (world-wide) 3

3a. Petiolar scale strongly reduced or absent (Figs. 143, 151); dorsal face of propodeum (when well defined) short (Fig. 143); mandible with 12-14 teeth in a decreasing size-series posteriorly along mandible, and lacking a distinct basal angle (Fig. 172) 4

3b. Petiolar scale present (Fig. 65) (although sometimes strongly inclined anteriorly (Fig. 17)); dorsal face of propodeum generally longer, occasionally short; mandibular teeth and basal angle variable 5

4a. Fifth gastral tergite ventral (Fig. 173); pronotum generally lacking erect hairs (world wide) ..... *Tapinoma*

4b. Fifth gastral tergite dorsal (Fig. 174); pronotum commonly with 2 to 10 erect hairs, rarely 0 or up to 20 (world wide, rare in New World) ..... *Technomyrmex*

5a. Third maxillary palp segment elongate, subequal in length to segments 4+5+6 (Fig. 175); propodeal angle in the form of a single, medial tooth or spine (Figs. 65, 66); apical tooth of mandible greatly enlarged (Fig. 176);

psammophore present, although sometimes weakly developed; clypeal setae elongate, surpassing the closed mandibles (New World) ..... *Dorymyrmex*

5b. Third maxillary palp segment subequal in length to segment 4, or absent; propodeal angle generally rounded, occasionally angular or with paired spines or protuberances, but never with a single tooth or spine; apical tooth of mandible usually subequal in size to, or only slightly larger than, subapical tooth (Fig. 177) (enlarged in some Australian species); psammophore absent (rarely elongate hairs on gula, but not forming a psammophore); clypeal setae generally short 6

6a. Propodeal spiracle located dorsally, near the dorsal propodeal surface when viewed in lateral profile (Figs. 17, 178, 179) 7

6b. Propodeal spiracle located laterally, well below the dorsal propodeal surface when viewed in lateral profile (Fig. 112) 10

7a. Propodeum rounded, without spines, protuberances or other ornamentation (Fig. 73) ..... *Ecphorella*

7b. Propodeum commonly with distinct spines (Fig. 178) or protuberances (Fig. 179), less often with lateral angles and/or a medial carina 8

8a. Propodeal spiracle located mediolaterally along dorsal face of propodeum (Fig. 17); anterior clypeal border with a distinct, medial notch (Fig. 16) (sub-Saharan Africa) ..... *Axinidris*

8b. Propodeal spiracle located posteriorly along dorsal face of propodeum, near junction of dorsal and declivitous faces (Figs. 178, 179); anterior clypeal border even or sinuate, without a distinct notch (Figs. 81, 157) (Australia, New Guinea, Solomon Islands) 9

9a. Propodeum with distinct spines directed posteriorly (Fig. 178); propodeal spiracle located distal of base of spine (Fig. 178); eyes approximately round (Fig. 81) (Australia) ..... *Froggattella*

9b. Propodeal angle distinct, rounded, with protuberances bearing the propodeal spiracles (Fig. 179); eyes elongate (Fig. 157) (Australia, New Guinea, Solomon Islands) ..... *Turneria*

10a. Compound eyes absent; frontal lobes very close together, the posteromedial portion of the clypeus long and narrow (Fig. 1); palp formula 2:3; entire body covered with dense, short pubescence (South America) ..... *Anillidris*

10b. Compound eyes present; frontal lobes widely spaced; palps variable; body at most covered with sparse erect and/or appressed hairs 11

11a. Metanotal groove reduced to a suture, mesonotum and propodeum forming a continuous surface in profile (Fig. 112) (holarctic) .... *Liometopum*

11b. Metanotal groove present as either a notch (Figs. 122, 129) or an angle (Figs. 32, 105) between the mesonotum and propodeum 12

12a. Anterior clypeal margin with 2 to about 12 ventrally curved (rarely nearly straight) hairs which are approximately the same length as the closed mandibles; first gastral segment projecting anteriorly and concealing (or nearly concealing) the petiole in dorsal view 13

12b. Anterior clypeal border with 2 to 20 short, straight (rarely curved) hairs which are much shorter than the closed mandibles; first gastral segment generally vertical, or occasionally projecting anteriorly, and not concealing the petiole in dorsal view 15

13a. Medial hypostoma present (Fig. 169); pronotum with at least a pair of long, erect hairs (New World) ..... *Forelius*

13b. Medial hypostoma notched or absent (Figs. 120, 171); pronotum without erect hairs (Old World) 14

14a. Palp formula 4:3 or 2:2; mandibles with 5 to 6 teeth and 0 to 5 denticles; fourth gastral sternite flat across posterior border ..... *Bothriomyrmex*

14b. Palp formula 6:4; mandibles with 7 to 8 teeth and 2 to 5 denticles; fourth gastral sternite keel-shaped posteriorly ..... *Loweriella*

15a. Palp formula 5:3; anterior clypeal border with 8 to 20 very short, straight setae which only slightly surpass the anterior clypeal margin; mandibles with about 11 to 14 teeth and no denticles; metanotal groove a distinct, deep trough or notch depressed below the level of the adjacent mesosomal notum (Fig. 129); monomorphic (Australia) ..... *Papyrius*

15b. Palp formula 6:4, or if reduced, then workers polymorphic; anterior clypeal border with 2 to 16 short, straight erect setae which noticeably surpass the anterior clypeal margin; mandibles with 5 to 12 teeth and generally at least a few denticles; metanotal groove a distinct angle (Fig. 90) or a narrow groove or notch (Fig. 122) 16

16a. Declivitous face of propodeum concave; mesosomal dorsum more or less flat; metanotal groove notch-like (Fig. 122) (Japan south to Australia) ..... *Ochetellus*

16b. Declivitous face of propodeum convex (rarely nearly flat); mesosomal dorsum with the propodeum below the mesonotum; metanotal groove angular (Fig. 90) 17

17a. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder (Fig. 89); anteromedial clypeal margin generally with a central projection, either pointed or rounded (sometimes weakly developed and present in the form of lateral concavities joined medially by a convexity, or rarely absent) (Fig. 89) 18

17b. Anterolateral clypeal margin either even with, or anterior to, the mediolateral region (Fig. 89); anteromedial clypeal margin without a projection, broadly concave to convex (Fig. 39) 20

18a. Anterior clypeal margin broadly concave, without a central projection or convexity (Fig. 8); mesonotum divided into two distinct regions, an anterior convex section followed by a posterior flat section (Fig. 9) .... *Anonychomyrma* (in part)

18b. Anterior clypeal margin generally with a distinct central projection, or if reduced and apparently absent, then the entire mesonotum is uniformly convex and not divided into subregions (Fig. 136) (a distinct central projection is always present in specimens with a mesonotum as described in 18a) 19

19a. Compound eyes in a relatively posterior position on head (Figs. 89, 95); monomorphic (rarely polymorphic); dorsum of petiole vertical to moderately inclined anteriorly (Fig. 90) (rarely strongly inclined anteriorly); vertex generally convex, occasionally weakly concave (Fig. 89) ..... *Iridomyrmex*

19b. Compound eyes in a relatively anterior position on head (Fig. 135); polymorphic; dorsum of petiole strongly inclined anteriorly (Fig. 136); vertex concave (Fig. 135) ..... *Philidris*

20a. Anterior clypeal setae moderately curved ventrally; fourth gastral sternite flat posteriorly; mandibles with 4 to 5 teeth and 4 to 5 denticles; dorsal face of propodeum shorter than declivitous face (Fig. 40); erect pronotal hairs absent (Australia) ..... *Doleromyrma*

20b. Anterior clypeal setae straight; fourth gastral sternite keel-shaped posteriorly; mandibles with 5 to 10 teeth and 0 to 13 denticles; dorsal face of propodeum generally subequal to, or longer than, declivitous face (Figs. 7, 25); erect pronotal hairs present or absent (world wide) 21

21a. Anterior clypeal border with a broad, medial concavity (Fig. 104); mandibles with 5 to 8 teeth and 5 to 13 denticles; apical tooth of mandible elongate and much longer than subapical tooth (Fig. 180) (native to New World, now widespread) ..... *Linepithema*

21b. Anterior clypeal border generally flat or convex medially (Fig. 24), if broadly concave, then the anterolateral region is very slightly posterior to the mediolateral region and separated from it by a weak concavity; mandible with 5 to 10 teeth and 0 to 4 denticles; apical tooth of mandible at most only slightly longer than subapical (Figs. 177, 181) 22

22a. Polymorphic, majors with ocelli; apical tooth of mandible generally subequal in size to subapical (Fig. 177); scale of petiole strongly inclined anteriorly (Fig. 25) (Central and South America) ..... *Azteca*

22b. Monomorphic, ocelli absent (rarely polymorphic and majors with ocelli); apical tooth of mandible slightly longer than subapical (Fig. 181); scale of petiole vertical to moderately inclined anteriorly (Fig. 7) (Southeast Asia to Australia) ..... *Anonychomyrma* (in part)

Key to dolichoderine genera based on queens

(Key does not include *Ecphorella* or *Loweriella*, the queens of which are unknown.)

1a. Medial hypostoma notched (similar to Fig. 168) (almost always ergatoid (worker-like, without wings or axillary sclerites), rarely fully winged) (New Guinea, New Caledonia, Australia) ..... *Leptomyrmex*

1b. Medial hypostoma generally entire (Fig. 169), sometimes grooved (Fig. 170) or completely absent (Fig. 171), but never notched (almost always fully winged and with an enlarged mesosoma) 2

2a. Anterior clypeal margin with a lateral shoulder (sometimes weakly developed) (Figs. 83, 91, 130, 137) (Indo-Australian region) 3

2b. Anterior clypeal margin without a lateral shoulder (Figs. 10, 26, 152) (world wide) 9

3a. Erect mesoscutal hairs absent; mandible with the basal angle weakly defined and the basal margin denticulate along its entire surface; venter of petiole without a lobe (Australia, New Guinea, Solomon Islands) ..... *Turneria* (in part)

3b. Erect mesoscutal hairs present, 6 to about 70; mandible with the basal angle generally distinct (one exception) and the basal margin denticulate distally only; venter of petiole with a well developed lobe (occasionally reduced or absent) 4

4a. Anterior clypeal margin with a central projection (sometimes present as a broad, nearly flat convexity, but always separated from the lateral regions by concave regions) (Figs. 83, 91, 137) 5

4b. Anterior clypeal margin even, weakly concave to weakly convex (the convexity continuous with the lateral regions and not separated by concavities) (Figs. 123, 130) 7

5a. Anterior clypeal margin with less than 5 erect setae; propodeal angle distinct; dorsum of petiole rounded; venter of petiole without a lobe (Fig. 84); first gastral segment smooth near the petiolar insertion (Australia) ..... *Froggattella*

5b. Anterior clypeal margin with more than 6 erect setae; propodeal angle indistinct; dorsum of petiole angular; venter of petiole with at least a weak lobe (Fig. 92); first gastral segment with a groove near the petiolar insertion 6

6a. Vertex convex to flat; apical tooth of mandible elongate compared to subapical tooth ..... *Iridomyrmex*

6b. Vertex generally concave; apical tooth of mandible subequal in size compared to subapical tooth ..... *Philidris* (in part)

7a. Palp formula reduced to 5:3 (Australia) ..... *Papyrius*

7b. Palp formula 6:4 8

8a. Anterior axillar suture angular medially (Fig. 182); first gastral segment with a groove or indentation for the reception of the entire height of the petiole (Japan south to Australia) ..... *Ochetellus*

8b. Anterior axillar suture straight (Fig. 183); first gastral segment with a groove or indentation for the reception of the basal portion of the petiole ..... *Philidris* (in part)

9a. Fifth gastral tergite dorsal, gaster with five apparent tergites (Fig. 174) (world wide, rare in New World) ..... *Technomyrmex*

9b. Fifth gastral tergite either ventral or vertical, gaster with four apparent tergites (Fig. 173) 10

10a. Venter of petiole without a lobe of any kind (Fig. 52) 11

10b. Venter of petiole with at least a weak lobe (Figs. 27, 34) 14

11a. Anterolateral hypostoma in the form of an expanded flange directed anteroventrally (Fig. 164) (world wide) ..... *Dolichoderus*

11b. Anterolateral hypostoma reduced to a thin sclerite (Fig. 166) 12

12a. Propodeal spiracle dorsal and medial along dorsal propodeal face (Fig. 19) (sub-Saharan Africa) ..... *Axinidris*

12b. Propodeal spiracle lateral and ventral of the propodeal dorsum (Figs. 11, 160) (Indo-Australian region) 13

13a. Mandible with the apical tooth slightly longer than the subapical, the basal angle distinct, and the basal margin denticulate distally, smooth proximally; erect mesoscutal hairs abundant (Southeast Asia to Australia) ..... *Anonychomyrma* (in part)

13b. Mandible with the apical tooth subequal in length to the subapical, the basal angle weakly defined, and the basal margin denticulate along its entire surface; erect mesoscutal hairs absent (Australia, New Guinea, Solomon Islands) ..... *Turneria* (in part)

14a. Palp formula reduced (less than 6:4) 15

14b. Palp formula 6:4 17

15a. Palp formula 3:4 (South America) ..... *Anillidris*

15b. Palp formula 4:3 or 2:2 16

16a. Anterior clypeal setae 8 to about 10, straight; medial hypostoma entire (Fig. 169) (Central and South America) ..... *Azteca* (in part)

16b. Anterior clypeal setae 2 to 6, moderately curved ventrally; medial hypostoma absent (Fig. 171) (Europe east to Australia) .. *Bothriomyrmex*

17a. Anterior clypeal setae strongly curved ventrally; psammophore present; third maxillary palp segment subequal to or longer than the combined lengths of segments 4+5+6 (Fig. 175) (New World) ..... *Dorymyrmex*

17b. Anterior clypeal setae at most weakly curved ventrally; psammophore absent; third maxillary palp segment subequal in length to segment 4. 18

18a. Petiolar scale strongly inclined anteriorly and with the anterior face much shorter than the posterior face (Figs. 11, 145) 19

18b. Petiolar scale at most moderately inclined anteriorly but with the anterior and posterior faces approximately the same length (Fig. 107) 22

19a. Radial cell open; anterior clypeal setae about 6, about as long as closed mandibles, and moderately ventrally curved (New World) .... *Forelius* (in part)

19b. Radial cell closed; anterior clypeal setae generally greater than about 8, short, and straight (if less than 8, long or curved, than the basal mandibular angle is absent) (world wide) 20

20a. Basal angle of mandible indistinct; dorsal propodeal face shorter than declivitous face; petiolar scale reduced or absent (Fig. 147) (world wide) ..... *Tapinoma*

20b. Basal angle of mandible distinct; dorsal propodeal face subequal to or longer than the declivitous face; petiolar scale present (Fig. 11) 21

21a. Axilla broad medially, the posterior suture weakly convex to nearly straight (occasionally slightly angular) and subparallel with, but not approaching, the anterior suture (Fig. 183) (Southeast Asia to Australia) .... *Anonychomyrma* (in part)

21b. Axilla narrowed medially, the posterior suture convex or angular and always approaching (sometimes touching) the anterior suture (Fig. 184) (Central and South America) ..... *Azteca* (in part)

22a. Declivitous face of propodeum flat; first gastral segment projecting anteriorly; erect mesoscutal hairs reduced, less than about 6 (Australia) ..... *Doleromyrma*

22b. Declivitous face of propodeum convex; first gastral segment vertical; erect mesoscutal hairs generally more than about 6 (occasionally reduced to about 2) 23

23a. Anterior clypeal setae moderately curved ventrally; basal margin of mandible smooth; wing with an open radial cell, 1 cubital cell and 0 discoidal cells (New World) ..... *Forelius* (in part)

23b. Anterior clypeal setae straight; basal margin of mandible with denticles; wing with a closed radial cell, 2 or 3 cubital cells and 1 or 2 discoidal cells 24

24a. Episternal suture weakly developed anteriorly; propodeal angle indistinct (Southeast Asia to Australia) ..... *Anonychomyrma* (in part)

24b. Episternal suture complete; propodeal angle distinct (New World and holarctic) 25

25a. Mandibular teeth in two size classes (6 to 8 larger teeth, 7 to 11 smaller denticles) (similar to Fig. 180); apical tooth elongate and much longer than the subapical; axilla with a suture medially (New World) ..... *Linepithema*

25b. Mandibular teeth in a single, continuous size class (7 to 9 teeth and no denticles) (similar to Fig. 177); apical tooth only slightly longer than the subapical; axilla entire (holarctic) ..... *Liometopum*

Key to dolichoderine genera based on males

(Key does not include *Ecphorella* or *Loweriella*, the males of which are unknown.)

1a. Mandible with at most a single tooth or denticle 2

1b. Mandible with 2 or more teeth or denticles, often more than 5 9

2a. Mandible without an apical tooth, tip of mandible round (sometimes with the third and fourth funicular segments bent and forming an angle between them) 3

2b. Mandible with a distinct apical tooth; or, if the apical tooth is absent, then the third and fourth funicular segments are straight, never bent 5

3a. First funicular segment cylindrical; medial hypostoma notched (Fig. 168); declivitous face of propodeum flat (Fig. 101) (New Guinea, New Caledonia, Australia) ..... *Leptomyrmex* (in part)

3b. First funicular segment barrel-shaped; third and fourth funicular segments straight; medial hypostoma entire (Fig. 169); declivitous face of propodeum concave (sometimes only weakly) 4

4a. Petiolar scale rounded dorsally; venter of petiole with a slight or reduced lobe (Fig. 86); first gastral segment vertical (Australia) ..... *Froggattella*

4b. Petiolar scale angular dorsally; venter of petiole with a well developed lobe (Fig. 162); first gastral segment elongate posteriorly (Australia, New Guinea, Solomon Islands) ..... *Turneria*

5a. Petiolar scale either a blunt angle dorsally, or spined with a single tooth or projection; venter of petiole with a well developed lobe (Fig. 29); first gastral segment with a groove or indentation for the reception of the entire height of the petiole; second funicular segment barrel- shaped (Central and South America) ..... *Azteca* (in part)

5b. Petiolar scale rounded or ridged dorsally; venter of petiole with at most a slight or reduced lobe; first gastral segment smooth and without a groove or indentation; second funicular segment cylindrical 6

6a. Palp formula 6:4; fore wing radial cell closed 7

6b. Palp formula 5:3; fore wing radial cell open 8

7a. Petiole expanded laterally along its entire height and with the dorsal surface very broad relative to ventral regions; anterior axillar suture generally angular medially; first gastral segment elongate posteriorly (Japan south to Australia) ..... *Ochetellus* (in part)

7b. Petiole not unduly expanded dorsally and with the dorsal regions the same width or narrower than ventral regions; anterior axillar suture straight medially; first gastral segment vertical ..... *Iridomyrmex* (in part)

8a. Scape longer than the length of funicular segments 2+3 (Fig. 78); first funicular segment cylindrical or cone-shaped; second funicular segment with a lateral bend; fore wing without a closed discoidal cell; hind wing without cells (New World) ..... *Forelius* (in part)

8b. Scape shorter than the length of funicular segments 2+3 (Fig. 132); first funicular segment barrel-shaped; second funicular segment straight; fore wing with 1 closed discoidal cell; hind wing with 2 closed cells (Australia) ..... *Papyrius*

9a. Second funicular segment with a lateral bend 10

9b. Second funicular segment straight 11

10a. Palp formula 6:4; third maxillary palp segment longer than the combined length of segments 4+5; hind wing with 2 closed cells (New World) .... *Dorymyrmex*

10b. Palp formula 5:3; third maxillary palp segment subequal in length to segment 4; hind wing without closed cells (New World) .... *Forelius* (in part)

11a. Petiole expanded laterally along its entire height and with the dorsal surface very broad relative to ventral regions; mandibles with at most 5 teeth (Japan south to Australia) ..... *Ochetellus* (in part)

11b. Petiole not unduly expanded dorsally and with the dorsal regions the same width or narrower than ventral regions; number of mandibular teeth variable 12

12a. Digitus linear, without a down-turned tip (tip sometimes slightly swollen);

second funicular segment barrel-shaped ..... *Azteca* (in part)

12b. Digitus with at least a slight ventral arch; second funicular segment cylindrical 13

13a. Petiolar scale strongly inclined anteriorly (Fig. 147); first gastral segment projecting anteriorly 14

13b. Petiolar scale vertical (Fig. 36); first gastral segment vertical or elongate posteriorly 16

14a. Scape much longer than the length of funicular segments 1+2+3 (Fig. 146); mandible with less than 16 teeth; petiolar scale reduced (world wide) ..... *Tapinoma*

14b. Scape shorter than the length of funicular segments 2+3 (Fig. 20); mandible with more than 17 teeth; petiolar scale present 15

15a. Petiolar scale rounded and forming an even arch dorsally; venter of petiole without a lobe (Fig. 21); first gastral segment projecting anteriorly, but not concealing the petiole in dorsal view, and with a groove or indentation for the reception of the basal portion of the petiole; fore wing with 1 closed discoidal cell (sub-Saharan Africa) ..... *Axinidris*

15b. Petiolar scale ridged and with a distinct angle dorsally; venter of petiole with a slight or reduced lobe (Fig. 155); first gastral segment projecting anteriorly and concealing the petiole in dorsal view, and with a groove or indentation for the reception of the entire height of the petiole; fore wing without closed discoidal cells (world wide, rare in New World) .... *Technomyrmex*

16a. Medial hypostoma absent (Fig. 171); palp formula 4:2 or 2:2; mandible with less than 4 teeth (rarely with 3 and a very small fourth tooth) (Old World) ..... *Bothriomyrmex*

16b. Medial hypostoma present (Figs. 168, 169); palp formula 6:4, rarely 3:4; mandible generally with more than 5 teeth 17

17a. Medial hypostoma notched (Fig. 168) (New Guinea, New Caledonia, Australia) ..... *Leptomyrmex* (in part)

17b. Medial hypostoma entire (Fig. 169) 18

18a. Inner margin of compound eye angular (Fig. 53); anterior hypostoma in the form of an expanded flange (Fig. 164); mandibles with more than 20 teeth (world wide) ..... *Dolichoderus*

18b. Inner margin of compound eye flat (Fig. 115); anterior hypostoma reduced to a thin sclerite (Fig. 166); mandibles usually with less than about 16 teeth (rarely with up to about 25) 19

19a. Scape about the same length as funicular segments 1+2+3 (Fig. 115); axilla constricted medially and therefore absent dorsally; first gastral segment with a groove or indentation; parameres enlarged (holarctic) .... *Liometopum*

19b. Scape shorter than the length of funicular segments 2+3 (Fig. 93); axilla with anterior and posterior sutures parallel and complete dorsally; first gastral segment smooth; parameres normal sized 20

20a. Basal angle of mandible indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle; posterior margin of subgenital plate with a "V"-shaped notch .... *Iridomyrmex* (in part)

20b. Basal angle of mandible distinct (with a well developed tooth or angle separating the masticatory and basal margins) or weakly defined by a denticle (or if indistinct, venter of petiole with a well developed lobe); posterior margin of subgenital plate concave 21

21a. Basal margin of mandible denticulate; first funicular segment cylindrical or cone-shaped (Southeast Asia to Australia) ..... *Anonychomyrma*

21b. Basal margin of mandible smooth; first funicular segment barrel-shaped 22

22a. Palp formula 3:4 (South America) .....*Anillidris*

22b. Palp formula 6:4 23

23a. Mandible with less than 8 teeth and the apical tooth much larger than the subapical; first gastral segment vertical (Australia) .....*Doleromyrma*

23b. Mandible with more than 8 teeth and the apical tooth only slightly larger than the subapical; first gastral segment elongated posteriorly 24

24a. Second funicular segment more than three times as long as broad; basal angle of mandible weakly defined by a denticle; dorsum of petiolar scale rounded; attachment of petiole and gaster narrow (New World, with a widespread tramp species) ..... *Linepithema*

24b. Second funicular segment about twice as long as broad; basal angle of mandible absent; dorsum of petiolar scale angular; attachment of petiole and gaster broad (Indo-Australian region) ..... *Philidris*

TAXONOMIC DISCUSSION

Genus *Anillidris* Santschi (Figs. 1-5)

Anillidris Santschi 1936: 414. Type Species: *Anillidris bruchi* Santschi (by monotypy).

[Syn. of *Linepithema* Mayr by Kusnezov 1958b: 273, reinstated by Brown 1973: 169.]

Diagnosis

Worker: Frontal lobes very close together; central region of clypeus raised, with a distinct medial trough and lateral ridges; compound eyes absent; palp formula 2:3; entire body covered with dense, short, erect pubescence. Known only from Argentina and Brazil.

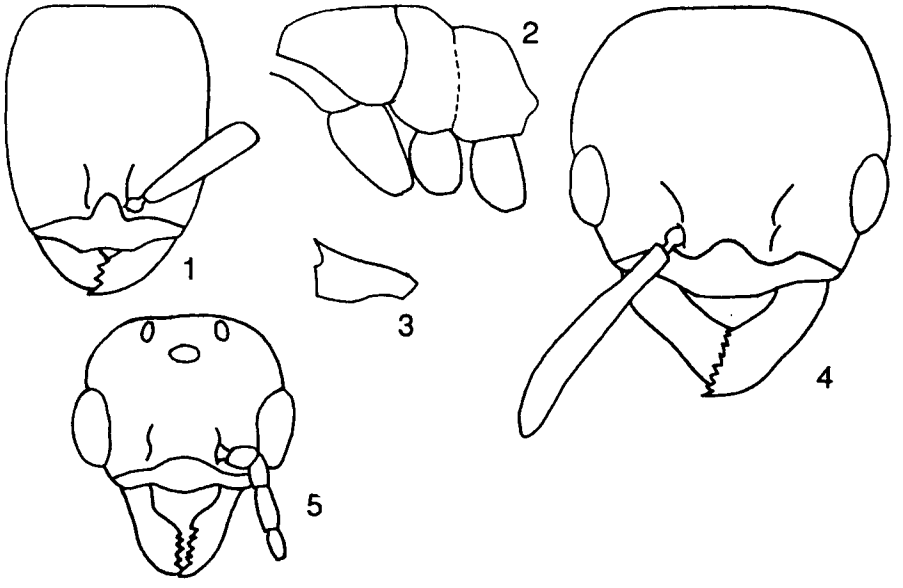
Queen: Palp formula 3:4; anterior clypeal margin with about 22 erect hairs.

Male: Palp formula 3:4; mandible with 6 to 7 teeth, 1 denticle, and a distinct basal angle; fore wing with 2 closed cubital cells and 1 closed discoidal cell.

Description

WORKER.

HEAD. Vertex weakly convex. Compound eyes and ocelli absent. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-third its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae about 4; short, less than twice the maximum scape diameter; moderately curved ventrally. Posterior clypeal margin even with or posterior to the posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 2:3 (Santschi 1936). Mandible with 4 teeth and 3 denticles. Apical tooth subequal in length to the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded. Mesopleural process absent. Declivitous face of propodeum



Figs. 1-5: 1, Full face view of *Anillidris* worker (Misiones, Argentina); 2, Lateral view of *Anillidris* worker mesosoma (Misiones, Argentina); 3, Lateral view of *Anillidris* worker petiole (Misiones, Argentina); 4, Full face view of *Anillidris* queen (Misiones, Argentina); 5, Full face view of *Anillidris* male (Misiones, Argentina).

weakly convex; dorsal face convex, subequal in length to the declivitous face. Propodeal angle distinct. Mesosomal spines and tooth absent. Erect pronotal hairs numerous; very short, less than the maximum scape width. Dorsal promesonotal junction with the pronotum and mesonotum even. Metanotal groove reduced to a suture and with the mesonotum and propodeum forming a continuous, uninterrupted surface. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a slight or weakly developed lobe. GASTER. First tergite damaged in available material. Fifth tergite ventral, gaster with 4 apparent tergites. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number unknown. Integument thin and flexible, weakly sculptured.

QUEEN.

HEAD. Vertex weakly convex. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin even with the mediolateral

region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae about 22; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin even with or posterior to the posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 3:4 (Santschi 1936). Mandible with 8 teeth and no denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded. Episternal suture complete. Mesopleural process absent. Axilla parallel (very narrow across dorsal surface) and entire. Anterior axillar suture straight. Declivitous face of propodeum convex; dorsal face convex, subequal in length to the declivitous face. Propodeal angle indistinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs absent. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cell. *Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct* angle dorsally; vertical and not inclined anteriorly. Venter with a slight or weakly developed lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment barrel-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 6; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 3:4 (Santschi 1936). Mandible with 6-7 teeth and 1 denticle. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded. Episternal suture present, complete. Axilla parallel

and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex. Propodeal angle indistinct. WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; vertical and not inclined anteriorly. Venter with a well developed lobe. Attachment to gaster broad. GASTER. First segment elongated posteriorly, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate with a "V"-shaped notch. Paramere entire. Digitus linear, with a slight ventral arch. Ventral lobe of volsella present as concave lobe.

LARVAE: Unknown.

Discussion

Anillidris is known from a single species and a limited number of collections in Argentina and Brazil. The genus is defined by the unique characters listed in the Diagnosis above. The workers are one of the most unusual in the subfamily, and are very similar to the formicine genus *Acropyga*. The worker material examined during this study was damaged, and neither an acidopore nor the typical dolichoderine slit-like gastral terminus could be observed. However, the worker-associated queen material was in very good condition and possessed the dolichoderine gaster, providing clear evidence that this taxon does belong to the Dolichoderinae. The morphological similarity of the *Anillidris* worker to workers of *Acropyga* is presumably a convergence caused by similar hypogeic habits.

The placement of *Anillidris* within the subfamily has been problematical. Santschi (1936) tentatively placed it near *Bothriomyrmex*, presumably based on the reduced number of palp segments and the thoracic profile. With the examination of the proventriculus and wings of the queen and male, Santschi revised his opinion and placed *Anillidris* near *Dolichoderus* and *Leptomyrmex* (Santschi 1937). Kusnezov (1958b) placed *Anillidris* in synonymy with *Linepithema*, but listed no characters to support his decision. Kempf (1972) agreed with this synonymy, while Brown (1973) and Snelling (1981) disagreed and treated both *Anillidris* and *Linepithema* as valid genera. The genus is in fact morphologically very different from all others in the subfamily (see Diagnosis above) and should be treated as distinct. Unfortunately, the large number of autapomorphic characters present in all castes make placement of *Anillidris* within the subfamily difficult.

Little is known about the habits of *Anillidris*. A colony has been collected under a large rock (Borgmeier 1937), while other data suggests that they are subterranean in moist areas (Kusnezov 1953b) and lestobiotic (Santschi 1937).

Distribution: Loreto, Misiones Prov., Argentina (type locality); Nova Teutonia

(=Nueva Teutonia), Santa Caterina State, Brazil (Borgmeier 1937).

Genus *Anonychomyrma* Donisthorpe (Figs. 6-15, Table 3)

Anonychomyrma Donisthorpe 1947: 588 (conditional syn. (not available) of *Iridomyrmex* by Brown 1973: 178, full genus by Shattuck 1992a). Type species: *Anonychomyrma myrmex* Donisthorpe (by monotypy).

Diagnosis

Worker: Mandible with apical tooth slightly longer than subapical, basal angle distinct and with a well developed tooth or angle separating the masticatory and basal margins, and basal margin denticulate along entire surface; gastral compression absent (gaster circular in cross section); fourth gastral sternite keel-shaped posteriorly; petiolar scale vertical and varying from not inclined anteriorly to moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. New Guinea, the Solomon Islands and Australia.

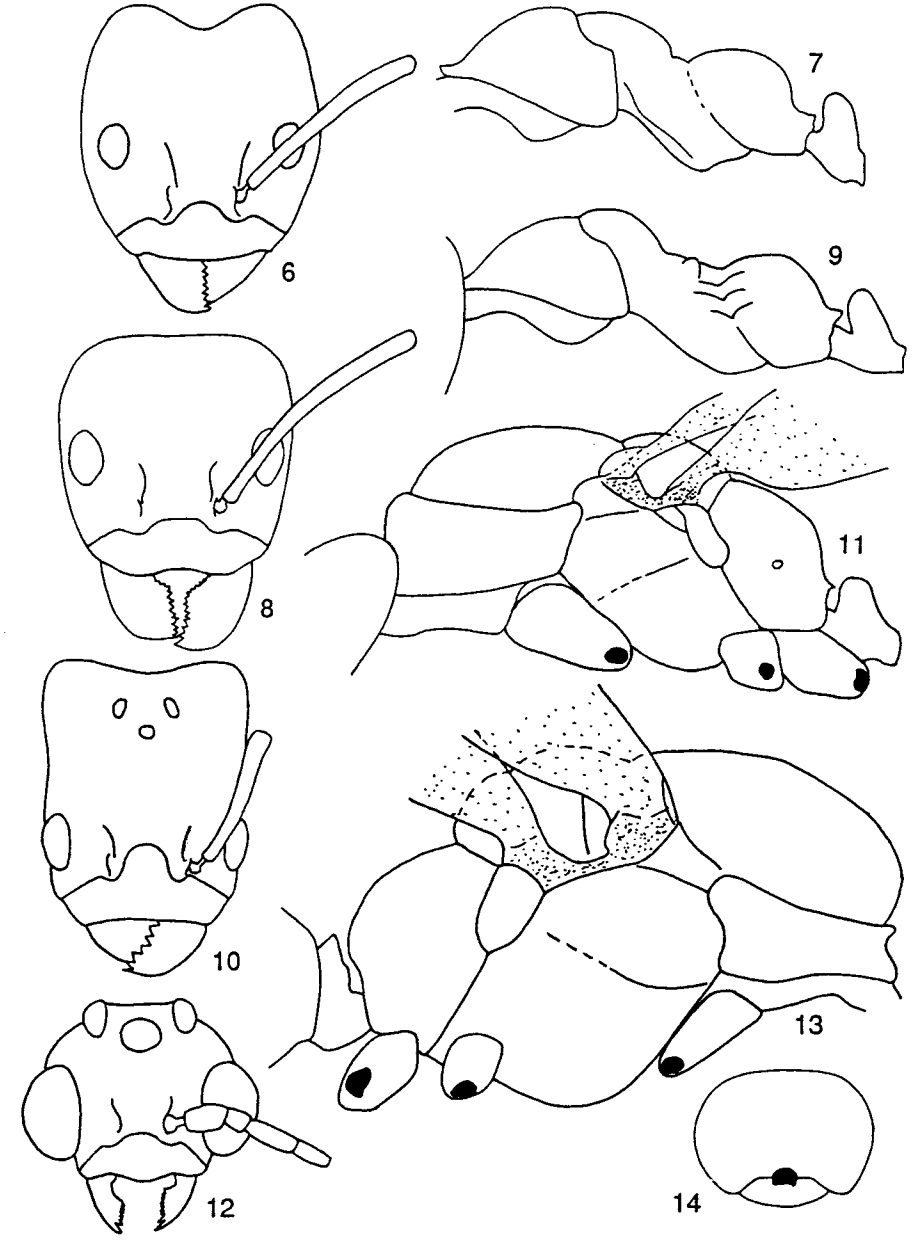
Queen: Anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region, and the entire margin with 14 to 26 short erect setae; dorsal face of propodeum longer than declivitous face; 28 to 40 erect hairs on the mesoscutum.

Male: Mandible with 5 to 9 teeth, 0 to 4 denticles, a distinct basal angle (or if the angle is weakly defined, the masticatory and basal margins are readily separable), and with the basal margin denticulate along its entire surface.

Description

WORKER.

HEAD. Vertex weakly convex to concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin even with the mediolateral region and with the corners expanded slightly anterior of the mediolateral region (sometimes with the lateral region very slightly posterior of the mediolateral region). Anteromedial clypeal margin entire, without a central notch or concavity of any type, or less commonly with a broad, shallow concavity. Anterior clypeal setae 6-16; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire (rarely with a small "V"-shaped notch). Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 5-10 teeth and



Figs. 6-14: 6, Full face view of *Anonychomyrma* worker (Queensland, Australia); 7, Lateral view of *Anonychomyrma* worker mesosoma (Queensland, Australia); 8, Full face view of *Anonychomyrma* worker (Irian Jaya, Indonesia); 9, Lateral view of *Anonychomyrma* worker mesosoma (Irian Jaya, Indonesia); 10, Full face view of *Anonychomyrma* queen (Solomon Islands); 11, Lateral view of *Anonychomyrma* queen mesosoma (Solomon Islands); 12, Full face view of *Anonychomyrma* male (Queensland, Australia); 13, Lateral view of *Anonychomyrma* male mesosoma (Queensland, Australia); 14, Anterior view of first gastral segment of *Anonychomyrma* (Queensland, Australia).

0-5 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum weakly convex to flat; dorsal face convex, longer than to subequal in length to the declivitous face. Propodeal angle distinct to indistinct. Mesosomal spines and tooth absent. Erect pronotal hairs 4-70; elongate, much longer than the maximum scape width, or less commonly short, about as long as maximum scape width. Dorsal pro-mesonotal junction with the mesonotum above the pronotum, or with the pronotum and mesonotum even. Metanotal groove forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle lateral and ventral of the dorsal surface, or dorsal and lying on the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; rounded and forming an even arch dorsally, or ridged and with a distinct angle dorsally; vertical and not inclined anteriorly to moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. Venter with a weakly to well developed lobe, or less commonly without a lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole (occasionally smooth and without a groove or indentation). Anterior tergosternal suture of the first segment extending laterally from the helcium, without or with at most a very weak dorsal arch. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite keel-shaped posteriorly. GENERAL CHARACTERS. Worker caste monomorphic (rarely polymorphic). Chromosome number 8 (n=8, 2n=16, *A. itinerans*, Crozier 1968a; 2n=16, *A. itinerans*-group, sp. ANIC-10, Imai *et al.* 1977). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round; with short pile; smooth, without sculpture; and with short, lateral phragma. Bulb completely hidden by cupola in lateral view. Occlusory tract absent.

QUEEN.

HEAD. Vertex weakly concave to concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type, or less commonly with a broad, shallow concavity. Anterior clypeal setae 14- 30; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin posterior of the anterior surfaces of the antennal socket cavities.

Table 3. Major characters differing among workers of *Anonychomyrma*, *Iridomyrmex*, *Papyrius* and *Philidris*.

Character	*Anonychomyrma*	*Iridomyrmex*	*Papyrius*	*Philidris*
Position of compound eyes	anterior	posterior	anterior	anterior
Worker caste	monomorphic	monomorphic	monomorphic	polymorphic
Anterolateral clypeus	even with or anterior to mediolateral margin	posterior to mediolateral margin	posterior to mediolateral margin	posterior to mediolateral margin
Anteromedial clypeus	entire	toothed	entire	weakly convex to toothed
Palp formula	6:4	6:4	5:3	6:4
Basal mandibular margin	denticulate	partially denticulate	smooth	partially denticulate
Inclination of petiolar scale	none to moderately anterior	none to moderately anterior	none	strongly anterior
First gastral suture near helcium	horizontal, flat	arched dorsally	arched dorsally	arched dorsally
Fourth gastral sternite	keel-shaped	flat	flat	flat

Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire or occasionally very slightly notched. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7-9 teeth and 0-4 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete but weakly developed anteriorly. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel or very weakly constricted medially, and entire or with a suture medially. Anterior axillar suture straight. Declivitous face of propodeum convex or occasionally weakly concave; dorsal face convex, longer than the declivitous face. Propodeal angle distinct or indistinct. Propodeal suture weakly developed or absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs 28-50; short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 1-2 cubital and 1 discoidal

cell. Hind wing with 2-3 cells. PETIOLE. Scale present; rounded and forming an even arch dorsally or ridged and with a distinct angle dorsally; vertical and not inclined to strongly inclined anteriorly (if inclined, the anterior face is much shorter than the posterior face). Venter with or without a well developed, rounded lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of either the basal portion or the entire height of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment cylindrical or cone- shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 4; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with 5-9 teeth and 0-4 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins, or weakly defined by a denticle (but with the masticatory and basal margins readily separable). Basal margin denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel, and entire or with a suture medially. Anterior axillar suture straight or angular medially. Declivitous and dorsal faces of propodeum convex. Propodeal angle indistinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; rounded and forming an even arch dorsally; vertical and not inclined anteriorly. Venter with or without a well developed lobe. Attachment to gaster broad. GASTER. First segment vertical and not concealing the petiole in dorsal view, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave. Paramere divided by a membranous region. Digitus with a down-turned tip. Cuspis parallel with digitus. Ventral lobe of volsella present as concave lobe. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances absent. Body hairs sparse; simple;

short. 9 spiracular pairs. Antennae short.

