TAXONOMY OF *MYRMECIA* FABRICIUS (HYMENOPTERA : FORMICIDAE)

by

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ABSTRACT

The taxonomy of _Myrmecia_ Fabricius is examined using characters from a variety of sources (i.e. scanning electron microscopy of workers, dissection of male terminalia, karyotype analysis, behavioural observations). Sixty species, including seven which were undescribed (_sp.8_, _sp.9_, _sp.12_, _sp.14_, _sp.15_, _sp.16_, _sp.17_), are recognized from workers alone, but these are not all equivalent to biological species. Biological species which cannot be distinguished by their workers are discussed collectively as _sensu lato_ (_s.l._) species (i.e. species in the broad sense). Six species which can only be recognized by their male terminalia or karyotypes are identified (_decipiens_, _desertorum_, _gilberti_, _sp.7_, _sp.11_, _sp.13_), and a number of others are suspected, because many widespread species exhibit considerable variation in chromosome number, worker colouration or behaviour (especially nest structure). Two other new species (_sp.M1_, _sp.M2_) are known only from males, but these may later be associated with workers which are already described. Species descriptions include information about literature synonymies, type specimens, worker morphology, geographic distribution, male terminalia, karyotypes, subspecific taxa, nest structure and biological references. Workers of 31 species are illustrated by scanning electron microscopy, male terminalia of 50 species are described and 22 species are karyotyped. Keys to species based on workers and male terminalia are presented. Chromosome numbers ranged from $2n = 10$ to $2n = 82$ and chromosome rearrangements detected include Robertsonian rearrangements, pericentric inversions, complex translocations and a chromosome deletion.

Characters of the male terminalia are used to place the species in 19 species groups of which 12 are monotypic, but two relatively speciose (i.e. the *vindex* and *pilosula* groups, 16 species each). The species groups are divided amongst two subgenera, *Myrmecia*, *s.s.* and *Promyrmecia*, which correspond to the bulldog ants and jumpers respectively.

Where possible, plesiomorphic (relatively primitive) and apomorphic (relatively derived) states are identified for the characters examined. These characters are used to construct a cladistic classification. It is postulated that the ancestral *Myrmecia* was a non-jumper, whose workers were all about the same size (i.e. with no identifiable subcastes) and of similar dimensions to extant jumpers. Subgenus *Promyrmecia* has developed prosalience (jumping) as a second form of locomotion with only slight change in size, while *Myrmecia*, *s.s.* remains incapable of prosalience and has developed two worker subcastes, one similar in size to the jumpers but the other much larger.

Hypotheses for the directionality of ant karyotype evolution are examined in detail. Evidence supports the fission hypothesis for ants as a whole and this can be extrapolated with caution to *Myrmecia*. The plesiomorphic *Myrmecia* karyotype was probably near n = 5 (N.F. = 20).

Miscellaneous observations which are discussed include morphometric analyses of *fuscipes* and *nigriceps*, *s.l.* colonies, and occurrences of eucharitine wasp parasites, light-coloured workers, multiple queens and a large carabid beetle within *Myrmecia* nests.

STATEMENT OF RESPONSIBILITY

To the best of my knowledge and belief, this thesis contains no material previously published or written by another person and contains no material which has been accepted for the award of any other degree or diploma in any university, except where due reference is made in the text.

Graeme Philip Browning
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1. INTRODUCTION

Bulldog ants and jumpers of the genus Myrmecia Fabricius are a conspicuous feature of the Australian biota because of their large size, colouration which is sometimes striking (at least amongst ants), pronounced aggressiveness, ability to sting and relative abundance of various species. They are undoubtedly important in many ecosystems as predators of invertebrates, and males of one species are orchid pollinators (Peakall, 1984a,b). Myrmecia are especially interesting to myrmecologists because, excepting the extraordinarily archaic Nothomyrmecia Clark, they are '... generally accepted as being the most primitive ... [ants]' (Imai et al., 1977). However, despite their conspicuousness and scientific interest, the taxonomy of Myrmecia is poorly developed, which led Gray (1974a) to exaggerate that '... the taxonomic status of the Myrmecia is one of confusion and near chaos.' To understand how this situation arose I examined the history of Myrmecia taxonomy.

The first bulldog ant to be described was Formica gulosa Fabricius, 1775 from specimens collected in 1770 by Banks and Solander during James Cook's voyage of discovery to eastern Australia. A second species, Formica forficata Fabricius, 1787, was also described before Fabricius (1804) decided that these forms were sufficiently distinct from all other ants to warrant a new genus, Myrmecia. He designated gulosa as the type and described a third species (esuriens Fabricius). No additional species were described during the next 50 years, but Latreille (1805) included gulosa in Eciton Latreille, and Illiger (1807) placed all three species in Ponera Latreille.

More bulldog ants, and the first jumpers, were described as

Myrmecia species by Smith (1858), who also mistakenly described a jumper male as *Ponera ruginoda*. Roger (1861a, 1861b), Mayr (1862, 1866, 1870, 1876), Lowne (1865), Emery (1883, 1895, 1898) and Forel (1893, 1894, 1900, 1907, 1910) described further species, subspecies, races and varieties before Emery (1911) listed 52 available names for *Myrmecia* and attempted the first infrageneric classification. Emery recognized three subgenera: (1) *Myrmecia*, *s.s.* (type species *gulosa*); (2) *Promyrmecia* (type species *aberrans* Forel); and (3) *Pristomyrmecia* (type species *mandibularis* Smith). The majority of species were placed in subgenus *Myrmecia*, which he divided into seven species groups. Wheeler (1922), realizing that two of these groups consisted of jumpers, decided that they should not be grouped with the others, which were all bulldog ants. For these he erected a fourth subgenus, *Halmamyrmecia* (type species *pilosula* Smith[*]). *Pristomyrmecia* and *Halmamyrmecia* were reduced to synonyms of *Promyrmecia* by Clark (1925). Meanwhile, further forms were described by Forel (1913a, 1913b, 1915, 1922), Emery (1914), Wheeler (1915, 1933), Crawley (1921, 1922a, 1925b), Viehmeyer (1924), Santschi (1928) and Clark (1929, 1934a, 1934b, 1938).

In 1943, Clark raised *Promyrmecia* to full generic rank and revised the new genus. He recorded 55 forms, of which 24 were new, and placed them in seven species groups. This was followed by his monographic revision of *Myrmecia* and *Promyrmecia* (Clark, 1951). Clark recognized 59 forms of *Myrmecia* (22 new species) and placed them in five species groups. Three new species and an eighth species group of *Promyrmecia* were also recognized.

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[*] Brown (1953a) mistakenly states that *nigrocincta* Smith is the type species of subgenus *Halmamyrmecia*.

Brown (1953a) examined the couplet used by Clark (1951, p. 20) to separate the two genera and summarized the characters as follows: '... (1) fraction of length by which the antennal scape surpasses the occipital border, (2) distinctness of metanotum, and (3) size, as mirrored in total length.' He appraised each of these characters critically and rejected Clark's and other divisions for lack of evidence. Consequently all bulldog ants and jumpers are now contained in a single genus, *Myrmecia*, with no recognized subgenera. Neither Clark's (1943, 1951) nor Emery's (1911) species groups have been used by subsequent authors and a comparison of the two classifications (fig. 1) demonstrates their incongruity. Since Clark's revisions only two new *Myrmecia* have been described by Brown (1953b) and Douglas and Brown (1959). Taylor and Brown (1985), in their checklist of available names for Australian ants, listed 141 names for *Myrmecia* and assigned them to 85 species, using the taxonomic decisions of Clark (1951) and Brown (1953b) for the synonymies. This checklist does not include *apicalis* Emery from New Caledonia which is the only non-Australian *Myrmecia*. Nor does it include one infrasubspecific name (*violacea* Forel, 1915) which is rightly considered to be unavailable following Article 45 of the International Code of Zoological Nomenclature (Third Edition).

The current status of *Myrmecia* taxonomy is that there are 142 available names which are assigned to 86 species and five subspecies (Taylor, 1987). Infrageneric classifications have been attempted but these have either been disputed or have fallen into disuse. None can be considered satisfactory.

The further development of *Myrmecia* taxonomy will involve three more or less distinct processes: (1) delimiting the biological species involved; (2) assigning names to these species and determining