Discussion

Anonychomyrma was established by Donisthorpe (1947), in its own tribe, for a single male specimen from Papua New Guinea. The specimen was described in detail, but no discussion was given to justify its status as a separate genus. The tribe was defined simply by the character "male tarsi without claws". This genus has received almost no attention since its establishment, other than being placed in conditional synonymy with *Iridomyrmex* by Brown (1973).

Recently however, Shattuck (1992a) transferred a number of species from *Iridomyrmex* to *Anonychomyrma*. This has expanded the genus considerably, and it now includes 29 described species distributed from Malaysia to the Solomon Islands and Australia. The transfer was based on examination of complete nest series (containing workers, queens and males) and morphological differences between *Anonychomyrma* and *Iridomyrmex* in all three castes. Specimens of *Anonychomyrma* can be diagnosed by the characters listed above. The workers and queens of *Anonychomyrma* differ from *Iridomyrmex* in the placement of the compound eyes, the configuration of the anterior clypeal and basal mandibular margins, and the shape of the fourth gastral sternite (see also Table 3). Additionally, the workers of *Anonychomyrma* have the pronotum, mesonotum and propodeum strongly arched whereas these regions in *Iridomyrmex* are generally only weakly arched. The males of these two genera differ in the configuration of the mandibles (number of teeth and configuration of the basal angle and margin), posterior margin of the subgenital plate, digitus, and ventral lobe of the volsella (see extended descriptions for details). Curiously, while tarsal claws are greatly reduced in the type species of *Anonychomyrma*, as noted by Donisthorpe (1947), all other known males have normally developed claws.

Anonychomyrma species are common in moist to semi-arid forested areas (and are less common in rain forests). They form conspicuous foraging trails on the ground and tree trunks and nest in the soil as well as arboreally.

Anonychomyrma differs from *Iridomyrmex* in habitat preferences and general ecology. *Anonychomyrma* prefers moister sites and is more often arboreal, while *Iridomyrmex* occurs primarily in drier sites and is predominantly terrestrial. Thus, ecological differences corroborate the morphological features which allow recognition of these two distinct groups.

Distribution: Malaysia and Sumatra east to New Guinea, the Solomon Islands and Australia (Fig. 15).

Genus *Axinidris* Weber (Figs. 16-23)

Axinidris Weber 1941:192. Type species: *Axinidris acholli* Weber (by

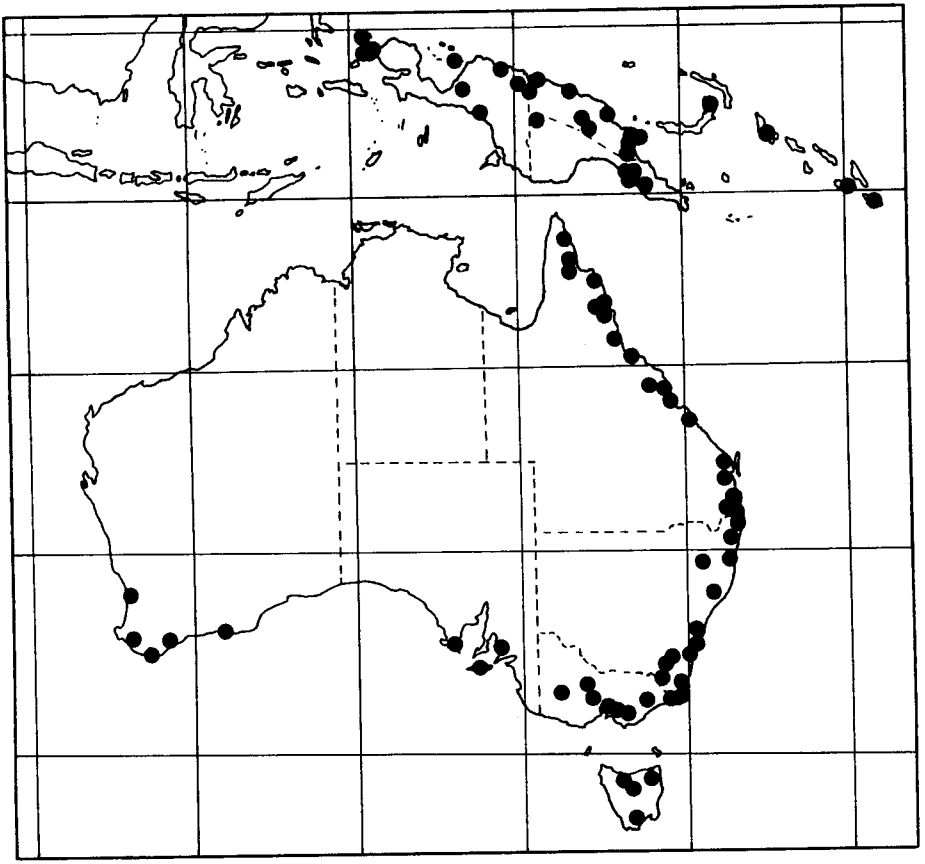


Fig. 15: Distribution of *Anonychomyrma* material examined during this study. (The types of three species here treated as belonging to *Anonychomyrma* lack specific locality data and are not included in the above map. The localities are Malacca, Sulawesi and Sumatra.)

monotypy).

Diagnosis

Worker: Anteromedial clypeal margin with a distinct notch separated from the general outline by distinct, angular corners; propodeum armed with short, rounded spines located near the dorsal margin of the declivitous face (occasionally spines elongate, reduced to angles, or absent); propodeal spiracle located dorsally and medially along the dorsal face of the propodeum and with at least the anterior margin raised on a slight projection (thus directing the spiracular opening posteriorly); medial region of propodeum (between the propodeal spines, when present) with a longitudinal carina (occasionally

expanded into a dorsal flange, or absent; if absent, propodeum with lateral angles); petiolar node broadly rounded dorsally and strongly inclined anteriorly. Sub-Saharan Africa.

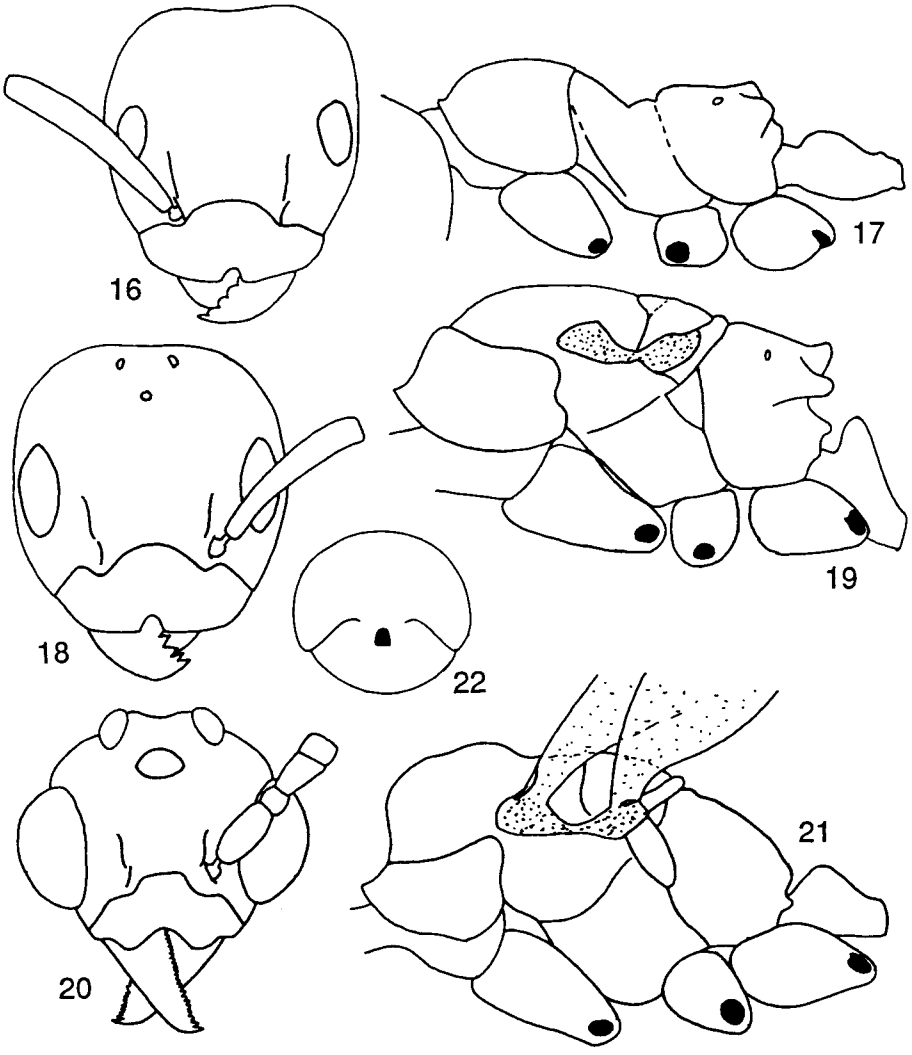
Queen: Anteromedial clypeal margin with a distinct notch separated from the general outline by distinct, angular corners; propodeal spiracles located dorsally and medially along the dorsal face of the propodeum; declivitous face of propodeum concave; first gastral segment projecting anteriorly, but not concealing petiole in dorsal view; hind wing without closed cells; propodeum with or without spines or angles.

Male: Anteromedial clypeal margin with a distinct notch separated from the general outline of the margin by distinct, angular corners; mandible with about 27 teeth and no denticles; first gastral segment strongly inclined anteriorly (but not concealing the petiole in dorsal view), and with a groove or indentation for the reception of the basal portion of the petiole; petiolar node strongly inclined anteriorly and with the anterior face much shorter than the posterior face; hind wing without closed cells.

Description

WORKER.

HEAD. Vertex flat to weakly concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin with a distinct, central notch separated from the general outline of the margin by distinct, angular corners. Anterior clypeal setae 2-12; about the same length as the closed mandibles (sometimes with a few additional short hairs); moderately curved ventrally. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with about 6 teeth and about 3 denticles. Apical tooth subequal in length to the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins. Basal margin denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum flat; dorsal face convex to flat, subequal in length to (rarely longer than) the declivitous face. Propodeal angle distinct. Pronotal spines absent (but ridged laterally in some species). Erect pronotal hairs 0-8; short, about as long as maximum scape width or elongate and much



Figs. 16-22: 22, Full face view of *Axinidris murielae* worker; 17, Lateral view of *Axinidris murielae* worker mesosoma; 18, Full face view of *Axinidris* queen (Gabon); 19, Lateral view of *Axinidris* queen mesosoma (Gabon); 20, Full face view of *Axinidris* male (Ivory Coast); 21, Lateral view of *Axinidris* male mesosoma (Ivory Coast); 22, Anterior view of first gastral segment of *Axinidris murielae*.

longer than the maximum scape width. Mesonotal spines absent. Propodeal spines present and distinct, or reduced to protuberances (and with a central, dorsal ridge or plate). Propodeal tooth absent. Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove forming a distinct

angle between the mesonotum and propodeum. Metanotal spiracle dorsal and lying on the dorsal surface when viewed in lateral profile. Propodeal spiracle dorsal and medially along the basal propodeal face. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; rounded and forming an even arch dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter without a lobe. GASTER. First tergite projecting anteriorly, but not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Anterior tergosternal suture of the first segment absent immediately lateral of the helcium and with the lateral section of the suture terminating immediately above the helcium. Fifth tergite vertical and with the distal terminus of the gaster not well defined. Gastral compression dorsoventral. Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number unknown. Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Not examined.

QUEEN.

HEAD. Vertex flat to weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin with a distinct, central notch separated from the general outline of the margin by distinct, angular corners. Anterior clypeal setae 6-16; short, less than twice the maximum scape diameter to about the same length as the closed mandibles; straight. Posterior clypeal margin posterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 8-9 teeth and no denticles. Apical tooth slightly longer than the subapical tooth. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete. Mesopleural process absent. Axilla absent dorsally. Declivitous face of propodeum concave; dorsal face weakly convex (sometimes with a central carina or plate), longer than the declivitous face. Propodeal angle distinct. Propodeal suture absent. Pronotal spines absent. Erect mesoscutal hairs 0-4; when present short, less than twice the maximum scape diameter. Propodeal spines present as protuberances. Propodeal tooth absent. Propodeal spiracle dorsal and medial along the dorsal face. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 1 cubital and 1 discoidal cell. Hind wing cells absent. PETIOLE. Scale present; rounded and forming an even arch dorsally, ridged

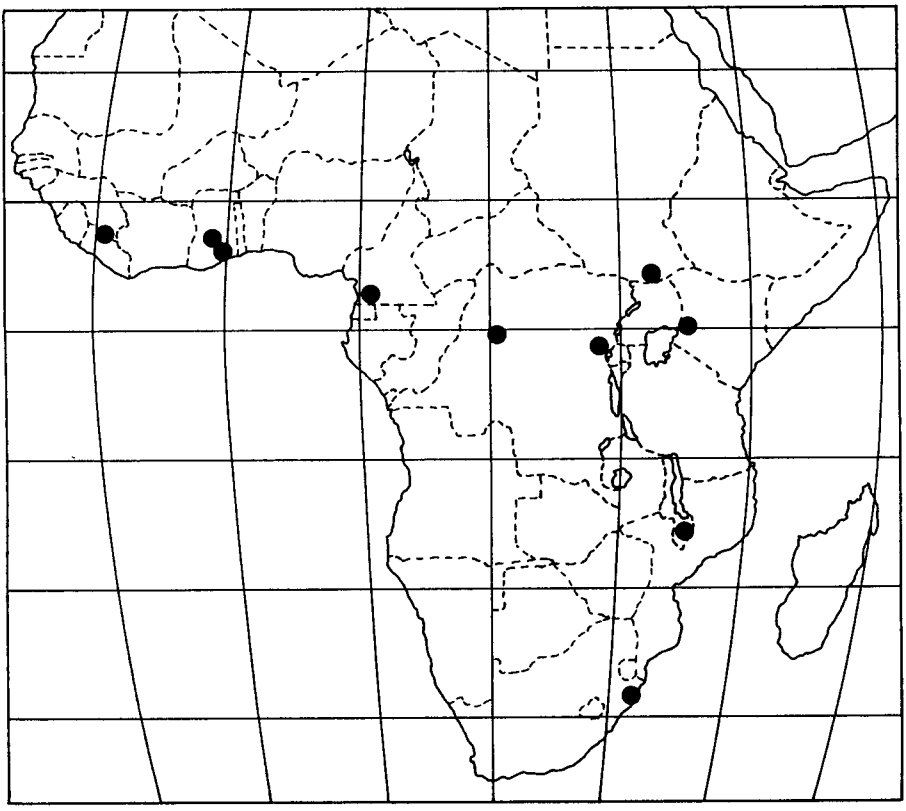


Fig. 23: Distribution of *Axinidris* material examined during this study.

and with a distinct angle dorsally, or spined and with a double tooth or projection dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter without a lobe. GASTER. First segment projecting anteriorly, but not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Fifth tergite vertical and with the distal terminus of the gaster not well defined (additionally, the sclerite is reduced longitudinally). Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment cylindrical or cone- shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin with a distinct, central notch separated from the

general outline of the margin by distinct, angular corners. Anterior clypeal setae about 10; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with about 27 teeth and no denticles. Apical tooth slightly longer than the subapical tooth. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Axilla constricted medially, and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex. Propodeal angle indistinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing cells absent. PETIOLE. Scale present; rounded and forming an even arch dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter without a lobe. Attachment to gaster narrow. GASTER. First segment projecting anteriorly, but not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. GENITALIA. Pygostyles present. Posterior margin of subgenital plate with a "V"-shaped notch. Paramere entire. Digitus with a down-turned tip. Cuspis ventral of digitus. Ventral lobe of volsella present as concave lobe. Aedeagus without ventral teeth.

LARVAE: Unknown.

Discussion

The genus *Axinidris* was established by Weber (1941) for two specimens of a single species collected in southern Sudan. Recently, *Axinidris* was revised (Shattuck 1991) and expanded to include 13 species, nine of which were newly described. It is now clear that this genus occurs throughout sub-Saharan Africa.

The worker caste of *Axinidris* can be distinguished from all other dolichoderines based on the dorsal propodeal spiracular placement, the angles or spines near the propodeal angle and the strongly anteriorly inclined and dorsally rounded petiolar node. Additionally, most species have a medial plate or carina on the propodeum. The propodeal spines and medial plate are extremely large in the type species (*A. acholli*) however these characters are less dramatic in most *Axinidris* species.

The limited biological information available for *Axinidris* species suggests that they nest and forage arboreally. This likely accounts for the low number of collections of these widely distributed ants.

Distribution: Africa from Liberia east to southern Sudan and Kenya, south to South Africa (Fig. 23).

Genus *Azteca* Forel (Figs. 24-30)

Azteca Forel 1878b:384. Type species: *Liometopum xanthochroum* Roger (by orig. desig.).

Diagnosis

Worker: Polymorphic, majors with ocelli; anterolateral clypeal margin with the corners expanded anterior of the mediolateral region; vertex concave; petiolar scale strongly inclined anteriorly, and with a distinct ventral node; dorsal face of propodeum longer than declivitous face; mandible with 7-9 teeth and no denticles, and with the apical tooth subequal in size to the subapical; metanotal groove forming a distinct angle between the mesonotum and propodeum. Central and South America.

Queen: Propodeal angle indistinct; petiolar scale strongly inclined anteriorly and with the anterior face much shorter than the posterior face; venter of petiole with a well developed, rounded lobe; wing with one closed cubital cell.

Male: Second funicular segment barrel-shaped; petiolar scale with a blunt angle or a single tooth or projection dorsally; pygostyles vestigial; mandible with 1 to 4 teeth and 0 to about 3 denticles; first gastral segment vertical (not concealing the petiole in dorsal view), and with a groove or indentation for the reception of the entire height of the petiole.

Description

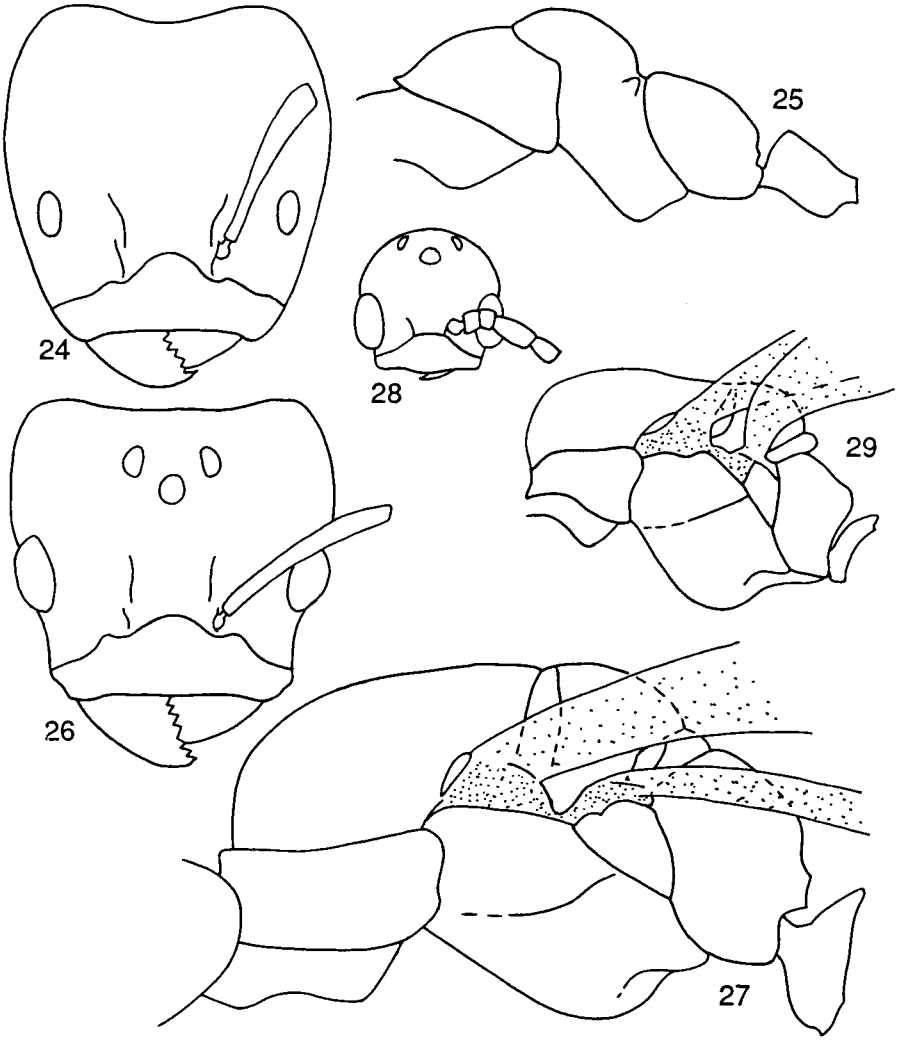
WORKER.

HEAD. Vertex weakly to strongly concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli present (in majors). Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin even with the mediolateral region and commonly with the corners expanded slightly anterior of the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 6-14; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4, 5:3, 4:3 or 4:2 (rarely 5:3 partly fused into 4:3). Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7-9 teeth and no denticles. Apical tooth subequal in length to the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin varying from smooth (without teeth or denticles) to denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or

angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum convex; dorsal face flat or convex, longer than the declivitous face. Propodeal angle indistinct to moderately distinct. Mesosomal spines and tooth absent. Erect pronotal hairs 4-20 (rarely absent); when present elongate, much longer than the maximum scape width. Dorsal pro-mesonotal junction with the pronotum and mesonotum even, or with the mesonotum above the pronotum. Metanotal groove forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle dorsal and lying on the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum (sometimes appearing dorsal because of reduction of dorsal propodeum). Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a well developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium, without or with at most a very weak dorsal arch. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression lateral, dorsoventral, or absent (gaster circular in cross section). Fourth sternite keel-shaped posteriorly. GENERAL CHARACTERS. Worker caste polymorphic. Chromosome number unknown. Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola slightly broader than bulb; excised; with short pile; smooth, without sculpture; and without phragma. Bulb exposed in lateral view. Longitudinal muscle No. 1 present. Occlusory tract present.

QUEEN.

HEAD. Vertex weakly convex to weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin even with the mediolateral region, or occasionally with the corners expanded slightly anterior of the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 8-10; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4 or 4:3 (and possibly others, see worker description). Third maxillary palp segment (when present) subequal in length to segment 4. Fifth maxillary palp segment (when present) at the apical extreme of segment 4. Mandible with 7-8 teeth and 0-1 denticles. Apical tooth subequal in length to, to slightly longer than, the



Figs. 24-29: 24, Full face view of *Azteca* worker (Panama); 25, Lateral view of *Azteca* worker mesosoma (Panama); 26, Full face view of *Azteca* queen (Panama), 27, Lateral view of *Azteca* queen mesosoma (Panama); 28, Full face view of *Azteca* male (Paraguay); 29, Lateral view of *Azteca* male mesosoma (Paraguay).

subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin varying from smooth (without teeth or denticles) to denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete. Mesopleural process absent. Anteromedial mesosternum

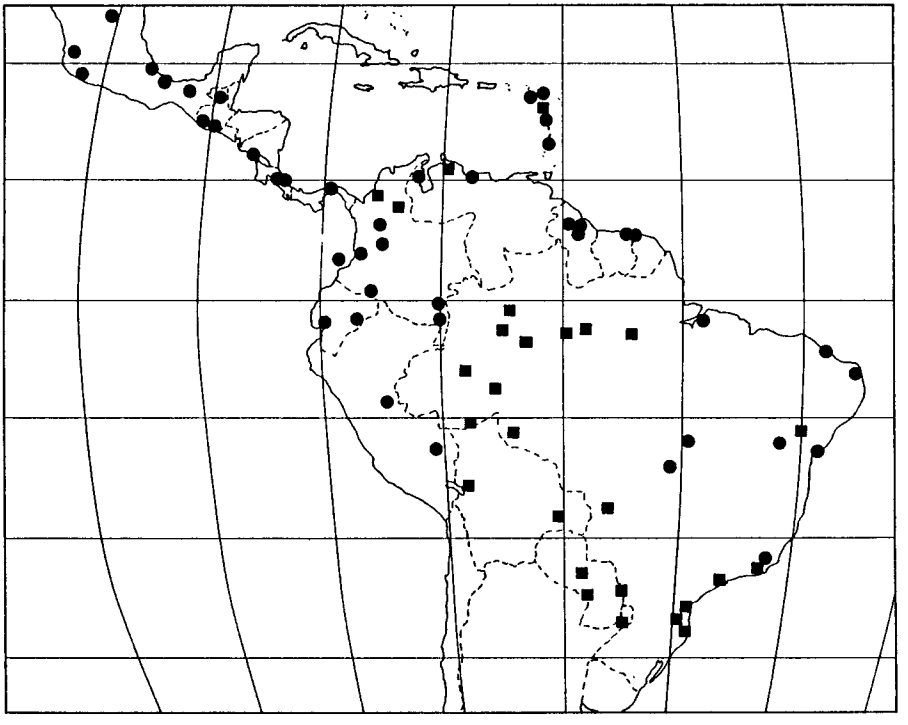


Fig. 30: Distribution of *Azteca*. Closed circles indicate examined material. Closed squares indicate literature records believed to be reliable.

even with the lateral regions. Axilla subparallel (very weakly constricted), constricted medially, or absent dorsally; when present, entire. Anterior axillar suture (when present) straight or angular medially. Declivitous face of propodeum convex; dorsal face convex, subequal in length to the declivitous face. Propodeal angle indistinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs about 16-100; short, less than twice the maximum scape diameter to elongate, more than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 1 cubital and 1-2 discoidal cells. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a well developed, rounded lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Fifth tergite vertical and with the distal terminus of the gaster not

well defined. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment barrel-shaped. Second funicular segment barrel-shaped, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 4-10; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin even with or anterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4 or 5:3 (and possibly others, see worker description). Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with 1-4 teeth and 0 - about 3 denticles. Apical tooth distinct. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel or constricted medially, and entire. Anterior axillar suture straight. Declivitous face of propodeum convex; dorsal face convex, subequal in length to the declivitous face. Propodeal angle distinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 1-2 discoidal cells. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; a blunt angle dorsally, or spined with a single tooth or projection dorsally; vertical and not inclined anteriorly. Venter with a well developed lobe. Attachment to gaster broad. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. GENITALIA. Pygostyles vestigial. Posterior margin of subgenital plate convex or even across entire width. Paramere entire. Digitus linear, without a down-turned tip; tip sometimes slightly swollen. Cuspis absent. Ventral lobe of volsella present as a swelling. Aedeagus with ventral teeth.

LARVA.

Shape crematogastroid. Protuberances present as 2 bosses located ventrolaterally on prothorax. Body hairs sparse and moderately abundant; simple and hooked; short and elongate. 10 spiracular pairs. Antennae large.

Discussion

Azteca is the second largest genus in the Dolichoderinae, with about 130 described species. The worker caste can generally be recognized in the field

by its cordate-shaped head, large foraging columns and habit of running with the gaster raised. *Azteca* workers are most similar to those of the Old World genus *Anonychomyrma*, but are separable based on the presence of ocelli in larger workers (ocelli are also present in one species of *Anonychomyrma*), a smaller subapical mandibular tooth, a strongly anteriorly inclined petiolar node, and a polymorphic worker caste. Additionally, the *Azteca* proventriculus is distinct in having the copula excised laterally, without phragma, and only slightly broader than the bulb; the bulb being exposed in lateral view; and the presence of an occlusory tract.

Species boundaries within *Azteca* are still poorly understood. The only comprehensive revision dates from 1893 (Emery 1893) and covers 25 of the 130 described species. The taxonomic understanding of this group is hindered by worker polymorphism, geographic variation, and the large number of species. In a recent taxonomic study, Longino (1989) synonymized two species and 12 subspecies under two valid names, but stated that each of his "species" may in reality represent a series of sibling species. Much work remains to be done to resolve these taxonomic problems.

All known species are arboreal, nesting in living or dead wood, or external carton nests. Some species exhibit obligate associations with myrmecophytes, especially of the genus *Cecropia*. Feeding habits are generalized with foraging occurring both arboreally and on the ground.

Distribution: Central Mexico south to Paraguay and southern Brazil (Fig. 30).

Genus *Bothriomyrmex* Emery (Figs. 31-38, Table 4)

Bothriomyrmex Emery 1869:117. Type Species: *Bothriomyrmex costae* Emery (by monotypy).

Chronoxenus Santschi 1920:202 (as subgenus of *Bothriomyrmex*, conditional syn. (not available) by Brown 1973:179). Type Species: *Bothriomyrmex myops* Forel (desig. by Donisthorpe 1944a:102). [NEW SYNONYMY]

Diagnosis

Worker: Palp formula 4:3 or 2:2; compound eyes with between 10 and about 40 ommitidia; mandibles with 5-6 teeth, 0-5 denticles, a distinct basal angle, and a smooth basal margin; frontal carinae reduced or absent; anterior clypeal margin with 2 to 12 downward curved hairs which are about the same length as the closed mandibles; medial hypostoma absent. Europe and northern Africa east through India to Taiwan, and south to Australia.

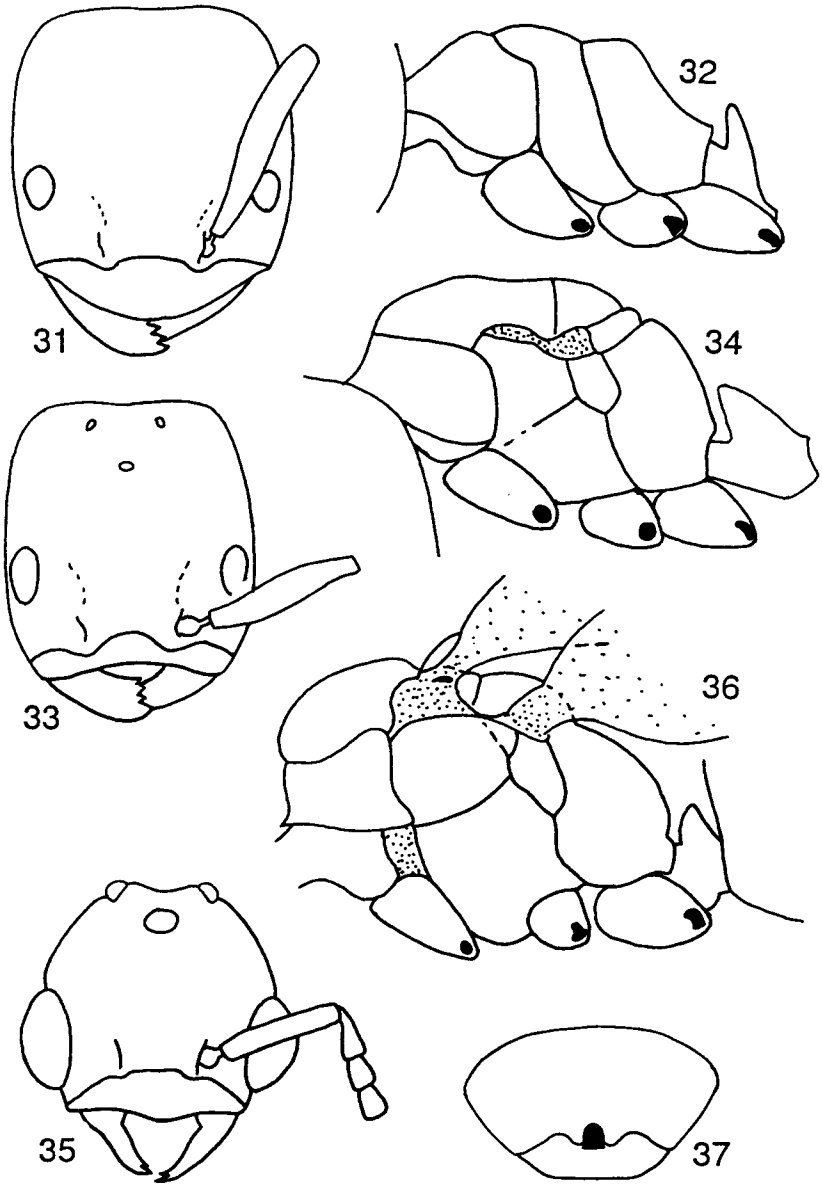
Queen: Palp formula 4:3 or 2:2; medial hypostoma absent; anterior clypeal margin with 2 to 6 moderately curved setae; apical tooth of mandible elongate and much longer than subapical; dorsal face of propodeum shorter than declivitous face.

Male: Medial hypostoma absent; palp formula 4:3 or 2:2; pygostyles vestigial.

Description

WORKER.

HEAD. Vertex weakly convex to weakly concave. Compound eyes present, approximately round (sometimes reduced to about 10 ommitidia, but always distinct); relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape relatively short, at most surpassing the vertex by less than one-half (often less than one-third) its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type, or with a broad, shallow concavity. Anterior clypeal setae 2-12; about the same length as the closed mandibles; moderately curved ventrally. Posterior clypeal margin even with or anterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina reduced or absent. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma absent. Psammophore absent. MOUTHPARTS. Palp formula 4:3 or 2:2. Third maxillary palp segment (when present) subequal in length to segment 4. Mandible with 5-6 teeth and 0-5 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum flat; dorsal face convex (sometimes weakly), shorter than the declivitous face. Propodeal angle indistinct to moderately distinct. Mesosomal spines and tooth absent. Erect pronotal hairs absent. Dorsal pro-mesonotal junction with the pronotum and mesonotum even, or with the mesonotum below the pronotum. Metanotal groove either reduced to a suture and with the mesonotum and propodeum forming a continuous, uninterrupted surface, or forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; ridged and with a distinct angle dorsally; varying from moderately inclined anteriorly (but with the anterior and posterior faces approximately the same length) to strongly inclined anteriorly (and with the anterior face much shorter than the posterior face). Venter with a well developed lobe. GASTER. First tergite projecting anteriorly and concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Anterior tergosternal suture of the first segment



Figs. 31-37: 31, Full face view of *Bothriomyrmex* worker (Queensland, Australia); 32, Lateral view of *Bothriomyrmex* worker mesosoma (Queensland, Australia); 33, Full face view of *Bothriomyrmex* queen (Queensland, Australia); 34, Lateral view of *Bothriomyrmex* queen mesosoma (Queensland, Australia); 35, Full face view of *Bothriomyrmex* male (Queensland, Australia); 36, Lateral view of *Bothriomyrmex* male mesosoma (Queensland, Australia); 37, Anterior view of first gastral segment of *Bothriomyrmex* (Queensland, Australia).

extending laterally from the helcium, either without a dorsal arch or with a distinct dorsal arch which is approximately the same height as the helcial dorsum. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression weakly dorsoventral. Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number 11 (n=11, *B.* sp., Hauschteck 1963; *B. gibbus*, Crozier 1975). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Not examined.

QUEEN.

HEAD. Vertex flat. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type, or with a broad, shallow concavity. Anterior clypeal setae 2-6; short, less than twice the maximum scape diameter to about the same length as the closed mandibles; moderately curved ventrally. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma absent. Psammophore absent. MOUTHPARTS. Palp formula 4:3 or 2:2. Mandible with 1-5 teeth (if 1 tooth, it is apical and the remainder of the masticatory border is smooth) and 0-4 denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla constricted medially. or absent dorsally (when present, entire). Declivitous and dorsal faces of propodeum convex to flat; dorsal face shorter than the declivitous face. Propodeal angle distinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs absent. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed or open. Fore wing with 1 cubital and 0-1 discoidal cells. Hind wing with 1-2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; varying from moderately inclined anteriorly (but with the anterior and posterior faces approximately the same length) to strongly inclined anteriorly (and with the anterior face much shorter than the posterior face). Venter with a well developed, rounded lobe. GASTER. First segment projecting anteriorly and concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Fifth tergite vertical and with the distal terminus of the gaster not well defined. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior

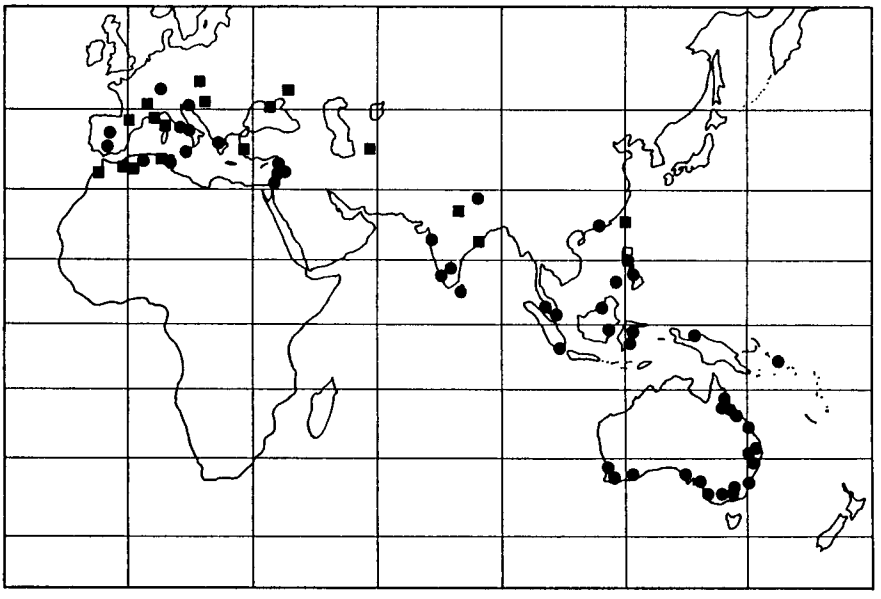


Fig. 38: Distribution of *Bothriomyrmex*. Closed circles indicate examined material. Closed squares indicate literature records believed to be reliable.

border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length much longer than the length of funicular segments 1+2+3 but not exceeding the vertex. First funicular segment cylindrical or cone-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 4-10; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma absent. MOUTHPARTS. Palp formula 4:2 or 2:2. Mandible with 2-3 teeth and no denticles (rarely with 3 teeth and a very small denticle). Apical tooth varying from slightly longer than, to elongate and much longer than, the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla constricted medially or absent dorsally. Anterior axillar suture straight. Declivitous face of

propodeum convex; dorsal face convex, subequal in length to the declivitous face. Propodeal angle distinct. WINGS. Radial cell closed or open. Fore wing with 1 cubital and 0-1 discoidal cells. Pterostigmal appendage absent. Hind wing with 1-2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; vertical and not inclined anteriorly. Venter with a well developed lobe. Attachment to gaster fairly broad, but with a distinct posterior petiolar face. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. GENITALIA. Pygostyles vestigial. Posterior margin of subgenital plate convex. Paramere entire. Digitus with a down-turned tip. Cuspis absent. Ventral lobe of volsella absent. Aedeagus without ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances present as 2 bosses located ventrolaterally on prothorax. Body hairs sparse; simple; short. 8 spiracular pairs. Antennae short.

Discussion

Bothriomyrmex is a moderate sized group widespread in the Old World and Australia. Workers are morphologically similar to those of *Doleromyrma* and smaller species of *Tapinoma* and *Technomyrmex*. They may be immediately recognized, however, by their smaller compound eyes, distinct basal mandibular angle, and 4:3 or 2:2 palp formula. For additional separatory characters, see Table 4.

In 1920, Santschi divided *Bothriomyrmex* into two subgenera, *Bothriomyrmex* (strict sense) and *Chronoxenus*. In the present study, all examined traits but one were either species-specific, or were shared between these two "subgenera." One character, a reduction in the number of maxillary and labial palp segments from 4:3 to 2:2, is the only attribute on which *Chronoxenus* is based. The fact that these two groups share numerous characters and that only a single derived feature can be used to separate them indicates that the species placed in *Chronoxenus* are a specialized subset of *Bothriomyrmex* (broad sense). On this basis, all species are here placed in the single genus *Bothriomyrmex*, confirming the conditional synonymy proposed by Brown (1973).

The taxonomic history of *Bothriomyrmex* was reviewed by Donisthorpe (1944a). (In this review, however, *B. meridionalis* is incorrectly listed as the type species, rather than *B. costae*.) The world fauna has been revised by Santschi (1920) and the European and Oriental species by Emery (1925).

Bothriomyrmex occurs in a wide variety of habitats, including grasslands, savanna woodlands, mallee forests, and lowland rain forests. Nests occur in the soil (with or without covering) or in rotten wood, and workers are known to forage on trees. At least some species are temporary social parasites of *Tapinoma* (Santschi 1906) or *Iridomyrmex* (strict sense) (Donisthorpe 1944a).

Distribution: Europe and northern Africa east through India to Taiwan, and south to Australia (Fig. 38).

Species Notes: The species described by Donisthorpe (1938b) as *Bothriomyrmex pallidus* (holotype worker [BMNH, examined] and 2 worker paratypes [BMNH, MCZC, examined] from Mt. Lina, 3500 ft, Cyclops Mts., Irian Jaya, Indonesia) is actually a formicine of the genus *Acropyga* and is here transferred to that genus as *Acropyga pallida* (Donisthorpe) (NEW COMBINATION).

Genus *Doleromyrma* Forel (Figs. 39-46, Table 4)

Doleromyrma Forel 1907: 28 (as subgenus of *Tapinoma*, syn. of *Iridomyrmex* in Emery 1912: 21, raised to full genus by Shattuck 1992a). Type species: *Tapinoma* (*Doleromyrma*) *darwinianum* Forel (by monotypy).

Diagnosis

Worker: First gastral segment projecting anteriorly, but generally not concealing petiole in dorsal view; anterior clypeal margin with moderately ventrally curved setae; mandibles with 4-5 teeth and 4-5 denticles; dorsal face of propodeum shorter than declivitous face; petiolar scale moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. Australia and New Zealand.

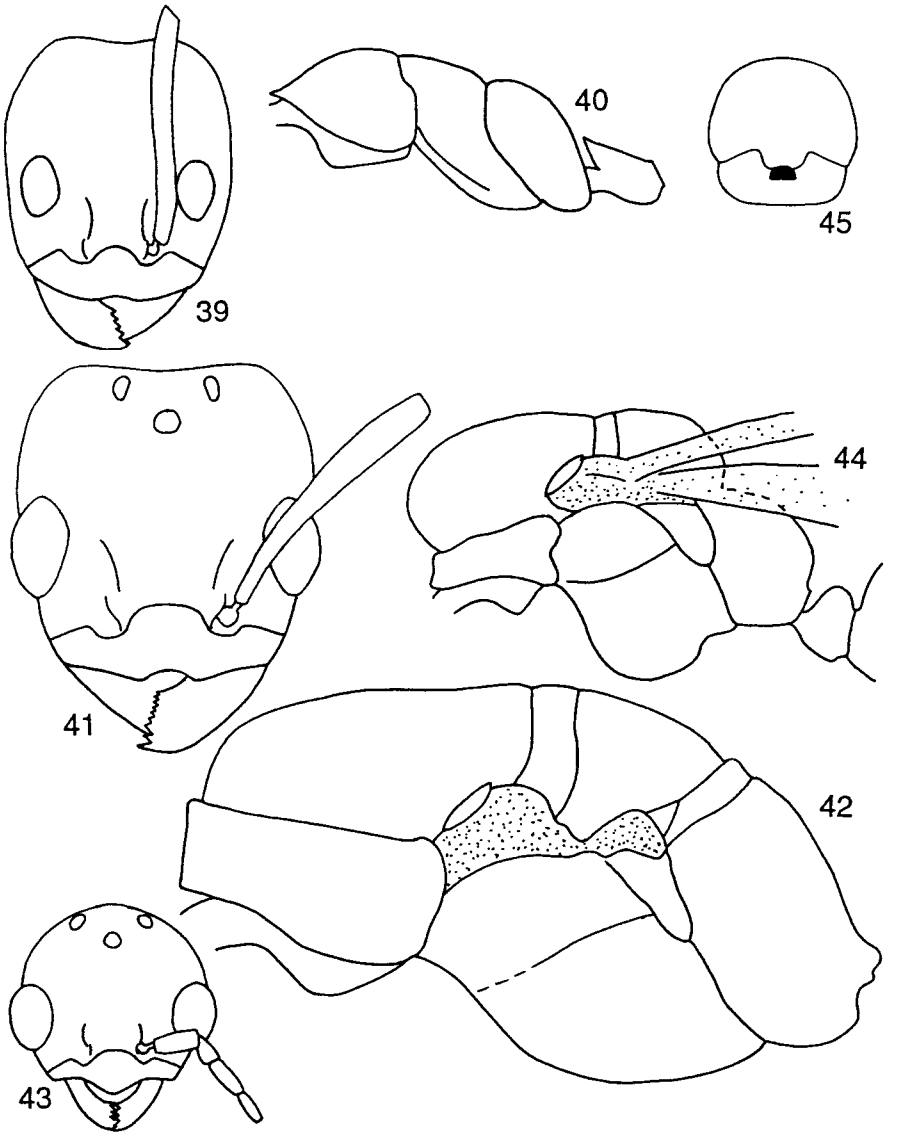
Queen: First gastral segment projecting anteriorly, but not concealing petiole in dorsal view; declivitous face of propodeum flat; mandibles with 8 teeth, 6 denticles, the basal angle weakly defined by a denticle, and the basal margin smooth and without teeth or denticles; dorsum of scale moderately inclined anteriorly but with the anterior and posterior faces of the scale approximately the same length.

Male: Mandible with an elongate apical tooth which is much longer than the subapical, and with a moderately to very distinct basal angle; venter of petiole with a well developed lobe; first gastral segment vertical and not concealing the petiole in dorsal view.

Description

WORKER.

HEAD. Vertex flat. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type (or sometimes with a very weak, narrow concavity). Anterior clypeal setae 6-8; short, less than twice the maximum scape diameter; moderately curved ventrally. Posterior clypeal margin between the anterior and posterior surfaces of the antennal



Figs. 39-45: 39, Full face view of *Doleromyrma* worker (Western Australia, Australia); 40, Lateral view of *Doleromyrma* worker mesosoma (Western Australia, Australia); 41, Full face view of *Doleromyrma* queen (New Zealand); 42, Lateral view of *Doleromyrma* queen mesosoma (New Zealand); 43, Full face view of *Doleromyrma* male (New Zealand); 44, Lateral view of *Doleromyrma* male mesosoma (New Zealand); 45, Anterior view of first gastral segment of *Doleromyrma* (Western Australia, Australia).

socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 4- 5 teeth and 4-5 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin denticulate distally, smooth proximally (sometimes entire surface nearly smooth). MESOSOMA. Posteroventral pronotum lateral, rounded. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum convex; dorsal face convex, shorter than the declivitous face. Propodeal angle moderately distinct. Mesosomal spines and tooth absent. Erect pronotal hairs absent. Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove forming a distinct angle between the mesonotum and propodeum (sometimes reduced). Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; ridged and with a distinct angle dorsally; moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. Venter with a well developed lobe. GASTER. First tergite projecting anteriorly, but not concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium in a distinct arch which extends dorsal of the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number 6 or 7 (n=7, 2n=14, *D.* "*darwinianus*-group" sp. ANIC-8, Imai *et al.* 1977; 2n=12, *D.* "*darwinianus*-group" sp. ANIC-9, Imai *et al.* 1977). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Not examined.

QUEEN.

HEAD. Vertex weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one- half scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 10-14; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion.

Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 8 teeth and 6 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle weakly defined by a denticle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous face of propodeum flat; dorsal face convex, subequal in length to the declivitous face. Propodeal angle distinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs 0-6. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cell. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. Venter with a well developed, rounded lobe. GASTER. First segment projecting anteriorly, but not concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment barrel-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 6; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin even with or anterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with 5-7 teeth and no denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle moderately to very distinct, with a distinct tooth or well defined angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel, very broad, and

entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face longer than the declivitous face. Propodeal angle distinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; vertical and not inclined anteriorly. Venter with a well developed lobe. Attachment to gaster broad. GASTER. First segment vertical and not concealing the petiole in dorsal view, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave. Paramere divided by a membranous region. Digitus with a weakly down-turned tip. Cuspis absent. Ventral lobe of volsella present as concave lobe. Aedeagus with ventral teeth.

LARVAE: Not examined.

Discussion

Doleromyrma contains a single described species and two "subspecies" and has received little attention in the literature. It was originally established as a subgenus of *Tapinoma* (Forel 1907), but was soon synonymized with *Iridomyrmex* (Emery 1912), a treatment followed by subsequent authors. This placement was based on overall similarity and the ill-defined nature of *Iridomyrmex,* and does not withstand close scrutiny. *Doleromyrma* differs from *Iridomyrmex* in numerous characters, including eye placement, configuration

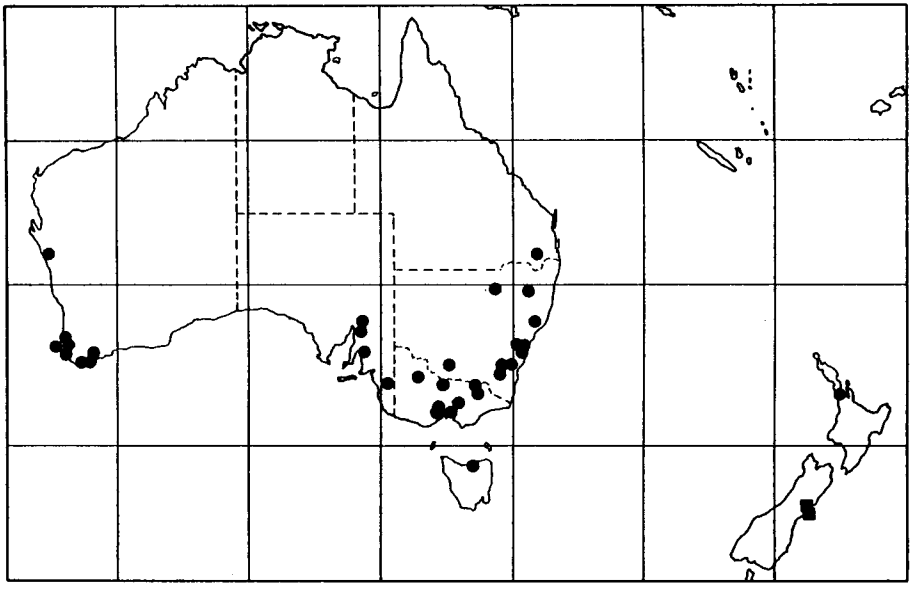


Fig. 46: Distribution of *Doleromyrma.* Closed circles indicate examined material. Closed squares indicate literature records believed to be reliable.

Table 4. Major characters differing among workers of *Bothriomyrmex, Doleromyrma, Loweriella, Tapinoma, and Technomyrmex.*

Character	*Bothriomyrmex*	*Doleromyrma*	*Loweriella*	*Tapinoma*	*Technomyrmex*
Palp formula	4:3 or 2:2	6:4	6:4	6:4	6:4, 5:3 or 4:3
Mandibular dentition	5-6 teeth, 0-5 denticles	4-5 teeth, 4-5 denticles	7-8 teeth, 2-5 denticles	3-7 teeth, about 7 denticles	7-10 teeth, 2-15 denticles
Basal mandibular angle	distinct	distinct	weakly defined	indistinct	weakly defined to indistinct
Basal mandibular margin	smooth	nearly smooth to partially denticulate	smooth	partially denticulate	smooth to denticulate
Setae on anterior clypeal margin	curved ventrally	curved ventrally	straight to weakly curved ventrally	straight	straight
Pronotal hairs	absent	absent	absent	generally absent	generally present
Petiolar scale	present, often inclined anteriorly	present, inclined anteriorly	present, inclined anteriorly	reduced or absent	reduced or absent
Fifth gastral tergite	ventral	ventral	ventral	ventral	dorsal
Fourth gastral sternite	flat	flat	keel-shaped	flat	flat

of the anterior clypeal border, and shape of the mesosoma and petiole, and is here removed from synonymy and treated as a valid genus.

Workers of *Doleromyrma* superficially resemble *Bothriomyrmex* or small *Tapinoma*, but differ in eye size, mandibular structure, palp formula or petiolar structure (see also Table 4). They are limited to southern Australia, although they have been introduced into New Zealand (Keall and Somerfield 1980). *Doleromyrma* species occur most commonly in dry forest areas, nesting in the soil under rocks or rotten logs.

Distribution: Southern Australia and New Zealand (Fig. 46).

Genus *Dolichoderus* Lund (Figs. 47-63)

Dolichoderus Lund 1831:130. Type species: *Formica attelaboides* Fabricius (by monotypy).

Hypoclinea "Foerst." Mayr 1855:377 (syn. of *Dolichoderus* by Forel 1878b:386, as subgenus of *Dolichoderus* by Emery 1894:228, syn. by Wheeler and Wheeler 1985:258). Type species: *Formica quadripunctata* Linnaeus (desig. by Wheeler 1911:165).

Monacis Roger 1862:233 (syn. of *Dolichoderus* by Forel 1878b:386, as subgenus of *Dolichoderus* in Emery 1894:228, syn. by Wheeler and Wheeler 1985:258). Type species: *Formica bispinosa* Olivier (desig. by Wheeler 1911:167).

Diabolus Karawajew 1926:424 (as subgenus of *Dolichoderus*, raised to full genus by Wheeler 1935:68) (preocc. by Grey 1841:400). Type species: *Dolichoderus* (*Diabolus*) *bifurcatus* Karawajew (by monotypy).

Acanthoclinea Wheeler 1935:69 (as subgenus of *Dolichoderus*, raised to full genus by Brown 1950:249, syn. by Wheeler and Wheeler 1985:258). Type species: *Dolichoderus doriae* Emery (by orig. desig.).

Diceratoclinea Wheeler 1935:69 (as subgenus of *Dolichoderus*, raised to full genus by Brown 1950:249, syn. by Wheeler and Wheeler 1985:258). Type species: *Dolichoderus scabridus* Roger (by orig. desig.).

Monoceratoclinea Wheeler 1935:68 (as subgenus of *Dolichoderus*, raised to full genus by Brown 1950:249, syn. by Wheeler and Wheeler 1985:258). Type species: *Dolichoderus* (*Hypoclinea*) *monoceros* Emery (by orig. desig.).

[*Irenae* Donisthorpe 1938a:502 (as subgenus of *Dolichoderus*, syn. of *Polyrhachis* by Brown 1973:181).]

Karawajewella Donisthorpe 1944b:59 (n. name for *Diabolus* Karawajew 1926 nec Grey 1841, syn. by Wheeler and Wheeler 1985:258).

Diagnosis

Worker: Anterior hypostoma in the form of an expanded flange directed anteroventrally (sometimes only weakly so); mesopleural process generally present, sometimes reduced to a blunt protuberance or swelling, occasionally

absent; spines sometimes present on thoracic dorsum; integument often strongly sculptured; mesosternum expanded anteriorly. World wide.

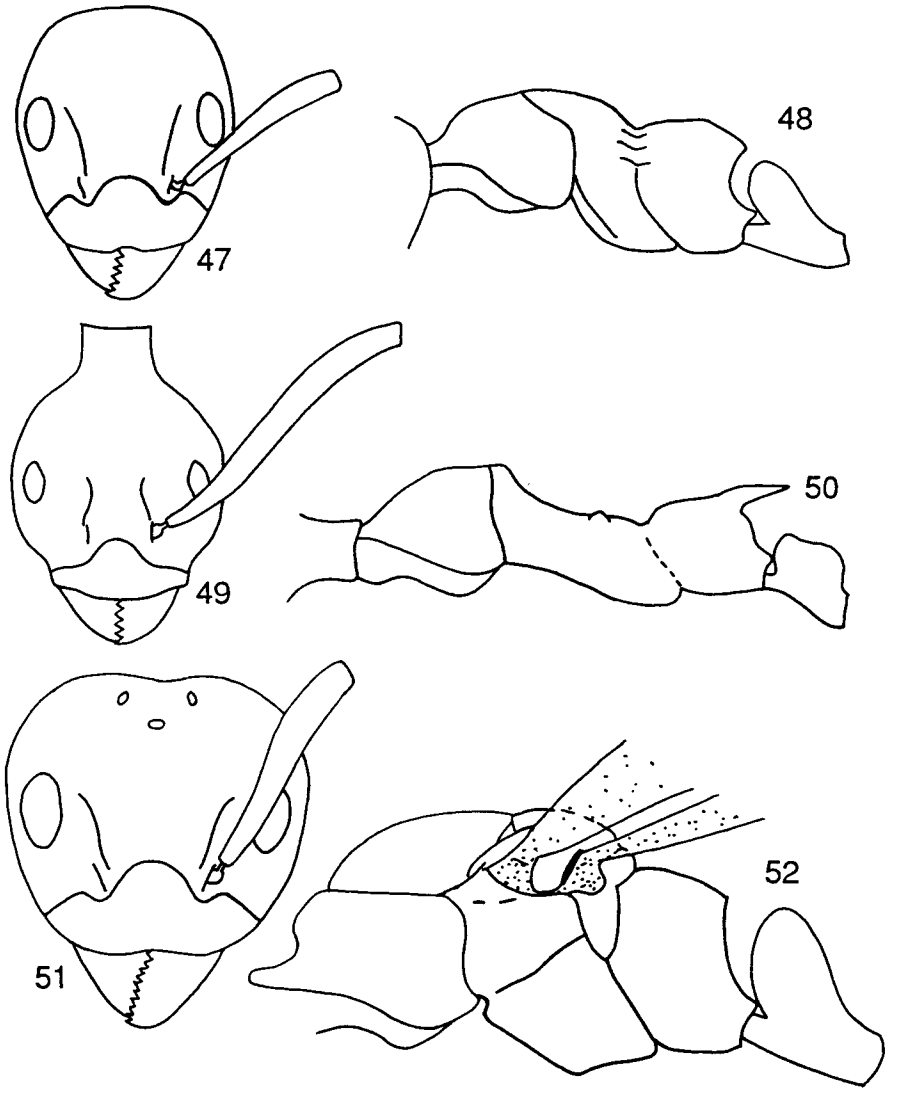
Queen: Anterior hypostoma in the form of an expanded flange directed anteroventrally (sometimes only weakly so); declivitous face of propodeum concave; mandible with 11 to 22 teeth and no denticles, and the apical tooth subequal in length to the subapical; venter of the petiole without a lobe.

Male: Inner margin of compound eye angular; anterior hypostoma in the form of an expanded flange directed anteroventrally; mandible with 25 to 27 teeth and no denticles, and with the basal margin denticulate along its entire surface; declivitous face of propodeum flat or concave.

Description

WORKER.

HEAD. Vertex convex to concave (occasionally drawn posteriorly into a neck). Compound eyes present, approximately round; position on head variable. Ocelli absent. Antennae 12 segmented. Scape relatively short, at most surpassing the vertex by less than one-half (often less than one-third) its length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder, or even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type, or with a broad, shallow concavity. Anterior clypeal setae 4-28; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin posterior of the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma in the form of an expanded flange directed anteroventrally. Medial hypostoma entire. Psammophore absent (rarely numerous elongate hairs on gula and ventral surface of mandibles). MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with about 11-13 teeth and no denticles. Apical tooth subequal in length to the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins, or weakly defined by a denticle. Basal margin denticulate along entire surface. MESOSOMA. Posteroventral pronotum elongate and expanded medially. Mesopleural process present (in the form of a spine, blunt protuberance, or lateral swelling), or absent. Anteromedial mesosternum expanded anteriorly relative to the lateral regions. Declivitous face of propodeum concave (rarely flat, nearly convex, or convex); dorsal face convex (rarely with a single, dorsal spine), subequal in length to the declivitous face. Propodeal angle distinct (sometimes with a ridge or carina). Pronotal spines present and distinct, or absent (sometimes with angles laterally). Erect pronotal hairs 20-35 (occasionally absent); short, about as long as maximum scape width to elongate and much



Figs. 47-52: 47, Full face view of *Dolichoderus mariae* worker; 48, Lateral view of *Dolichoderus mariae* worker mesosoma; 49, Full face view of *Dolichoderus attelaboides* worker; 50, Lateral view of *Dolichoderus attelaboides* worker mesosoma; 51, Full face view of *Dolichoderus* queen (Singapore); 52, Lateral view of *Dolichoderus* queen mesosoma (Singapore).

longer than the maximum scape width. Mesonotal spines present and distinct, reduced to protuberances, or absent. Propodeal spines present and distinct, or absent (in some, concave medially with lateral edges raised). Propodeal tooth absent. Dorsal pro-mesonotal junction variable, with the mesonotum

above or below the pronotum. Metanotal groove forming a distinct angle between the mesonotum and propodeum, or a narrow, distinct notch in the relatively flat dorsal mesosomal surface. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile, or dorsal and lying on the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; rounded and forming an even arch dorsally, ridged and with a distinct angle dorsally, or spined and with a single or double tooth or projection dorsally; moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. Venter without a lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view, smooth and without a groove or indentation or with a groove or indentation for the reception of the basal portion of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium, without or with at most a very weak dorsal arch. Fifth tergite ventral, gaster with 4 apparent tergites (sometimes narrowed longitudinally). Gastral compression lateral or dorsoventral. Fourth sternite keel-shaped posteriorly. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number 14-16 (2n=28, *D. quadripunctatus*, Imai 1969; 2n=30, *D. bituberculatus* (=*D. thoracicus*), Imai *et al.* 1985b; 2n=30, 31, 32 and 33, *D. bituberculatus* (=*D. thoracicus*), Imai *et al.* 1985a; n=14, *D. scabridus*, Crozier 1970a; 2n=28, *D. scabridus*, Imai *et al.* 1977). Integument thickened, often strongly sculptured. PROVENTRICULUS. Cupola narrow relative to bulb; round; with short pile; smooth, without sculpture; and without phragma. Bulb exposed in lateral view. Longitudinal muscle No. 1 present. Occlusory tract absent.

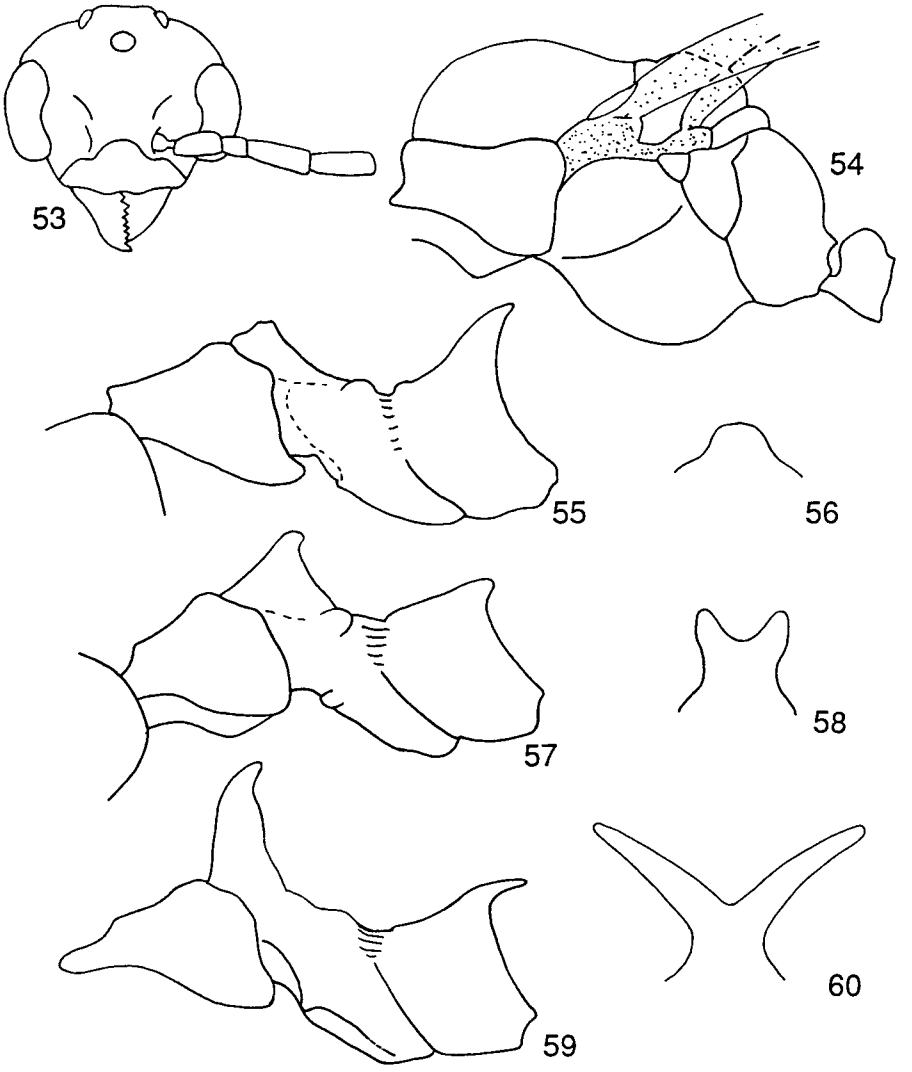
QUEEN.

HEAD. Vertex convex to weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape variable, short (surpassing the vertex by less than one-half scape length) or long (surpassing the vertex by more than one-half scape length). Anterolateral clypeal margin even with the mediolateral region, or with the corners expanded slightly anterior of the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 6-8; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin posterior of the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma in the form of an expanded flange directed anteroventrally. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 11-22 teeth and no denticles. Apical tooth subequal in length to the subapical tooth. Basal

angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin denticulate along entire surface. MESOSOMA. Posteroventral pronotum elongate and expanded medially. Episternal suture complete. Mesopleural process present or absent. Anteromedial mesosternum expanded anteriorly relative to the lateral regions. Axilla parallel or constricted medially, and entire. Anterior axillar suture straight. Declivitous face of propodeum concave; dorsal face convex, subequal in length to the declivitous face. Propodeal angle distinct. Propodeal suture complete (obscured near the metapleural gland bulb) or absent. Pronotal spines present and distinct, or absent. Erect mesocutal hairs 4-60; short, less than twice the maxmum scape diameter to elongate, more than twice the maximum scape diameter. Propodeal spines present as protuberances, or absent. Propodeal tooth absent. Propodeal spiracle laeral and ventral of the propodeal dorsum. Hind tibial spur wit well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cell. Hind wing with 2cells. PETIOLE. Scale present; rounded and forming an ven arch dorsally, ridged and with a distinct angle dorsally, or spined and with a single tooth or projection dorsally; vertical and not inclned anteriorly to strongly inclined anteriorly and with he anterior face much shorter than the posterior face. Venter without a lobe. GASTER. First segment vertical and not concealing the petiole in dorsal vie, smooth and without a groove or indentation r with a groove or indentation for the reception of the entire height of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral comression absent (gaster circular in cross section. Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye angular. Scape length at most only slightly longer than the length f funicular segments 1+2+3. First funicular segment cylindrial or cone-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at mos twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae about 5-7; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin posterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma in the form of an expanded flange directed anteroventrally. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with about 25-27 teeth and no denticles. Apical tooth varying from slightly longer than, to elongate and much longer than, the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin denticulate along entire surface. MESOSOMA.



Figs. 53-60: 53, Full face view of *Dolichoderus* male (ACT, Australia); 54, Lateral view of *Dolichoderus* male mesosoma (ACT, Australia); 55, Lateral view of *Dolichoderus coniger* worker mesosoma; 56, Anterior view of mesonotum (see also Fig. 55); 57, Lateral view of *Dolichoderus furcifer* worker mesosoma. 58, Anterior view of mesonotum (see also Fig. 57); 59, Lateral view of *Dolichoderus cuspidatus* worker mesosoma; 60, Anterior view of mesonotum (see also Fig. 59).

Posteroventral pronotum weakly expanded medially. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions, or weakly

expanded anteriorly relative to the lateral regions. Axilla constricted medially and entire. Anterior axillar suture straight. Declivitous face of propodeum flat to concave; dorsal face convex, subequal in length to the declivitous face. Propodeal angle distinct. WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; rounded and forming an even arch dorsally, or ridged and with a distinct angle dorsally; vertical and not inclined anteriorly. Venter without a lobe. Attachment to gaster narrow. GASTER. First segment elongated posteriorly to vertical and not concealing the petiole in dorsal view, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave or with a "V"-shaped notch. Paramere entire. Digitus with a down-turned tip. Cuspis parallel with digitus. Ventral lobe of volsella present as concave lobe. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances present or absent; when present, as 2 bosses located ventrolaterally on prothorax. Body hairs sparse; simple; short. 10 spiracular pairs.

Discussion

Dolichoderus is the largest genus in the subfamily and has a complex taxonomic history. It has been treated as either a single genus (Forel 1878b, Wheeler and Wheeler 1985), or as many as seven separate genera (Brown 1950). Recent authors have generally recognized two or three genera (Brown 1973, Snelling 1981, Hölldobler and Wilson 1990). An outline of the history of generic-level changes is given in Fig. 61. In this revision only one genus is recognized, *Dolichoderus* (broad sense).

All species of *Dolichoderus* (broad sense) share the characters listed in the Diagnosis above. Additionally, many have large dorsal mesosomal spines and well developed sculpturing (at least for a member of the Dolichoderinae). The development of an anterolateral expansion on the hypostoma and a convex anteromedial margin of the mesosternum are unique to the genus. These characters occur to varying degrees in all species examined in this study. Additionally, the structure of the proventriculus in *Dolichoderus* is unique within Dolichoderinae, although it is similar to some members of Formicinae.

The diverse views on the internal classification of *Dolichoderus* result from the rather striking variation in gross body shape, as well as the development of spines on various regions of the mesosoma. However, by classifying on the basis of spine development and overall shape, the phylogenetic relationships among the subgroups have been obscured. For example, I can find no character by which to define *Hypoclinea*, other than as an assemblage of taxa left after all distinctive groups are removed. Additionally, there are morphological clines between species currently placed in *Hypoclinea* and

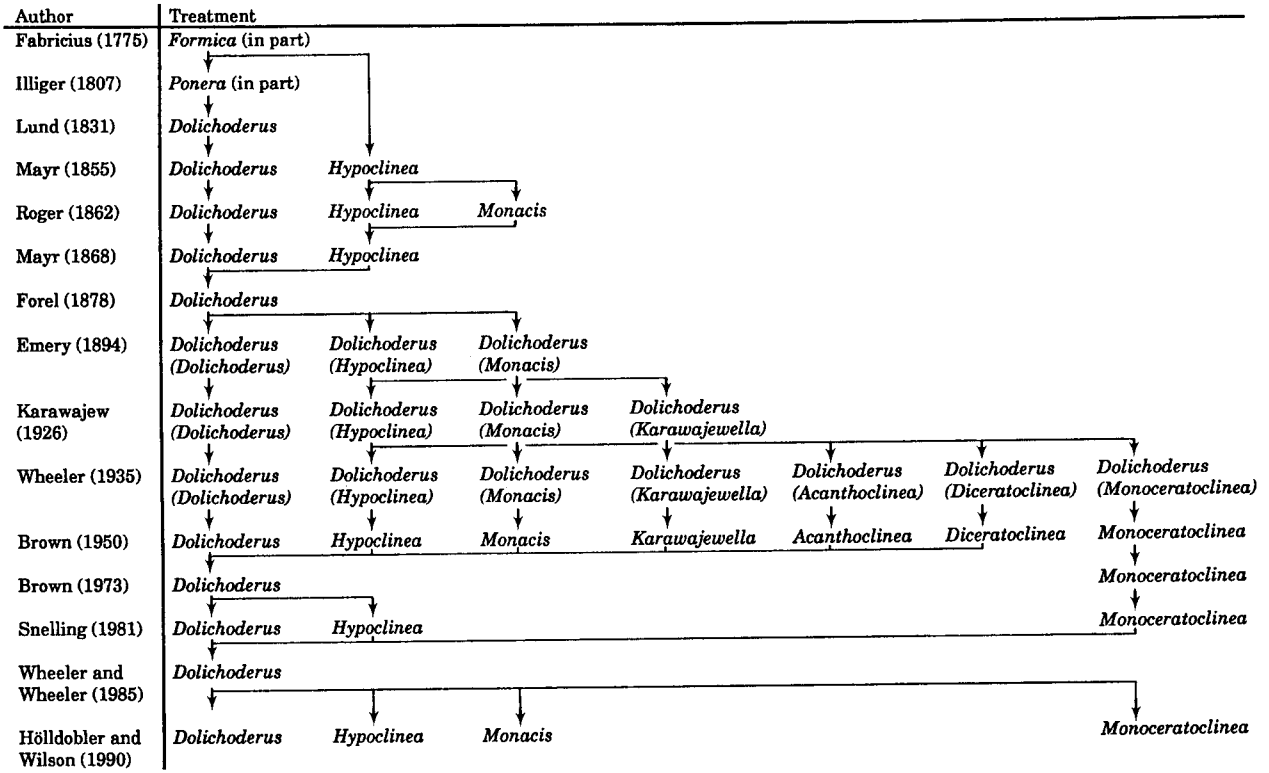


Fig. 61. Generic-level history of *Dolichoderus* and related groups. (The table includes only generic-level studies; individual species treatments may vary.)

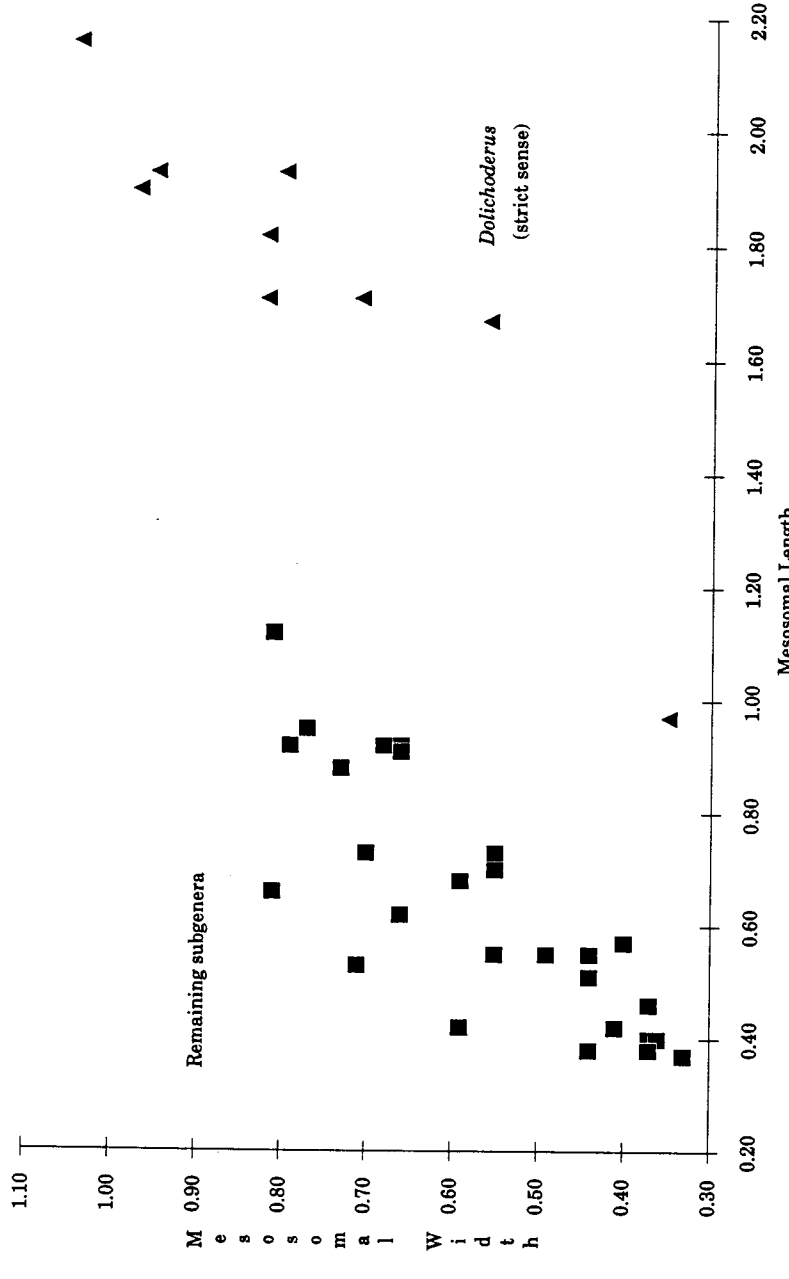


Fig. 62. Distribution of minimal mesosomal width and maximal mesosomal length for 20 species and 36 worker individuals of *Dolichoderus* (units are mm).

Karawajewella, and *Hypoclinea* and *Monacis.* These clines make placement of individual species within these groups difficult or arbitrary.

For example, an examination of *Hypoclinea* reveals that the species *gibbifer* (and *feae*), *coniger* and *brevithorax* form a graded series with increasing development of mesonotal spines, linking typical *Hypoclinea* with the well developed bifurcating spines found in *cuspidatus*, the type species of *Karawajewella* (see Figs. 55-60). Similarly, *debilis*, a species placed in *Monacis*, differs from typical *Hypoclinea* only in possessing pronotal spines. However, the queens of this species lack pronotal spines and are thus inseparable from *Hypoclinea* (strict sense) queens.

On the other hand some of the groups are phenetically distinct from *Hypoclinea.* The groups *Acanthoclinea* (paired spines on both the pronotum and propodeum), *Diceratoclinea* (paired spines on propodeum only), *Monoceratoclinea* (a single spine on the propodeum) and *Dolichoderus* (strict sense) (elongate mesosoma) are clearly distinguishable. The spinal development characterizing the former three groups is distinct. Similarly, the mesothoracic elongation of *Dolichoderus* (strict sense) separates it from other members in the group for all size classes (Fig. 62). While these groups are discernable their treatment as genera is still unacceptable as this would leave *Hypoclinea* paraphyletic. Therefore all groups are treated as members of the single genus *Dolichoderus.*

It should be stressed that the recognition of any of these groups of species is recommended only as a matter of taxonomic convenience as some may not form monophyletic groups. In fact, as discussed above, the species previously placed in *Hypoclinea* are almost certainly paraphyletic and an artificial aggregation of species. Additionally, it seems quite likely that detailed species-level studies will reveal additional sets of morphologically similar species, especially in the diverse Indo-Australian fauna.

Much of the species-level taxonomic work in *Dolichoderus* has been regional. The species formerly placed in *Dolichoderus* (strict sense) were reviewed by Kempf (1969), while those placed in "*Monacis*" were revised by Kempf (1959) with additional notes by Lattke (1986) and Harada (1987). The Australian fauna was examined by Clark (1930), while the North American species were reviewed by Johnson (1989a) and the east Asian species by Yasumatsu (1941). The remainder of the genus has received little attention, and there is serious need for a world-wide revision of the entire genus.

Species of *Dolichoderus* occur in forested areas, from dry savanna woodlands to rain forests. They nest either in the soil or arboreally, and sometimes use carton in nest construction. Workers can be quite common, foraging in columns on the ground or in trees, and are known to invade buildings. They are general scavengers and also tend aphids and coccids.

Distribution: In the New World, from southern Canada south to southern

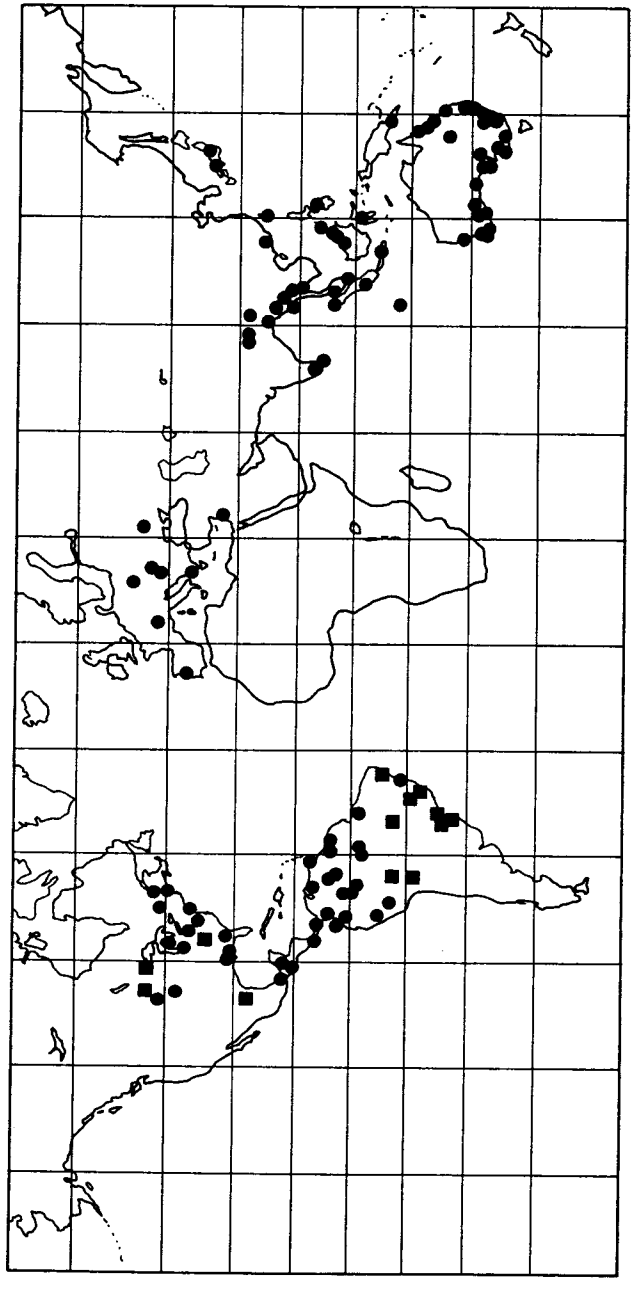


Fig. 63. Distribution of *Dolichoderus*. Closed circles indicate examined material. Closed squares indicate literature records believed to be reliable.