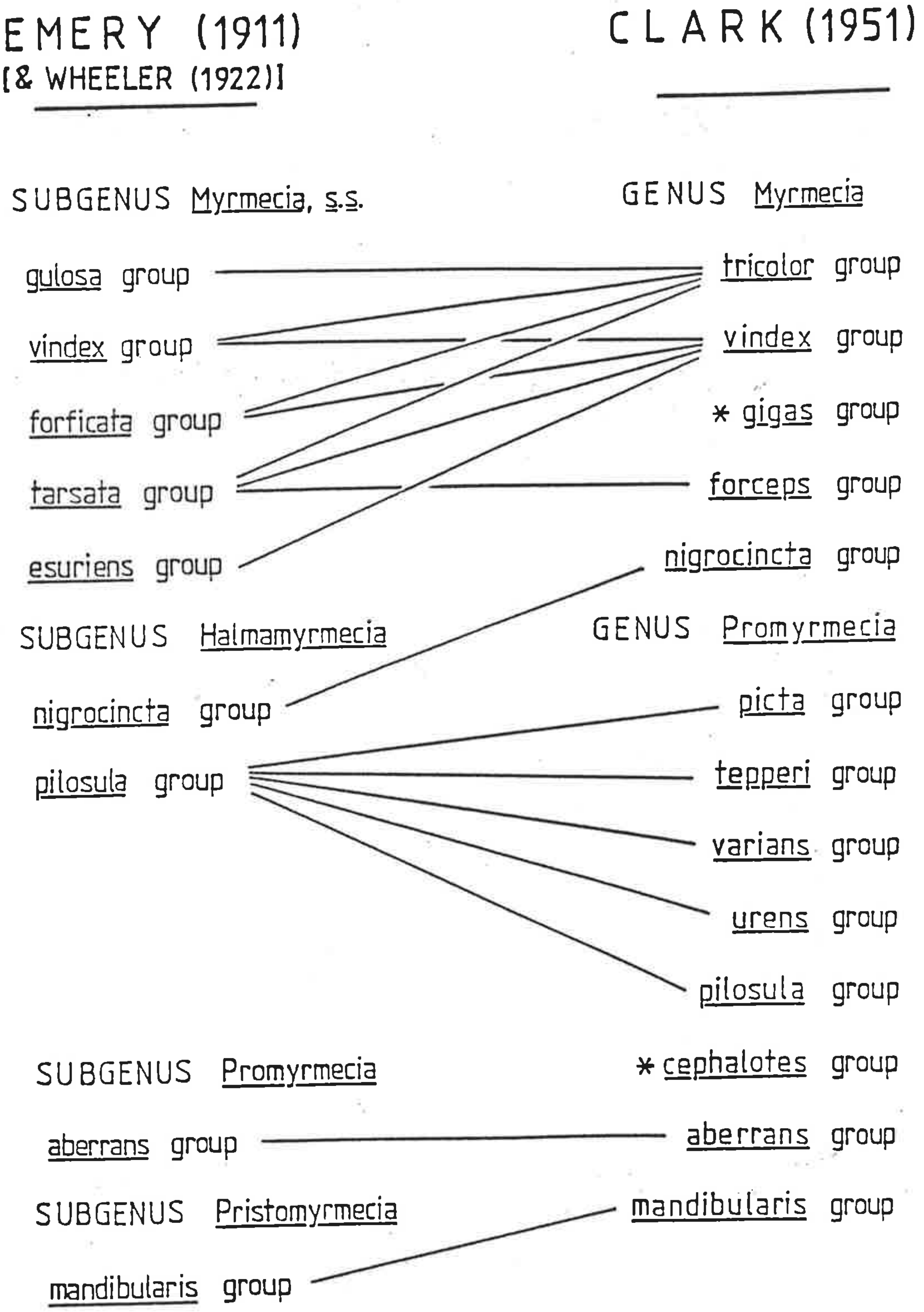

Figure 1. Comparison of the subgeneric classifications for *Myrmecia* proposed by Emery (1911) and Clark (1951). The Emery classification includes a slight modification by Wheeler (1922), who removed the *nigrocincta* and *pilosula* groups from subgenus *Myrmecia*, *s.s.* and placed them in a new subgenus, *Halmamyrmecia*. Lines indicate where species from each group of both classifications reside in the opposing classification. Groups asterisked in the Clark classification contain only species which were described subsequent to Emery's work.

synonymies; and (3) producing a stable infrageneric* classification.

Traditionally, ant taxonomists have concentrated almost entirely on morphological characters of the worker caste because this is by far the most common form encountered - and often the only one that has been collected. But unfortunately, as well as being highly variable, the worker is relatively simple in structure, as it possesses neither wings nor complex genitalia. Therefore in many genera, including Myrmecia, worker morphology does not well reflect the underlying genetic diversity. Many manifest species have almost identical workers.

The small differences between species, and the apparent intraspecific variability of many Myrmecia, have produced considerable nomenclatural problems. To solve these the valid biological species must first be identified, and decisions made as to which names belong to each. These decisions often require examination of the types because many original descriptions contain insufficient detail for us to be sure of their identity. Moreover, holotypes were designated in less than half of the original descriptions, so for the rest it will be necessary to designate lectotypes or neotypes.

Biological species could possibly be determined by means of an exhaustive study of worker morphology, but this would involve numerous measurements and comparisons before it could be assumed that intraspecific variation had been adequately assessed for all species. Even then, suspicion might remain that sibling species with indistinguishable worker morphologies had not been identified.

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* The retention of all bulldog ants and jumpers in a single genus is accepted here and it is recommended that this practice should continue unless thorough study provides a biological justification for splitting it (see Ehrlich and Murphy, 1983).

Fortunately, other taxonomic techniques are now available and some of these can reveal characters which are more likely to provide discernible expression of the underlying genetic differences. Examples are examination of male terminalia (genitalia and terminal gastric segments), karyotype analysis, isozyme studies and mitochondrial DNA sequencing. Coverage of all *Myrmecia* species by each of these techniques is beyond the scope of this study. Instead I have examined male terminalia and analysed karyotypes of all *Myrmecia* species for which I was able to obtain suitable material. The use of male terminalia to develop *Myrmecia* taxonomy was initially proposed by Brown (1953a) who said that '... it is entirely possible that study of the male genitalia, when a sufficient number of males becomes available, will demonstrate a set of cleavages that along with other characters will serve as discontinuities for the proper splitting of *Myrmecia* ...' The taxonomic information obtained from each technique varies, so their usefulness at different taxonomic levels is not the same. In general I expect that karyotype analysis will provide better criteria for distinguishing biological species, while male terminalia will furnish characters more suitable for splitting *Myrmecia* into infrageneric groups.

However, even if these techniques could be used to characterize all species, the problem of assigning names would remain, because karyotypes cannot be determined for any of the types, which are characteristically dried, and because males were included amongst the types of less than one-tenth of the available names. Some of these males cannot be located (e.g. *cephalotes* (Clark), *tepperi* Emery) and at least one type series' only male does not belong to the same species group as the worker syntypes (*pilosula*).

For many species, the process of assigning names and determining synonymies must ultimately involve comparisons between workers from the type series and workers associated with material showing karyotypes or male terminalia. These comparisons would best be made using scanning electron microscopy (SEM), but available techniques require that specimens be coated prior to examination. Most museums will not allow type specimens to be coated, although this policy could change in the future, especially if coatings are developed which can be easily removed or do not obscure colouration. Already several ant taxonomists consider SEM to be very useful (see Taylor and Beaton, 1970) and SE micrographs of holotypes have now been published for some species of *Orectognathus* Smith (Taylor and Lowery, 1972; Taylor, 1977, 1979), *Mesostruma* Brown (Taylor, 1973), *Amblyopone* Erichson (Taylor, 1978a), *Eurhopalothrix* Brown and Kempf (Taylor, 1980) and *Rhytidoponera* Mayr (Ward, 1980, 1984). Although SEM has not been used to examine types in this study, SE micrographs are presented for a representative selection of species. These can later be used to compare the studied species with type specimens.

Having delimited and described the subgenera, species groups, species and intraspecific forms of *Myrmecia* as I perceive them, the other main aim of this study was to convert the resulting phenetic classification into one reflecting phylogeny wherever practicable. This process is described fully in Chapter 4, but briefly, it involved determining polarities (from primitive to derived) for characters from worker morphology, male terminalia, karyotype and behaviour, then constructing a phylogeny which would account for the observed distributions of derived (apomorphic) character states. Generally, a taxon (or group of taxa) supported by numerous synapomorphies (shared derived features), from a variety of sources, is confidently considered to be monophyletic, while one based on a single synapomorphy has its monophyly assumed somewhat tentatively.

The overall aim of this study was to develop a classification for Myrmecia, based on its evolutionary history, using a range of taxonomic techniques, which is testable by examining further characters from an even wider variety of sources.

2. MATERIALS AND METHODS

2.1 Collection of specimens

Myrmecia were mainly collected during extensive field trips in South Australia and Western Australia and some in New South Wales, Queensland, Tasmania and Victoria. Two days searching in the Alice Springs area and a week of fieldwork near Darwin disclosed no *Myrmecia*. The later collecting was directed towards obtaining larvae and pupae for chromosome preparations, while earlier I especially sought males. Emphasis was also placed on collecting species of the *vindex* group, although specimens I encountered from other species groups were always taken.

Collecting was usually done during the warmer months (October - May) when males and brood are more likely to be present, but a few trips were scheduled during winter because cooler temperatures made excavation of large nests much simpler. The precise location of brood and males within the nest varied with the season and is related to the soil temperature profile. In winter, average air temperatures are less than those deep in the nest so that brood (if present) were usually located towards the bottom. However, during daylight hours of the warmer months, males and brood are often in the upper chambers where the temperature is higher and maturation thus accelerated. This is of course the part of the nest most vulnerable to predators. Consequently, if the nest is disturbed, the males rapidly retreat to the lower chambers and some workers quickly pick up the brood and follow, while others rush out to defend the nest. This behaviour was observed numerous times both in the field and in laboratory colonies. Because of this behavioural adaptation for the protection of males and brood, careful excavation of a nest will usually result in these being found in the lowest chambers. To be sure of collecting males and brood (if present), it was therefore unwise to attempt a careful excavation unless the nest was easily accessible. Indeed, for those nests located in hard soil, intertwined among rocks or tree roots, or possibly extending to a depth of several metres, such complete excavation was not practicable. When such nests were located it was often possible to quickly remove the top few decimetres of the nest - before brood could be carried away or males retreat - and any material thus exposed could be easily collected. This method generally gave adequate samples. On several occasions during this study males were seen at the entrances of nests (probably preparing to embark on mating flights) and once even pupae were found on the surface near a nest entrance (colony 430).

2.2 Curation of specimens

Most ants collected, including all males, were killed and preserved in 70% ethanol + 3% glycerol. Some of these were later dried and mounted on points. Considerable material was kept alive and maintained in laboratory colonies.

Each colony sampled (even if only a single specimen was found) was assigned a sequential colony number in my personal collection. This collection now contains material from over 500 colonies - most were collected by myself (often with volunteer assistance), but specimens donated by other biologists were also given colony numbers. These numbers appear often in the text below and are enclosed in square brackets (e.g. [293] represents the 293rd colony added to the collection). Collection data for nests is provided in Appendix 1.