Brazil. In the Old World, Europe east to the Black Sea, and India east and south to Australia (Fig. 63).

Species Notes: The following species, previously placed in *Hypoclinea*, *Iridomyrmex* or *Monacis*, are here transferred to *Dolichoderus* (all NEW COMBINATIONS): *curvilobus* (Lattke), *epetreia* (Lattke), *patens* (Mayr), *primitivus* (Wilson), *semirugosus* (Mayr), *superaculus* (Lattke), and *thoracicus borneonensis* (Roger) (from *Hypoclinea*); *mazaruni* (Donisthorpe) (from *Iridomyrmex*); *andinus* (Kempf), *caribbaea* (Wilson), *inpai* (Harada), *lobicornis* (Kempf), *omacanthus* (Kempf), *prolaminatus* (Wilson), *setosus* (Kempf) and *vilidus* (Kempf) (from *Monacis*). The following species are returned to *Dolichoderus* from *Hypoclinea* or *Monacis* (all REVISED COMBINATIONS): *abruptus* (F. Smith), *analis* Emery, *bidens* (Linnaeus), *bidens albatus* Viehmeyer, *bidens attenuatus* Forel, *bidens bahiana* Santschi, *bidens cogitans* Forel, *bidens ferrugineus* Forel, *bidens inferior* Mann, *bidens spurius* Forel, *championi* Forel, *championi ornatus* Mann, *championi trinidadensis* Forel, *diversus* Emery, *doloniger* (Roger), *germaini* Emery, *germaini garbei* Forel, *germaini leviusculus* Emery, *ghilianii* Emery, *grandii* Menozzi, *luederwaldti* Santschi, *luederwaldti lujae* Santschi, *lugens* Emery, *lutosus* (F. Smith), *lutosus nigriventris* Forel, *mesonotalis* Forel, *quadridenticulatus* (F. Smith), *quadridenticulatus gibbosoanalis* Forel, *quadridenticulatus integer* Forel, *quadridenticulatus nitidior* Emery, *simplex* Forel, and *ursus* (Mayr) (from *Hypoclinea*); *andinus* (Kempf), *debilis* Emery, *gagates* Emery, *lamellosus* (Mayr), *laminatus* (Mayr), *mucronifer* (Roger), *obscurus* (F. Smith), *rufescens* Mann, *schulzi* Emery, *septemspinosus* Emery, *spinicollis* (Latreille), *tristis* Mann, and *varians* Mann (from *Monacis*). The species name *D. gibbosus* (F. Smith 1858) is preoccupied by Latreille (1798) and is replaced by *D. quadridenticulatus* (Roger).

Genus *Dorymyrmex* Mayr (Figs. 64-71)

Dorymyrmex Mayr 1866: 494. Type species: *Dorymyrmex flavescens* Emery (by monotypy).

Psammomyrma Forel 1912: 43 (as subgenus of *Dorymyrmex*, conditional syn. (not available) by Brown 1973:184, syn. by Snelling and Hunt 1975:93). Type species: *Dorymyrmex planidens* Mayr (desig. by Wheeler 1913: 82).

Conomyrma Forel 1913: 350 (as subgenus of *Dorymyrmex*, raised to full genus by Kusnezov 1952: 429). Type species: *Prenolepis pyramica* Roger (by orig. desig.). [NEW SYNONYMY]

Araucomyrmex Gallardo 1919: 249 (as subgenus of *Dorymyrmex* by Santschi 1922: 365, raised to full genus by Kusnezov 1959:46, syn. by Snelling 1981:402). Type species: *Dorymyrmex tener* Mayr (by orig. desig.).

Ammomyrma Santschi 1922: 365 (as subgenus of *Dorymyrmex*, syn. of *Araucomyrmex* by Snelling and Hunt 1975: 93). Type species: *Dorymyrmex*

exsangius Forel (by orig. desig.).

Biconomyrma Kusnezov 1952: 429 (as subgenus of *Conomyrma*, raised to full genus by Kusnezov 1959: 50, syn. by Kempf 1972: 78). Type species: *Dorymyrmex pyramicus* var. *brunnea* Forel (desig. by Kusnezov 1959: 51).

Spinomyrma Kusnezov 1952:429 (as subgenus of *Dorymyrmex*, raised to full genus by Kusnezov 1956:30, syn. by Snelling and Hunt 1975:93). Type species: *Dorymyrmex alboniger* Forel (desig. by Kusnezov 1959:51).

Diagnosis

Worker: Angle of propodeum with a single medial dorsal spine or tooth; psammophore present, weakly to strongly developed; third maxillary palp segment elongate, subequal in length to segments 4+5+6; anterior clypeus margin with numerous elongate, curved hairs which extend beyond (rarely just to) the distal edge of closed mandibles; apical tooth of mandibles greatly elongate. North and South America.

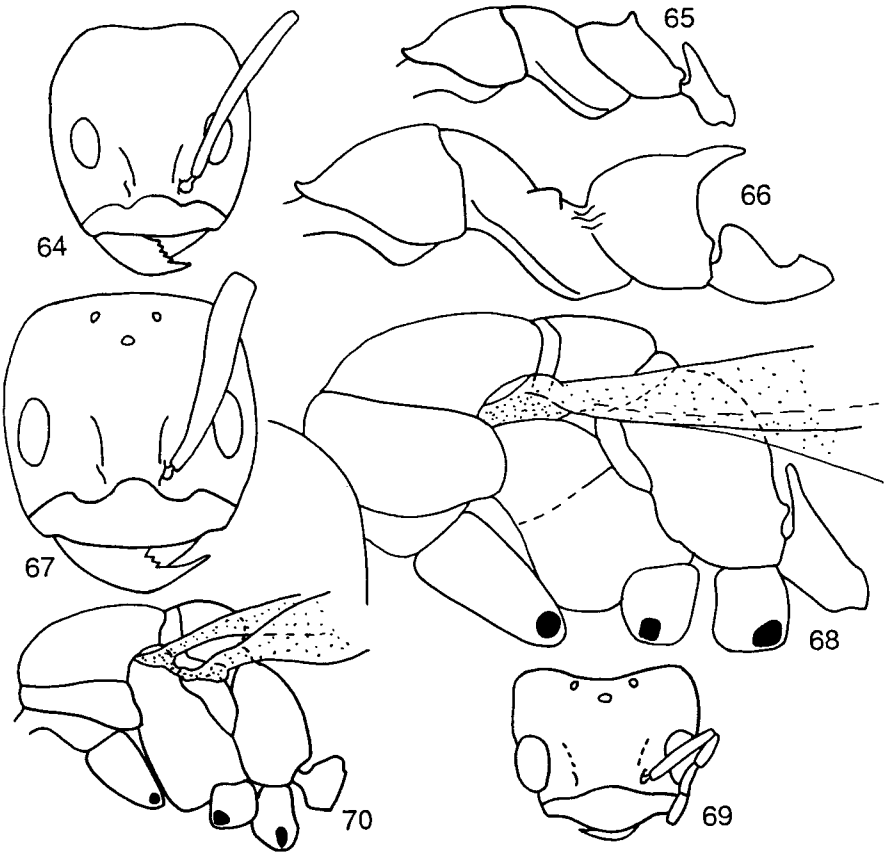
Queen: Anterior clypeal margin with long, strongly ventrally curved setae which surpass the distal edge of closed mandibles; psammophore present; third maxillary palp segment elongate and subequal to or longer than the combined lengths of segments 4+5+6.

Male: Third maxillary palp segment longer than the combined lengths of segments 4+5; anterior clypeal margin with moderately ventrally curved setae; second funicular segment with a lateral bend; pygostyles reduced; mandibles with 2 to 3 teeth and 2 denticles.

Description

WORKER.

HEAD. Vertex convex to weakly concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape relatively short, at most surpassing the vertex by less than one-half (often less than one-third) its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 4-12; long and surpassing the distal edge of the closed mandibles; strongly curved ventrally. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite (extending past the mandibular insertion in some South American species, but always thin). Medial hypostoma entire. Psammophore present (originating at extreme lateral edges of head or "V"-shaped and placed medially on under surface of head, and weakly to strongly developed). MOUTHPARTS. Palp formula 6:4 (distal 3rd and entire 4th maxillary segment sometimes flattened and expanded). Third maxillary palp segment subequal to or longer than the combined lengths of segments 4+5+6.



Figs. 64-70: 64, Full face view of *Dorymyrmex* worker (Colorado, USA); 65, Lateral view of *Dorymyrmex* worker mesosoma (Colorado, USA); 66, Lateral view of *Dorymyrmex* worker mesosoma (Catamarca, Argentina); 67, Full face view of *Dorymyrmex* queen (Catamarca, Argentina); 68, Lateral view of *Dorymyrmex* queen mesosoma (Catamarca, Argentina); 69, Full face view of *Dorymyrmex* male (Catamarca, Argentina); 70, Lateral view of *Dorymyrmex* male mesosoma (Catamarca, Argentina).

Fifth maxillary palp segment at the apical extreme of segment 4, or subapical and with a finger- like extension distal of the attachment point. Mandible with 6-7 teeth and 0-1 denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin varying from smooth (without teeth or denticles) to denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum convex to weakly concave; dorsal face convex

to flat, longer to slightly shorter than the declivitous face. Propodeal angle distinct. Mesosomal spines absent (but propodeal tooth present, spine-like or tooth-like, or rarely reduced to a slight raised angle). Erect pronotal hairs 0-6 (sometimes with a few additional hairs of varying lengths); when present elongate, much longer than the maximum scape width. Dorsal pro-mesonotal junction with the pronotum and mesonotum even (occasionally with either the pronotum or mesonotum slightly raised). Metanotal groove forming a distinct angle between the mesonotum and propodeum, or a distinct, deep trough or notch depressed below the level of the adjacent mesosomal notum. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile, or dorsal and lying on the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present or reduced; rounded and forming an even arch dorsally, or ridged and with a distinct angle dorsally; varying from moderately inclined anteriorly (but with the anterior and posterior faces approximately the same length) to strongly inclined anteriorly (and with the anterior face much shorter than the posterior face). Venter with a slight or weakly developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of either the basal portion or the entire height of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium in a distinct dorsal arch which varies from approximately the same height as, to noticeably dorsal of, the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites (sometimes narrowed longitudinally). Gastral compression lateral (greatly developed). Fourth sternite keel-shaped posteriorly. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number 9 or 13 (n=9, *D. ?pulchellus* and *?thoracicus*, Crozier 1970a; n=13, *D. bicolor*, Crozier 1970a). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round or lobed; with short pile; smooth, without sculpture; and with short, lateral phragma or without phragma. Bulb partially hidden by cupola in lateral view. Longitudinal muscle No. 1 absent. Occlusory tract absent.

QUEEN.

HEAD. Vertex convex. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae about 10-14; long and surpassing the distal edge of the closed mandibles; strongly curved ventrally. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire.

Psammophore present. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal to or longer than the combined lengths of segments 4+5+6. Fifth maxillary palp segment at the apical extreme of segment 4, or subapical and with a finger-like extension distal of the attachment point. Mandible with 5-7 teeth and 0-2 denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin varying from smooth (without teeth or denticles) to denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete to weak, nearly absent. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex. Propodeal angle indistinct. Propodeal suture absent. Mesosomal spines and tooth absent (but propodeal tooth sometimes present). Erect mesoscutal hairs 0-75; when present short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell open. Fore wing with 1-2 cubital and 0-1 discoidal cells. Hind wing with 1-2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally, or spined and with a single tooth or projection dorsally; moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. Venter with a well developed to slight or weakly developed lobe. GASTER. First segment projecting anteriorly and concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Fifth tergite vertical and with the distal terminus of the gaster not well defined. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length at most only slightly longer than the length of funicular segments 1+2+3. First funicular segment cylindrical or cone-shaped. Second funicular segment cylindrical and with a lateral bend. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae about 6; about the same length as the closed mandibles; moderately curved ventrally. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment longer than the combined lengths of segments 4+5. Fifth maxillary palp at the apical extreme of segment 4 (probably also

subapical and with a finger-like extension distal of the attachment point, but this could not be confirmed with available material). Mandible with 2-3 teeth and 2 denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous face of propodeum convex to concave; dorsal face convex, subequal in length to the declivitous face. Propodeal angle distinct. WINGS. Radial cell open. Fore wing with no cubital or discoidal cells. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; a blunt angle dorsally; vertical and not inclined anteriorly. Venter with a slight or weakly developed lobe. Attachment to gaster broad. GASTER. First segment elongated posteriorly or vertical and not concealing the petiole in dorsal view, smooth and without a groove or indentation or with a groove or indentation for the reception of the basal portion of the petiole. GENITALIA. Pygostyles present, reduced. Posterior margin of subgenital plate convex. Paramere entire. Digitus linear, with or without a down-turned tip (tip sometimes slightly swollen). Cuspis absent. Ventral lobe of volsella present as concave lobe. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances present as a single boss on posterior of body. Body hairs moderately abundant; simple; short. 10 spiracular pairs. Antennae short.

Discussion

Dorymyrmex is a moderate sized group found only in the New World. The group has been divided into as many as 5 genera and 2 subgenera, but most recently has been viewed as consisting of just two genera, *Dorymyrmex* and *Conomyrma* (Snelling 1981). The results of the present study indicate that there is a complex relationship between species in *Dorymyrmex* (strict sense) and *Conomyrma*, and that alternate arrangements of these species are plausible. As a result, *Conomyrma* is not regarded as distinct from *Dorymyrmex* and both are combined into the single genus *Dorymyrmex*.

Workers of *Dorymyrmex* (broad sense) are at once identifiable by the presence of a psammophore (sometimes reduced, but always present), an elongate third palp segment, and the development of a tooth or spine at the propodeal angle. It has been held that *Dorymyrmex* (strict sense) can be distinguished from *Conomyrma* (which includes *Araucomyrmex* (Snelling 1981)) based on the possession of the following set of characters: nodiform petiole, fifth segment of maxillary palp segment attached preapically to the

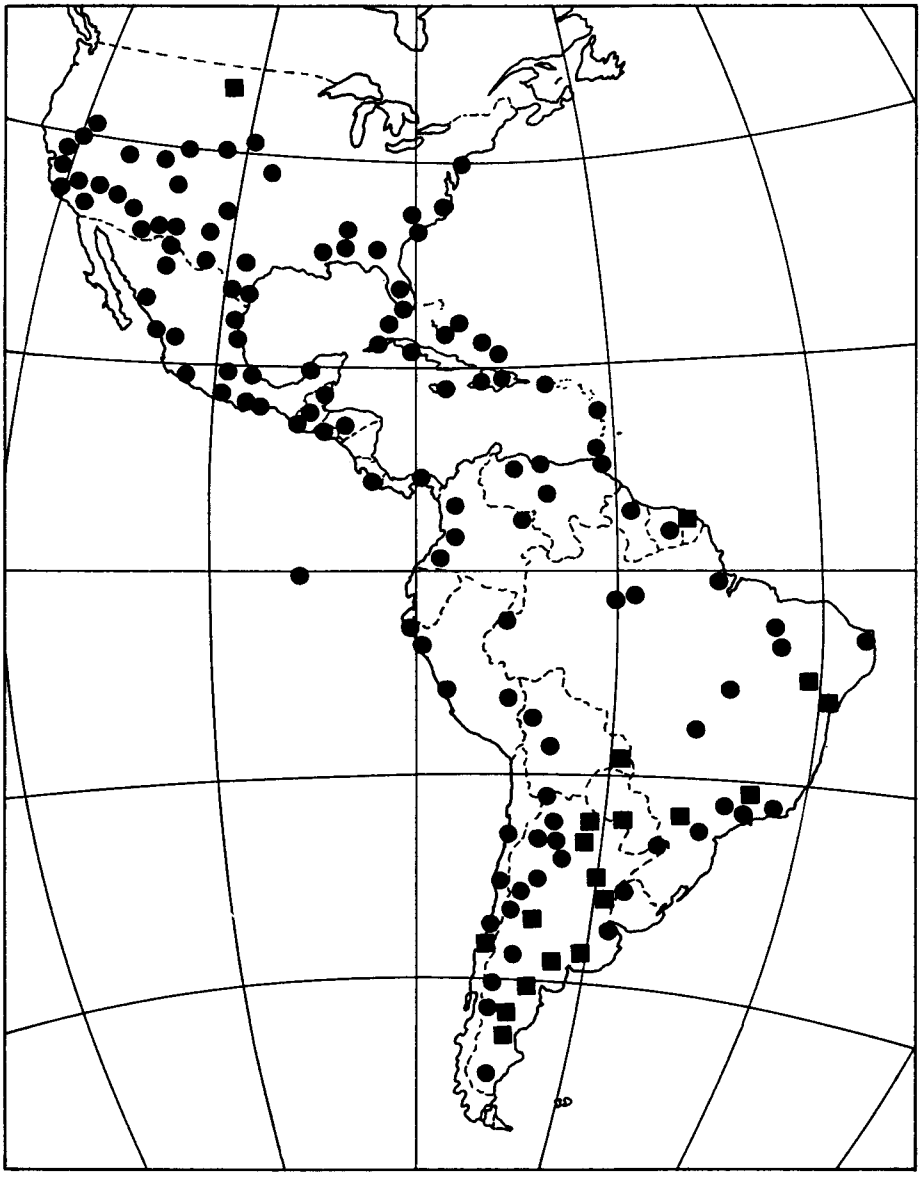


Fig. 71: Distribution of *Dorymyrmex*. Closed circles indicate examined material. Closed squares indicate literature records believed to be reliable.

fourth, and the deep impression of the metanotal groove (Snelling and Hunt 1975). However, at least one species placed in *Conomyrma* possesses a

combination of *Dorymyrmex* and *Conomyrma*-type characters. *D. bruchi* has the nodiform scale used to diagnose *Dorymyrmex* (strict sense) but the metanotal groove is only weakly depressed and the fifth maxillary palp segment is attached apically rather than subapically, characters diagnostic of *Conomyrma*. It is therefore not possible to place this species within either group as defined above.

Moreover, two other characters not addressed by the above authors suggest that an alternate arrangement of the species in these groups is possible. These characters are the form of the psammophore and the flattening of the fourth and fifth maxillary palp segments. Within *Dorymyrmex* (broad sense) the placement of the psammophore hairs follows two basic patterns: triangular and centrally located on the underside of the head, or quadrate and located at the lateral margins of the head. All *Dorymyrmex* (strict sense) have the hairs in the quadrate pattern, while both patterns occur in the species placed in *Conomyrma*. The second character, the flattening of the distal fourth and fifth palp segments, shows a similar pattern: all *Dorymyrmex* (strict sense) have these segments flattened, while *Conomyrma* have species with either normal or flattened segments. These patterns suggest that *Conomyrma* is paraphyletic; that is, some species (those with a quadrate psammophore and flattened palps) are more closely related to *Dorymyrmex* (strict sense) than to the *Conomyrma* species with triangular psammophore and normal palp segments. Thus recognizing *Conomyrma* obscures complex species-level relationships within this group. As a result all species are placed in a single genus, *Dorymyrmex*.

The taxonomic history of this group was reviewed by Snelling (1973) and Snelling and Hunt (1975). The only taxonomic change proposed since then has been the synonymy of *Araucomyrmex* under *Conomyrma* by Snelling (1981). I support the synonymies recognized by Snelling (1973), Snelling and Hunt (1975) and Snelling (1981) (but I do not regard *Conomyrma* as distinct from *Dorymyrmex*).

The species-level taxonomic knowledge within *Dorymyrmex* is fair for North America. The species of the eastern and southern United States have been reviewed by Trager (1988) and Johnson (1989b). Unfortunately, these two authors differ in their treatment of several taxa and only a complete review of the entire North American fauna will resolve these differences. The Central and South American fauna is essentially unknown, with the exception of Chile (Snelling (1975), Snelling and Hunt (1975)).

All species of *Dorymyrmex* are ground nesting and foraging and usually occur in drier habitats, especially grasslands. Nests are often in open areas without covering, and entrances are surmounted by an irregular mound of loose soil.

Distribution: North America from the northern United States south through-

out South America (Fig. 71).

Species Notes: The following species are here transferred from *Araucomyrmex* or *Conomyrma* to *Dorymyrmex* (all NEW COMBINATIONS): *hunti* (Snelling), *hypocritus* (Snelling), *incomptus* (Snelling), *pappodes* (Snelling), *pogonius* (Snelling) and *tener donisthorpei* (Santschi) (from *Araucomyrmex*); *bossutus* (Trager), *confusus* (Kusnezov), *elegans* (Trager), *grandulus* (Forel), *pyramicus nigriventris* (Kempf), and *spurius* (Kempf) (from *Conomyrma*). The following species are returned to *Dorymyrmex* from *Araucomyrmex* or *Conomyrma* (all REVISED COMBINATIONS): *antarcticus* Forel, *baeri* André, *chilensis* Forel, *coniculus* Santschi, *exsanguis* Forel, *fusculus* Santschi, *goetschi* Menozzi, *minutus* Emery, *richteri* Forel and *tener* Mayr (from *Araucomyrmex*); *bicolor* Wheeler, *biconis* Forel, *bituber* Santschi, *breviscapis* Forel, *brunneus* Forel, *carettei* Forel, *caretteoides* Forel, *flavopectus* M. R. Smith, *flavus* MacCook, *goeldii* Forel, *insanus* (Buckley), *jheringi* Forel, *pulchellus* Santschi, *pyramicus* (Roger), *santschii* Gallardo, *silvestrii* Gallardo, *steigeri* Santschi, *steigeri platensis* Gallardo, *thoracicus* Gallardo and *wolffhuegeli* Forel (from *Conomyrma*).

Genus *Ecphorella* Forel (Figs. 72-73)

Ecphorella Forel 1909:65 (as subgenus of *Tapinoma*, raised to full genus by Brown 1973). Type Species: *Tapinoma* (*Ecphorella*) *wellmani* Forel (by monotypy).

Diagnosis

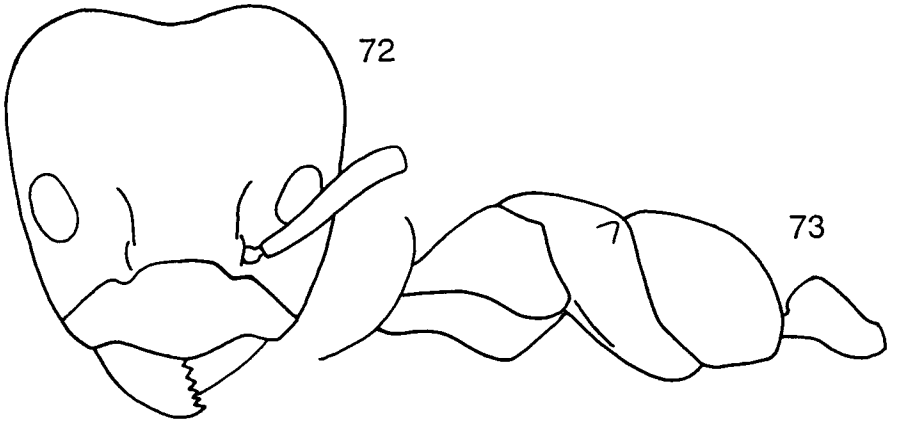
Worker: Vertex concave; anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region; palp formula reduced; metanotal groove a narrow, distinct notch in the relatively flat dorsal mesosomal surface; propodeal spiracle dorsal and posterior, near the propodeal angle; petiolar scale strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Known only from the type locality, Benguela, Angola.

Queen and male: Unknown.

Description

WORKER.

HEAD. Vertex concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-third its length. Anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae about 10; very short, only slightly surpassing the anterior clypeal margin; straight. Posterior clypeal margin



Figs. 72-73: 72, Full face view of *Ecphorella wellmani* worker; 73, Lateral view of *Ecphorella wellmani* worker mesosoma.

between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula reduced, but exact count not possible with existing material. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with about 7 teeth and no denticles (although basal regions of mandible obscured). Apical tooth slightly longer than the subapical tooth. Basal angle obscured in existing material. Basal margin obscured in existing material. MESOSOMA. Posteroventral pronotum lateral, rounded. Mesopleural process absent. Declivitous face of propodeum flat; dorsal face weakly convex, subequal in length to the declivitous face. Propodeal angle distinct. Mesosomal spines and tooth absent. Erect pronotal hairs about 25; elongate, slightly longer than the maximum scape width. Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove a narrow, distinct notch in the relatively flat dorsal mesosomal surface. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle dorsal and posterior, near the propodeal angle. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale reduced; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a well developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Anterior tergosternal suture of the first segment apparently extending laterally from the helcium in a distinct arch which extends

dorsal of the dorsal helcial surface (available material damaged). Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). GENERAL CHARACTERS. Chromosome number unknown. Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Not examined.

QUEEN: Unknown.

MALE: Unknown.

LARVAE: Unknown.

Discussion

Ecphorella was established as a subgenus of *Tapinoma* by Forel (1909) for a single worker specimen. Forel considered this subgeneric placement tentative pending the availability of additional material and the examination of the proventriculus. It is now some eighty years later and no further material has been collected.

Ecphorella was raised to full genus status without discussion by Brown (1973). Examination of the type specimen during this study indicates that the genus is distinct and separable from all other genera in the subfamily. (For a list of these characters, see the Diagnosis above.) Therefore, Brown's (1973) treatment of *Ecphorella* is confirmed and followed here.

Nothing is known about the biology of this genus.

Distribution: Benguela, Angola (known only from type material).

Genus *Forelius* Emery (Figs. 74-80, Table 5)

Forelius Emery 1888:389. Type species: *Iridomyrmex maccooki* Forel (by monotypy).

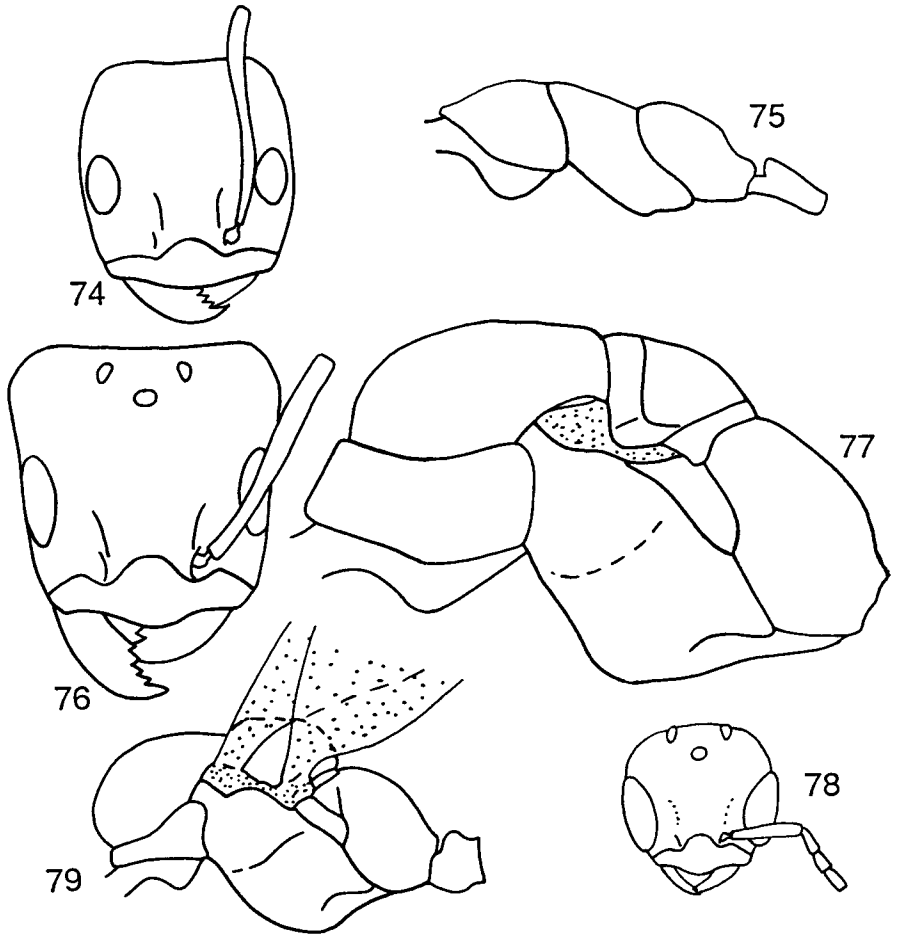
Amyrmex Kusnezov 1953a:333. Type species: *Amyrmex golbachi* Kusnezov (by monotypy). [NEW SYNONYMY]

Neoforelius Kusnezov 1953a:327. Type species: *Neoforelius tucumanus* Kusnezov (by monotypy). [NEW SYNONYMY]

Diagnosis

Worker: Anterior clypeal margin with long, ventrally curved setae which are about the same length as the closed mandibles; mandibles with 5 teeth and 0-2 denticles, a distinct basal angle, and a smooth basal margin; pronotum with 2 elongate hairs (at least 1/3 longer than others on the pronotum) (rarely more), and 1 to about 14 short hairs; petiolar scale reduced and strongly inclined anteriorly, or absent; first gastral segment projecting anteriorly and concealing petiole in dorsal view (anterior base visible in some species); propodeal spiracle sometimes elongate. North and South America.

Queen: Anterior clypeal margin with moderately ventrally curved setae which are about the same length as the closed mandibles; mandibles with 5 to



Figs. 74-79: 74, Full face view of *Forelius* worker (Tucuman, Argentina); 75, Lateral view of *Forelius* worker mesosoma (Tucuman, Argentina); 76, Full face view of *Forelius* queen (Tucuman, Argentina) 77, Lateral view of *Forelius* queen mesosoma (Tucuman, Argentina); 78, Full face view of *Forelius* male (Tucuman, Argentina); 79, Lateral view of *Forelius* male mesosoma (Tucuman, Argentina).

6 teeth, 0 to 2 denticles, and with the basal margin smooth and without teeth or denticles; petiolar scale vertical and not inclined anteriorly; fore wing with an open radial cell and without closed discoidal cells; hind wing with 1 closed cell.

Male: Second funicular segment with a lateral bend; palp formula 5:3; pygostyles vestigial; scape approximately the same length as funicular segments 1+2+3; anterior clypeal margin with setae which are approximately the same length as the closed mandibles; fore wing radial cell open; hind wing

without closed cells.

Description

WORKER.

HEAD. Vertex weakly convex to weakly concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 4-6 (rarely 8); about the same length as the closed mandibles; moderately curved ventrally. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent (but with between 2 and about 12 elongate hairs randomly placed on gula). MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 5-6 teeth and 0-2 denticles. Apical tooth subequal in length to, to elongate and much longer than, the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum convex to flat; dorsal face convex, longer or shorter than the declivitous face. Propodeal angle distinct or indistinct. Mesosomal spines and tooth absent. Erect pronotal hairs 2-16 (2 (rarely more) hairs elongate (at least 1/3 longer than any other hairs on the pronotum) and the remainder short). Dorsal pro-mesonotal junction with the mesonotum slightly above, or even with, the pronotum. Metanotal groove either forming a distinct angle between the mesonotum and propodeum, or reduced to a suture and with the mesonotum and propodeum forming a continuous, uninterrupted surface. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum (sometimes greatly elongate). Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present or reduced; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a well developed lobe. GASTER. First tergite projecting anteriorly and concealing the petiole in dorsal view (anterior base of pedicel visible in some species) and with a groove or indentation for the reception of the entire height of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium in

a distinct arch which extends dorsal of the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression dorsoventral. Fourth sternite keel- shaped posteriorly. GENERAL CHARACTERS. Worker caste monomorphic (rarely weakly polymorphic). Chromosome number 16 (n=16, *F. foetidus* (= *F. maccooki*), Crozier 1970a). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round; with short pile; smooth, without sculpture; and with short, lateral phragma. Bulb partially hidden by cupola in lateral view. Longitudinal muscle No. 1 present or absent. Occlusory tract absent.

QUEEN.

HEAD. Vertex flat to weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 6; about the same length as the closed mandibles; moderately curved ventrally. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 5-6 teeth and 0-2 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous face of propodeum convex; dorsal face convex, subequal in length to the declivitous face. Propodeal angle indistinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs about 6-30; short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell open. Fore wing with 1 cubital and no discoidal cells. Hind wing with 1 cell. PETIOLE. Scale present; either rounded and forming an even arch dorsally, or ridged and with a distinct angle dorsally; vertical and not inclined anteriorly. Venter with a well developed, rounded lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior

border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length at most only slightly longer than the length of funicular segments 1+2+3, or occasionally much longer than the length of funicular segments 1+2+3 but not exceeding the vertex. First funicular segment cylindrical or cone-shaped. Second funicular segment cylindrical and with a lateral bend. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 2-6; about the same length as the closed mandibles; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 5:3 (apparently 0:0 in *F. golbachi* (Kusnezov 1953a)). Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with 1-5 teeth and no denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle either distinct (with a well developed tooth or angle separating the masticatory and basal margins) or indistinct (with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle). Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous face of propodeum convex; dorsal face convex, longer than, to subequal in length to, the declivitous face. Propodeal angle distinct. WINGS. Radial cell open. Fore wing with 0-1 cubital and no discoidal cells. Pterostigmal appendage absent. Hind wing cells absent. PETIOLE. Scale present; rounded and forming an even arch dorsally; vertical and not inclined anteriorly. Venter with a slight or weakly developed lobe. Attachment to gaster broad. GASTER. First segment vertical and not concealing the petiole in dorsal view, smooth and without a groove or indentation. GENITALIA. Pygostyles vestigial. Digitus linear, with a slight ventral arch. Cuspis absent. Ventral lobe of volsella present as concave lobe. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances present or absent; when present, as a single boss located mid-dorsally on second abdominal tergite. Body hairs sparse; simple; short. 9 spiracular pairs. Antennae large or short.

Discussion

Forelius is a New World genus with disjunct North and South American populations. The genus is robust although one author has suggested that the

Table 5. Major characters differing between workers of *Forelius* and *Linepithema*.

Character	*Forelius*	*Linepithema*
Setae on anterior clypeal margin	long, ventrally curved	short, straight
Mandibular dentition	5-6 teeth, 0-2 denticles	5-8 teeth, 5-13 denticles
Basal mandibular margin	smooth	partially denticulate
First gastral tergite	projecting anteriorly	vertical
Gastral compression	dorsoventral	absent

two populations represent separate genera, and several species within the genus have been placed in three other genera, *Amyrmex*, *Iridomyrmex* and *Neoforelius*. The characters examined in this study indicate that *Forelius* is a distinct, easily recognized genus. Moreover, the transfer of *I. pruinosus* and *I. pruinosus analis* to *Forelius* by Wheeler and Wheeler (1986) is upheld, and the genera *Amyrmex* and *Neoforelius* are subsumed under *Forelius*.

Members of the genus *Forelius* are well adapted to xeric conditions and are seldom found in forested or moist sites. This has resulted in the North and South American populations of *Forelius* being geographically separated by the vast tropical regions of northern South America. An examination of material from both populations has made it clear, however, that *Forelius* is a well defined group of species separable from other dolichoderine genera (see Diagnosis above).

In 1958, Kusnezov (1958a) suggested that the North and South American species of *Forelius* be placed in separate genera, based on the configuration of the first cubital cell and the absence of a closed discoidal cell in South American species. In the present study, as with Brown and Nutting (1950), wing venation was found to be polymorphic with most taxa showing variation in the numbers of cubital and discoidal cells. However, a worker character not mentioned by Kusnezov (1958a), the elongate propodeal spiracular opening, is unique within the genus and limited to the South American species. This character does suggest that the South American species have diverged from those in North America and may form a monophyletic group, a result not unexpected in such a widely disjunct genus. However, no characters were found to suggest that the North American species form a monophyletic group.

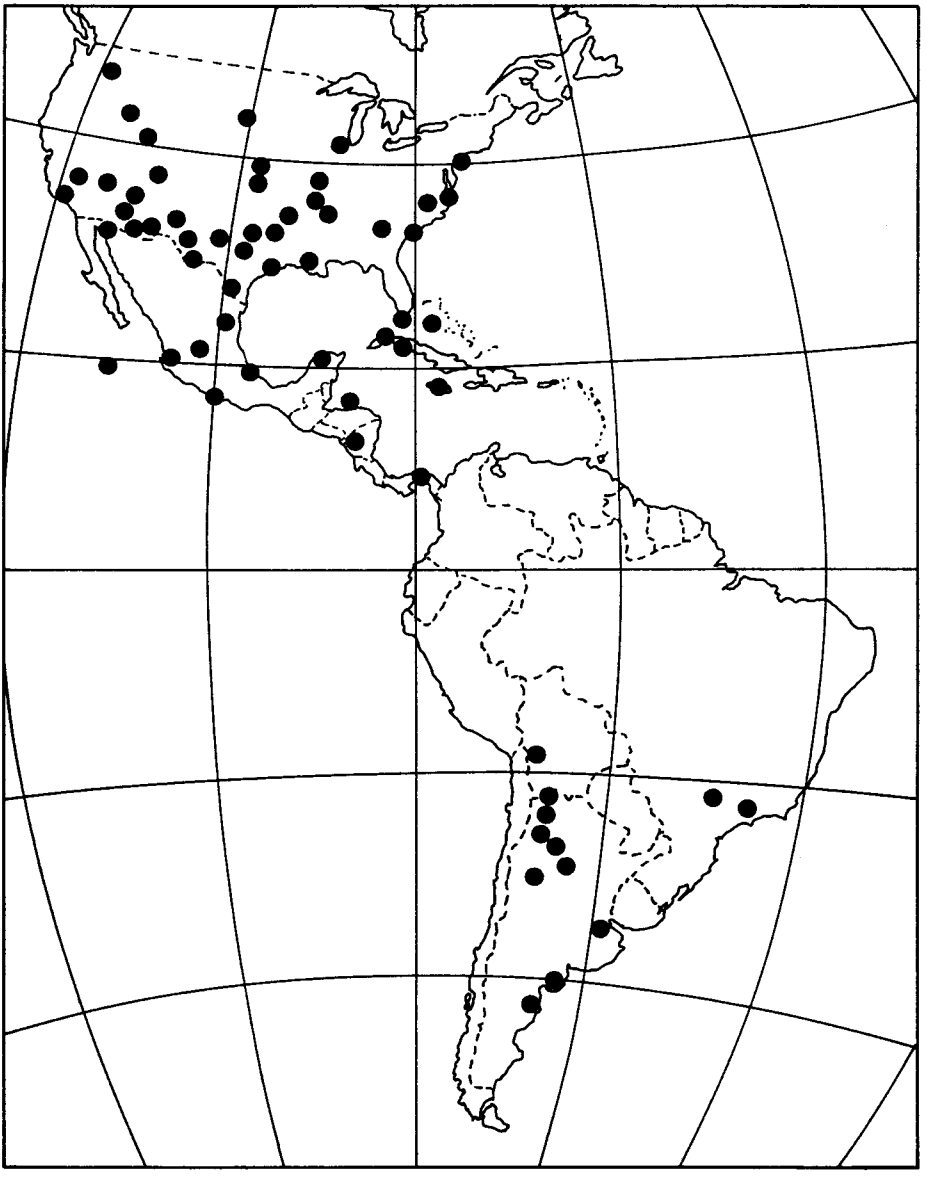


Fig. 80: Distribution of *Forelius* material examined during this study.

Therefore, as both of these groups are united by several synapomorphous characters, all species are here placed in a single genus, *Forelius*.

One North American species of *Forelius, F. pruinosus*, was placed in

Iridomyrmex (now *Linepithema*) based on superficial resemblance. This misplaced species weakened the generic concepts of both *Forelius* and *Iridomyrmex* and later caused Creighton (1950) to rely on minor pilosity differences when separating these genera, although he correctly stated that they differed in proventricular morphology. These generic concepts were accepted by most authors, presumably because of the difficulty in evaluating proventricular morphology combined with a lack of South American material for study.

The transfer of *Iridomyrmex pruinosus* (and its "subspecies" *analis*) to *Forelius* was suggested numerous times and several character systems indicated transfer was appropriate (overall morphology and habits by Creighton 1950 and Wheeler and Wheeler 1973, chemical systems by Blum *et al.* 1966). Nonetheless, the transfer of this species was not formally proposed until 1979 (Snelling and George) and finally published in 1986 (Wheeler and Wheeler). In the present study, the examination of additional South American material combined with the development of numerous external morphological characters supports the transfer of the North American species to *Forelius*.

Two *Forelius* species have been placed in their own genera, *Neoforelius* and *Amyrmex*. The genus *Neoforelius* was established by Kusnezov (1953a) for the single Argentinean species *N. tucumanus*. It was reported as differing from typical *Forelius* in its smaller body and the round rather than oval metanotal spiracles (?=propodeal spiracles). This separation from *Forelius* was based on weak characters which do not withstand close examination. This species shows all the characters used to diagnose *Forelius*, and it seems clear that Kusnezov's species is a small, pale representative of the genus. Therefore, *Neoforelius* is here considered a synonym of *Forelius*.

The genus *Amyrmex* was described by Kusnezov (1953a) from four males collected in the vicinity of Tucuman, Argentina and apparently has not been collected since. The specimens differ from typical *Forelius* males in having the apex of the cubital cell distal of the stigma, and in the morphology of the terminal segment of the tibia and claw. However, they are similar to *Forelius* in mandibular structure, profile of the pronotum and scutellum, the open radial cell, the number of closed cubital and discoidal cells, and the apparent length of the scape (based on Kusnezov's (1953a) figures). Although the wing venation is peculiar, in all other respects the specimens are typical of *Forelius*, and share all the characters used to diagnose this genus. *Amyrmex* is therefore considered a junior synonym of *Forelius*.

Species of *Forelius* are ground nesters and occur in drier habitats. Nests may be under rocks or in the soil with a small crater of loose soil at the entrance. Workers forage for honeydew and arthropods on the ground or in trees. They are usually active during the warmer parts of the day and forage singly or in columns.

Distribution: In the New World from the northern United States south to Panama, and in South America from southern Bolivia and Brazil south (Fig. 80).

Species Notes: The species previously placed in *Amyrmex* and *Neoforelius* are here transferred to *Forelius* (all NEW COMBINATIONS). These include *galbachi* (Kusnezov) (from *Amyrmex*) and *tucumanus* (Kusnezov) (from *Neoforelius*). The taxon *Iridomyrmex pruinosus* var. *analis* (André) is also transferred to *Forelius* (NEW COMBINATION).

Genus *Froggattella* Forel (Figs. 81-88)

Froggattella Forel 1902:459. Type Species: *Acantholepis kirbii* Lowne (by orig. desig.).

Diagnosis

Worker: Propodeum with elongate, flattened, posteriorly-directed spines; propodeal spiracles dorsal and posterior, located on the propodeal spines between 1/3 and 1/2 spine length distal of the base. Australia.

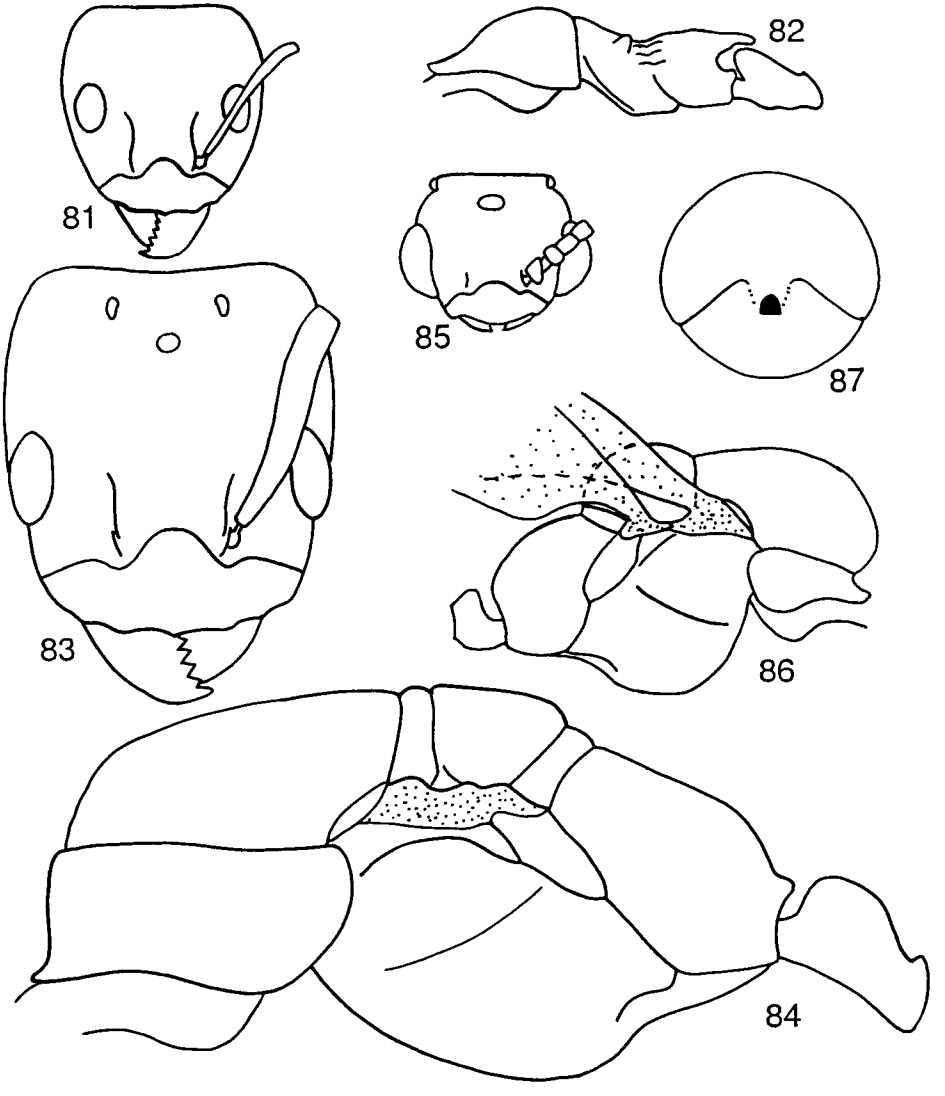
Queen: First gastral segment elongate posteriorly and smooth, without a groove or indentation near the petiolar insertion; anterior clypeal margin with a lateral shoulder, a central projection, either pointed or rounded (sometimes only feebly projecting), and 2 to 4 setae; dorsum of petiole rounded and venter without a lobe.

Male: Mandible without teeth or denticles (tip of mandible rounded and without a differentiated tooth); petiolar scale rounded and forming an even arch dorsally; venter of petiole with a slight or reduced lobe; first gastral segment vertical and not concealing the petiole in dorsal view.

Description

WORKER.

HEAD. Vertex weakly concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin with a central projection, either pointed or rounded (sometimes only feebly projecting). Anterior clypeal setae 0-4; when present short, less than twice the maximum scape diameter; straight. Posterior clypeal margin even with or posterior to the posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with about 9 teeth and no



Figs. 81-87: 81, Full face view of *Froggattella* worker; 82, Lateral view of *Froggattella* worker mesosoma; 83, Full face view of *Froggattella* queen; 84, Lateral view of *Froggattella* queen mesosoma; 85, Full face view of *Froggattella* male; 86, Lateral view of *Froggattella* male mesosoma; 87, Anterior view of first gastral segment of *Froggattella*. All from Queensland, Australia.

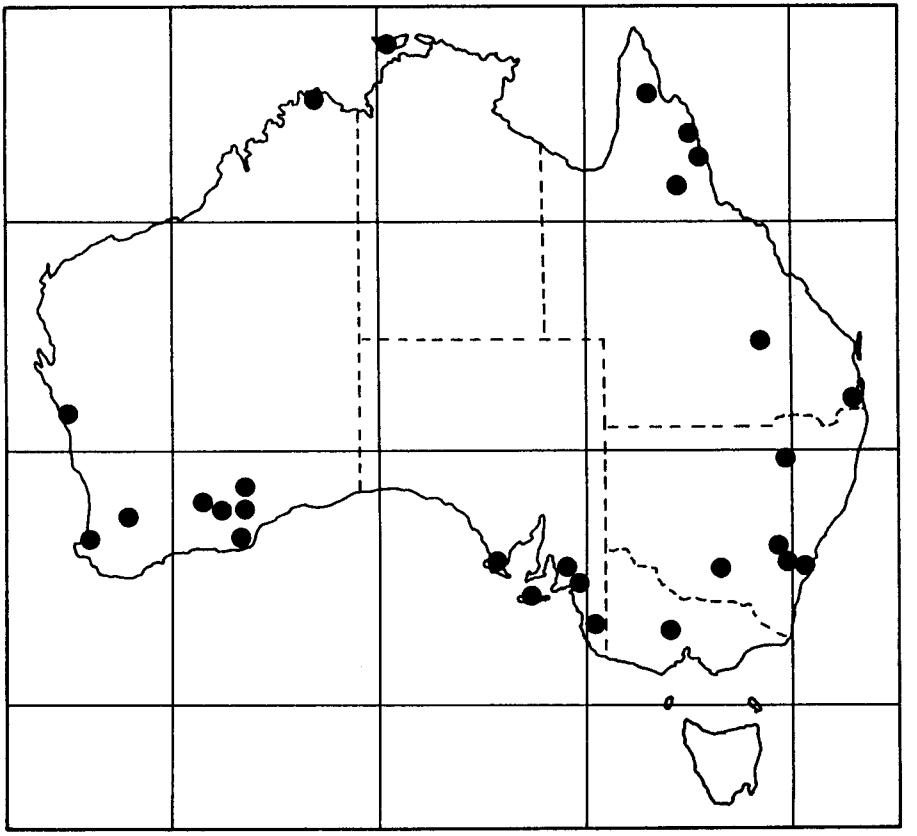


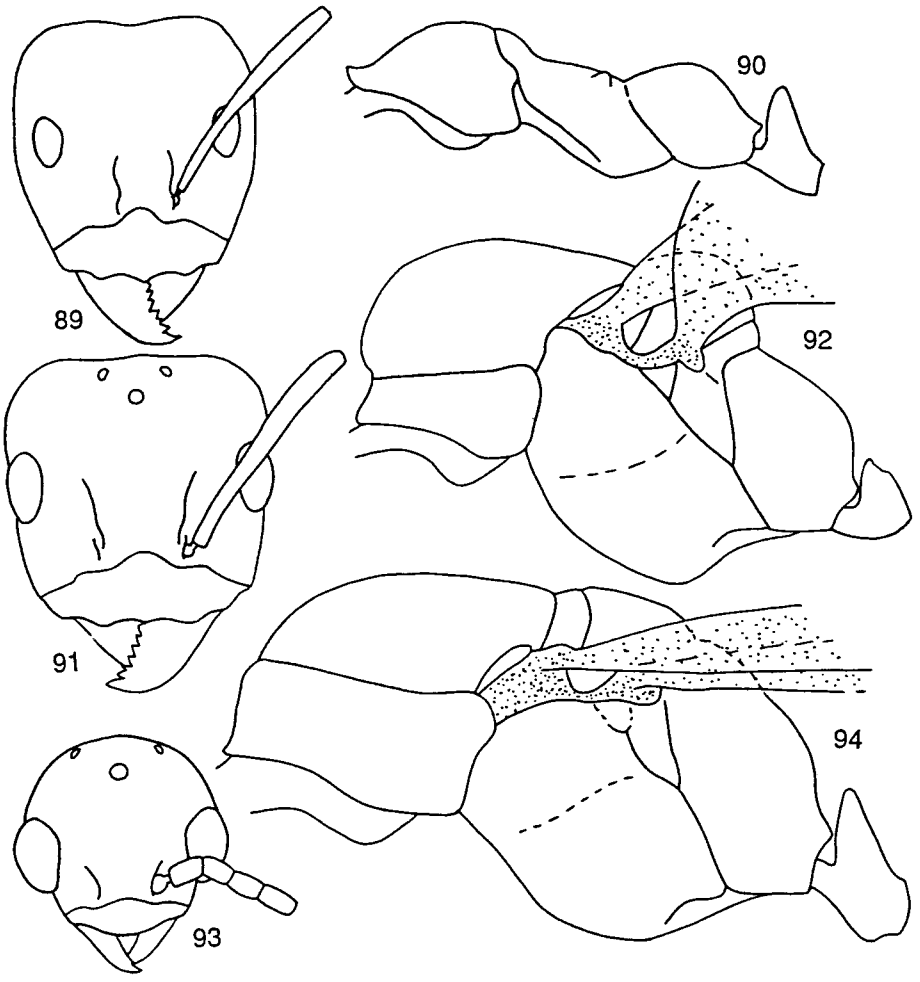
Fig. 88: Distribution of *Froggattella* material examined during this study.

denticles. Apical tooth subequal in length to the subapical tooth. Basal angle weakly defined by a denticle. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum concave; dorsal face convex, longer than the declivitous face. Propodeal angle distinct. Pronotal spines absent. Erect pronotal hairs about 20; elongate, much longer than the maximum scape width. Mesonotal spines absent. Propodeal spines present, distinct (dorsoventrally flattened, extending posteriorly). Propodeal tooth absent. Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle dorsal and lying on the dorsal surface when viewed in lateral profile. Propodeal spiracle dorsal and posterior, located on propodeal spines distal of base. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present;

rounded and forming an even arch dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a slight or weakly developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Anterior tergosternal suture of the first segment very weakly developed immediately lateral of the helcium and forming a distinct arch which extends dorsal of the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression dorsoventral. Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number unknown. Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round; with short pile; smooth, without sculpture; and with narrow phragma. Bulb completely hidden by cupola in lateral view. Longitudinal muscle No. 1 absent. Occlusory tract absent.

QUEEN.

HEAD. Vertex flat to weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin with a central projection, either pointed or rounded (sometimes only feebly projecting). Anterior clypeal setae 2-4; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin even with or posterior to the posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with about 6 teeth and no denticles. Apical tooth subequal in length to the subapical tooth. Basal angle weakly defined by a denticle. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete but weakly developed anteriorly. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face longer than the declivitous face. Propodeal angle moderately distinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs about 25; short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cell. Hind wing with 2 cells. PETIOLE. Scale present; rounded and forming an even arch dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter



Figs. 89-94: 89, Full face view of *Iridomyrmex* worker (New South Wales, Australia); 90, Lateral view of *Iridomyrmex* worker mesosoma (New South Wales, Australia); 91, Full face view of *Iridomyrmex* queen (Western Australia, Australia); 92, Lateral view of *Iridomyrmex* queen mesosoma (Western Australia, Australia); 93, Full face view of *Iridomyrmex* male (Victoria, Australia); 94, Lateral view of *Iridomyrmex* male mesosoma (Victoria, Australia).

without a lobe. GASTER. First segment elongated posteriorly, smooth and without a groove or indentation. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment barrel-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a notch or concavity of any type. Anterior clypeal setae 4-6; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible without teeth or denticles. Apical tooth absent (tip of mandible rounded and without a differentiated tooth). Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex. Propodeal angle indistinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; rounded and forming an even arch dorsally; vertical and not inclined anteriorly. Venter with a slight or weakly developed lobe. Attachment to gaster broad. GASTER. First segment vertical and not concealing the petiole in dorsal view, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave. Paramere divided by a membranous region. Digitus with a down-turned tip. Cuspis parallel with digitus. Ventral lobe of volsella present as weakly developed concave lobe. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances present as 6 bosses located mid-dorsally. Body hairs sparse; simple; short. 10 spiracular pairs. Antennae short.

Discussion

Froggattella is a small Australian genus immediately recognizable by the unique configuration of the propodeal spines and the propodeal spiracles. These spiracles are located on the spines distal of their bases, while in all other genera with propodeal spines the spiracles are located ventral of the spine bases.

This genus is widespread in Australia, but is sporadically distributed and not commonly collected. *Froggattella* species generally forage arboreally while nesting occurs either in the soil or arboreally. The species-level taxonomy is discussed by Wheeler (1936).

Distribution: Australia (Fig. 88)

Genus *Iridomyrmex* Mayr (Figs. 89-96, Table 3)

Iridomyrmex Mayr 1862:702. Type species: *Formica purpurea* F. Smith (desig. by Bingham 1903:297).

Diagnosis

Worker: Compound eyes placed relatively posteriorly on head; anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder; anteromedial clypeal margin with a central projection, either pointed or rounded (sometimes only feebly projecting). India east to China and south to Australia and New Caledonia.

Queen: Compound eyes relatively posterior on head; anterolateral clypeal margin posterior to the mediolateral areas and separated from it by a shoulder; anteromedial clypeal margin with a central projection, either pointed or rounded (sometimes only feebly projecting); apical tooth of mandible elongate and much longer than subapical.

Male: Mandible with 1 tooth (the apical) and no denticles (rarely with up to about 25 denticles); first gastral segment vertical and not concealing the petiole in dorsal view.

Description

WORKER.

HEAD. Vertex convex to weakly concave. Compound eyes present, approximately round; relatively posterior on head. Ocelli absent (rarely present). Antennae 12 segmented. Scape relatively short, at most surpassing the vertex by less than one-half (often less than one-third) its length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin with a central projection, either pointed or rounded (sometimes only feebly projecting). Anterior clypeal setae 6-15; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent (gula rarely with numerous short, erect, randomly placed hairs). MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with about 7-10 teeth and about 2-5 denticles. Apical tooth varying from slightly to much longer than the subapical tooth. Basal angle varying from distinct (with a well developed tooth or angle separating the masticatory and basal margins) to indistinct (with a relatively uninterrupted curve between the two margins).

Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum convex to flat; dorsal face convex, varying from longer than, to subequal in length to, the declivitous face. Propodeal angle distinct to indistinct (rarely expanded dorsally into a cone-like projection). Mesosomal spines and tooth absent. Erect pronotal hairs 0-80; when present, varying from short (about as long as maximum scape width) to elongate (much longer than the maximum scape width). Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle lateral and ventral of the dorsal surface, or dorsal and lying on the dorsal surface, when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; rounded and forming an even arch dorsally, or ridged and with a distinct angle dorsally; vertical and not inclined anteriorly to moderately inclined anteriorly but with the anterior and posterior faces approximately the same length (rarely strongly inclined anteriorly and with the anterior face much shorter than the posterior face). Venter with or without a well developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium in a distinct arch which extends dorsal of the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section) or weakly lateral. Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste monomorphic or rarely polymorphic. Chromosome number 9 (2n=18, *I. purpureus*-group, blue form, black form, Imai *et al.* 1977; 2n=18, *I. gracilis*-group, sp. ANIC-13, ANIC-14, ANIC-15, ANIC- 16, ANIC-17, Imai *et al.* 1977; n=9, 2n=18, *I. gracilis*(A), *gracilis*(B), *gracilis*(C), Crozier 1968a; 2n=18, *I. anceps*, Imai *et al.* 1984; 2n=48 (probably in error), *I. anceps*, Imai *et al.* 1985b; n=9, 2n=18, *I. detectus*- group (=*purpureus*-group), Crozier 1968a, Crozier 1968b; n=9, 2n=18, *I. mattiroloi*, Crozier 1968a). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round; with short pile; smooth, without sculpture; and with narrow phragma. Bulb completely hidden by cupola in lateral view. Longitudinal muscle No. 1 absent. Occlusory tract absent.

QUEEN.

HEAD. Vertex weakly convex to flat. Compound eyes relatively posterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal

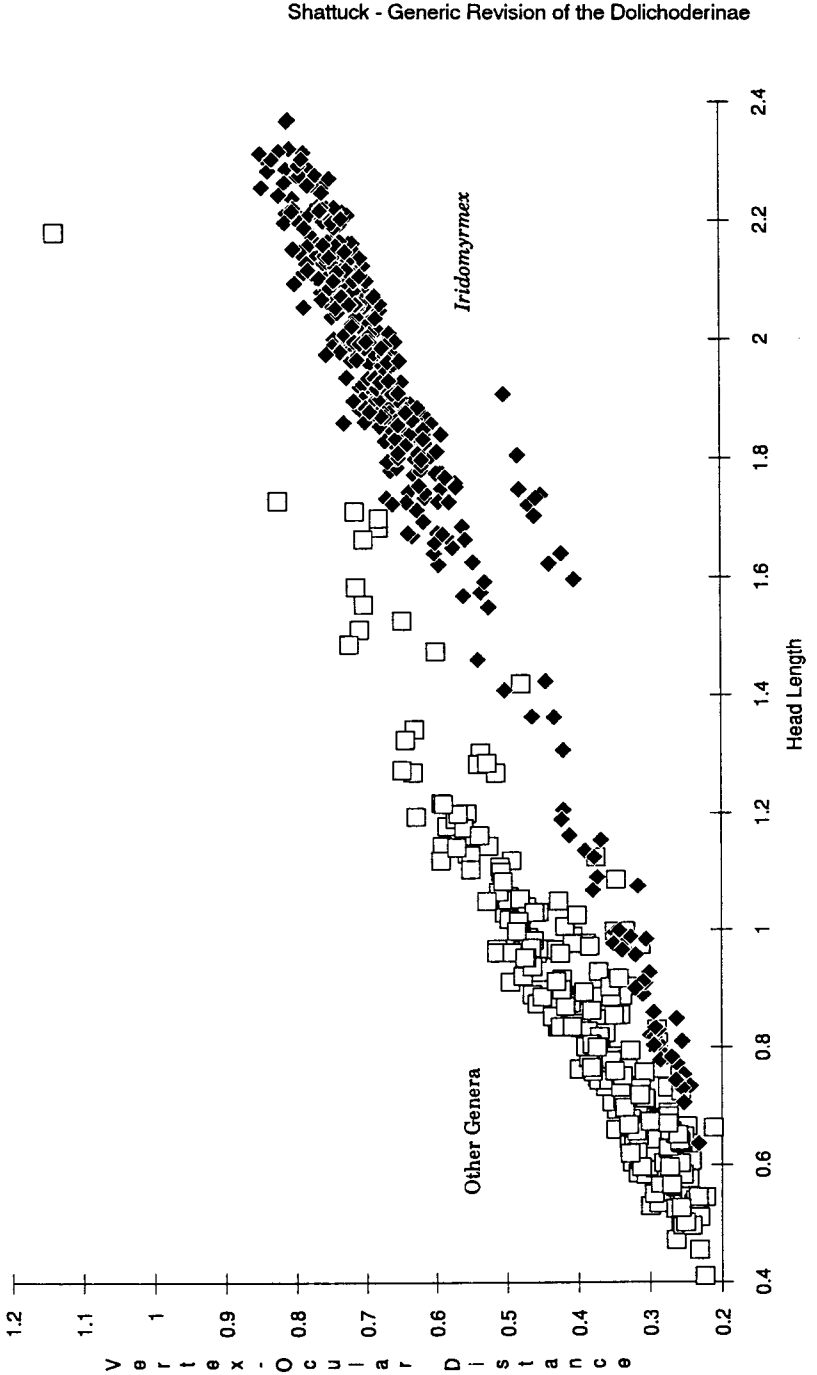


Fig. 95. Distribution of the vertex-ocular distance (measured from the posterior-most point of the head to the posterior-most point of the compound eye in full face view) and the head length (measured from the posterior-most point to the anterior-most point of the head excluding the mandibles in full face view) for 677 individual workers representing 126 species of Dolichoderinae (units are mm). Included genera are *Anonychomyrma, Bothriomyrmex, Doleromyrma, Dolichoderus, Dorymyrmex, Forelius, Froggattella, Iridomyrmex, Linepithema, Liometopum, Ochetellus, Papyrius, Philidris, Tapinoma,* and *Technomyrmex.*

margin with a central projection, either pointed or rounded (sometimes only feebly projecting). Anterior clypeal setae 8-16; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin posterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7- 9 teeth and 4-7 denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin varying from denticulate distally, smooth proximally to denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture weak, nearly absent. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel, and entire or with a suture medially. Anterior axillar suture straight or angular medially. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle indistinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs 6-60; short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 1-2 cubital and 1 discoidal cell. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; varying from vertical and not inclined anteriorly to moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. Venter with a well developed to slight or weakly developed lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of either the basal portion or the entire height of the petiole. Fifth tergite vertical and with the distal terminus of the gaster not well defined. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment cylindrical (or cone-shaped) or barrel-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 6- 8; with both short (about as long as the maximum diameter of the scape) and long (about the same length as the closed mandibles) hairs (sometimes only short hairs present); straight. Posterior clypeal margin even with or anterior to the anterior

surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with 1 tooth and no denticles (rarely about 25 denticles are present). Apical tooth distinct. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin smooth and without teeth or denticles (rarely denticulate along entire margin). MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture varying from present and complete to reduced and incomplete. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face longer than the declivitous face. Propodeal angle distinct or indistinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; rounded and forming an even arch dorsally, or ridged and with a distinct angle dorsally; vertical and not inclined anteriorly. Venter with or without a slight or weakly developed lobe. Attachment to gaster broad to intermediate. GASTER. First segment vertical and not concealing the petiole in dorsal view, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate with a "V"-shaped notch. Paramere divided by a membranous region. Digitus linear, with a slight ventral arch. Cuspis parallel with digitus. Ventral lobe of volsella absent. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances present as a single boss located mid-dorsally on abdominal tergite 2. Body hairs sparse; simple; short. 9 spiracular pairs. Antennae short.

Discussion

The genus "*Iridomyrmex*" has proven to be one of the most taxonomically challenging in the subfamily. It had long been suspected of being an assemblage of unrelated species (Brown 1958, Crozier 1968a, Brown 1977, Snelling and Hunt 1975). However, few suggestions have been put forth to resolve this problem even though there is no lack of available material; most larger museums have hundreds of specimens representing dozens of species. Moreover, there is no lack of taxonomically useful characters, as detailed examination revealed numerous character systems which vary among species. In this study the 152 described species and subspecies previously placed in *Iridomyrmex* are considered to belong to seven separate genera. The majority of taxa (62) remain in *Iridomyrmex* (strict sense).

To resolve the genus, homogeneous sets of morphologically divergent species were removed. As groups were separated, the patterns of character distribution became clearer. In the final analysis the original "*Iridomyrmex*-group" was split into seven genera: *Anonychomyrma* (30 described taxa), *Doleromymra* (3), *Iridomyrmex* (strict sense) (62), *Linepithema* (28), *Ochetellus* (10), *Papyrius* (6) and *Philidris* (14). Three of these, *Ochetellus*, *Papyrius* and *Philidris*, are newly described (Shattuck 1992a), two, *Linepithema* and *Anonychomyrma*, are greatly expanded from their previous concepts, and one, *Doleromyrma*, is removed from synonymy.

Members of *Iridomyrmex* may be separated from other members of the subfamily by the configuration of the anterior clypeal margin and the relatively posterior placement of the compound eyes on the head capsule (Fig. 95) (see also the above Diagnosis and Table 3). While the generic- level understanding of these ants is improved greatly by the above changes, the species-level knowledge is very poor. The genus has not received comprehensive taxonomic attention and specific identifications are very difficult. It is hoped that this new generic concept will allow detailed studies to proceed.

While *Iridomyrmex* species are widely distributed in the Oriental region, they are far more common and diverse in Australia and form one of the most ecologically important groups of terrestrial invertebrates in many habitats. *Iridomyrmex* occurs throughout Australia, with the exception of wet sclerophyll forests and rain forests, and species densities of up to 12 to 15 species at a given site are not uncommon (Andersen 1983, P. J. M. Greenslade, pers. comm.). Nests are located in soil, with or without covering, and can contain up to 300,000 individuals (Ettershank 1971). Colonies are often spread over wide areas with multiple nests connected by well defined paths. Workers forage in columns as general scavengers, or tend aphids and coccids.

Distribution: India east to China and south to Australia and New Caledonia (Fig. 96).

Genus ***Leptomyrmex*** Mayr (Figs. 97-103)

Leptomyrmex Mayr 1862: 695. Type Species: *Formica erythrocephala* Fabricius (by monotypy).

Diagnosis

Worker: Antennal scapes elongate, surpassing the vertex by more than one-half their length; medial hypostoma notched; mandibles with 7 to 15 teeth and 5 to 12 denticles; anterior tentorial pit located laterally, near the mandibular insertion (mid-way between mandibular insertion and antennal socket in some species). New Guinea, New Caledonia, Australia.

Queen: Usually worker-like, differing as follows: mesosoma slightly enlarged; ocelli present (see Discussion below).

Male: Funicular segments 2 and 3 more than twice as long as broad; anterior

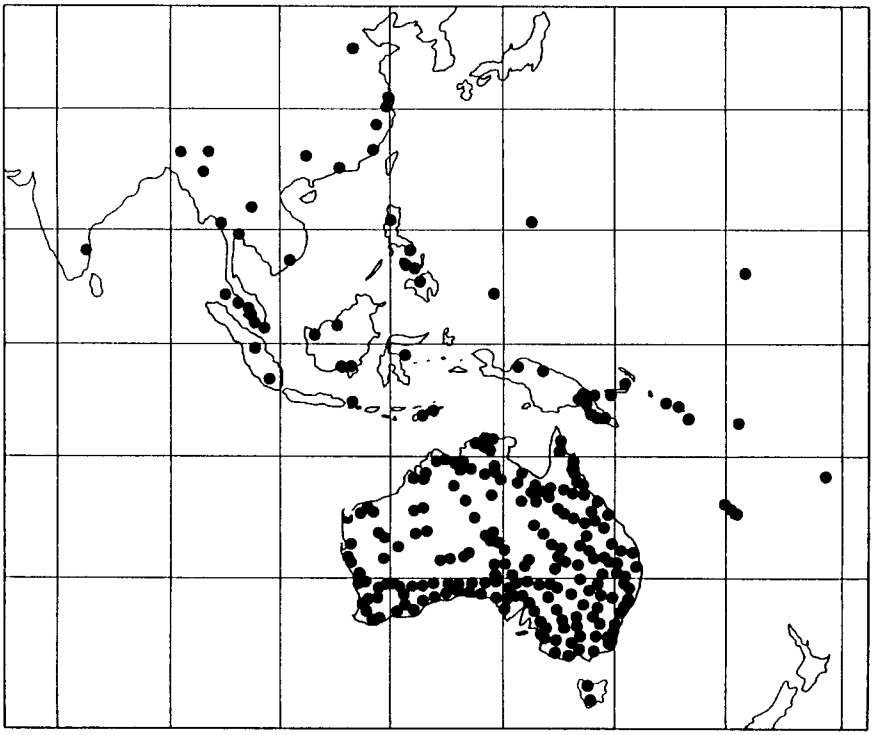


Fig. 96: Distribution of *Iridomyrmex* material examined during this study.

tentorial pit near the lateral junction of the gena and clypeus (near the mandibular insertion); medial hypostoma notched; pterostigmal appendage generally present (although sometimes reduced), but absent in at least one species.

Description

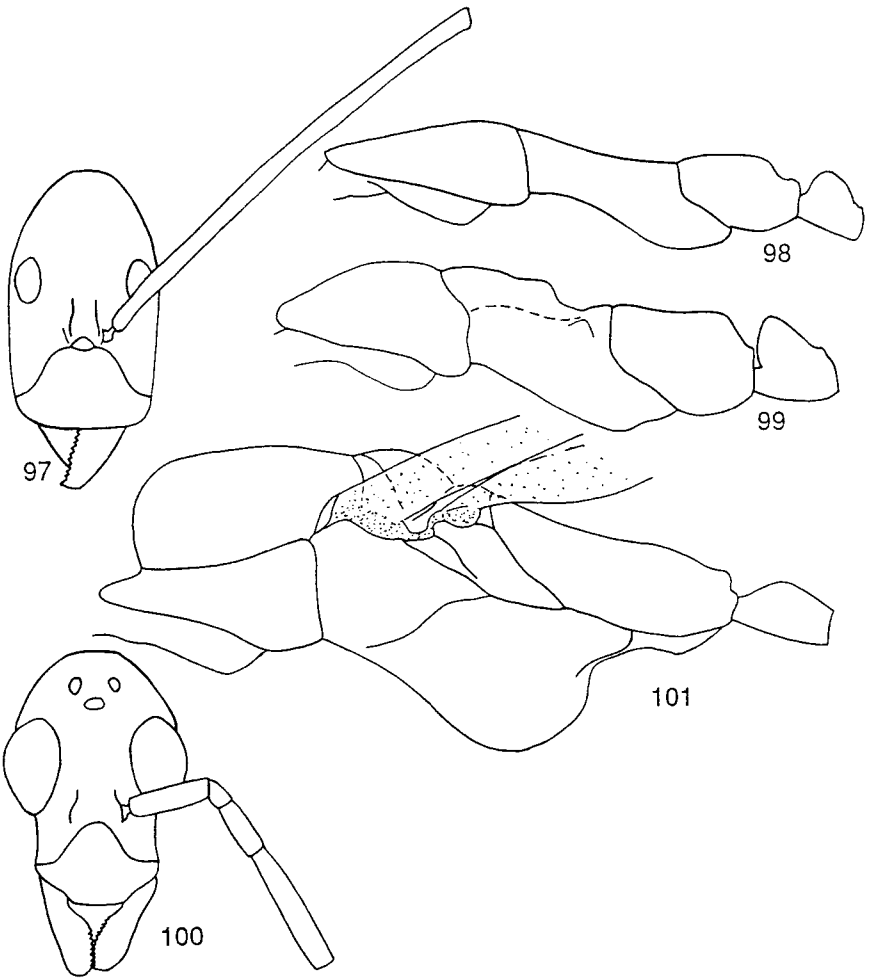
WORKER.

HEAD. Vertex convex to very weakly concave. Compound eyes present, approximately round; relatively posterior on head. Ocelli absent. Antennae 12 segmented. Scape long, surpassing the vertex by about one- half its length or more. Anterolateral clypeal margin even with the mediolateral region (sometimes with a very weakly developed shoulder). Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 2-9; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin even with or anterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit near the lateral junction of the gena and clypeus (near the mandibular insertion). Frontal carina present. Anterolateral

hypostoma reduced to a thin sclerite (rarely slightly expanded, but never tooth-like). Medial hypostoma notched. Psammophore absent. MOUTHPARTS. Palp formula 6:4 (very rarely 5:4). Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7-15 teeth and 5-12 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle weakly defined by a denticle. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum weakly expanded medially. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum flat; dorsal face weakly convex to concave, longer than the declivitous face. Propodeal angle distinct (sometimes only weakly). Mesosomal spines and tooth absent. Erect pronotal hairs absent (rarely with numerous short, erect hairs). Dorsal pro-mesonotal junction with the pronotum and mesonotum even, or rarely with the mesonotum above the pronotum. Metanotal groove forming a distinct angle between the mesonotum and propodeum (often reduced and with the mesosomal dorsum nearly flat). Metanotal spiracle dorsal and lying on the dorsal surface when viewed in lateral profile, or rarely lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with reduced barbules (barbules often absent from basal half). PETIOLE. Scale present; rounded and forming an even arch dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with or without a slight or weakly developed lobe. GASTER. First tergite elongated posteriorly, smooth and without a groove or indentation. Anterior tergosternal suture of the first segment extending laterally from the helcium, without or with at most a very weak dorsal arch. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression lateral. Fourth sternite keel- shaped posteriorly. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number 12 (n=12, *L. erythrocephalus*, Imai *et al.* 1977). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola narrow relative to bulb; round; with long pile; smooth, without sculpture; and without phragma. Bulb exposed in lateral view. Longitudinal muscle No. 1 present. Occlusory tract present.

QUEEN.

The majority of species have ergatoid queens which differ from the worker caste in being slightly larger, having ocelli, and in having an enlarged mesosoma. The fully-winged form is as follows: HEAD. Vertex flat to weakly concave. Compound eyes relatively posterior on head. Antennae 12 segmented. Scape long, surpassing the vertex by more than one-third scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae about 20; short, less than twice the maximum



Figs. 97-101: 97, Full face view of *Leptomyrmex pallens* worker; 98, Lateral view of *Leptomyrmex pallens* worker mesosoma; 99, Lateral view of *Leptomyrmex* queen mesosoma (New South Wales, Australia); 100, Full face view of *Leptomyrmex* male (New South Wales, Australia); 101, Lateral view of *Leptomyrmex* male mesosoma (New South Wales, Australia).

scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit midway between the antennal socket and mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma notched. Psammophore absent.

MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with about 5-7 teeth and about 14 denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin with denticles limited to near the angle. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla constricted medially; entire. Anterior axillar suture straight. Declivitous face of propodeum flat to weakly concave. Dorsal face flat; longer than the declivitous face. Propodeal angle distinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs absent. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with reduced barbules (absent from basal third). PETIOLE. Scale present; ridged and with a distinct angle dorsally; moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. Venter with a well developed, rounded lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and smooth and without a groove or indentation. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite keel-shaped posteriorly.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment cylindrical or cone- shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 more than twice as long as broad. Third and fourth funicular segments bent and forming an angle between them (angle either between segments, or at the distal end of segment 3). Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 0-6; when present short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin even with or anterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit near the lateral junction of the gena and clypeus (near the mandibular insertion). Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma notched. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with no teeth (except apical, if present) and about 0-26 denticles. Apical tooth absent (tip of mandible rounded, or occasionally angular) or rarely well defined and much longer than the subapical tooth. Basal angle either indistinct (with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle) or weakly defined by a denticle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal

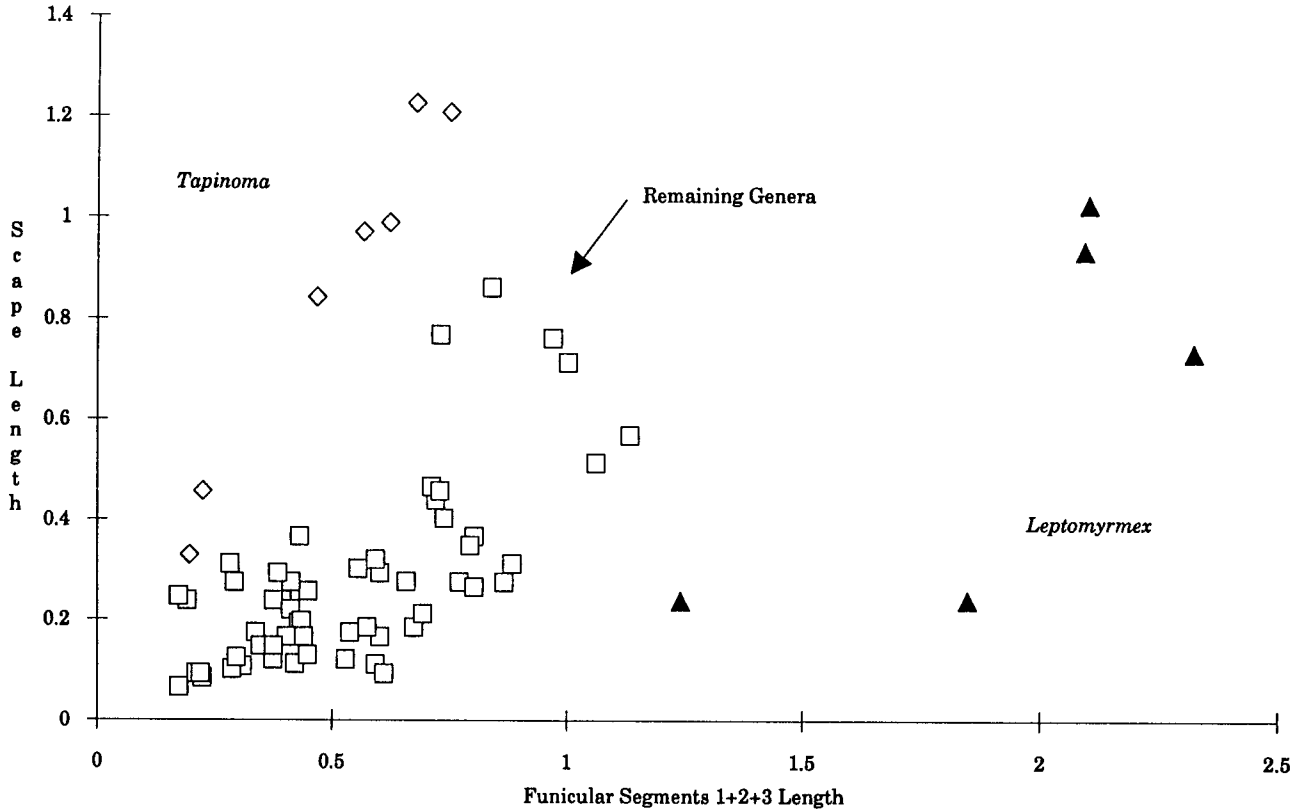


Fig. 102. Distribution of the scape length and combined length of funicular segments 1+2+3 for males of 77 species of Dolichoderinae (units are mm).

suture present and complete (but weak posteriorly), or reduced and incomplete. Anteromedial mesosternum even with the lateral regions. Axilla absent dorsally. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum flat; dorsal face longer than the declivitous face. Propodeal angle indistinct. WINGS. Radial cell closed. Fore wing with no cubital or discoidal cells (rarely with 2 cubital and 1 discoidal cell). Pterostigmal appendage present (although sometimes reduced), or rarely absent. Hind wing with 2 cells. PETIOLE. Scale present; rounded and forming an even arch dorsally; vertical and not inclined anteriorly. Venter with a slight or weakly developed lobe. Attachment to gaster narrow. GASTER. First segment elongated posteriorly, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate convex to even across entire width. Paramere weakly divided (distinctly divided in a few small species). Digitus with a down-turned tip (sometimes also with a dorsal tooth). Cuspis parallel with digitus. Ventral lobe of volsella present as concave lobe (sometimes elongate and finger-like). Aedeagus with ventral teeth.