2.3 Other specimens examined

An estimated 10,000 dried and alcohol preserved specimens in museum collections were also examined in this study. Collection data for about 2,000 colonies represented in museums are listed in the 'Material examined' sections of Chapter 3. Colonies were not recorded if: (1) they came from localities which had already been recorded; (2) their localities could not be mapped because they were not listed in the gazetteers and atlases which I consulted; or (3) they belonged to very common species which had already been recorded a number of times from nearby localities. The data has been condensed using abbreviations, museum acronyms and collector acronyms, as defined at the end of this chapter and in Appendices 2 and 3 respectively.

2.4 Maintenance of laboratory colonies

When practicable, forty or so workers, the queen (if captured) and brood were kept alive so that they might produce males (for dissections of male terminalia) or prepupae (for chromosome preparations). These colony fragments were kept in modified Freeland nests (fig. 2; see Freeland, 1958), 'plant pot' nests of my own design (fig. 3) or plastic containers of various shapes and sizes.

The modified Freeland nests and plastic containers were kept in the laboratory at about 20°C, while plant pot nests were buried in soil outside, up to the rim of the pot. The plant pot nests proved to be the most successful type of enclosure because they provided the colony fragment with a temperature and humidity profile similar to that in field nests. Workers were therefore able to select optimal conditions for brood development. Colony fragments kept in these nests often successfully produced adults from eggs laid in captivity.

In contrast, brood of colony fragments kept in plastic containers was forced to develop at about 20°C and in a humidity which depended on how much moisture was present in the container when the lid was replaced. Sometimes pupae were produced from eggs laid in these nests

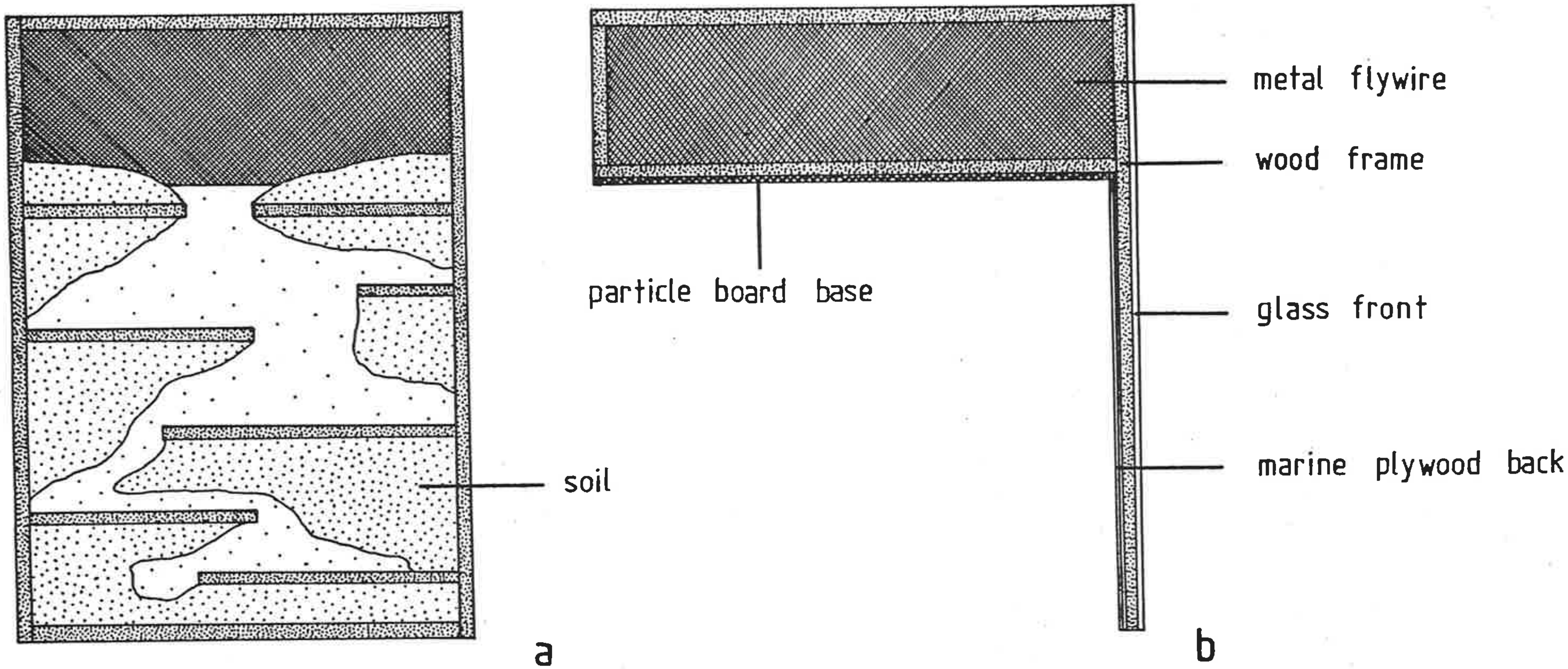


Figure 2. A modified Freeland nest: (a) front view; and (b) side view.

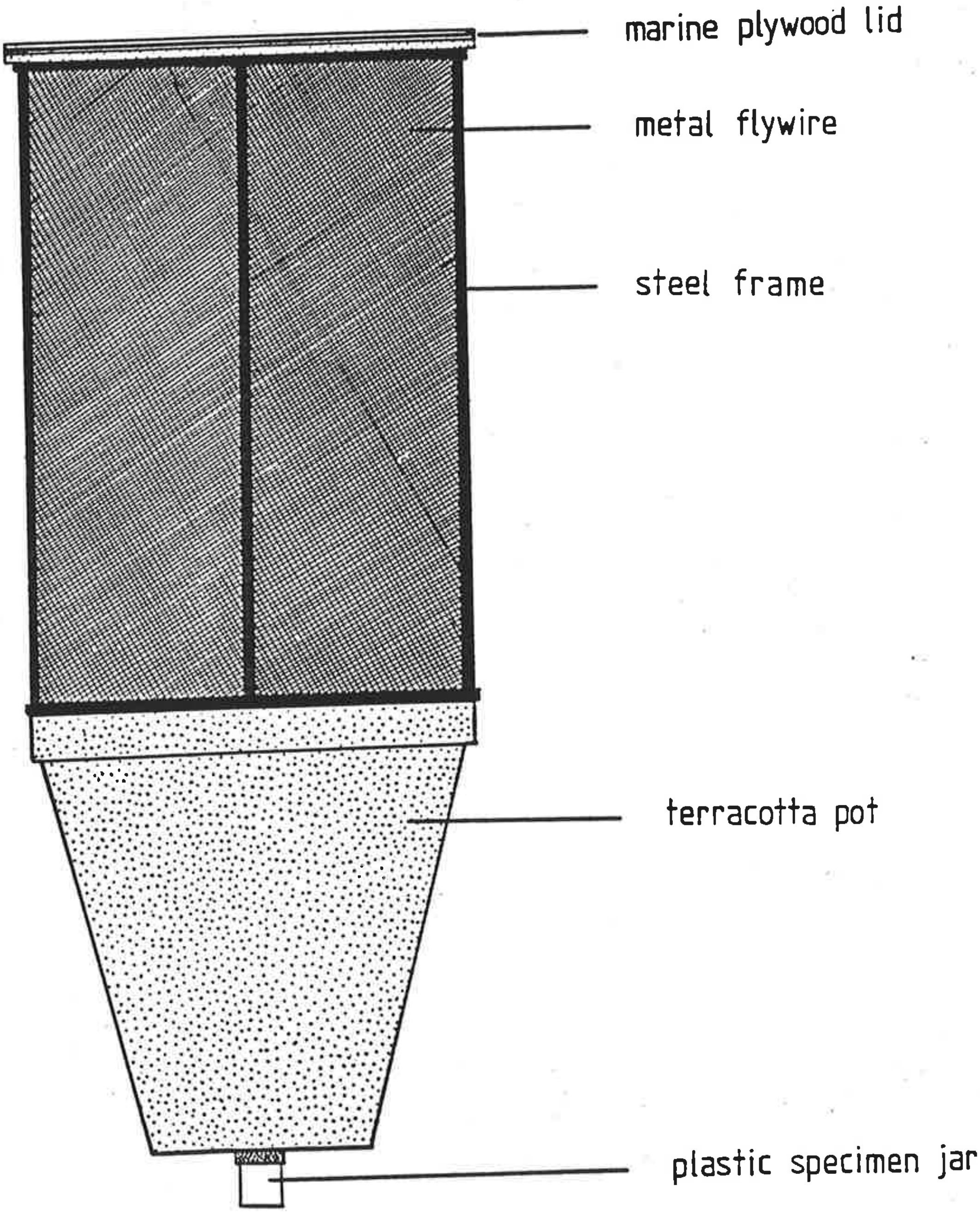


Figure 3. A 'plant pot' nest. The plastic specimen jar has its bottom cut away and replaced by metal flywire to enable good drainage. Its lid has a hole of equal diameter to the hole in the bottom of the terracotta pot and is joined to the pot with silicone sealant. Normally the nest is buried up to the top of the pot, but if it is lifted out of the ground the specimen jar can be unscrewed and pupae tipped out.

but usually the larvae perished before pupation. Colony fragments collected with pupae and placed in plastic containers usually produced some adults before the remaining pupae died.

Like plant pot nests, modified Freeland nests provided the ants with a range of humidities, but they were kept at a constant temperature of about 20°C, and colony fragments housed in them only produced adults from eggs occasionally. Adult mortality was greatest in plastic containers and least in plant pot nests.

2.5 Wax-casting and recovery of specimens

During the study one polydomous (multi-nest) colony was cast in paraffin wax using the technique of Salinitri (1976). It was then excavated and transported back to the laboratory for reconstruction and photographing. Afterwards it was cut into a number of sections which were melted separately so that the location of specimens in the nest could be recorded. Specimens thus freed from the wax were washed in xylene (twice) and absolute alcohol (five times), then stored in 70% alcohol. The size of workers in various parts of the colony was later analysed (see Chapter 3).

2.6 Identification

The species examined were identified as far as possible using Clark's (1951) revision, Brown's (1953b) revisionary notes, and the original species descriptions. In the course of this work all Myrmecia types located in Australia have been examined, including 76 of the 143 holotypes or syntype series, but of the types in museums/institutes overseas so far I have only seen one holotype and two paratype males. Species which could be confidently named were assigned conventional scientific names, but those which seem to be undescribed and those which could not be confidently named were referred to species codes (e.g.

Myrmecia sp.12 (ANIC), *Myrmecia sp.M1* (GPB)).

The codes that include '(ANIC)' follow a formal numbering system, developed by R.W. Taylor (see Imai et al., 1977), which provides ant species in the Australian National Insect Collection (ANIC) with provisional but constant 'handles' until formal names can be assigned to them. The other type of code, which includes '(GPB)', was given to two species which are each known from a single male. The numbers given to these species are prefixed by an 'M' to indicate that they are based on males only. There is currently no provision for numbering such species in the ANIC system.

Vouchers from all but one species studied have been deposited under the appropriate names or codes in the ANIC, while a voucher for the other species (*sp.M2* (GPB)) is in the Museum of Comparative Zoology, Harvard, U.S.A. In addition to white labels with species identification and collection data, these specimens bear a green label which reads *'Voucher specimen, Browning Ph.D. thesis, University of Adelaide, 1987'*.

2.7 Procedure for recognizing species (based on workers)

In the procedure I adopted for recognizing species I began by preparing a list that included all species recognized by Clark (1951) and the more recently described *flammicollis* Brown and *inquilina* Douglas and Brown. Workers of each of these putative species (except *inquilina*, a workerless social parasite) were examined and an assessment was made as to whether: (1) it appeared to contain material belonging to only one species; and (2) it was sufficiently distinct from all similar putative species to warrant its recognition as a separate species. This process enabled recognition of species which can be distinguished on the basis of worker morphology alone. Because museum collections usually consist of worker specimens only, I refer to these species as museum species.

As stated earlier, unfortunately, not all biological species of *Myrmecia* have workers which can be distinguished, so that museum species in this genus are not always equivalent to biological species (*sensu* Mayr, 1942; see below). Therefore, museum species actually include two different types of 'species': (1) those which are equivalent to a single biological species; and (2) those which are equivalent to more than one biological species. In this study, the second type are referred to as *sensu lato* species (or species in the broad sense). Consequently, if a museum species is known, because of inconsistencies in its male terminalia or karyotype, to contain more than one biological species, its name is followed by the abbreviation '*s.l.*' (e.g. *nigriceps* Mayr, *s.l.*). Conversely, all species names which are not followed by such an abbreviation are considered to be biological species. In a few cases the abbreviation *s.s.* (*sensu stricto*, in the narrow sense) is appended to a species name (e.g. *nigriceps*, *s.s.*) to indicate that it is the nominate biological species within a *sensu lato* species that is being discussed.

2.8 Criteria for recognizing species groups

The criteria used for recognizing species groups are phenetic, based on similarities in the male terminalia. A group is recognized if all species examined have male terminalia that are broadly similar but distinct from those of all other groups. Species whose male terminalia are unknown are placed within groups, based on phenetic similarity between workers, or placed in separate groups if their workers are sufficiently distinct. The *auriventris* group is the only group delimited just on worker morphology.

2.9 Compilation of descriptions

In Chapter 3 descriptions are given for species which can be recognized from worker morphology alone and for three others whose workers either do not exist (*inquilina*, a workerless social parasite) or are unknown (*sp.M1* and *sp.M2*). Each description consists of eleven parts as detailed below.

2.9.1 Literature synonymy

This contains all published references which are taxonomically important. Other references are listed separately as 'Biological references (including unpublished theses)'. The symbols ☿, ♀ and ♂ enclosed in square brackets (sometimes in combination) may appear once after each valid name and indicate the first paper to describe worker, female (queen) and male respectively. If papers deal with larvae, male terminalia or karyotypes, this too is indicated in square brackets.

2.9.2 Type data

For valid names the following details of the primary type(s) are given: (1) status and sex (or caste) (e.g. syntype workers (15) or holotype female); (2) type locality, date of collection and collector's name; and (3) location of type(s), indicated by museum acronyms as listed in Appendix 2. Types which I have examined are indicated in round brackets following their details. New synonymies are indicated, and any old synonymies are attributed to the original proposer - both are enclosed in square brackets after the type details.

2.9.3 Worker diagnosis

Worker diagnoses are given for all undescribed species, the 30 species I have illustrated by SEM, and any species with more than one colour form. For other species whose workers are known a reference is given to the most recent description by Clark (1951) or Brown (1953b).

Specimens for SEM work were removed from the alcohol, dried, mounted on points, coated with 5 nm of carbon by thread evaporation and sputter coated with 30 nm of gold. SE micrographs were prepared with a J.E.O.L. JSM U3 microscope, equipped with a vice-like stage to hold the wide end of a point, at an accelerating voltage of 15kV.

The micrographs do not carry scale lines or a magnification factor. This follows a recommendation by Taylor (1985) which is accompanied by a full discussion of their inappropriateness. In summary, the reasons for not using scale lines or magnification factors are: (1) any scale line can be accurate for only one of the infinite number of planes which could be specified normal to the viewing axis because of the enormous depth of field possible in a SE micrograph; and (2) it is not possible to gain identical orientation for the specimens illustrated, yet even a very small amount of tilt can noticeably distort shapes or alter linear measurements between reference points. Absolute scale is indicated instead by stating in each figure caption a series of measurements and indices, determined directly from the specimens themselves, using an optical stereomicroscope fitted with an electronic measuring device. Measurements were made to the nearest hundredth of a millimetre.

The following measurements, illustrated in fig. 4, were taken for each specimen illustrated by SEM:

TL	Total length - sum of axial lengths of body tagmata, including head and closed mandibles, but not extruded parts of the sting.
ML	Mandible length - length of mandible, from posteriormost point to apex, measured in same plane as HL.
HL	Head length - length of head proper, measured in full-face (dorsal) view, from anterior clypeal margin to midpoint of occipital margin.

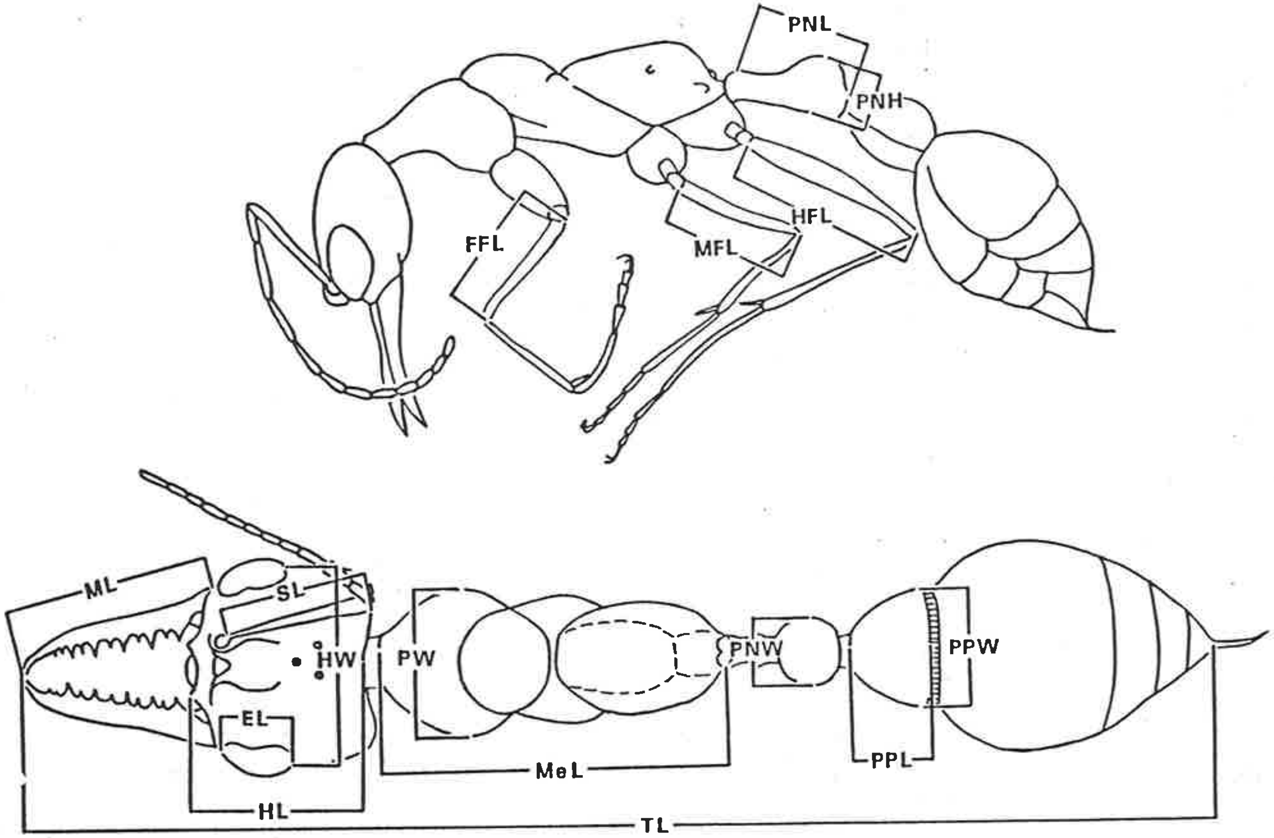


Figure 4. Dorsal and lateral views of a *Myrmecia* worker illustrating the measurements taken from the gold-plated specimens illustrated by SEM in Chapter 3 and/or used in the analysis of worker size variation in Chapter 4. TL = total length, ML = mandible length, HL = head length, HW = head width, SL = scape length, MeL = mesosoma length, PW = pronotum width, PNH = petiolar node height, PNL = petiolar node length, PNW = petiolar node width, EL = eye length, PPL = postpetiole length, PPW = postpetiole width, FFL = front femora length, MFL = middle femora length, HFL = hind femora length.