LARVA.

Shape leptomyrmecoid. Protuberances present or absent; when present, as a single boss located ventrally on prothorax. Body hairs numerous; simple; short. 10 spiracular pairs.

Discussion

The genus *Leptomyrmex* is one of the most distinct in the subfamily. All species can be recognized by the relatively large number of mandibular teeth and denticles, the elongate scapes, and the notched medial hypostomal border. Additionally, most workers can be recognized by their large size, elongate legs, and coloration (black, orange, or bicolored black and orange).

Most *Leptomyrmex* species are morphologically similar in size and overall appearance, and have ergatoid (worker-like) queens. However, several species (as yet undescribed) are much smaller, have fully winged queens, and superficially resemble *Iridomyrmex*. These species do not, however, belong in *Iridomyrmex* based on their possession of the following *Leptomyrmex* character states: mandibular dentition, anterior clypeal margin configuration, elongate scapes, elongate head, cleft medial hypostomal margin, anterior tentorial pit location, keeled fourth gastral sternite, reduced hind tibial spurs, and replete formation in the workers. Additionally, the males of typical *Leptomyrmex* possess elongate flagellomeres relative to the scape length (Fig. 102), and the males of these small species are similar, although the flagellomeres are not quite as long as in other species. These "smaller" *Leptomyrmex* species possess no diagnostic *Iridomyrmex* characters and at best exhibit only generalized *Iridomyrmex* features (small body size, and the configuration of the pro- mesonotal junction, lateral mesonotal spiracle, petiolar node, and first

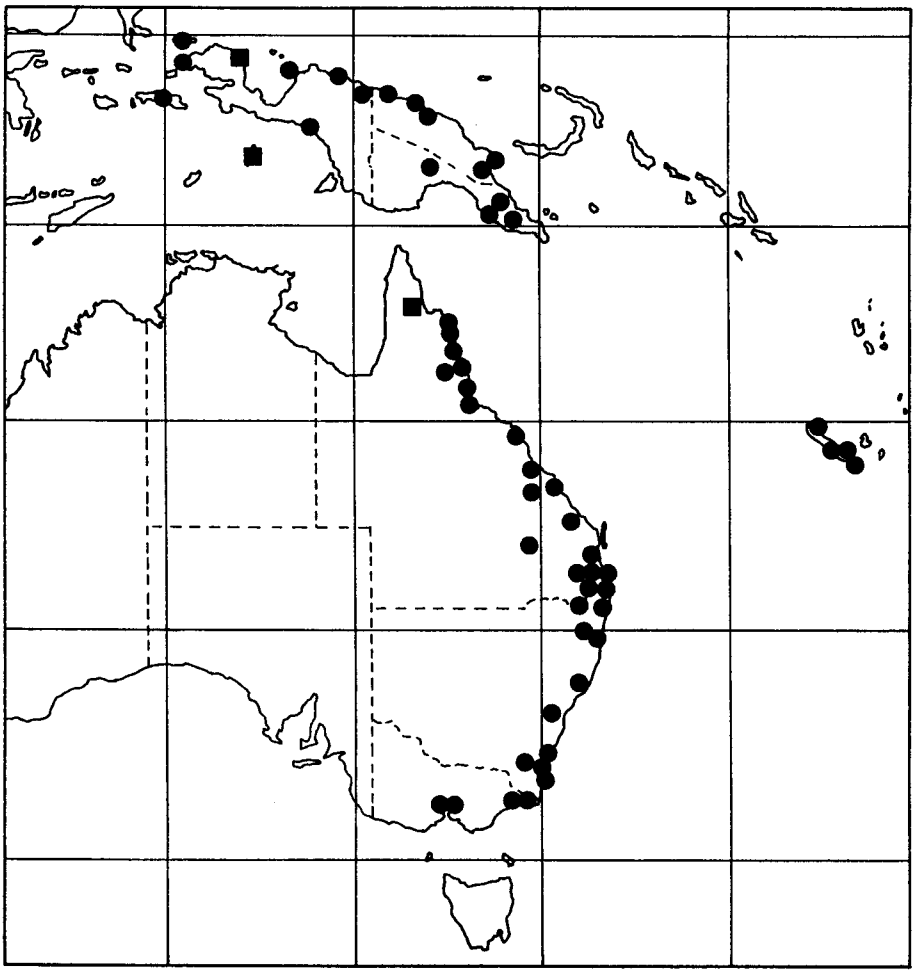


Fig. 103: Distribution of *Leptomyrmex*. Closed circles indicate examined material. Closed squares indicate literature records believed to be reliable.

gastral tergite).

The species of *Leptomyrmex* were revised by Wheeler (1934). Unfortunately, Wheeler made extensive use of color-based subspecies and the group is now in need of revisionary work.

This genus is now limited to wet sclerophyll or rain forests of New Guinea (and nearby islands), eastern Australia, and New Caledonia. *Leptomyrmex* was previously much more widely distributed based on fossils found in the Dominican Republic amber (Baroni Urbani 1980, Baroni Urbani and Wilson 1987). Workers forage singly or in small groups on the ground, and nest in the

soil or in dead wood, either standing or on the ground.

Distribution: Seram, New Guinea, eastern Australia, and New Caledonia (Fig. 103).

Species Notes: The species *Formica flavitarsus* F. Smith is transferred from *Camponotus* to *Leptomyrmex* (NEW COMBINATION).

Genus *Linepithema* Mayr (Figs. 104-110, Tables 5-6)

Linepithema Mayr 1866: 496. Type species: *Linepithema fuscum* Mayr (by monotypy).

Diagnosis

Worker: Mandible with 5 to 8 teeth, 5 to 13 denticles, and the apical tooth elongate and much longer than the subapical; anteromedial clypeal margin with a broad, shallow concavity; gastral compression absent (gaster circular in cross section); fourth gastral sternite keel-shaped posteriorly. Central and South America, with an introduced species in North America, Europe, Canary Islands, Azores, southern Africa, Australia and Hawaii.

Queen: Mandible with 6 to 8 teeth, 7 to 11 denticles, and the apical tooth elongate and much longer than the subapical; axilla with a suture medially; petiolar scale vertical and not inclined anteriorly; venter of the petiole with a slight or reduced lobe.

Males related to *L. fuscum*: Paramere with the gonostylus elongated into an articulating finger-like structure; digitus elongate; axilla with a suture medially; venter of petiole without a lobe.

Males related to *L. humile*: Pygostyles present, reduced; petiolar scale a blunt angle dorsally; mandibles with 1 tooth (the apical), 6 to 14 denticles, and the basal angle weakly defined by a denticle.

Description

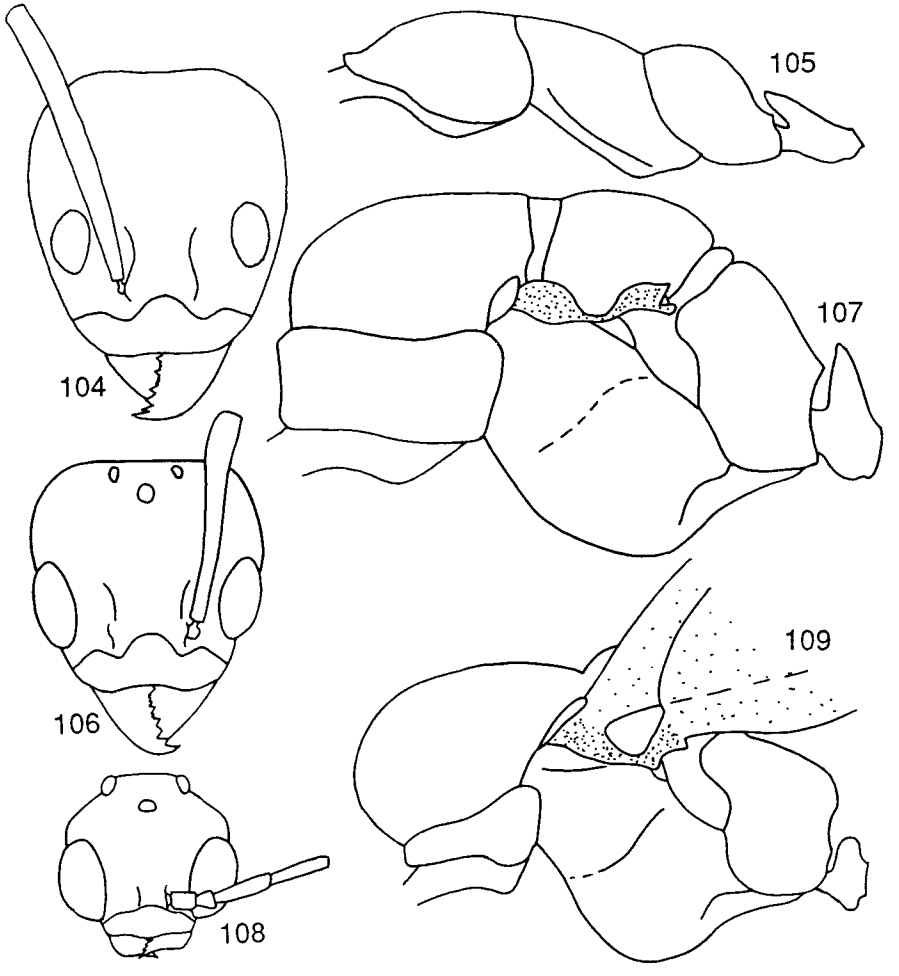
WORKER.

HEAD. Vertex convex to weakly concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin with a broad, shallow concavity. Anterior clypeal setae 8-12; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of

segment 4. Mandible with 5-8 teeth and 5-13 denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle either distinct (with a well developed tooth or angle separating the masticatory and basal margins) or weakly defined by a denticle. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle distinct or indistinct. Mesosomal spines and tooth absent. Erect pronotal hairs 0-6 (generally 2); elongate, much longer than the maximum scape width. Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle either lateral and ventral of the dorsal surface, or dorsal and lying on the dorsal surface, when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; rounded and forming an even arch dorsally, or ridged and with a distinct angle dorsally; varying from moderately inclined anteriorly (but with the anterior and posterior faces approximately the same length) to strongly inclined anteriorly (and with the anterior face much shorter than the posterior face). Venter with a slight to well developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of either the basal portion or the entire height of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium in a dorsal arch which is approximately the same height as the helcial dorsum. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite keel-shaped posteriorly. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number 8 or 9 (n=8, 2n=16, *L. humile*, Crozier 1968a; n=9, *L. piliferum*, sp. nr. *piliferum*, Crozier 1970a). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round; with short pile; smooth, without sculpture; and with short, lateral phragma. Bulb completely hidden by cupola in lateral view. Occlusory tract absent.

QUEEN.

HEAD. Vertex flat to weakly concave. Compound eyes relatively anterior on head. antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 6-15; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin even with or posterior to the posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion.



Figs. 104-109: 104, Full face view of *Linepithema humile* worker; 105, Lateral view of *Linepithema humile* worker mesosoma; 106, Full face view of *Linepithema humile* queen; 107, Lateral view of *Linepithema humile* queen mesosoma; 108, Full face view of *Linepithema humile* male; 109, Lateral view of *Linepithema humile* male mesosoma.

Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 6-8 teeth and 7-11 denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle varying from distinct (with a well developed tooth or angle separating the masticatory and basal margins) to weakly defined by a denticle. Basal margin

Table 6. Major morphological differences between *L. fuscum* group and *L. humile* group males.

Character	*L. fuscum*-group	*L. humile*-group
Axilla	Divided medially	Entire
Declivitous face of propodeum	Convex	Convex or concave
Propodeal angle	Indistinct	Distinct
Number of fore wing cubital cells	2	1
Dorsal petiolar node	Rounded	Bluntly angular
Ventral petiolar lobe	Absent	Well developed
Pygostyles	Well developed	Reduced
Digitus	Elongate	Short
Gonostylus	Finger-like	Short, triangular
Cuspis	Absent	Present
Ventral lobe of volsella	Present as a weakly concave lobe	Present as a swelling

varying from denticulate distally, smooth proximally to denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and with a suture medially. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle distinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs 2-25; short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cell. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; vertical and not inclined anteriorly.

Venter with a slight or weakly developed lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat (sometimes weakly concave). Scape length shorter than the length of funicular segments 2+3. First funicular segment barrel-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 more than twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 8; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin anterior to the posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with 1 tooth (the apical) and 6-14 denticles. Apical tooth varying from subequal in length to, to slightly longer than, the subapical tooth (occasionally elongate and much longer than the subapical tooth). Basal angle weakly defined by a denticle. Basal margin smooth and without teeth or denticles (or occasionally with a few small denticles near the basal angle). MESOSOMA. Posteroventral pronotum lateral, rounded. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel and with or without a suture medially. Anterior axillar suture straight. Declivitous face of propodeum convex or concave; dorsal face convex, longer than the declivitous face. Propodeal angle distinct or indistinct. WINGS. Radial cell closed. Fore wing with 1-2 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; either rounded and forming an even arch dorsally, or forming a blunt angle dorsally; vertical and not inclined anteriorly. Venter with or without a well developed lobe. Attachment to gaster narrow. GASTER. First segment elongated posteriorly, smooth and without a groove or indentation. GENITALIA. Pygostyles present, often reduced. Posterior margin of subgenital plate concave. Paramere triangular and very weakly divided, or with the gonostylus elongated into an articulating finger-like structure. Digitus with a down-turned tip. Cuspis absent or ventral of digitus. Ventral lobe of volsella present as either a weakly concave lobe or as a swelling. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances present as a single boss located mid-dorsally on abdominal tergite 1. Body hairs sparse; simple or bifid; short. 9

spiracular pairs. Antennae short.

Discussion

Linepithema was established by Mayr (1866) for several male specimens collected in the higher regions of the Andes Mountains. The genus remained virtually unknown after its establishment and was never associated with workers or queens. During the present study complete nest series became available thanks to the collecting efforts of W. L. Brown and J. Lattke. These nest series secured the relationship of *Linepithema* males to workers previously placed in *Iridomyrmex*.

With this association established, a detailed morphological analysis showed that the New World "*Iridomyrmex*" species were distinct from the Old World species and actually belonged to the genus *Linepithema* (Shattuck 1992a). Significant differences between Indo-Australian *Iridomyrmex* and New World *Linepithema* were found in the structure of the anterior clypeal margin, mandibular morphology and compound eye placement, among others. Thus the New World species previously placed in *Iridomyrmex* were transferred to *Linepithema*. While *Linepithema* is distinct, some species have been confused with *Forelius*. A table listing major characters separating these two genera is provided (Table 5).

The workers and queens of *Linepithema* are morphologically very similar. The males, however, show a distinct morphological divergence not seen in other genera. Males can be divided into two distinct groups: those related to *L. humile* and those related to *L. fuscum*. The differences between these groups are summarized in Table 6. The *L. humile*-group males are typical for the subfamily in most morphological traits. On the other hand, the *L. fuscum*-group males are morphologically distinct from the *L. humile*-group.

L. fuscum-group males are unique in having an elongate digitus and the gonostylus finger-like. Additionally, these species have only been collected from the higher regions of the Andes Mountains. This information suggests that the *L. fuscum*-group may be a specialized, high altitude- adapted group with a morphologically divergent male caste. However, since no autapomorphic characters could be found for the *L. humile*-group, all species are here placed in the single genus *Linepithema*.

Ecologically, most species of *Linepithema* are poorly known. They are reported to nest in trees under bark, in cavities of bamboo, and in arboreal ferns. In Puerto Rico, *L. melleum* nests in decayed branches on trees, as well as rotten limbs on the ground (R. Snelling, pers. comm.). However, the biology of one species is well known. The Argentine ant, *L. humile*, is a widespread pest species. It can occur at very high population densities in both urban and rural areas, and has been documented to have a negative impact on local, native plant (Bond and Slingsby 1984) and ant faunas (Ward 1987). This species

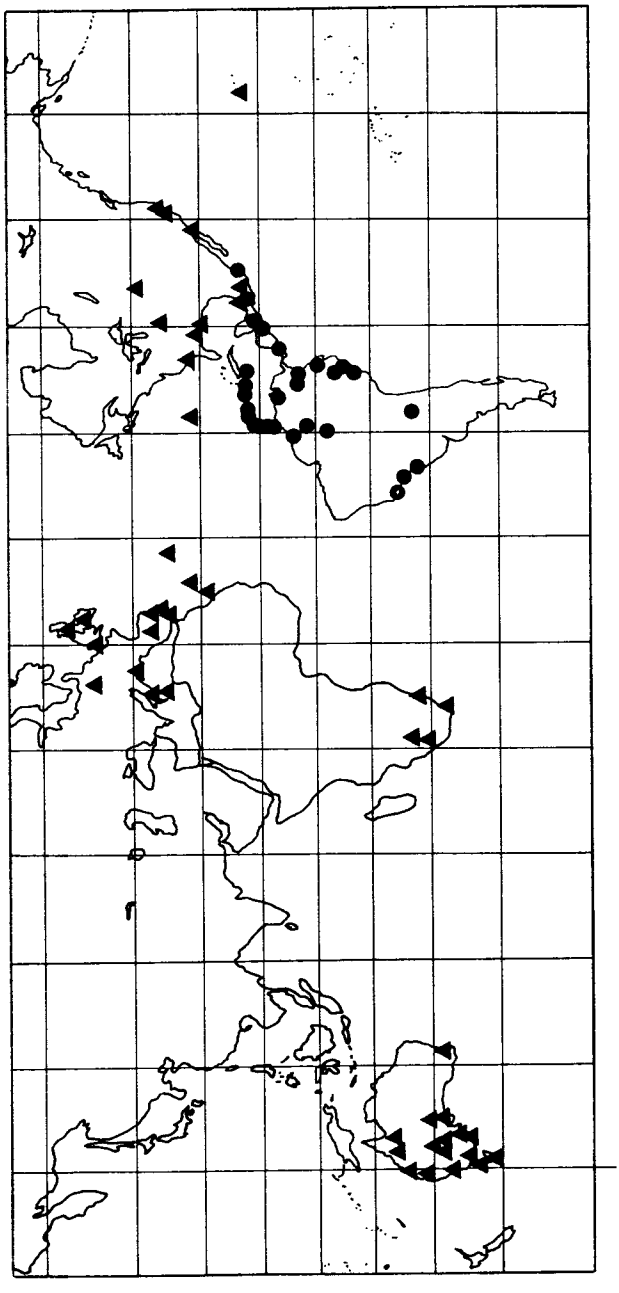


Fig. 110. Distribution of *Linepithema*. Closed circles indicate examined material. Closed triangles indicate examined, human-introduced populations.

forms multi-nest colonies with numerous queens and can monopolize resources by rapidly recruiting workers to newly found food sources.

Distribution: Central and South America, with an introduced species in North America, Europe, Canary Islands, Azores, southern Africa, Australia and Hawaii (Fig. 110).

Genus *Liometopum* Mayr (Figs. 111-117)

Liometopum Mayr 1861:25,38. Type species: *Formica microcephala* Panzer (by monotypy).

Ctenobethylus Brues 1939:261 (syn. of *Iridomyrmex* by Brown 1977:214). Type species: *Ctenobethylus succinalis* Brues (by monotypy). [NEW SYNONYMY]

Diagnosis

Worker: Polymorphic, majors with ocelli; anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region; anteromedial clypeal margin with a broad, shallow concavity; mandible with about 7 to 9 teeth, an indistinct basal angle, and 3 to 5 denticles on the basal margin; metanotal groove reduced to a suture and with the mesonotum and propodeum forming a continuous, uninterrupted surface; petiolar scale vertical and not inclined anteriorly. Western North America from southern Canada south to central Mexico; Italy east to the Caspian Sea; eastern India east through southern China.

Queen: Venter of the petiole with a well developed, angular lobe; 75 to 100 short, erect hairs on the mesoscutum; anteromedial clypeal margin with a broad, shallow concavity; basal angle of mandible indistinct, with a relatively uninterrupted curve between the masticatory and basal margins; petiolar scale vertical and not inclined anteriorly.

Male: Basal margin of mandible denticulate distally, smooth proximally; episternal suture reduced or absent; fore wing with two closed cubital cells; paramere enlarged.

Description

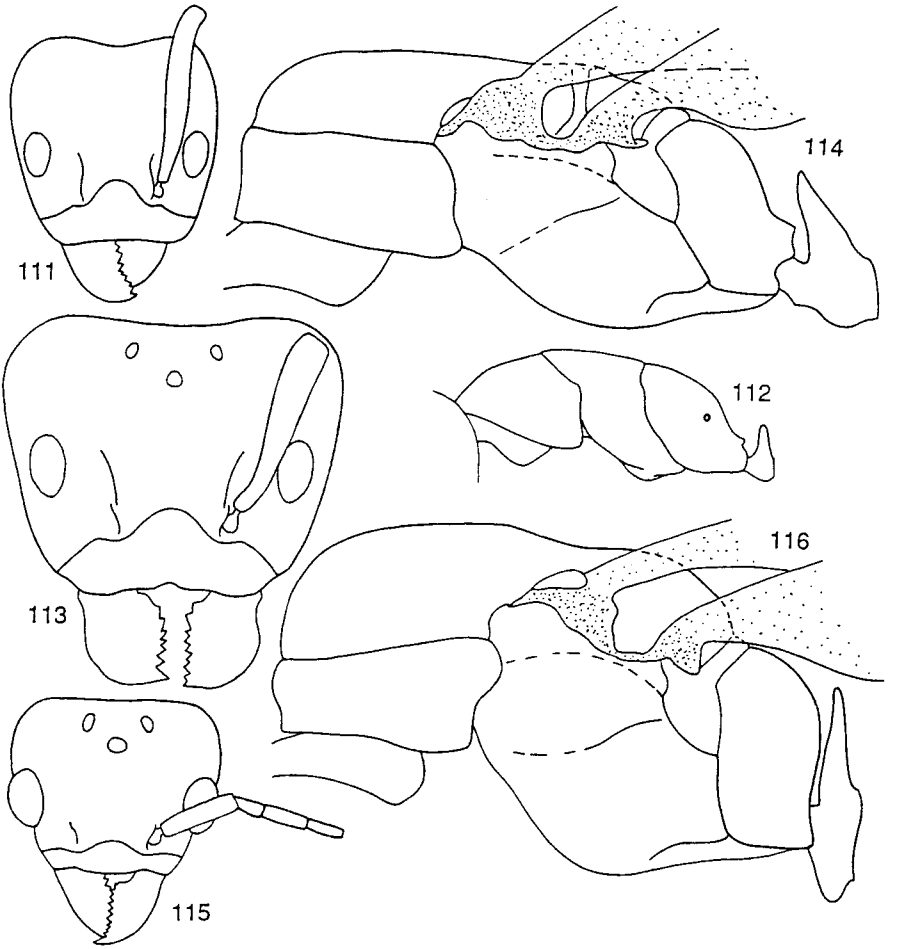
WORKER.

HEAD. Vertex concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli present (in majors). Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region. Anteromedial clypeal margin with a broad, shallow concavity. Anterior clypeal setae 6-12; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin even with or posterior to the posterior surfaces of the antennal socket cavities. Anterior

tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7-9 teeth and no denticles. Apical tooth subequal in length to the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins. Basal margin denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle indistinct. Mesosomal spines and tooth absent. Erect pronotal hairs 16-45; elongate, much longer than the maximum scape width. Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove reduced to a suture and with the mesonotum and propodeum forming a continuous, uninterrupted surface. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; ridged and with a distinct angle dorsally (tapering dorsally into a broad point); vertical and not inclined anteriorly. Venter with a slight or weakly developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium in a distinct arch which extends dorsal of the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite keel-shaped posteriorly. GENERAL CHARACTERS. Worker caste polymorphic. Chromosome number unknown. Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round; with long pile; smooth, without sculpture; and without phragma. Bulb exposed in lateral view. Longitudinal muscle No. 1 present. Occlusory tract present.

QUEEN.

HEAD. Vertex weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one- half scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin with a broad, shallow concavity. Anterior clypeal setae about 10; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent.



Figs. 111-116: 111, Full face view of *Liometopum occidentale* worker; 112, Lateral view of *Liometopum occidentale* worker mesosoma; 113, Full face view of *Liometopum occidentale* queen; 114, Lateral view of *Liometopum occidentale* queen mesosoma; 115, Full face view of *Liometopum occidentale* male; 116, Lateral view of *Liometopum occidentale* male mesosoma.

MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7-9 teeth and no denticles. Apical tooth slightly longer than the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture com-

plete. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle distinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs about 75-100; short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 2 cubital and 1-2 discoidal cells. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally (narrowed dorsolaterally); vertical and not inclined anteriorly. Venter with a well developed, angular lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Fifth tergite vertical and with the distal terminus of the gaster not well defined. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length at most only slightly longer than the length of funicular segments 1+2+3. First funicular segment cylindrical or cone-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 10-20; short, about twice antennal diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with 7-10 teeth and 0-1 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture reduced and incomplete (always weakly developed posteriorly), or absent. Anteromedial mesosternum even with the lateral regions. Axilla constricted medially and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle distinct. WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cells. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally, or spined and with a double tooth or

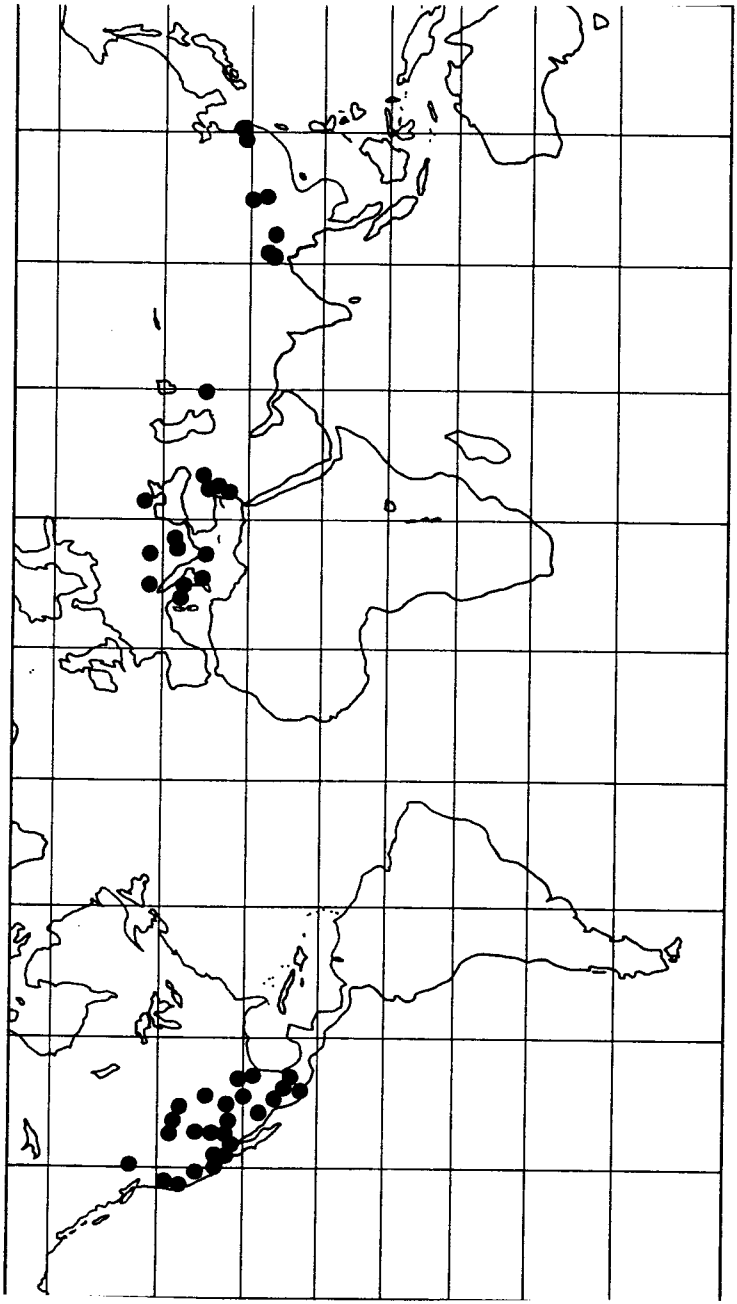


Fig. 117. Distribution of *Liometopum* material examined during this study.

projection dorsally; vertical and not inclined anteriorly. Venter with a well developed lobe. Attachment to gaster narrow. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave or with a "V"-shaped notch. Paramere entire (but with a very weak suture). Digitus with a down-turned tip. Cuspis slightly ventral of digitus. Ventral lobe of volsella present as concave lobe. Aedeagus with ventral teeth.

LARVA.

Body hairs sparse; simple; short. 10 spiracular pairs. Antennae large.

Discussion

Liometopum is a small, morphologically homogeneous set of species. The group has a Holarctic distribution and is well represented in the fossil record. Workers can be recognized by the configuration of the anterior clypeal margin and the even arch of the dorsal mesosomal surface (see Diagnosis for additional details). In the field, these ants are very aggressive. They attack when the nest or foraging column is disturbed, and produce a strong, distinctive odor.

The North American species have been revised and their biologies discussed by Wheeler (1905). An updated key was provided by Creighton (1950).

Most species of *Liometopum* occur in drier forested areas and they are often associated with oak or pine. These ants form large, arboreal nests and forage epigeically in columns. (However, one North American species, *L. apiculatum*, is apparently primarily a ground nester.) The nest chambers are often located in inaccessible regions of tree boles and are difficult to collect.

Distribution: Western North America from southern Canada south to central Mexico; Italy east to the Caspian Sea; eastern India east through southern China (Fig. 117).

Species Notes: The species *Iridomyrmex goepperti* (Mayr) was transferred to *Liometopum* by Shattuck (1992a). The species *Ctenobethylus succinalis* Brues was synonymized under *I. geopperti* (Mayr) by Brown (1977), and is retained as such in the present study. Therefore, the genus *Ctenobethylus* is a synonym of *Liometopum* (NEW SYNONYMY) rather than of *Iridomyrmex*.

Genus *Loweriella* gen. nov. (Figs. 118-120, Table 4)

Loweriella gen. nov. Type species: *Loweriella boltoni* sp. nov. (by present desig.).

Diagnosis

Worker: Medial hypostoma notch-like, absent posteromedially and weakly developed anterolaterally near the anterior corners of the notch; anterior

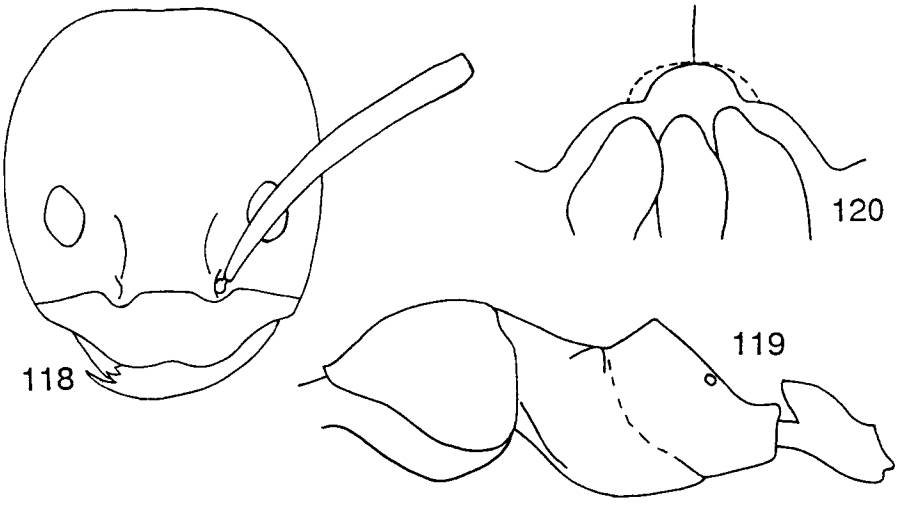
clypeal setae 8-10, straight or slightly curved ventrally, the central pair about the same length as the closed mandibles, the lateral setae shorter; compound eyes small, with about 35-40 ommitidia; palp formula 6:4; apical mandibular tooth elongate, noticeably longer than the subapical tooth; dorsal face of propodeum shorter than the declivitous face and separated from it by a distinct ridge or carina (see also Table 4).

Queen and male: Unknown.

Description

WORKER.

HEAD. Vertex convex (with a very slight central concavity). Compound eyes present, approximately round; small, with about 35-40 ommitidia; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin entire and with a slight, shallow medial concavity. Anterior clypeal setae 8-10; the central pair about the same length as the closed mandibles, the lateral setae shorter; straight or slightly curved ventrally. Posterior clypeal margin even with or anterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma notch-like, absent posteromedially and weakly developed anterolaterally near the anterior corners of the notch. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7-8 teeth and 2-5 denticles. Apical tooth elongate, noticeably longer than the subapical tooth. Basal angle weakly defined by a denticle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous and dorsal faces of propodeum flat; dorsal face shorter than the declivitous face. Propodeal angle a distinct ridge or carina. Mesosomal spines and tooth absent. Erect pronotal hairs absent. Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle dorsal and lying on the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum (although located posteriorly near the declivitous face). Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a well developed lobe. GASTER. First tergite projecting anteriorly, concealing all but the extreme



Figs. 118-120: 118, Full face view of *Loweriella boltoni* worker (holotype from Sarawak, Malaysia); 119, Lateral view of *Loweriella boltoni* worker mesosoma (holotype from Sarawak, Malaysia); 120, Ventral view of anterior section of *Loweriella boltoni* worker head (Brunei).

anterior region of the petiole in dorsal view; with a groove or indentation for the reception of the entire height of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium in a distinct arch which extends dorsal of the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite keel-shaped posteriorly. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number unknown. Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Not examined.

QUEEN: Unknown.

MALE: Unknown.

LARVAE: Unknown.

Discussion

Loweriella is a small genus containing a single known species which has been collected from rainforest areas. The worker is similar to *Bothriomyrmex* in having a broadly convex anterior clypeal margin, elongate anterior clypeal setae, an anteriorly-placed posterior clypeal margin, relatively small compound eyes, and in the overall shapes of the mesosomal profile, petiole and first gastral segment. However, *Loweriella* differs from *Bothriomyrmex* in having well developed frontal carina; the medial hypostoma notched rather than completely absent; the mandible with a greater number of teeth, a relatively larger apical tooth and a more poorly defined basal mandibular angle; a 6:4 palp formula; and having a keel- shaped fourth gastral sternite (see

also Table 4). These differences allow ready separation of *Loweriella* and *Bothriomyrmex* and suggest that each is distinct from the other.

The single species of *Loweriella* (described below) is known from only three collections made in rainforests. It has been found in leaf litter and at the base of a tree. Nothing else is known of its biology.

Distribution: Known only from northern Sarawak, Malaysia and Brunei (see Type Material below).

Species Notes: The single known species of *Loweriella, L. boltoni* (NEW SPECIES) is as follows. *Measurements* (holotype followed by the range for 11 paratype workers, in mm; see Shattuck (1990) for details of measurement methods and abbreviations): LES 0.04 (0.04-0.05), EW 0.06 (0.05-0.07), ES 0.29 (0.28-0.31), HW 0.49 (0.48-0.51), OOD 0.29 (0.28-0.30), EL 0.11 (0.10-0.12), OCD 0.09 (0.08-0.10), CL 0.10 (0.10-0.12), HL 0.59 (0.57-0.61), SL 0.55 (0.52-0.55), PnL 0.27 (0.25-0.28) ML 0.19 (0.16-0.20), PpL 0.27 (0.24- 0.28) CI 0.83 (0.82-0.85), OI 0.54 (0.49-0.62), SI 1.11 (1.06-1.11). *Description*: The following characters are in addition to those of the generic description above. Posterior regions of head, dorsum of pronotum and entire mesothorax and propodeum very weakly coriarious, anterior regions of head and ventrolateral area of pronotum smooth. Entire body except ventrolateral pronotum covered with course, suberect to decumbent hairs. Color light yellowish-brown. This species may be separated from other dolichoderines using the characters listed above under the generic diagnosis.

Type material: Holotype worker from MALAYSIA: Sarawak, 4th Division, Gunong Mulu National Park, R. G. S. Expedition, Long Pala, 19.ix.1977, lowland rainforest, base of tree (B. Bolton) (in BMNH); 14 paratype workers, same data as holotype (11 individuals in BMNH, 3 individuals in MCZC); 2 paratype workers, same data as holotype except 29.ix.1977, leaf litter (in BMNH); 5 paratype workers from BRUNEI: Kuala Belalong, UBD Field Centre, 4°33'N 115°08'E, Nov. 1991, rainforest (A. N. Andersen) (3 individuals in ANIC, 2 individuals in A. N. Andersen personal coll., Darwin, Australia).

Genus *Ochetellus* Shattuck (Figs. 121-127)

Ochetellus Shattuck 1992a. Type species: *Hypoclinea glabra* Mayr (by orig. desig.).

Diagnosis

Worker: Metanotal groove a narrow, distinct notch in the relatively flat dorsal mesosomal surface; declivitous face of propodeum concave; petiolar scale vertical and not inclined anteriorly, narrowed longitudinally, expanded dorsolaterally; anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder; anteromedial clypeal margin with a broad, shallow concavity. Japan south through Burma and the Philippines to

Australia and Fiji.

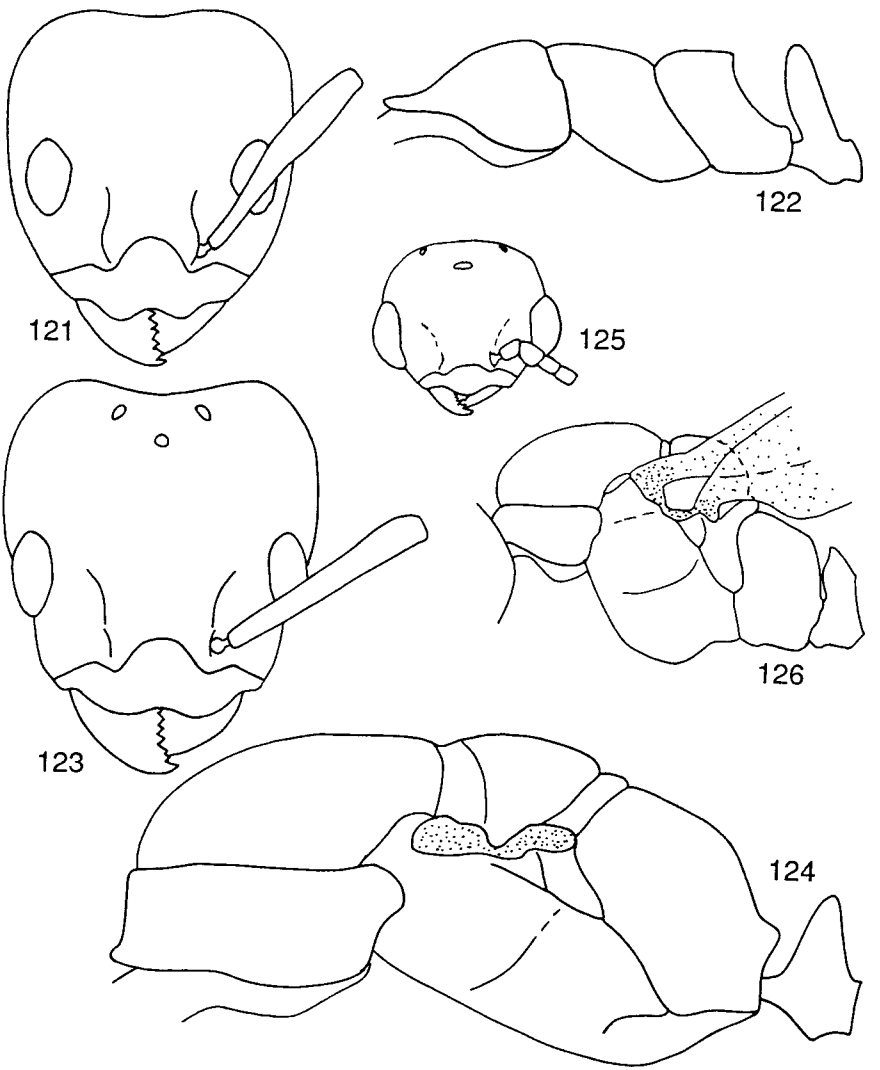
Queen: Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder; anteromedial clypeal margin with a broad, shallow concavity; dorsal face of propodeum longer (occasionally shorter) than declivitous face; petiolar scale moderately inclined anteriorly but with the anterior and posterior faces approximately the same length; anterior axillar suture angular medially (occasionally weakly developed).