HW	Head width - maximum width of head, measured in full-face view, excluding eyes.
SL	Scape length - length of first antennal segment, excluding basal constriction.
MeL	Mesosoma length - maximum length of mesosoma from anterior pronotal border (excluding neck) to posterior propodeal border, measured in dorsal view.
PW	Pronotum width - maximum width of pronotum, measured in dorsal view.
PNH	Petiolar node height - maximum height of petiolar node, from summit of node to ventral surface, excluding subpetiolar process, measured in lateral view.
PNL	Petiolar node length - length of node, from midponts of maximum curvature where anterior and posterior faces of node meet anterior and posterior peduncles, measured in lateral view.
PNW	Petiolar node width - maximum width of petiolar node, measured in dorsal view.

The indices which were calculated from these measurements were:

CI	Cephalic index - (HW/HL) X 100
MI	Mandibular index - (ML/HL) X 100
MI2	Mandibular index (2) - (ML/HW) X 100
SI	Scape index - (SL/HL) X 100
PNI	Petiolar node index - (PNW/PNL) X 100
PNI2	Petiolar node index (2) - (PNH/PNL) X 100
MeI	Mesosomal index - (PW/MeL) X 100

An additional six measurements, also illustrated in fig. 4, were taken for some specimens in the analysis of size variation in workers (Chapter 3). These were:

EL Eye length - maximum length of eye, measured in dorsal view.

PPL Postpetiole length - maximum length of postpetiole, measured in dorsal view.

PPW Postpetiole width - maximum width of postpetiole, measured in dorsal view.

FFL Front femora length - maximum length of front femora, measured in full-leg (lateral) view.

MFL Middle femora length - maximum length of middle femora, measured in full-leg view.

HFL Hind femora length - maximum length of hind femora, measured in full-leg view.

2.9.4 Material examined

Localities of all specimens examined are listed in alphabetical order within states. Those from which I have specimens in my personal collection are followed by the colony number(s) in square brackets. Others are followed by collector and museum acronyms in round brackets. The absence of a museum acronym implies that the specimen is in the ANIC. Any registered specimens (namely some from the Tasmanian Museum, Hobart and the British Museum, London) also have their museum registration (or accession) number included. When material from a locality includes primary types of a valid name they are indicated in square brackets, and 'MT', 'SEM' and 'K' in square brackets respectively show that male terminalia, SE micrographs or karyotypes have been prepared. After 'MT' the number of males dissected and date(s) of collection appear, and 'SEM' and 'K' are followed by the number and type of specimens used. The inclusion within square brackets of '♂ only' indicates that only males from that locality (and no workers or queens) have been examined. If, because the male terminalia and/or karyotype are known, a population can be assigned to a biological species within a sensu lato species, then that too is indicated by the name of the species in square brackets.

The localities are marked on distribution maps for each species. When a distribution disagrees with those published by Taylor and Brown (1985) I have included notes in square brackets outlining the discrepancies.

2.9.5 Male terminalia

Where known, the dissected male terminalia are described and illustrated.

Male terminalia were prepared for dissection by: (1) cutting or pulling the posterior half of the gaster away from either spirit specimens, or dried specimens which had been softened in a humid atmosphere for 24 hours; (2) boiling the separated part in 10% caustic potash (potassium hydroxide) for 30-60 minutes; (3) placing it in glacial acetic acid for at least several hours; and (4) transferring the part gaster to clove oil for at least 24 hours. After this time the attached sternites and tergites were removed using jewellers forceps to leave the intact genitalia. The basal ring was also removed using jewellers forceps, then the rest of the genitalia were sliced along the sagittal plane using a piece of razor blade held in a pin vice. The three valves (outer, middle and inner) of one half were then eased apart using jewellers forceps.

The ninth sternite, eighth sternite, fused ninth and tenth tergites and inner valve were mounted in DPX on a slide under a coverslip. The basal ring, and outer and middle valves were not flat enough for mounting in this way so were instead cleaned in alcohol and transferred to glycerol.

The terminalic parts were drawn using a Wild-Heerbrugg M3 dissecting microscope with drawing tube attached. Where thickness of the specimen permitted, details were added or clarified after examination using an Olympus H4 compound microscope. Drawings of each of the terminalic parts (except the basal ring) were made for at least one species of each group (except the *auriventris* group). For one species (*fuscipes* Clark), dorsal, ventral and lateral views of the intact genitalia were also drawn (fig. 61a-c). A scale line is given for the illustrations of the intact genitalia only, but if required the scales of the other drawings can be calculated by multiplying the length of the scale line by 1.0 for figs 62-84, 1.5 for figs 85-94, 2.0 for figs 95-97, 2.5 for figs 98 and 100, and 3.0 for figs 99 and 101.

Various terminologies have been used for the male terminalia of Hymenoptera (e.g. Snodgrass, 1941, 1957; Michener, 1944, 1956; Smith, 1969, 1970a, 1970b; Matsuda, 1976, pp 379-383) based on different theories concerning their origin. Unfortunately, there is still no generally accepted theory for the origin of external insect genitalia (e.g. compare Smith, 1969 and Matsuda, 1976, pp 86-91) and until this is so a stable terminology is unlikely to be agreed upon. However, for taxonomic purposes unstable and cumbersome terminologies are unsuitable and I have preferred a much simpler terminology, based on that used previously for descriptions of ant terminalia (e.g. Forbes, 1967; Ford and Forbes, 1980). In morphology the male terminalia of *Myrmecia* are typically formicid (see Clausen, 1938; Snodgrass, 1941; Krafchick, 1959) and the parts can be easily homologized with those of other ants. Thus, it will be easy for later workers to substitute their terms for those used below.

2.9.6 Karyotypes

Where known the karyotype is described and usually illustrated by karyograms and idiograms.

Chromosome preparations were made from the cerebral ganglia of worker and male prepupae using a slight variation of a technique developed by A.D. Bishop (pers. comm.) which he based on the 'improved air-drying technique' of Imai et al. (1977). The best preparations were made from prepupae which had shed their meconium 3-6 days earlier (i.e. 6-9 days after producing a cocoon). Older material had a diminishing number of mitotic divisions while ganglia of younger prepupae and larvae were too small and diffuse to be manipulated by this technique. Some preparations were made from male prepupae which developed in laboratory colonies from worker-laid eggs.

The steps are: (1) Dissect out the ganglia in hypotonic solution (1% w/v sodium citrate solution) in a small petri dish using jewellers forceps, and remove as much as possible of the fat body, tracheae and epithelial membranes. The dissection should be done under a dissecting microscope with light from above and against a black background. Care should be taken to avoid heating the solution and tissue by either keeping incandescent bulbs about 30 cm from the dissection or using a cold light source. (2) Transfer the ganglia to fresh hypotonic solution and leave for 45 minutes at room temperature. (3) Transfer to colchicine-hypotonic solution (0.005% colchicine in 1% sodium citrate solution) for 15 minutes. (4) Transfer through three changes of acetic ethanol (1:3, glacial acetic acid : absolute ethanol). Allow 2 minutes in the first and about 15 minutes in each of the second and third. (5) Transfer to a pre-cleaned slide (washed in detergent solution, rinsed in distilled water, and stored in absolute alcohol) which has been freshly rinsed in acetic ethanol and wiped. (6) Incline the slide lengthwise at about 30° to a piece of tissue and apply 12-16 drops of fixative (4:2:1, glacial acetic acid : absolute ethanol : distilled water) above the ganglia (not directly onto the ganglia) so that it runs over them. (7) Drain the fixative by inclining the slide lengthwise to 90° for a few seconds, then add 1-2 more drops of fixative and dissociate ganglia using glass mounted minuten pins. This step should be done thoroughly but quickly, ensuring that the fixative does not evaporate completely. (8) Immediately add 2 drops of glacial acetic acid and after 20 seconds again drain off fixative by inclining the slide laterally to 90°. Then place slide horizontally and allow it to dry completely. (9) The glass mounted minuten pins can then be pushed through tissue paper soaked in fixative to clean them before commencing the next preparation.

The number of the preparation was inscribed on the slide using a diamond pencil and repeated with a felt tip pen. No coverslip was used and oil was placed directly on the preparation for examination by light microscopy using an oil immersion lens. The oil could be removed if necessary by dipping the slide in xylene.

It was rarely possible to count the number of chromosomes present in the cells by just looking through the microscope because of the large number (e.g. 2n = 82 for one species) and overlap between their arms. Therefore suitable cells were routinely photographed and then the photographs were photocopied so that each chromosome could be marked as it was counted. Rarely were all chromosome counts from one slide identical. This could be due to a number of factors: (1) one chromosome could totally overlay another or overlay it enough to give the appearance of a single chromosome; (2) a chromosome might not adhere to the slide after fixation; (3) a chromosome might be on the slide but be separated from the rest of the chromosomes due to the bursting of the cell membrane during hypotonic treatment; (4) a chromosome could become mixed with those from another cell for the same reason; and (5) chromosomes from two cells could be adjacent or interspersed so that they could not be distinguished. The first three factors would lead to counts slightly less than the actual number of chromosomes present in the cell before treatment, the fourth would lead to counts of slightly more than the actual number and the last would give a count about double the actual number from one cell. In addition the actual number of chromosomes in a cell could be slightly more or less than the number which is normal for a slide due to unequal division of the chromosomes into the daughter cells during mitosis. And some cells might actually have twice the normal number of chromosomes if, during mitosis, all the chromosomes finished in one daughter cell. Consequently, the finding of variable chromosome numbers on the same slide is not exceptional. Thus, it is the range of numbers found that is used to determine the chromosome number which is presumed to be normal for a species. The normal number is usually the most common, or modal, number counted. Counts often show less than this number, but only rarely are more chromosomes found. Hence, if the modal number is also the highest it is likely that this is the normal count for a species. When I describe karyotypes in Chapter 3, I include the counts from all cells observed so that an estimate of the reliability of my count can be made.

To classify the chromosomes found in this study I measured the lengths of the short and long arms, which can be abbreviated as 's' and 'l' respectively. Based on the arm ratio ($a = l / s$), which reflects the position of the centromere, chromosomes can be classified as one of five types: (1) metacentric (M; $1.0 < a \leqslant 1.4$; i.e. long and short arms more or less equal in length); (2) submetacentric (SM; $1.4 < a \leqslant 3.0$; i.e. long arm noticeably longer than short arm); (3) subtelocentric (ST; $3.0 < a \leqslant 11.0$; i.e. long arm much longer than short arm); (4) acrocentric (A; $11.0 < a < \infty$; i.e. with very small short arms); or (5) telocentric (T; $a = \infty$; i.e. no short arms). The values of the arm ratios which assume critical values for classifying the chromosomes were determined as illustrated in fig. 5. In this study it was not possible to distinguish acrocentrics from telocentrics so I assumed that all chromosomes had at least minute short arms and ignored the telocentric category. For the purposes of discussion it was sometimes necessary to use a broader classification of chromosomes into two types: (1) 'metacentrics' ($\overline{M}$), which include metacentrics, submetacentrics and subtelocentrics; and (2) 'acrocentrics' ($\overline{A}$), which include acrocentrics and telocentrics.

When counting chromosomes in a karyotype it is often possible to detect chromosome polymorphisms. Chromosome polymorphisms which have been found in ants are due to the following rearrangements: (1) Robertsonian rearrangements; (2) pericentric inversions; (3) saltatory changes of constitutive heterochromatin; (4) simple reciprocal translocations; (5) complex translocations, often accompanied by the loss of genetic material; (6) supernumerary (B-) chromosomes; and (7) chromosome deletions (Imai et al., 1977). I will not describe rearrangements (4) and (6) here, because neither were detected in this study and have not been found in any Myrmecia.

Robertsonian rearrangements is used as a general term to cover the processes of centric fusion, centric fission and centric dissociation. Imai et al. (1977) provide indirect evidence which suggests that centric

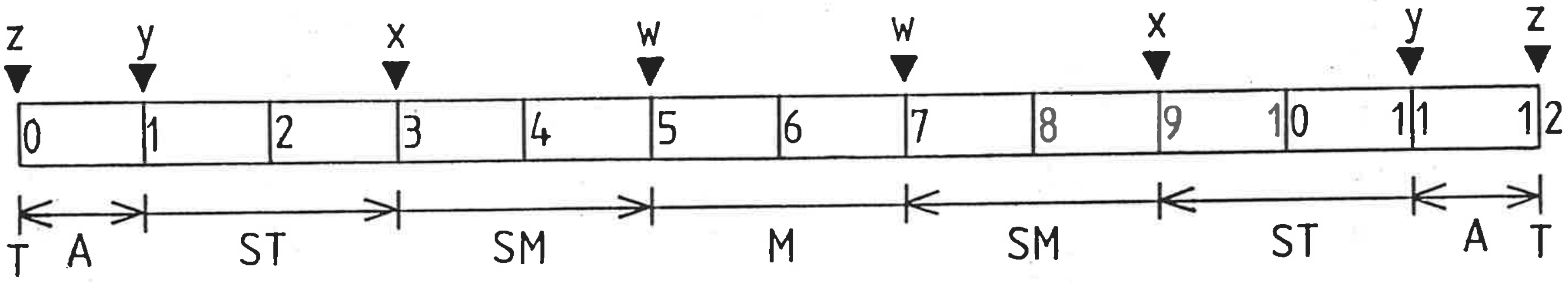


Figure 5. Hypothetical chromosome (12 units long) illustrating where the centromere would be positioned for metacentrics (M), submetacentrics (SM), subtelocentrics (ST), acrocentrics (A) and telocentrics (T). Changeover points between chromosome types are labelled w, x, y and z. The arm ratios at these critical points are: $a_w = 7/5 = 1.4$, $a_x = 9/3 = 3.0$, $a_y = 11/1 = 11.0$ and $a_z = 12/0 = \infty$.

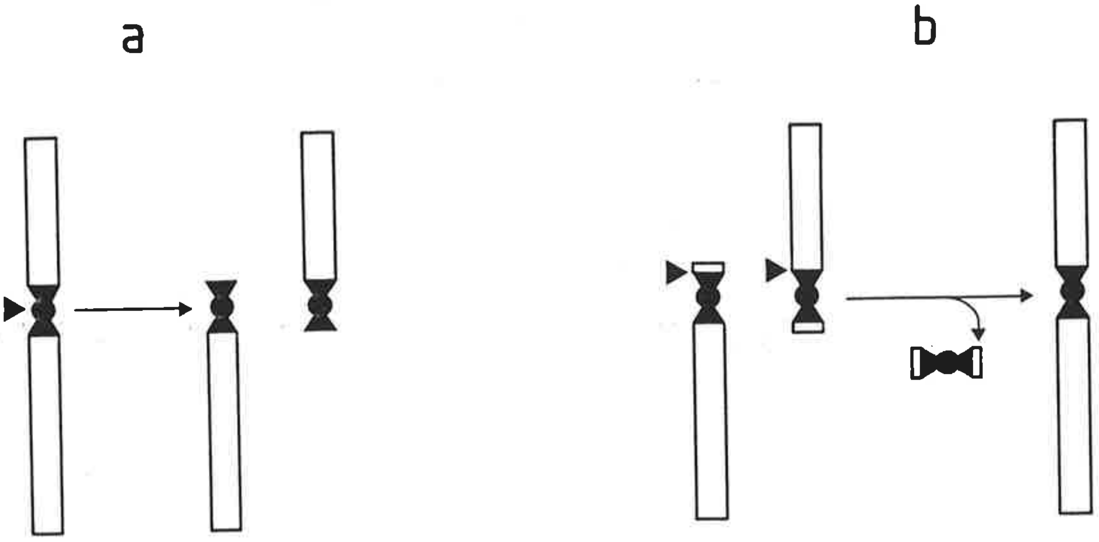
dissociation can be excluded as a significant type of rearrangement in ant karyotype evolution, and I found no contradictory evidence, so I will discuss centric fissions and centric fusions only.

During centric fission, as envisaged by Imai et al. (1977), a break occurs through the centromere (fig. 6a) of a 'metacentric' chromosome to form two telocentrics, which may have centromeres that are too small to function adequately. Tandem growth of constitutive heterochromatin then converts the telocentrics into two acrocentrics with fully functional centromeres. The result of centric fission is that a 'metacentric' chromosome is split into two 'acrocentrics'.

Centric fusion can occur when two 'acrocentrics' break close to their centromeres (fig. 6b). The two long arms fuse and result in a large 'metacentric' chromosome, while the two short arms join to form a very small chromosome that may be lost without any genetic damage to the organism. Centric fusion has the opposite result to centric fission because it joins two 'acrocentrics' into one 'metacentric'.

In this study, I considered that a Robertsonian rearrangement had been detected when I found that a karyotype included an unpaired 'metacentric' and two unpaired 'acrocentrics' whose individual total lengths matched each of the arms of the 'metacentric'. I was unable to determine whether the rearrangements had involved splitting or joining of chromosomes.

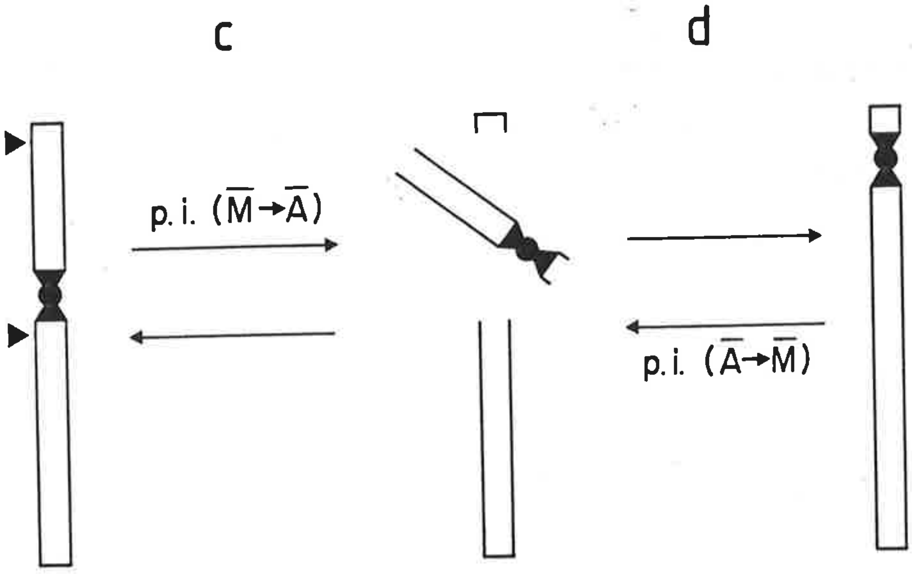
During pericentric inversion two breaks occur on the same chromosome, one on either side of the centromere, and the middle segment (including the centromere) is inverted (fig. 6c-d). This usually results in a morphological change in the chromosome because the centromere position and arm ratios are altered. Depending on where the breaks occur, pericentric inversion can shift the centromere closer to



CENTRIC
FISSION

CENTRIC
FUSION

ROBERTSONIAN
REARRANGEMENTS



PERICENTRIC INVERSION

the middle or nearer to one end. Pericentric inversions which do not shift the centromere occur if the two breaks are equidistant from the centromere, but cannot be detected unless banding patterns are observed. However, when gross morphological change occurs - such as when 'acrocentrics' are converted to 'metacentrics' (p.i. $(\overline{A}\rightarrow\overline{M})$ or 'metacentrics' are converted to 'acrocentrics' (p.i. $(\overline{M}\rightarrow\overline{A})$ - detection of pericentric inversion polymorphisms is possible because the karyotype will include two unpaired chromosomes of equal length but different arm ratios. It is rarely possible to determine whether the inversion has increased or decreased the arm ratio.