Male: Petiole expanded laterally along entire height, and with the dorsal surface very broad; anterior axillar suture angular medially; mandible with 1 tooth (the apical) and 0 to 4 denticles.

Description

WORKER.

HEAD. Vertex weakly convex to weakly concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin with a broad, shallow concavity. Anterior clypeal setae 2-8; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin posterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 6-8 teeth and 1-3 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum concave; dorsal face convex, shorter than the declivitous face. Propodeal angle distinct (with a sharp angle or carina at juncture). Mesosomal spines and tooth absent. Erect pronotal hairs absent. Dorsal pro-mesonotal junction with the pronotum and mesonotum even, or occasionally with the mesonotum below the pronotum. Metanotal groove a narrow, distinct notch in the relatively flat dorsal mesosomal surface. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; rounded and forming an even arch dorsally (narrowed longitudinally, expanded dorsolaterally); vertical and not inclined anteriorly.



Figs. 121-126: 121, Full face view of *Ochetellus* worker (South Australia, Australia); 122, Lateral view of *Ochetellus* worker mesosoma (South Australia, Australia); 123, Full face view of *Ochetellus* queen (Queensland, Australia); 124, Lateral view of *Ochetellus* queen mesosoma (Queensland, Australia); 125, Full face view of *Ochetellus* male (Queensland, Australia); 126, Lateral view of *Ochetellus* male mesosoma (Queensland, Australia).

Venter with or without a slight or weakly developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of either the basal portion or the entire height of the petiole. Anterior tergosternal suture of the first segment extending laterally

from the helcium in a distinct arch which extends dorsal of the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression dorsoventral. Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number 14 (n=14, 2n=28, *O. itoi*, Imai and Yosida 1964, Imai 1969; *O. glaber*, Crozier 1968a). Integument thin and flexible, weakly sculptured. PROVENTRICLUS. Cupola much broader than bulb; round; with short pile; smooth, without sculpture; and with narrow phragma. Bulb completely hidden by cupola in lateral view. Longitudinal muscle No. 1 absent. Occlusory tract absent.

QUEEN.

HEAD. Vertex weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one- half scape length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin with a broad, shallow concavity. Anterior clypeal setae 10- 14; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin posterior of the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7- 9 teeth and 0-3 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete but weakly developed anteriorly. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture angular medially (occasionally only weakly). Declivitous face of propodeum weakly convex to flat; dorsal face convex, longer than the declivitous face (or occasionally shorter than the declivitous face). Propodeal angle indistinct. Propodeal suture weakly developed to absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs about 15-70; varying from short (less than twice the maximum scape diameter) to elongate (more than twice the maximum scape diameter). Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cell. Hind wing with 2 cells. PETIOLE. Scale present; weakly ridged and with a distinct angle dorsally; moderately inclined anteriorly but with the anterior and posterior faces approximately the same length. Venter with a well developed, rounded lobe. GASTER. First segment vertical and not concealing the petiole in dorsal

view and with a groove or indentation for the reception of the entire height of the petiole. Fifth tergite vertical and with the distal terminus of the gaster not well defined. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment barrel-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 6; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin anterior of the posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with 1 tooth and 0-4 denticles. Apical tooth distinct. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture angular medially. Declivitous and dorsal faces of propodeum convex. Propodeal angle indistinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally, expanded laterally along entire height, and with the dorsal surface very broad; vertical and not inclined anteriorly. Venter with a slight or weakly developed lobe. Attachment to gaster broad. GASTER. First segment elongated posteriorly, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate even across entire width. Paramere divided by a membranous region. Digitus with a down-turned tip. Cuspis absent. Ventral lobe of volsella absent. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances present as 5 bosses located mid-dorsally on thoracic tergite 2 and abdominal tergites 1-4. Body hairs sparse; simple; short. 9 spiracular pairs. Antennae short.

Discussion

Ochetellus is a recently described genus (Shattuck 1992a) consisting of seven species and 3 subspecies previously placed in *Iridomyrmex*. The

placement of this group in *Iridomyrmex* illustrates the previously ill- defined nature of that taxon as *Ochetellus* differs markedly from *Iridomyrmex* in numerous characters, including the placement of the compound eye, configuration of the anterior clypeal margin and petiolar node, and mesosomal profile.

Ochetellus workers superficially resemble small workers of *Dolichoderus* in their mesosomal profile (relatively flat mesosomal dorsum and concave declivitous propodeal face) but can be separated by their generally smaller size and the unique petiole, which is narrowed longitudinally and expanded dorsolaterally. The head shape, while not diagnostic, tends to appear flattened dorsoventrally, giving a thinner profile than in most dolichoderine genera.

This genus is found in forested areas with colonies occurring under rocks, in dead wood or in soil. Workers forage arboreally or epigeically, often forming conspicuous foraging columns. *Ochetellus* commonly forage in houses where they show a preference for fluids and sweets.

Distribution: Japan south through Burma and the Philippines to Australia and Fiji (Fig. 127). Also known from the United States (Smith 1979) and New Zealand (Brown 1958), but there seems little doubt that these are human introductions, as both of the populations are limited to urban areas and are not known to occur in natural, undisturbed habitats.

Genus *Papyrius* Shattuck (Figs. 128-134, Table 3)

Papyrius Shattuck 1992a. Type species: *Iridomyrmex nitida* Mayr (by orig. desig.).

Diagnosis

Worker: Palp formula 5:3; anterior clypeal margin with 8 to 20 very short, straight setae; metanotal groove a distinct, deep trough or notch depressed below the level of the adjacent mesonotum and propodeum; mandibles with 11 to 14 teeth, about 3 denticles, the apical tooth elongate and much longer than subapical, and the basal angle weakly defined by a denticle; petiolar scale vertical and not inclined anteriorly. New Guinea and Australia.

Queen: Palp formula 5:3; anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder; anterior clypeal margin with 0 to 4 setae; wing radial cell open.

Male: Palp formula 5:3; anterior axillar suture angular medially; mandible with a single tooth (the apical); fore wing radial cell open.

Description

WORKER.

HEAD. Vertex concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral

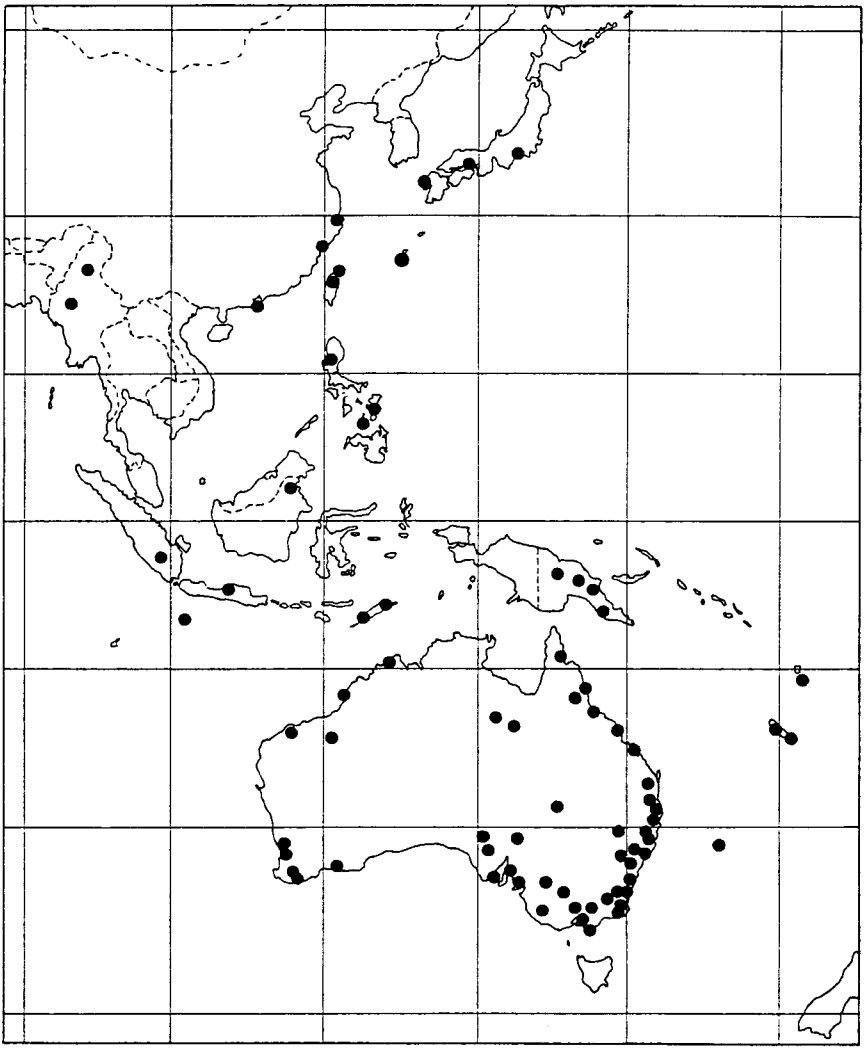


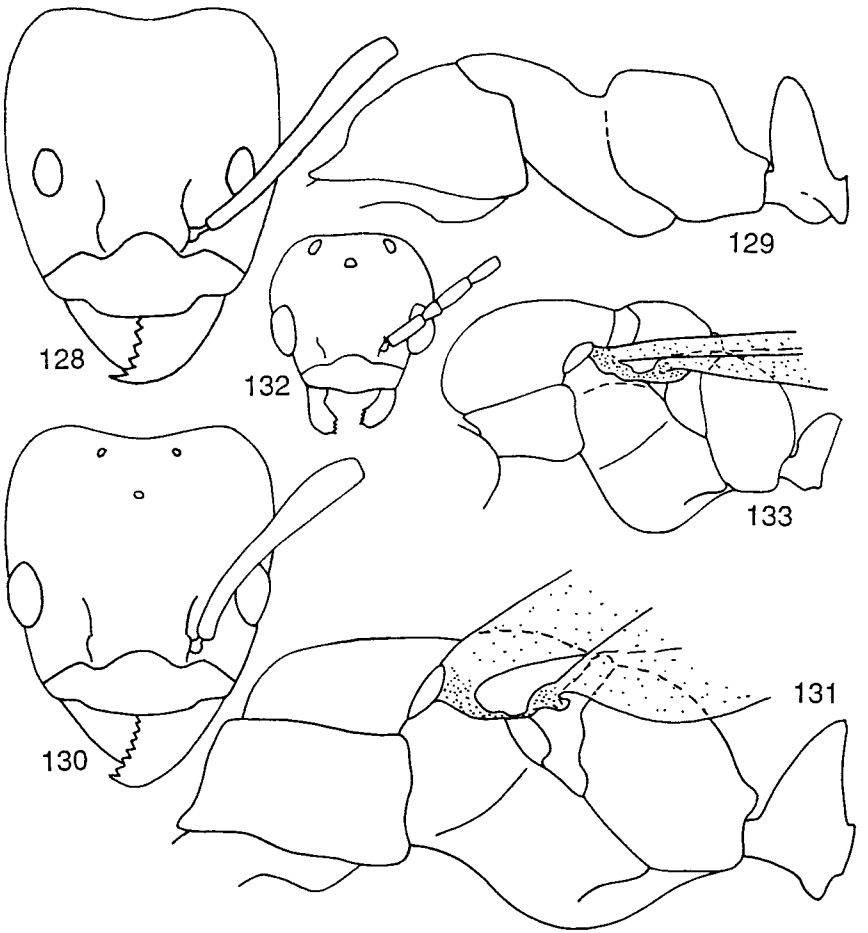
Fig. 127: Distribution of *Ochetellus* material examined during this study.

clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 8- 20; very short, only slightly surpassing the anterior clypeal margin; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion.

Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 5:3. Third maxillary palp segment subequal in length to segment 4. Mandible with 11- 14 teeth and about 3 denticles. Apical tooth elongate and much longer than the subapical tooth. Basal angle weakly defined by a denticle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum flat; dorsal face flat to weakly concave, subequal in length to the declivitous face. Propodeal angle distinct. Mesosomal spines and tooth absent. Erect pronotal hairs absent. Dorsal pro-mesonotal junction with the mesonotum above the pronotum. Metanotal groove a distinct, deep trough or notch depressed below the level of the adjacent mesosomal notum. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; rounded and forming an even arch dorsally (but narrowed dorsally); vertical and not inclined anteriorly. Venter with a well developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium in a distinct arch which extends dorsal of the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression slightly dorsoventral. Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number 8 (n=8, *P. nitidus*, Crozier 1968a; 2n=16, *P. nitidus*, Imai *et al.* 1977). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round; with short pile; smooth, without sculpture; and with narrow phragma. Bulb completely hidden by cupola in lateral view. Longitudinal muscle No. 1 absent. Occlusory tract absent.

QUEEN.

HEAD. Vertex weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one- half scape length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 0-4; when present short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 5:3. Third maxillary palp segment subequal in length to segment



Figs. 128-133: 128, Full face view of *Papyrius* worker (South Australia, Australia); 129, Lateral view of *Papyrius* worker mesosoma (South Australia, Australia); 130, Full face view of *Papyrius* queen (Queensland, Australia); 131, Lateral view of *Papyrius* queen mesosoma (Queensland, Australia); 132, Full face view of *Papyrius* male (New South Wales, Australia); 133, Lateral view of *Papyrius* male mesosoma (New South Wales, Australia).

4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with about 9 teeth and about 4 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin varying from smooth (without teeth or denticles) to denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal

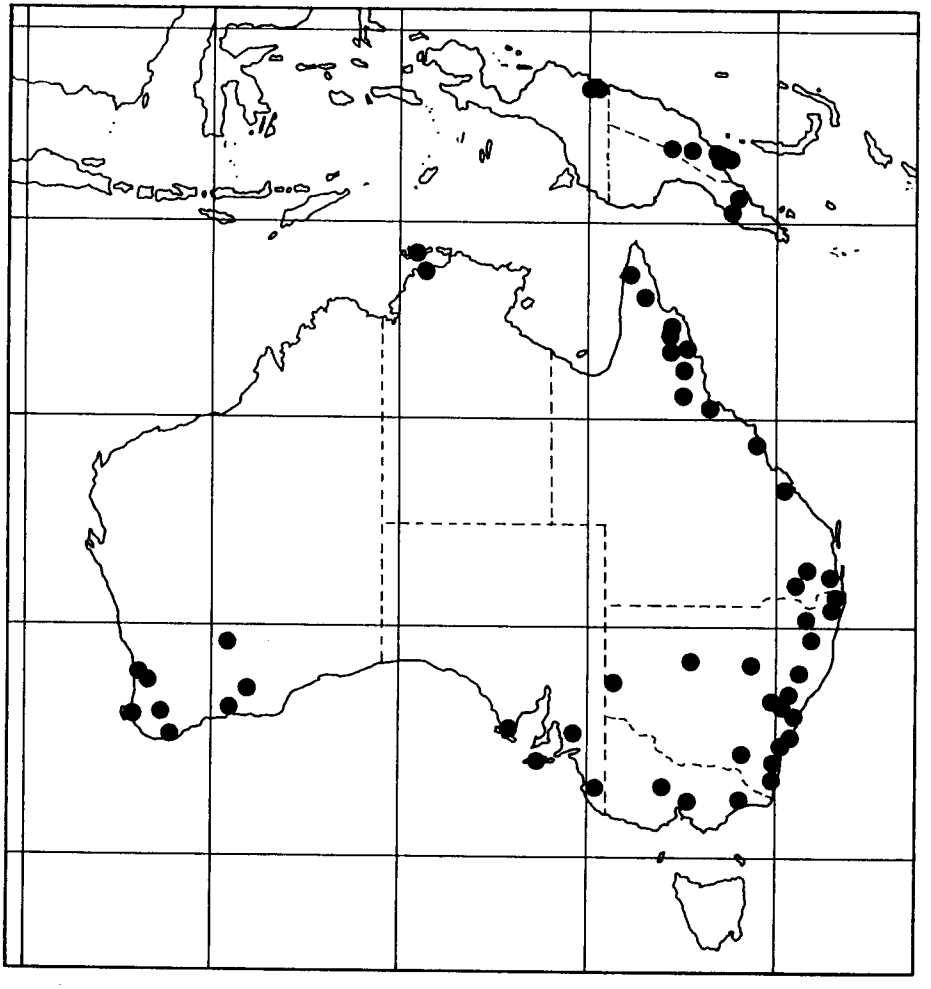


Fig. 134: Distribution of *Papyrius* material examined during this study.

suture weak, nearly absent. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face longer than the declivitous face. Propodeal angle indistinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs about 30-50; short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell open. Fore wing with 1 cubital and 1 discoidal cell.

Hind wing with 2 cells. PETIOLE. Scale present; rounded and forming an even arch dorsally, or weakly ridged and with an angle dorsally; vertical and not inclined anteriorly. Venter with a well developed, rounded lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3. First funicular segment barrel-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 2-6; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin even with or anterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 5:3. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with 1 tooth and no denticles, and with an enlarged ventral lobe. Apical tooth distinct. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture angular medially. Declivitous and dorsal faces of propodeum convex; dorsal face shorter than the declivitous face. Propodeal angle distinct. WINGS. Radial cell open. Fore wing with 1 cubital and 1 discoidal cells. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; vertical and not inclined anteriorly. Venter with a slight or weakly developed lobe. Attachment to gaster broad. GASTER. First segment elongated posteriorly, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave. Paramere divided by a membranous region. Digitus with a down-turned tip. Cuspis parallel with digitus. Ventral lobe of volsella present as weakly concave lobe. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances absent. Body hairs sparse; simple; short. 9 spiracular pairs. Antennae short.

Discussion

The six taxa placed in the recently described genus *Papyrius* were removed from *Iridomyrmex* by Shattuck (1992a). *Papyrius* differs from true species of *Iridomyrmex* in more than 12 characters, including the placement of the compound eyes, configuration of the anterior clypeal border, palp formula, mandibular structure, and configuration of the mesosomal dorsum (see Diagnosis and Table 3). Analysis of these characters demonstrates that both *Papyrius* and *Iridomyrmex* possess unique features allowing definition of each group independent of the other, and therefore, both are separate and distinct genera.

Papyrius occurs only in Australia and New Guinea. Members of this genus are found primarily in forested areas, where they nest in dead wood, either standing or on the ground. *Papyrius* species commonly use plant fibers to construct carton covers over nest sites and feeding areas.

Distribution: New Guinea and Australia (Fig. 134).

Genus *Philidris* Shattuck (Figs. 135-141, Table 3)

Philidris Shattuck 1992a. Type species: *Formica cordata* F. Smith (by orig. desig.).

Diagnosis

Worker: Polymorphic (less commonly monomorphic), majors with ocelli; compound eyes placed relatively anterior on head; anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder; anteromedial clypeal margin with a central projection, either pointed or rounded (sometimes only feebly projecting); mandibles with 10 to 12 teeth, 0 to 3 denticles, and the basal angle weakly defined by a denticle. Extreme eastern India east through southeast Asia to the Philippine Islands, northern Australia and the Solomon Islands.

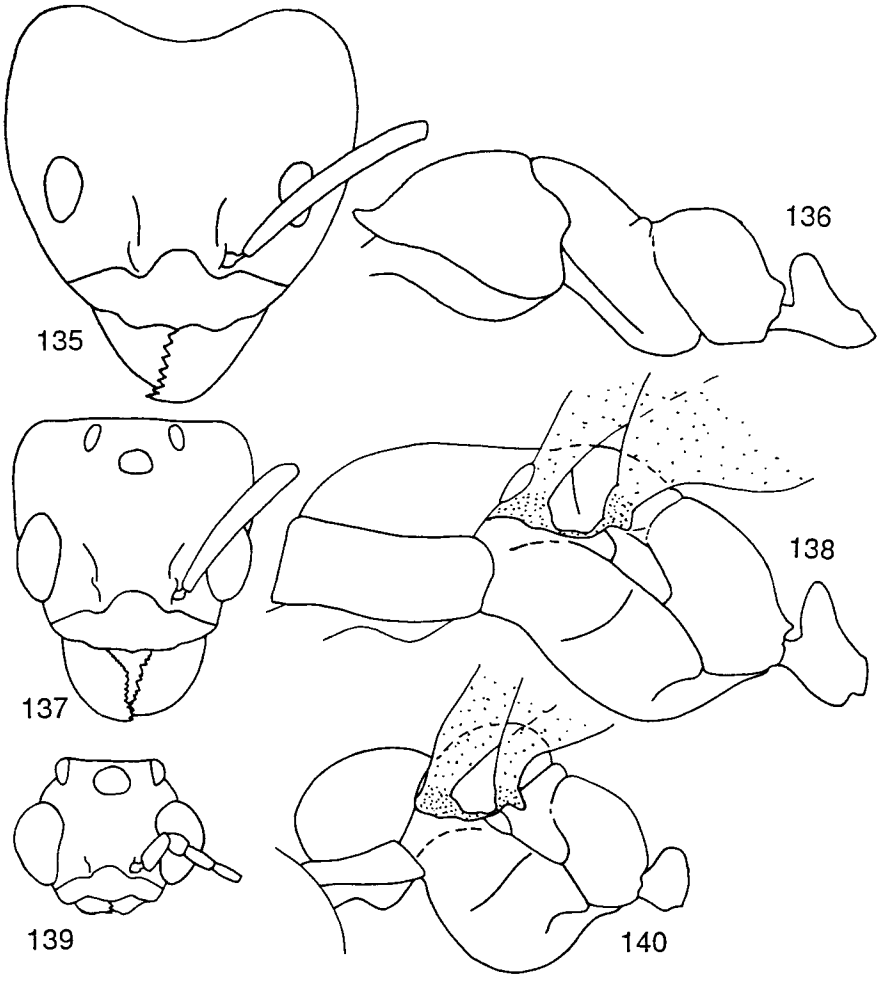
Queen: Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder (sometimes weakly developed); anterior clypeal margin with about 20 short, erect setae; mandible with 7 to 10 teeth, 2 or 3 denticles, and the apical tooth subequal in length to the subapical; about 20 to 50 short, erect setae on mesoscutum; first gastral segment with a partial groove for the reception of the basal portion of the petiole.

Male: Mandible with one tooth (the apical), about 10 to 12 denticles, and with the apical tooth subequal to or longer than the subapical tooth or denticle; venter of petiole with a well developed lobe; first gastral segment elongate posteriorly.

Description

WORKER.

HEAD. Vertex concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli present (in major). Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin with a central projection, either pointed or rounded (often weakly developed). Anterior clypeal setae 4-10; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 10-12 teeth and 0-3 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle weakly defined by a denticle. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle indistinct. Mesosomal spines and tooth absent. Erect pronotal hairs 8-24; elongate, much longer than the maximum scape width. Dorsal pro-mesonotal junction with the pronotum and mesonotum even, or with the mesonotum above the pronotum. Metanotal groove forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle dorsal and lying on the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a well developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Anterior tergosternal suture of the first segment extending laterally from the helcium in a distinct arch which extends dorsal of the dorsal helcial surface. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste polymorphic or less commonly monomorphic. Chromosome number 8 (2n=16, *P. cordatus*, Imai *et al.* 1985a, Tjan *et al.* 1986). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round; with short pile; smooth, without sculpture; and with very broad phragma. Bulb completely hidden by cupola in lateral view. Occlusory tract absent.



Figs. 135-140: 135, Full face view of *Philidris* worker (Papua New Guinea); 136, Lateral view of *Philidris* worker mesosoma (Papua New Guinea); 137, Full face view of *Philidris* queen (Papua New Guinea); 138, Lateral view of *Philidris* queen mesosoma (Papua New Guinea); 139, Full face view of *Philidris* male (Papua New Guinea); 140, Lateral view of *Philidris* male mesosoma (Papua New Guinea).

QUEEN.

HEAD. Vertex weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one- half scape length. Anterolateral clypeal margin posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin either entire (without a central notch or concavity of any type) or with

a central projection, either pointed or rounded (sometimes only feebly projecting). Anterior clypeal setae 20; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin even with or posterior to the posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7- 10 teeth and 2-3 denticles. Apical tooth subequal in length to the subapical tooth. Basal angle distinct, with a well developed tooth or angle separating the masticatory and basal margins. Basal margin denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture varying from complete (but weakly developed anteriorly) to weak and nearly absent. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle indistinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs about 20-50; short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cells. Hind wing with 2-3 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; varying from moderately inclined anteriorly (but with the anterior and posterior faces approximately the same length) to strongly inclined anteriorly (and with the anterior face much shorter than the posterior face). Venter with a well developed, rounded lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat (or sometimes weakly angular). Scape length shorter than the length of funicular segments 2+3. First funicular segment barrel-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 4; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular

insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with one tooth (the apical) and about 10-12 very small denticles. Apical tooth (or denticle) subequal in length to, or slightly longer than, the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex. Propodeal angle indistinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; vertical and not inclined anteriorly. Venter with a well developed lobe. Attachment to gaster broad. GASTER. First segment elongated posteriorly, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave. Paramere divided by a weak membranous region. Digitus linear, with a slight ventral arch. Cuspis parallel with digitus. Ventral lobe of volsella present as concave lobe. Aedeagus with ventral teeth.

LARVA.

Protuberances present as 5 bosses located mid-dorsally. Body hairs sparse; simple; short.

Discussion

Members of the genus *Philidris* were recently removed from the genus *Iridomyrmex* (Shattuck 1992a). *Philidris* differs from *Iridomyrmex* in the placement of the compound eyes, the shape of the vertex, the prevalence of worker caste polymorphism, and the degree of anterior inclination of the petiolar scale (see Diagnosis and Table 3). Additionally, workers of this genus tend to have a larger number of long, erect pronotal hairs compared to *Iridomyrmex* species. Using the above characters *Philidris* can be readily separated from *Iridomyrmex* (without rendering the latter paraphyletic) and is here treated as a distinct genus.

Philidris is most common in forested areas where it is often associated with myrmecophytes (especially of the genus *Myrmecodia*). Unfortunately, the species within this genus have received little attention, either biologically or taxonomically.

Distribution: Extreme eastern India east through southeast Asia to the Philippine Islands, northern Australia and the Solomon Islands (Fig. 141).

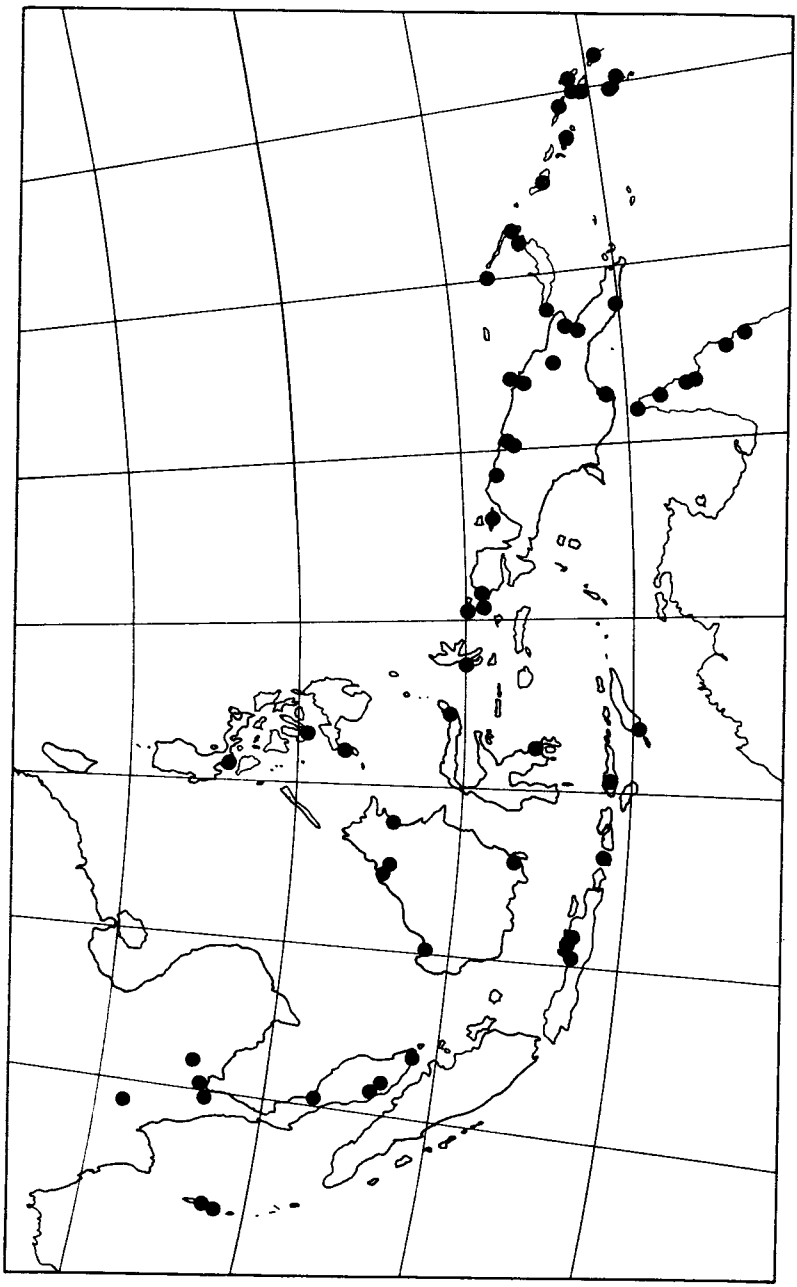


Fig. 141. Distribution of *Philidris* material examined during this study.

Genus *Tapinoma* Förster (Figs. 142-149, Table 4)

Tapinoma Förster 1850:43. Type species: *Tapinoma collina* Förster (by monotypy).

Micromyrma Dufour 1857:60 (syn. by Mayr 1868:428, as subgenus of *Tapinoma* by Emery 1887:363, syn. by Wheeler 1911:167). Type species: *Micromyrma pygmaea* Dufour (by monotypy).

Semonius Forel 1910:21. Type species: *Semonius schultzei* Forel (by monotypy). [NEW SYNONYMY]

Tapinoptera Santschi 1925:348 (as subgenus of *Tapinoma*, syn. in Brown 1973:185). Type species: *Tapinoma vexatum* Santschi (by monotypy).

Zatapinoma Wheeler 1928:20. Type species: *Zatapinoma annandalei* Wheeler (by monotypy). [NEW SYNONYMY]

Neoclystopsenella Kurian 1955:133 (syn. by Brown 1988:337). Type species: *Neoclystopsenella luffae* Kurian (by monotypy).

Diagnosis

Worker: Mandibles with 3 to 7 teeth, about 7 denticles, and the basal angle indistinct and with a relatively uninterrupted curve between the masticatory and basal margins; petiolar scale reduced or absent; first gastral segment projecting anteriorly and concealing petiole in dorsal view; dorsal face of propodeum shorter than declivitous face; erect hairs generally lacking on pronotum. World wide.

Queen: Gastral compression dorsoventral; petiolar scale reduced or absent; dorsal face of propodeum shorter than declivitous face; first gastral segment projecting anteriorly and concealing petiole in dorsal view; basal angle of mandible indistinct, with a relatively uninterrupted curve between the masticatory and basal margins.

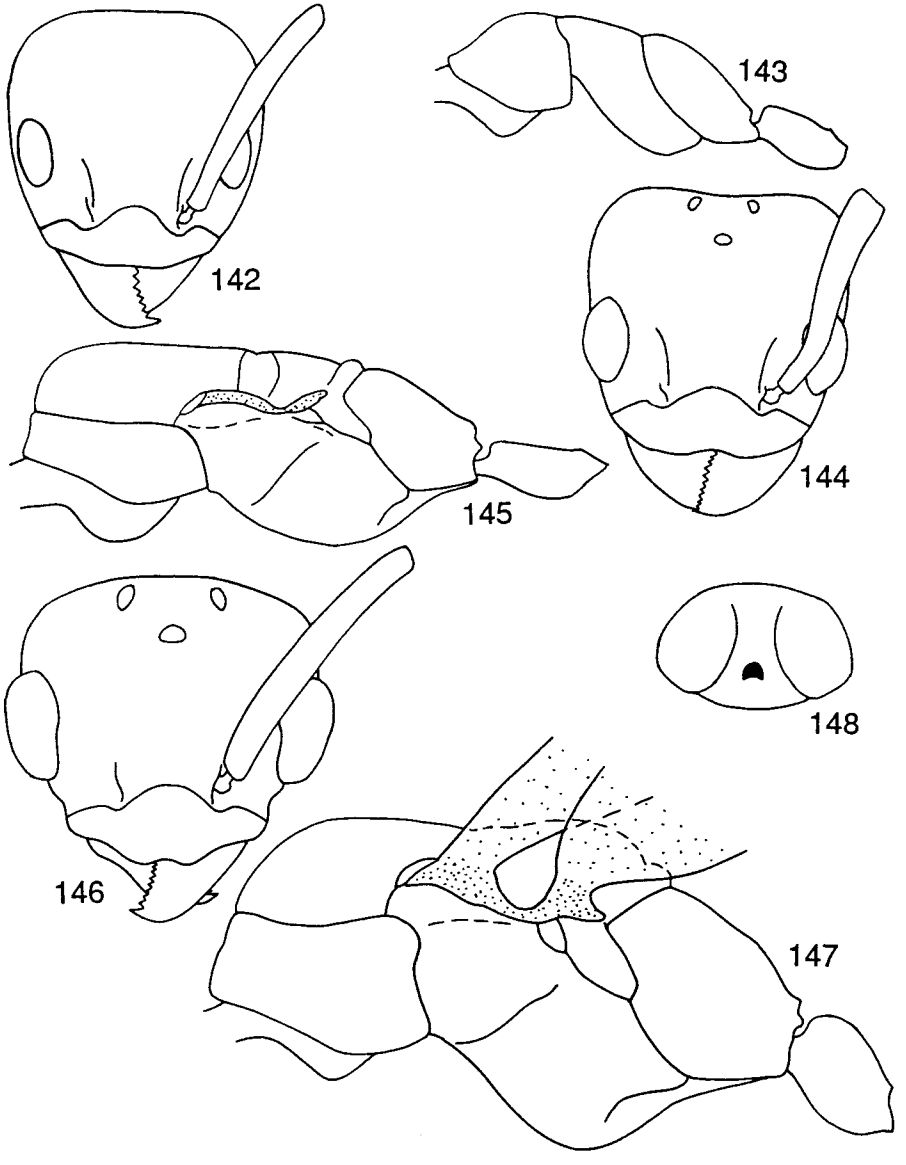
Male: Scape length much longer than the length of funicular segments 1+2+3; petiolar scale reduced, strongly inclined anteriorly; first gastral segment projecting anteriorly, sometimes concealing the petiole in dorsal view; mandible with 8 to 15 teeth and 0 to 3 denticles.

Description

WORKER.

HEAD. Vertex slightly convex to concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented (occasionally 11, rarely 8 segmented). Scape relatively short, at most surpassing the vertex by less than one-half (often less than one-third) its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin variable, either entire, without a central notch or concavity of any type; with a broad, shallow concavity; or with a distinct, central

notch separated from the general outline of the margin by distinct, angular corners. Anterior clypeal setae 2-6 (or absent); short, less than twice the maximum scape diameter or about the same length as the closed mandibles; straight or moderately curved ventrally. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 3-6 (rarely 7) teeth and about 7 denticles. Apical tooth varying from subequal in length to, to slightly longer than, the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins. Basal margin varying from denticulate distally, smooth proximally to denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous and dorsal faces of propodeum convex to flat; dorsal face shorter than the declivitous face. Propodeal angle distinct (rarely with a dorsal lip or tooth). Mesosomal spines absent (propodeum rarely with a dorsal tooth). Erect pronotal hairs absent (rarely 2 to 12); when present elongate, much longer than the maximum scape width. Dorsal pro- mesonotal junction with the pronotum and mesonotum even, or with the mesonotum slightly above the pronotum. Metanotal groove either reduced to a suture (and with the mesonotum and propodeum forming a continuous, uninterrupted surface) or forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle lateral and ventral of the dorsal surface when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale absent to reduced; when present, ridged and with a distinct angle dorsally, and strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a slight to well developed lobe. GASTER. First tergite projecting anteriorly and concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Anterior tergosternal suture of the first segment absent immediately lateral of the helcium and with the lateral section of the suture extending anterodorsally and terminating near the dorsal surface of the gaster. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression dorsoventral. Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste monomorphic or rarely dimorphic. Chromosome number 5, 7, 8 or 9 (2n=10, *T. melanocephalum*, Imai *et al.* 1984, Imai *et al.* 1985b; n=5, *T. melanocephalum*, Crozier 1970b; n=8, *T. sessile*, Crozier 1970b; 2n=16, *T. sessile*, Taber and Cokendolpher 1988; 2n=10, *T. indicum*,



Figs. 142-148: 142, Full face view of *Tapinoma sessile* worker; 143, Lateral view of *Tapinoma sessile* worker mesosoma; 144, Full face view of *Tapinoma* queen (New South Wales, Australia); 145, Lateral view of *Tapinoma* queen mesosoma (New South Wales, Australia); 146, Full face view of *Tapinoma sessile* male; 147, Lateral view of *Tapinoma sessile* male mesosoma; 148, Anterior view of first gastral segment of *Tapinoma sessile*.

Imai *et al.* 1984; n=7, *T. indicum*, Crozier 1975; n=8, *T. erraticum*, Crozier 1975; n=9, *T. nigerrimum*, *T. simrothi*, Crozier 1975). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola slightly broader than bulb; round; with short pile; smooth, without sculpture; and without phragma. Bulb exposed in lateral view. Longitudinal muscle No. 1 present. Occlusory tract absent.

QUEEN.

HEAD. Vertex convex to weakly concave. Compound eyes relatively anterior on head. Antennae 11 or 12 segmented (probably also 8, see worker description). Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin variable, either entire (without a central notch or concavity of any type) with a broad, shallow concavity, or with a distinct, central notch separated from the general outline of the margin by distinct, angular corners. Anterior clypeal setae 4-10; short, less than twice the maximum scape diameter to about the same length as the closed mandibles; straight to moderately curved ventrally. Posterior clypeal margin posterior of the anterior posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 4-9 teeth and 0-12 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin varying from denticulate distally, smooth proximally to denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture complete. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel or absent dorsally (when present, entire). Anterior axillar suture when present straight. Declivitous and dorsal faces of propodeum convex; dorsal face shorter than the declivitous face. Propodeal angle distinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs 0-20; when present short, less than twice the maximum scape diameter. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 1-2 cubital and 0-1 discoidal cells. Hind wing with 1-2 cells. PETIOLE. Scale reduced or absent; when present, ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a slight to well developed lobe. GASTER. First segment projecting anteriorly and concealing the petiole in dorsal view and with a groove or indentation for

the reception of the entire height of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression dorsoventral. Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Antennae 13 segmented (probably also with fewer segments, see worker description). Scape length much longer than the length of funicular segments 1+2+3 and exceeding the vertex. First funicular segment cylindrical or cone-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin variable, either entire (without a central notch or concavity of any type) or with a distinct, central notch separated from the general outline of the margin by distinct, angular corners. Anterior clypeal setae 4; varying from short (about as long as the maximum diameter of the scape) to about the same length as the closed mandibles; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with about 8- 15 teeth and 0-3 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel or constricted medially, and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face shorter than the declivitous face. Propodeal angle indistinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 0-1 discoidal cells. Pterostigmal appendage absent. Hind wing with 0, 1 or 2 cells. PETIOLE. Scale reduced; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a slight to weakly developed lobe. Attachment to gaster narrow. GASTER. First segment projecting anteriorly and sometimes concealing the petiole in dorsal view, and with a groove or indentation for the reception of the entire height of the petiole. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave. Paramere divided by a membranous region (but only weakly in some species). Digitus with a down-turned tip. Cuspis absent. Ventral lobe of volsella present as concave lobe. Aedeagus with ventral teeth.