Imai et al. (1977) found evidence, in a number of ant species, of polymorphisms involving pairs of chromosomes with *saltatory changes* (different amounts) *of constitutive heterochromatin*. In this type of polymorphism one chromosome of a pair appears to have increased the amount of heterochromatin in its short arm by tandem gene duplication or saltatory replication. It is also possible that in some instances the polymorphism may have arisen by deletion of heterochromatin from one chromosome of the pair. Such polymorphisms are suspected when two chromosomes, which can only be paired with each other (because the rest of the chromosomes have already been matched in pairs), have one arm the same length but the other markedly different. This can be confirmed if the constitutive heterochromatin is stained by Giemsa as sometimes occurs during routine staining, and the unequal arms stain darkly (i.e. C-positive).

Complex translocations, are rearrangements that involve at least three breaks and exchange of segments between chromosomes. Imai et al. (1977) found one complex translocation polymorphism in *Myrmecia*, which converted three homologous pairs of chromosomes into six chromosomes of different lengths. Having obtained good C-banding for these karyotypes, they were able to suggest a plausible description for the breaks and exchanges which could be involved in the rearrangement. Two karyotypes examined in this study contained six chromosomes which could not be paired, and appeared to be due to the same or a similar complex translocation.

Chromosome deletions can be detected when a karyotype contains an unpaired chromosome. The possibility that such a chromosome is supernumerary and has resulted from non-disjunction should be considered, but can be excluded if the chromosome is different in size to all others in the complement.

The best photograph for each species was used to prepare a karyogram by cutting around the individual chromosomes and matching the pairs as closely as possible, using their size and centromere position. Idiograms were prepared from these karyograms by measuring the relative lengths on either side of the centromere and expressing them as a percentage of the total chromosome length (%TCL) within the cell.

2.9.7 Taxa included

Biological species, colour forms and cytotypes recognized within each museum species are listed with notes as to status.

2.9.8 Nest structure

Descriptions are given for each species.

2.9.9 Biological references

Any references that are biological rather than taxonomic in content, and all unpublished theses, are listed for each species.

2.9.10 Comments

Comments made include: (1) status of the species; (2) reasons for making or accepting synonymies, and (3) any unusual features.

2.10 Procedure for recognizing biological species

To recognize biological species within *sensu lato* species I made use of the generally accepted biological species definition. According to Mayr (1940, 1963), '... species are groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups ...' Consequently, determining whether two populations belong to the same biological species requires that an assessment be made about whether individuals from the two populations are capable of producing fertile offspring. Unfortunately, I only observed copulatory behaviour between captive *Myrmecia* males and queens on a few occasions and no offspring were produced as a result. I attempted to employ the forced copulation technique of Cupp et al. (1973), used by them to produce hybrid offspring between the fire ants, *Solenopsis richteri* Forel and *S. invicta* Buren, but this was not successful. The technique involved (1) anaesthetizing a virgin queen with carbon dioxide, (2) decapitating a male, (3) with jewellers forceps, grasping the queen by the wings in one hand and the male by the mesosoma in the other, and (4) presenting the queen's gaster to the male terminalia. In a number of attempts using various species in the *vindex* group I was unable to get the male terminalia to grasp the females gaster as occurs during copulation.

To try to make crosses in the field was impracticable because (1) the populations produced reproductives at slightly different times of the year, (2) the populations were sometimes separated by thousands of kilometres, and (3) the mating flights occurred on only a few nights of each year when the right combination of temperature, humidity and wind conditions were available.

Consequently, to determine biological species, I had to rely upon other, less direct methods to estimate whether populations were capable of interbreeding. Although their workers were indistinguishable, some biological species had male terminalia which were easily separated. In these cases a morphological species concept was used to estimate the biological species involved.

When karyotypes were available they were of considerable value for assessing the interbreeding potential of two populations. For the populations to be capable of interbreeding, the karyotypes must be sufficiently similar for their gametes to cross-fertilize and form zygotes which can undergo meiosis. If the chromosomes in the karyotypes are morphologically too dissimilar, the chromosomes will be unable to pair during synapsis, a critical part of meiosis. Determining when two karyotypes are too dissimilar to partake in meiosis is difficult because of the possibilities that chromosomes of dissimilar morphology and size may still form bivalents and trivalents if large amounts of their DNA can be aligned. Consequently, if only a few chromosome rearrangments separate two karyotypes it is likely that the populations possessing them can potentially interbreed, but if they are separated by many rearrangements then they almost certainly belong to distinct biological species. The types of rearrangements which distinguish karyotypes in ants are usually Robertsonian rearrangements or pericentric inversions. Robertsonian rearrangements offer less barriers to meiosis than do pericentric inversions because their products can still form trivalents during synapsis, but the products of pericentric inversions pair with some difficulty (fig. 7) and often have problems later in meiosis due to crossing-over.

When two populations are sympatric it is possible to determine whether chromosome polymorphisms indicate that they belong to separate

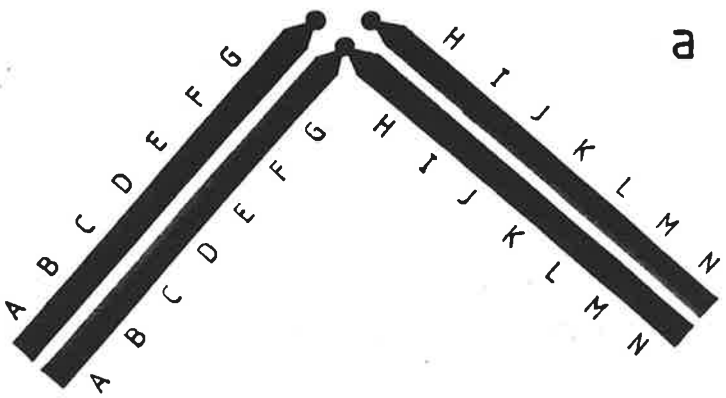
Figure 7. Drawings of heterozygote chromosomes when paired in meiosis:

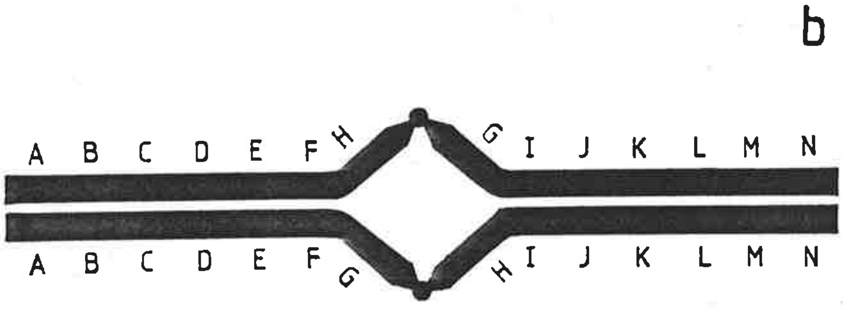
(a) Robertsonian rearrangement - all genes pair - minimal meiotic difficulties;

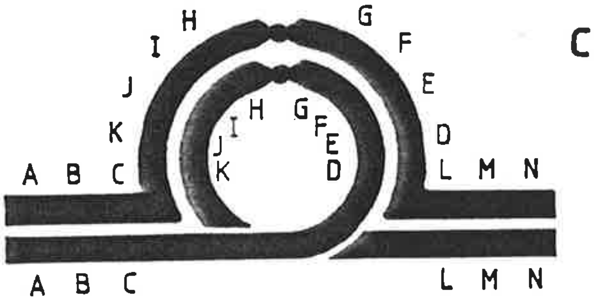
(b) Pericentric inversion when inverted region is very small - genes in inverted region unable to pair - minimal meiotic difficulties;

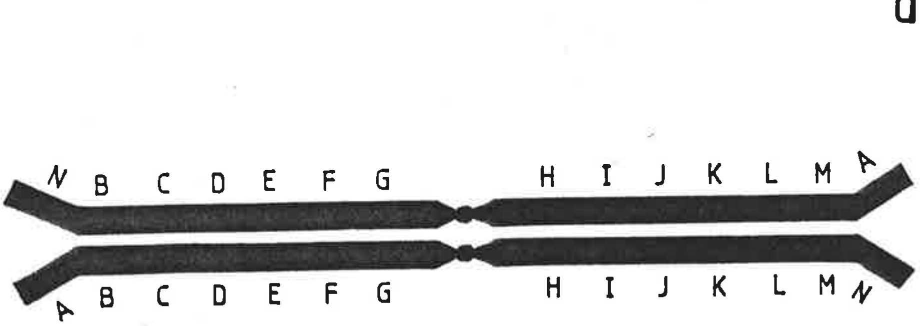
(c) Pericentric inversion when inverted region is large enough for maneuvering - one chromosome buckles, while its partner loops, enabling them to pair gene for gene - considerable difficulties likely later in meiosis, because crossing-over can result in unbalanced recombinant chromosomes; and

(d) Pericentric inversion when inverted region is very large - genes in the inverted region pair, but the uninverted ends cannot - considerable difficulties likely later in meiosis, because crossing-over can result in unbalanced recombinant chromosomes.


a
A B C D E F G
A B C D E F G
H I J K L M N
H I J K L M N


b
A B C D E F H
G I J K L M N
A B C D E F G
H I J K L M N


c
A B C K J I H
G F E D L M N
J I H G F E D K
A B C
L M N


d
N B C D E F G
H I J K L M A
A B C D E F G
H I J K L M N

species by looking for nests which are heterozygous for the polymorphism. For example, ten nests are karyotyped at one locality and six are homozygous for a certain chromosome rearrangement (i.e. pericentric inversion, Robertsonian rearrangement) and the other four are homozygous for its absence. The failure to find any nests which are heterozygous strongly indicates that the two populations are not interbreeding, because if they were, it would be expected that they would be in Hardy-Weinberg equilibrium. Therefore the number of nests without the rearrangement, heterozygous for the rearrangement and homozygous for the rearrangement should approach 1.6, 4.8 and 3.6 respectively. These expected values are determined from the Hardy-Weinberg Law ($p^2 + 2pq + q^2 = 1$, where p and q are the relative frequencies of gametes with and without the rearrangement). The χ^2-test can be used to evaluate the departure of the observed numbers from those which can be calculated from the known values of p and q ($p = 0.4$ and $q = 0.6$). The χ^2 value is the sum of (observed - expected)^2/ expected for each class. In this example χ^2 is
$(4 - 1.6)^2/ 1.6 + (0 - 4.8)^2/ 4.8 + (6 - 3.6)^2/ 3.6 =$
$3.6 + 4.8 + 1.6 = 10.0$, which far exceeds the minimum value of 3.84 (one degree of freedom, 5% significance level) required to reject the hypothesis that the two populations are interbreeding. Furthermore, in Table 1 it can be seen that the value of 3.84 is exceeded whenever four or more nests have been karyotyped and nests homozygous for both presence and absence of a rearrangement have been found, but no heterozygotes are known. However, Bodmer and Cavalli-Sforza (1976, p. 722) state that the χ^2-test should not be fully trusted in such examples unless the number of nests expected in the least common of the three classes (two homozygous and one heterozygous) is at least 5.0.