LARVA.

Shape dolichoderoid. Protuberances present as a single boss on posterior

Fig. 149. Distribution of *Tapinoma*. Closed circles indicate examined material. Closed triangles indicate examined, human-introduced populations.

of body. Body hairs sparse; simple; short. 9 spiracular pairs. Antennae short.

Discussion

Tapinoma is a large, diverse genus which occurs throughout the world. Workers can be separated from those of all other dolichoderine genera based on the lack of a petiolar node (occasionally greatly reduced), the lack of a basal mandibular angle, and the four apparent gastral tergites (see also the Diagnosis above). A table of characters (Table 4) is provided to emphasize differences between *Tapinoma* workers and those of the superficially similar genera *Bothriomyrmex*, *Doleromyrma* and *Technomyrmex*.

The concept of *Tapinoma* is here expanded to include the five species formerly placed in *Semonius* and *Zatapinoma*. *Semonius* and *Zatapinoma* were established based solely on single character systems. *Semonius* was defined by the reduction of antennal segments from 12 to 11 and *Zatapinoma* by the formation of a phragmotic worker caste. Other than these single characters the species in these two genera display all the characters used to diagnose *Tapinoma*, including the unique elongate scape of the male. Recognition of these two genera renders *Tapinoma* paraphyletic, and makes it impossible to define *Tapinoma* without reference to *Semonius* and *Zatapinoma*. Therefore *Semonius* and *Zatapinoma* are subsumed under *Tapinoma*.

Tapinoma is morphologically diverse and some species tend to form groups within the genus. Four groups based on single character systems can be noted: (i) small species with the mandibular teeth in a uniform, decreasing size series along the masticatory margin, (ii) species with a distinct clypeal notch, (iii) species with a phragmotic soldier caste and (iv) species with reduced antennal segment numbers. These groups may be monophyletic, but a number of species cannot be placed in any of these groups. As a result these groups should be considered preliminary until the entire genus is examined and the unplaced species are better understood.

Species of *Tapinoma* utilize a wide variety of nest sites, including open soil, soil covered with rocks, wood or other plant material, rotten or dead wood, plant stems, or almost any appropriately-sized preformed cavity. Nests are of moderate to large size, and may contain up to several hundred dealate queens. *Tapinoma* are general scavengers, but have a preference for honeydew and often tend aphids or coccids. One species, *T. melanocephalum*, is a tramp species widely distributed by commerce throughout tropical regions.

Distribution: World-wide south of approximately 55° N (absent from Antarctica) (Fig. 149).

Species notes: The following species are here transferred from *Semonius* or *Zatapinoma* to *Tapinoma* (all NEW COMBINATIONS): *glaucus* (Viehmeyer) and *schultzei* (Forel) (from *Semonius*); *annandalei* (Wheeler), *wheeleri* (Mann) and *williamsi* (Wheeler) (from *Zatapinoma*).

The species *Tapinoma panamense* and *T. canalis* were established by Wheeler (1934, 1942) from material collected on Barro Colorado Island, Panama. An examination of the type material (first pointed out to me by R. Snelling) has revealed that both names are based on the same type series, and are therefore objective synonyms [NEW SYNONYMY]. Wheeler apparently overlooked his earlier description of *T. panamense* when he described *T. canalis.* This is confirmed by the almost identical original descriptions, and the fact that the description of *T. canalis* distinguishes it from other similar Central American species of *Tapinoma*, but does not mention *T. panamense.* To secure the identities of these names, LECTOTYPES have been selected from material in MCZC.

The name *Tapinoma dimmocki* (Wheeler) is here synonymized under *Tapinoma sessile* (Say) [NEW SYNONYMY]. Originally described as *Bothriomyrmex dimmocki* Wheeler (1915), it was transferred to *Tapinoma* by Emery (1925), and then treated as *incertae sedis* in Dolichoderinae by Smith (1958). An examination of the type material of *dimmocki* [1 worker, 1 alate queen and 3 dealate queens in MCZC] reveals that the worker is *Tapinoma sessile.* The queens are typical of *Tapinoma*, although they are smaller than normal *T. sessile* queens. Wheeler (1915) made no special mention of the queens to indicate that they were in any way unusual. Based on Wheeler's treatment of the species and on the examination of the type material, I here designate the MCZC *dimmocki* worker as LECTOTYPE and synonymize the species under *Tapinoma sessile* (Say).

Genus *Technomyrmex* Mayr (Figs. 150-156, Table 4)

Technomyrmex Mayr 1872: 147. Type species: *Technomyrmex strenua* Mayr (by monotypy).

Engramma Forel 1905: 180. Type species: *Engramma lujae* Forel (by monotypy). [NEW SYNONYMY]

Aphantolepis Wheeler 1930: 44 (syn. by Brown 1953:5). Type Species: *Aphantolepis quadricolor* Wheeler (by monotypy).

Diagnosis

Worker: Fifth gastral tergite dorsal; petiolar scale reduced or absent; first gastral segment projecting anteriorly and concealing petiole in dorsal view; anteromedial clypeal margin with a broad, shallow concavity, or with a distinct, central notch separated from the general outline of the margin by indistinct, arched corners; dorsal face of propodeum shorter than declivitous face; generally 2 to 10 erect hairs on pronotum. Primarily Old World, with one species in Central America and a widespread tramp species.

Queen: Petiolar scale reduced; fifth gastral tergite dorsal; dorsal face of propodeum shorter than declivitous face; first gastral segment projecting

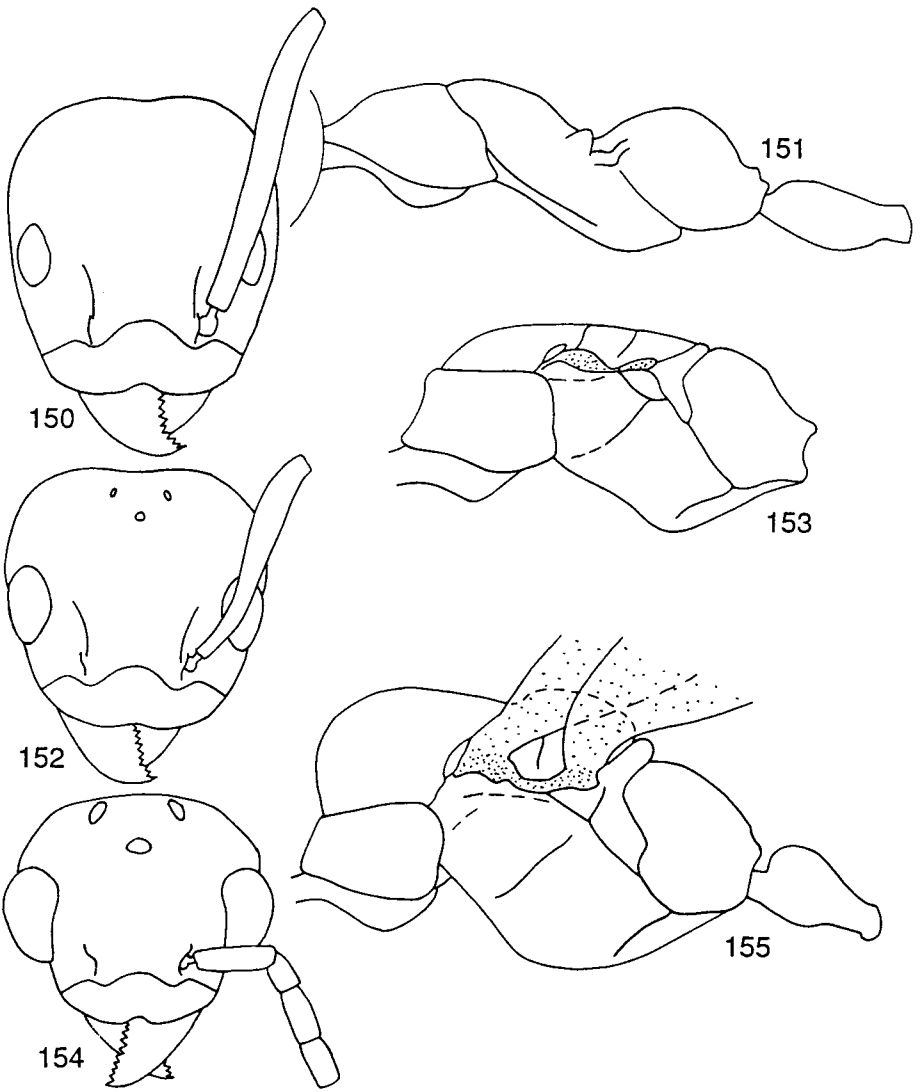
anteriorly and concealing petiole in dorsal view; basal angle of mandible indistinct, with a relatively uninterrupted curve between the masticatory and basal margins; hind wing without closed cells.

Male: Anteromedial clypeal margin with a broad, shallow concavity; mandible with about 19 teeth, and with the basal margin denticulate along the entire surface; petiolar scale strongly inclined anteriorly; first gastral segment projecting anteriorly, concealing the petiole in dorsal view; hind wing without closed cells.

Description

WORKER.

HEAD. Vertex convex to weakly concave. Compound eyes present, approximately round; relatively anterior on head. Ocelli absent. Antennae 12 segmented. Scape relatively short, at most surpassing the vertex by less than one-half (often less than one-third) its length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin with either a broad, shallow concavity, or with a distinct, central notch separated from the general outline of the margin by indistinct, arched corners. Anterior clypeal setae 6-12; short, less than twice the maximum scape diameter to about the same length as the closed mandibles; straight. Posterior clypeal margin posterior of the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present.Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4, 5:3 or 4:3. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 7-10 teeth and 2-15 denticles. Apical tooth subequal in length to, to slightly longer than, the subapical tooth. Basal angle weakly defined by a denticle to indistinct, with a relatively uninterrupted curve between the two margins. Basal margin varying from smooth (without teeth or denticles) to denticulate along entire surface. MESOSOMA. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum convex; dorsal face convex to flat, shorter than the declivitous face (sometimes only slightly). Propodeal angle distinct. Mesosomal spines and tooth absent. Erect pronotal hairs 2-10 (sometimes 0, rarely up to 20); short, about as long as maximum scape width. Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle either lateral and ventral of the dorsal surface, or dorsal and lying on the dorsal surface, when viewed in lateral profile. Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale reduced or absent; when



Figs. 150-155: 150, Full face view of *Technomyrmex* worker (Queensland, Australia); 151, Lateral view of *Technomyrmex* worker mesosoma (Queensland, Australia); 152, Full face view of *Technomyrmex* queen (Solomon Islands); 153, Lateral view of *Technomyrmex* queen mesosoma (Solomon Islands); 154, Full face view of *Technomyrmex* male (Queensland, Australia); 155, Lateral view of *Technomyrmex* male mesosoma (Queensland, Australia).

present, angular and only slightly visible in profile; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a slight or weakly developed lobe. GASTER. First tergite projecting anteriorly and concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. Anterior tergosternal suture of the first segment absent immediately lateral of the helcium and with the lateral section of the suture extending anterodorsally and terminating near the dorsal surface of the gaster. Fifth tergite dorsal, gaster with 5 apparent tergites. Gastral compression dorsoventral or rarely lateral. Fourth sternite flat across entire posterior border (some species with fan of erect hairs around apex of gastral sternite 4, similar to many formicines). GENERAL CHARACTERS. Worker caste monomorphic or rarely polymorphic. Chromosome number 8, 9, 14 or 15 (2n=16, *T. albipes*, Imai *et al.* 1977, Imai *et al.* 1984; n=9, 2n=18, *T. albipes*, Crozier 1968a; 2n=28, *T.* sp.1, Imai *et al.* 1985b; 2n=30, *T.* sp.2, Imai *et al.* 1985b; 2n=30, *T.* sp.1, Imai *et al.* 1985a; 2n=28, *T. bicolor* group, Imai *et al.* 1984). Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; lobed; with short pile; with hexagonal sculpturing; and without phragma. Bulb partially hidden by cupola in lateral view. Longitudinal muscle No. 1 absent. Occlusory tract absent.

QUEEN.

HEAD. Vertex flat to weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin even with the mediolateral region. Anteromedial clypeal margin variable, either entire (without a central notch or concavity of any type); with a broad, shallow concavity; with a distinct, central notch separated from the general outline of the margin by indistinct, arched corners; or with a distinct, central notch separated from the general outline of the margin by distinct, angular corners. Anterior clypeal setae 6-12; short, less than twice the maximum scape diameter to about the same length as the closed mandibles; straight. Posterior clypeal margin posterior of the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4 (and possibly others, see worker description). Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with about 4-16 teeth and about 0-16 denticles. Apical tooth subequal in length to, to slightly longer than, the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin varying from denticulate distally, smooth proximally to denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture com-

Fig. 156. Distribution of *Technomyrmex*. Closed circles indicate examined material. Closed squares indicate literature records believed to be reliable. Closed triangles indicate examined, human-introduced populations.

plete. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla constricted medially or rarely parallel, and entire. Anterior axillar suture straight. Declivitous face of propodeum convex to flat; dorsal face convex, shorter than the declivitous face. Propodeal angle distinct or indistinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs 0-30; when present, varying from short (less than twice the maximum scape diameter) to elongate (more than twice the maximum scape diameter). Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 1 cubital and 0-1 discoidal cells. Hind wing cells absent. PETIOLE. Scale reduced; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with or without a slight or weakly developed lobe. GASTER. First segment projecting anteriorly and concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Fifth tergite dorsal, gaster with 5 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length of funicular segments 2+3 (rarely slightly shorter than the length of funicular segments 1+2+3 and surpassing the vertex). First funicular segment cylindrical or cone-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin with a broad, shallow concavity, or less commonly entire, without a central notch or concavity of any type. Anterior clypeal setae 4-8; short, about as long as the maximum diameter of the scape and about the same length as the closed mandibles (both lengths present); straight. Posterior clypeal margin even with or anterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4 or 5:4 (and possibly others, see worker description). Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with about 19 teeth and no denticles. Apical tooth slightly longer than the subapical tooth. Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin denticulate along entire surface, or rarely denticulate distally, smooth proximally. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel or constricted medially and entire. Anterior axillar suture straight. Declivitous and

dorsal faces of propodeum convex; dorsal face shorter than the declivitous face. Propodeal angle indistinct. WINGS. Radial cell closed. Fore wing with 1 cubital and no discoidal cells. Pterostigmal appendage absent. Hind wing cells absent. PETIOLE. Scale present; ridged and with a distinct angle dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a slight or weakly developed lobe. Attachment to gaster narrow. GASTER. First segment projecting anteriorly and concealing the petiole in dorsal view and with a groove or indentation for the reception of the entire height of the petiole. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave or with a "V"-shaped notch. Paramere entire. Digitus with a down-turned tip. Cuspis ventral of digitus. Ventral lobe of volsella absent. Aedeagus with ventral teeth.

LARVA.

Shape pheidoloid or dolichoderoid. Protuberances present as a single boss on posterior of body. Body hairs sparse; simple; short. 9 spiracular pairs. Antennae short.

Discussion

Technomyrmex is a large, widespread genus that has received little taxonomic attention. This genus can be most easily separated from other dolichoderines based on the configuration of the gaster. The terminal gastral tergite is dorsal, giving the gaster a five-segmented appearance in dorsal view. In a few African species, the fifth gastral tergite is positioned more vertically than in most other members of the genus, but the tergite is still just visible in dorsal view.

Two genera have been subsumed under *Technomyrmex*, *Engramma* and *Aphantolepis*. *Engramma* was established by Forel (1905) for the single species *lujae*. Over the next few decades several species accumulated in the genus. The supposed uniting character was the palp formula 4:3 in the worker. (Most Dolichoderinae have a palp formula of 6:4.) However, in the present study examination of these species reveals that they share the following characters typical of *Technomyrmex*: notched anterior clypeal margin with elongate, flattened hairs; low, compact propodeum; weakly concave vertex; arched mesonotum; and dorsally placed fifth gastral tergite. Additionally, the habits of nesting arboreally and using carton in nest construction are shared between these groups. Finally, only one of the species placed in *Engramma* has a palp formula of 4:3. Of the material examined only *lujae* has a palp formula of 4:3, the remaining species have formulas of either 5:3 or 6:4. Therefore, the number of characters shared in common between *Engramma* and *Technomyrmex*, and the derived nature of the palp formula reduction, suggests that species formerly placed in *Engramma* are at best only divergent *Technomyrmex*.

The genus *Aphantolepis* was described by Wheeler (1930) from a single worker. Wheeler mistakenly placed this genus in Formicinae, apparently based on the semi-circle of erect hairs on the fifth gastral sternite, a trait now known to occur in several species of *Technomyrmex*. *Aphantolepis* was correctly recognized as a synonym of *Technomyrmex* by Brown (1953) as it possesses all the characters used to diagnose *Technomyrmex*.

Two species of *Technomyrmex*, *T. albipes* and *T. fulvus*, have distribution patterns that are of special note. *T. albipes* is a tramp species which has become widespread in tropical regions. It can be quite common in disturbed habitats and is known to survive in cold climates by occupying greenhouses. For example, it has become established in the Conservatory at Golden Gate Park, San Francisco, California, Miami, Florida (Deyrup 1991) and in Kew Gardens, London, England.

Technomyrmex fulvus, and its subspecies *sublucidus*, were described from Barro Colorado Island, Panama. This occurrence of an apparently native species of *Technomyrmex* in the New World tropics presents an interesting situation because the group is otherwise entirely Old World. Taxonomically, this species is clearly a *Technomyrmex*. While it has been placed in *Tapinoma*, it cannot remain in that genus because the fifth gastral tergite is dorsal, the sculpturing is heavier than that found in *Tapinoma*, and there are erect hairs on the pronotum, a character seldom found in *Tapinoma*. Moreover, the proventricular cupola of *fulvus* is lobed and the bulb is partially hidden by the cupola in lateral view, characters common to other members of *Technomyrmex* but unknown in *Tapinoma*. The likelihood that *T. fulvus* is introduced is remote as it is distinct from all other species of *Technomyrmex* examined during this study. The occurrence of *Technomyrmex* species in the New World presents a biogeographic challenge, one that will require a more thorough study of the entire genus.

Species of *Technomyrmex* are most common in moist, forested regions. They nest in the soil, in twigs or branches, or in carton nests under leaves or on tree trunks. They are general scavengers and often forage in columns. At least one species is known to have ergatoid males (Terron 1972), and ergatoid queens have been collected in Papua New Guinea (P. S. Ward, pers. comm.).

Distribution: The majority of species occur from Africa, east through southern Asia, to Australia (Fig. 156). A single species (with one subspecies) is known from Panama, and is the only native New World species. A tramp species (*T. albipes*) has been widely distributed by human activity, and is known from California and Florida (Deyrup 1991), USA, London, England, and many Pacific Islands (Wilson and Taylor 1967).

Species notes: The following species are transferred from *Engramma*, *Iridomyrmex* or *Tapinoma* to *Technomyrmex* (all NEW COMBINATIONS): *allatus* (Stitz), *gowdeyi* (Wheeler), *griseopubens* (Wheeler), *ilgi* (Forel), *ilgi*

stygius (Santschi), *incisus* (Mukerjee), *kohli* (Forel), *laurenti* (Emery), *laurenti congolensis* (Forel), *lujae* (Forel), *lujae pulliceps* (Santschi), *lujae wasmanni* (Forel), *tailori* (Santschi), *wolfi* (Forel), *zimmeri* (Forel), and *zimmeri okiavoensis* (Forel) (from *Engramma*); *fulvus* (Wheeler), *fulvus sublucidus* (Wheeler), *pratense* (F. Smith), *setiferus javanus* (Forel), *sundaicus* (Emery), *voeltzkowi* (Forel), and *voeltzkowi rhodesiae* (Forel) (from *Tapinoma*); *wheeleri* (Emery) (from *Iridomyrmex*).

Genus *Turneria* Forel (Figs. 157-163)

Turneria Forel 1895a:419. Type species: *Turneria bidentata* Forel (by monotypy).

Diagnosis

Worker: Compound eyes elongate; propodeum with protuberances bearing the propodeal spiracle; anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region (rarely posterior to the mediolateral regions); declivitous face of propodeum concave. Papua New Guinea, Solomon Islands, Australia.

Queen: Anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region; mandible with apical tooth subequal in length to subapical, and the basal angle weakly defined by a denticle; petiolar scale rounded and forming an even arch dorsally; venter of petiole without a lobe; mandible with 7 teeth and 4 denticles.

Male: Mandible without teeth or denticles (tip of mandible rounded and without a differentiated tooth); venter of petiole with a well developed lobe.

Description

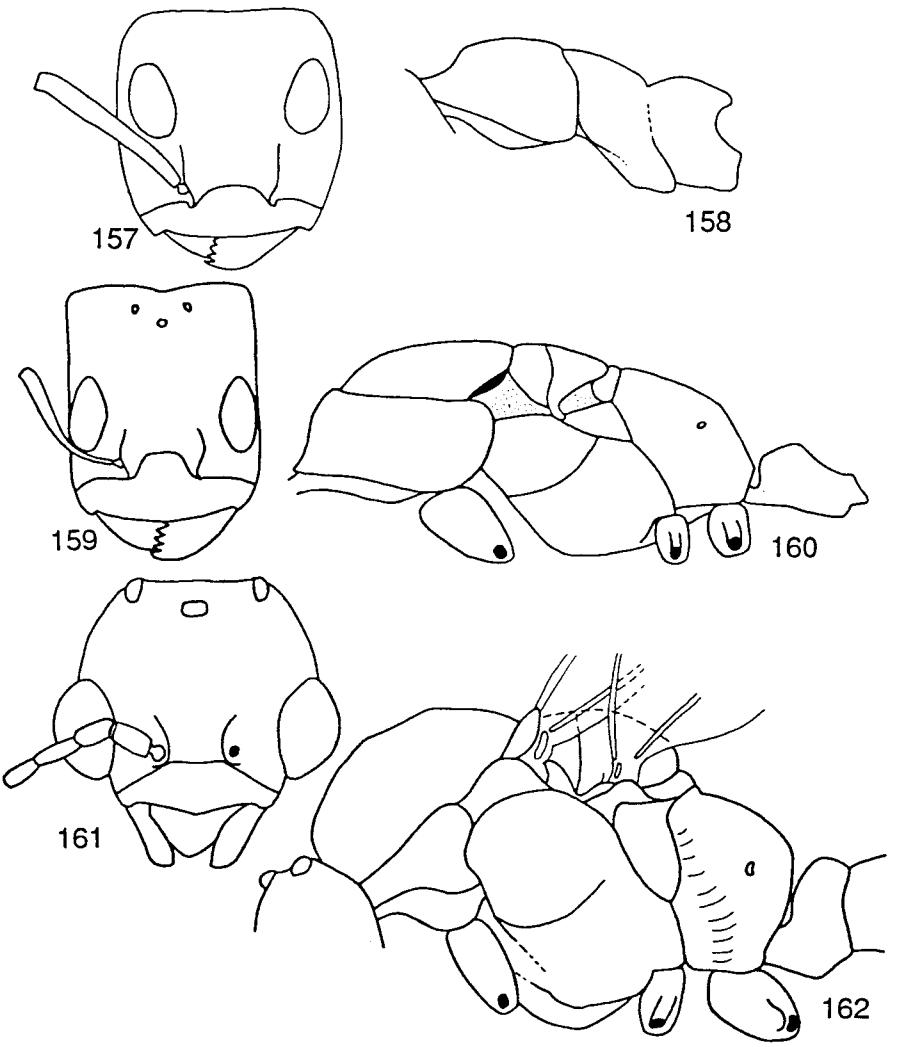
WORKER.

HEAD. Vertex flat to weakly concave. Compound eyes present, elongate; relatively posterior on head. Ocelli absent. Antennae 12 segmented. Scape short, at most surpassing the vertex by less than one-third its length. Anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region, or rarely posterior to the mediolateral region and separated from it by a shoulder. Anteromedial clypeal margin entire, without a central notch or concavity of any type, or rarely with a broad, shallow concavity. Anterior clypeal setae 10-16; short, less than twice the maximum scape diameter to about the same length as the closed mandibles; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Frontal carina present. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment

4. Fifth maxillary palp segment at the apical extreme of segment 4. Mandible with 5 teeth and 5-6 denticles. Apical tooth slightly longer than the subapical tooth. Basal angle weakly defined by a denticle. Basal margin denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Declivitous face of propodeum concave; dorsal face convex, subequal in length to, or longer than, the declivitous face. Propodeal angle distinct. Pronotal spines absent. Erect pronotal hairs usually absent (present in one undescribed species). Mesonotal spines absent. Propodeal spines present as protuberances. Propodeal tooth absent. Dorsal pro-mesonotal junction with the pronotum and mesonotum even. Metanotal groove forming a distinct angle between the mesonotum and propodeum. Metanotal spiracle dorsal and lying on the dorsal surface when viewed in lateral profile. Propodeal spiracle dorsal and posterior, near the propodeal angle. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). PETIOLE. Scale present; rounded and forming an even arch dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter with a well developed lobe. GASTER. First tergite vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of either the basal portion or entire height of the petiole. Anterior tergosternal suture of the first segment absent immediately lateral of the helcium and with the lateral section of the suture terminating immediately above the helcium. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border. GENERAL CHARACTERS. Worker caste monomorphic. Chromosome number unknown. Integument thin and flexible, weakly sculptured. PROVENTRICULUS. Cupola much broader than bulb; round; with short pile; smooth, without sculpture; and with narrow phragma. Bulb completely hidden by cupola in lateral view. Longitudinal muscle No. 1 absent. Occlusory tract absent.

QUEEN.

HEAD. Vertex flat to weakly concave. Compound eyes relatively anterior on head. Antennae 12 segmented. Scape short, surpassing the vertex by less than one-half scape length. Anterolateral clypeal margin with the corners expanded slightly anterior of the mediolateral region. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 12; short, less than twice the maximum scape diameter; straight. Posterior clypeal margin between the anterior and posterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. Psammophore absent. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth



Figs. 157-162: 157, Full face view of *Turneria postomma* worker; 158, Lateral view of *Turneria postomma* worker mesosoma; 159, Full face view of *Turneria dahlii* queen; 160, Lateral view of *Turneria dahlii* queen mesosoma; 161, Full face view of *Turneria pacifica* male; 162, Lateral view of *Turneria pacifica* male mesosoma.

maxillary palp segment at the apical extreme of segment 4. Mandible with 7 teeth and 4 denticles. Apical tooth subequal in length to the subapical tooth. Basal angle weakly defined by a denticle. Basal margin denticulate along entire surface. MESOSOMA. Posteroventral pronotum lateral, rounded or

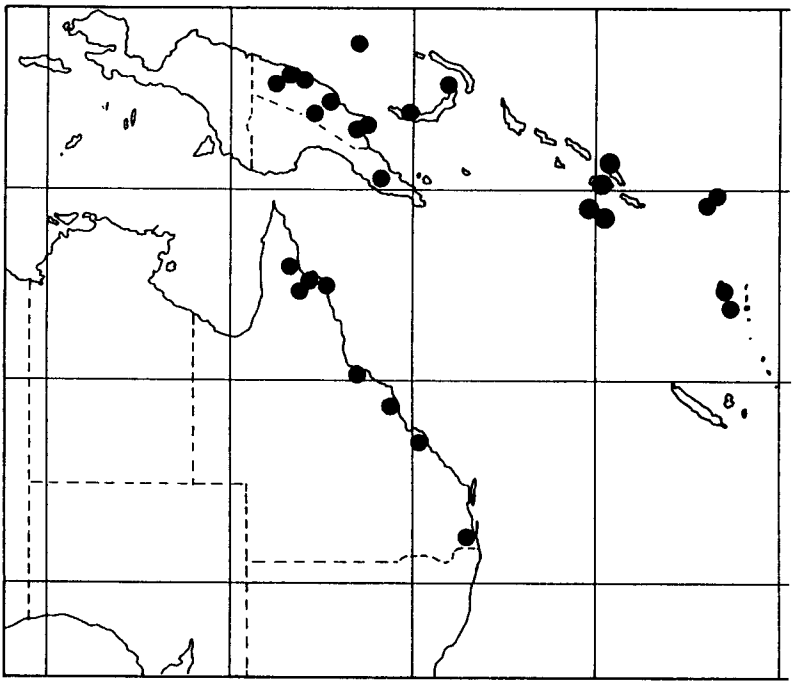


Fig. 163: Distribution of *Turneria* material examined during this study.

angled. Episternal suture complete to weak, nearly absent. Mesopleural process absent. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle indistinct. Propodeal suture absent. Mesosomal spines and tooth absent. Erect mesoscutal hairs absent (possibly present in one undescribed species; see worker description). Propodeal spiracle lateral and ventral of the propodeal dorsum. Hind tibial spur with well developed barbules along entire inner surface (except extreme base). WINGS. Radial cell closed. Fore wing with 2 cubital and 1 discoidal cell. Hind wing with 2 cells. PETIOLE. Scale present; rounded and forming an even arch dorsally; strongly inclined anteriorly and with the anterior face much shorter than the posterior face. Venter without a lobe. GASTER. First segment vertical and not concealing the petiole in dorsal view and with a groove or indentation for the reception of the basal portion of the petiole. Fifth tergite ventral, gaster with 4 apparent tergites. Gastral compression absent (gaster circular in cross section). Fourth sternite flat across entire posterior border.

MALE.

HEAD. Inner margin of eye entire, flat. Scape length shorter than the length

of funicular segments 2+3. First funicular segment barrel-shaped. Second funicular segment cylindrical, straight. Funicular segments 2 and 3 at most twice as long as broad. Third and fourth funicular segments straight. Anteromedial clypeal margin entire, without a central notch or concavity of any type. Anterior clypeal setae 4-6; short, about as long as the maximum diameter of the scape; straight. Posterior clypeal margin even with or anterior to the anterior surfaces of the antennal socket cavities. Anterior tentorial pit nearer the antennal socket than the mandibular insertion. Anterolateral hypostoma reduced to a thin sclerite. Medial hypostoma entire. MOUTHPARTS. Palp formula 6:4. Third maxillary palp segment subequal in length to segment 4. Fifth maxillary palp at the apical extreme of segment 4. Mandible with no teeth or denticles. Apical tooth absent (tip of mandible rounded and without a differentiated tooth). Basal angle indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle. Basal margin smooth and without teeth or denticles. MESOSOMA. Posteroventral pronotum lateral, rounded or angled. Episternal suture present, complete. Anteromedial mesosternum even with the lateral regions. Axilla parallel and entire. Anterior axillar suture straight. Declivitous and dorsal faces of propodeum convex; dorsal face subequal in length to the declivitous face. Propodeal angle distinct. WINGS. Radial cell closed. Fore wing with 1 cubital and 1 discoidal cell. Pterostigmal appendage absent. Hind wing with 2 cells. PETIOLE. Scale present; ridged and with a distinct angle dorsally; vertical and not inclined anteriorly. Venter with a well developed lobe. Attachment to gaster broad. GASTER. First segment elongated posteriorly, smooth and without a groove or indentation. GENITALIA. Pygostyles present. Posterior margin of subgenital plate concave. Paramere divided by a membranous region. Digitus linear, with a slight ventral arch. Cuspis ventral of digitus. Ventral lobe of volsella present as a swelling. Aedeagus without ventral teeth.

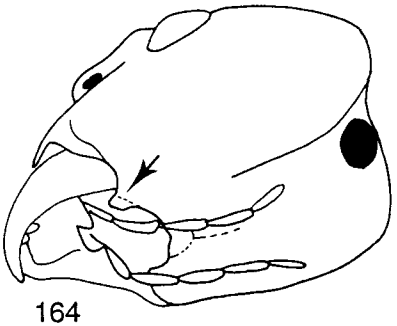
LARVA.

Shape dolichoderoid. Protuberances present as 2 bosses located mid-dorsally. Body hairs sparse; simple; short. 10 spiracular pairs. Antennae short.

Discussion

The genus *Turneria* was established by Forel (1895a) for the single Australian species *T. bidentata*. In a recent revision, Shattuck (1990) found the genus to contain a total of 6 species. (Recent collecting has revealed additional undescribed species in Australia and New Guinea.) Members of *Turneria* are easily recognized by their elongate compound eyes and the placement of the propodeal spiracles dorsally and posteriorly on protuberances located at the propodeal angle.

This genus has a restricted distribution as it is known only from Papua New Guinea, northeastern Australia, the Solomon Islands and Vanuatu. All known



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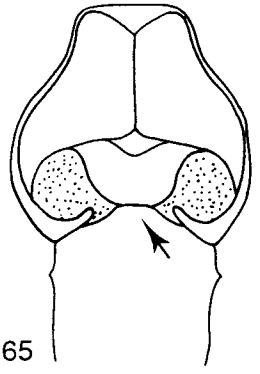

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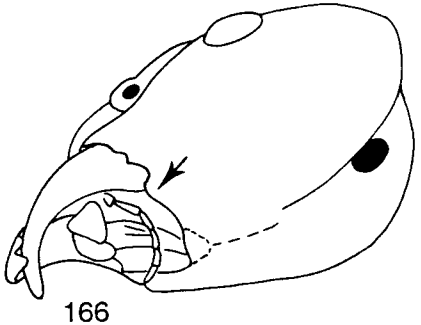

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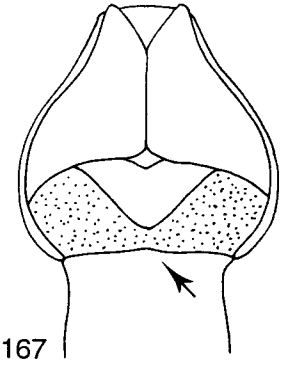

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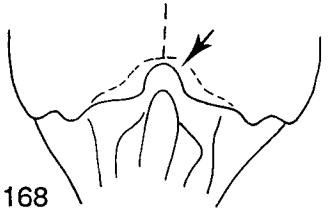

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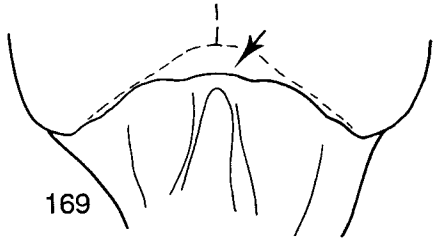

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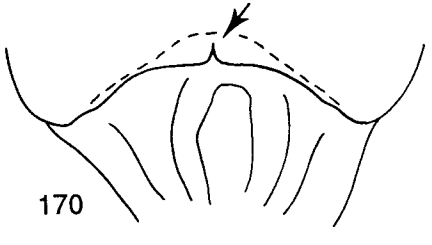

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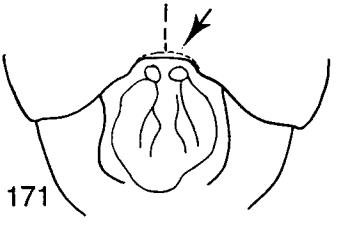

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species are arboreal in parklands and primary or secondary rain forests, often nesting in dead twigs. *Turneria* is not commonly collected, although this is likely due to their arboreal habits and not to their scarcity.

Distribution: Papua New Guinea south into northern Australia, and east to Vanuatu (Fig. 163).

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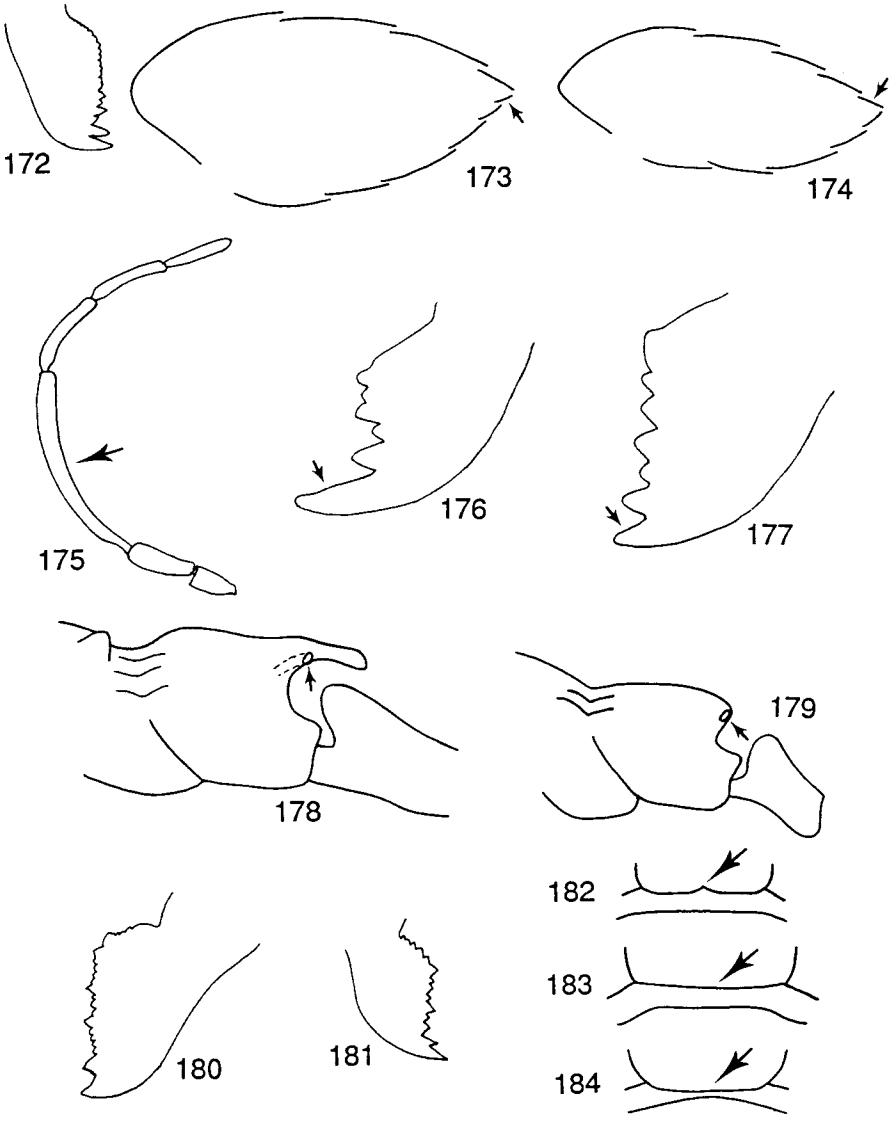
Figs. 164-171: 164, Anteroventral surface of worker head (*Dolichoderus*). Arrow indicates expanded hypostomal tooth; 165, Ventral view of anterior worker mesosoma with legs removed (*Dolichoderus*). Arrow indicates expanded mesosternal margin; 166, Anteroventral surface of worker head (*Iridomyrmex*). Arrow indicates anterolateral hypostomal margin; 167, Ventral view of anterior worker mesosoma with legs removed (*Iridomyrmex*). Arrow indicates mesosternal margin; 168, Ventral view of worker head (*Leptomyrmex*). Arrow indicates notched medial hypostomal border; 169, Ventral view of worker head (*Iridomyrmex*). Arrow indicates entire medial hypostoma; 170, Ventral view of worker head (*Anonychomyrma*). Arrow indicates grooved medial hypostoma; 171, Ventral view of worker head (*Bothriomyrmex*). Arrow indicates absent medial hypostoma.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Figs. 172-184: 172, Mandible of *Tapinoma* worker; 173, Diagrammatic cross section of gaster of worker (*Tapinoma*). Arrow indicates fifth tergite; 174, Diagrammatic cross section of gaster of worker (*Technomyrmex*). Arrow indicates fifth tergite; 175, Maxillary palp of *Dorymyrmex* worker. Arrow indicates elongate third segment; 176, Mandible of *Dorymyrmex* worker. Arrow indicates enlarged apical tooth; 177, Mandible of *Azteca* worker. Arrow indicates apical tooth; 178, Posterior mesosoma of *Froggattella*. Arrow indicates spiracular opening; 179, Posterior mesosoma of *Turneria*. Arrow indicates spiracular opening; 180, Mandible of *Linepithema humile* worker; 181, Mandible of *Anonychomyrma* worker; 182, Dorsal view of *Ochetellus* queen mesosoma. Arrow indicates anterior axillar suture; 183, Dorsal view of *Anonychomyrma* queen mesosoma. Arrow indicates anterior axillar suture; 184, Dorsal view of *Azteca* queen mesosoma. Arrow indicates anterior axillar suture.

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