TABLE 1. χ^2 values calculated from the Hardy-Weinberg Law for various combinations of nests with and without a rearrangement when no heterozygotes are found. Underlined values support the hypothesis that the nests are from two non-interbreeding populations.

		NUMBER OF NESTS WITHOUT REARRANGEMENT									
		1	2	3	4	5	6	7	8	9	10
	1	2.0									
	2	3.0	4.0								
NUMBER	3	4.0	5.0	6.0							
OF	4	5.0	6.0	7.0	8.0						
NESTS	5	6.0	7.0	8.0	9.0	10.0					
HOMOZYGOUS	6	7.0	8.0	9.0	10.0	11.0	12.0				
FOR	7	8.0	9.0	10.0	11.0	12.0	13.0	14.0			
REARRANGEMENT	8	9.0	10.0	11.0	12.0	13.0	14.0	15.0	16.0		
	9	10.0	11.0	12.0	13.0	14.0	15.0	16.0	17.0	18.0	
	10	11.0	12.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0

In Table 2 it is evident that this second condition is not satisfied unless at least ten nests in each of the homozygous classes are karyotyped and no heterozygous nests are found. Unfortunately, I was never able to karyotype this number of nests from the same area so that I was unable to employ the χ^2-test in this way. Instead I had to rely upon making a decision about whether two karyotypes were sufficiently different to render them incapable of interbreeding. For allopatric populations this was the only criterion available for making such an assessment. As an arbitrary rule, I did not recognize *Myrmecia* populations as distinct biological species on the basis of karyotype alone, unless they differed by at least ten Robertsonian rearrangements

TABLE 2. Minimum number of nests in any of the three classes as expected from the Hardy-Weinberg for various combinations of nest numbers. Underlined values support the hypothesis that the nests are from two non-interbreeding populations.

		NUMBER OF NESTS WITHOUT REARRANGEMENT										
		10	11	12	13	14	15	16	17	18	19	20
	10	5.00										
	11	4.76	5.50									
NUMBER	12	4.55	5.26	6.00								
OF	13	4.34	5.04	5.76	6.50							
NESTS	14	4.17	4.84	5.54	6.26	7.00						
HOMOZYGOUS	15	4.00	4.65	5.33	6.04	6.76	7.50					
FOR	16	3.85	4.48	5.14	5.83	6.53	7.26	8.00				
REARRANGEMENT	17	3.70	4.32	4.97	5.63	6.32	7.03	7.76	8.50			
	18	3.57	4.17	4.80	5.45	6.13	6.82	7.53	8.26	9.00		
	19	3.45	4.03	4.65	5.28	5.94	6.62	7.31	8.03	8.76	9.50	
	20	3.33	3.90	4.50	5.12	5.76	6.43	7.11	7.81	8.53	9.26	10.0

or five pericentric inversions in the haploid condition. I consider this to be a conservative approach.

2.11 Abbreviations

Most abbreviations which are used in the text and appendices are listed below. However, these do not include acronyms for museums and collectors which are listed in Appendices 2 and 3 respectively.

A	acrocentric chromosome
$\bar{A}$	"acrocentric" chromosome in the broad sense (i.e. acrocentric or telocentric)
A.C.T., ACT	Australian Capital Territory
auct.	*auctorum* (of authors)

cf.	*confer*
CI	cephalic index
C.P., CP	Conservation Park
cu	collector unknown
du	date (of collection) unknown
E	East
emend.	emendation
et al.	*et alii*
fig./figs	figure/figures
gp	group
HL	head length
HW	head width
H.S., HS	Homestead
M	metacentric chromosome
$\overline{M}$	"metacentric" chromosome in the broad sense (i.e. metacentric, submetacentric or subtelocentric)
MeI	mesosomal index
MeL	mesosoma length
MI	mandibular index
MI2	mandibular index (2)
ML	mandible length
N	north
NE	north east
N.F.	*nombre fondamental*
N.P., NP	National Park
n / 2n	haploid / diploid chromosome number
nr	near
N.R., NR	Nature Reserve
N.S.W., NSW	New South Wales
N.T., NT	Northern Territory
NW	north west
p./pp	page/pages
pers. comm.	personal communication
pl./pls	plate/plates
PNH	petiolar node height
PNI	petiolar node index
PNI2	petiolar node index (2)
PNL	petiolar node length

PNW	petiolar node width
P.S.	Pumping Station
PW	pronotum width
Qld	Queensland
R.H., RH	Rockhole
R.S., RS	Railway Siding
S	south
S.A., SA	South Australia
SE	south east
SE micrographs	scanning electron micrographs
SEM	scanning electron micoscopy
S.F., SF	State Forest
SI	scape index
SL	scape length
SM	submetacentric chromosome
sp. *nov*.	*species novum* (new species)
ST	subtelocentric chromosome
s.*l*.	*sensu lato* (in the broad sense)
sp./spp	species/species (plural)
sp. *indet*.	*species indeterminata* (indeterminate species)
s.*s*.	*sensu stricto* (in the narrow sense)
subsp.	subspecies
SW	south west
syn. *nov*.	*synonym novum* (new synonym)
Tas., Tas	Tasmania
TL	total length
T.S.	Tracking Station
var.	variety
Vic., Vic	Victoria
W	West
W.A., WA	Western Australia
W.H., WH	Waterhole
♀/♀♀	female/females
♂/♂♂	male/males
⚲/⚲⚲	worker/workers

3. WORKER MORPHOLOGY

3.1 Introduction

In this chapter I present descriptions of 60 *Myrmecia* species which can be recognized from workers alone. I also describe two species which are known only from males (*sp.M1* and *sp.M2*), a species which is workerless and known only from queens (*inquilina*) and two indeterminate species which are almost certainly synonyms of species from the *forficata* group. Six other biological species which can only be recognized by their male terminalia and/or karyotypes are dealt with under the descriptions of species which have identical workers (e.g. *desertorum* Wheeler, *nigriceps*, *s.s.*, *sp.11* (ANIC) and *sp.13* (ANIC) are all dealt with under *nigriceps*, *s.l.*). This brings my determination of the number of biological species in *Myrmecia* to 69. Taylor (1978b) estimated a similar number (about 65), but Taylor (1987) catalogued 86.

The species descriptions are ordered alphabetically within species groups (with undescribed species placed last) and the ordering of groups is taxonomic (see Chapter 4). My procedures for recognizing species groups and species are outlined in Chapter 2 and justifications for individual cases are presented in the 'Comments' sections below. All illustrations for this chapter are grouped together at its end so that comparisons can be made more easily.

3.1.1 Scanning electron microscopy of workers

Scanning electron micrographs of whole workers are presented for 31 species, including at least one species from each species group (except the *picta* group). These are the first taxonomic illustrations of *Myrmecia* prepared by SEM. For most species only one specimen has been illustrated but, as stated earlier, *Myrmecia* workers are thought to be highly variable. Consequently, four specimens of one species (*fuscipes*; from three localities) have been illustrated, in an attempt to give some idea of the amount of variation which may be expected. As an initial attempt to quantify the size differences between species a series of ten measurements (defined in Chapter 2) were taken from each specimen illustrated by SEM (Appendix 4). These were used to calculate seven indices (also defined in Chapter 2) which are listed in Appendix 5. The same seven indices were calculated separately for each of Clark's (1951) figures of *Myrmecia* workers (Appendix 6). The values for indices obtained from my measurements and Clark's figures are compared in Table 3 to provide a first approximation of the ranges expected within species groups. Size variation in workers of *fuscipes* and *nigriceps*, *s.l.* is investigated by morphometric analysis later in this chapter.

3.1.2 Male terminalia

Descriptions and illustrations of the dissected male terminalia (genitalia and terminal gastral segments) have been published for only two *Myrmecia* species (*vindex* Smith and *tarsata* Smith; Forbes, 1967). In addition, Emery (1911) figured the intact genitalia of *pyriformis* Smith, and Gray (1966) sketched outlines of several segments of the terminalia of *hillstonensis* (unpublished name) [= *dispar* (Clark)]. And more recently, Browning (1979) described the terminalia of 18 species: *fuscipes* [included *fuscipes* and *nigriceps*, *s.s.*]; *vindex* var. *basirufa* Forel [= *vindex*]; ?*gracilis* Emery [= *rufinodis* Smith]; *gulosa*; *pyriformis*; *tarsata*; *forceps* Roger; *nigriscapa* Roger; *pulchra* Clark; *nigrocincta*; *sp.10* (ANIC) [= *sp.17* (ANIC)]; *sp.A* [= *fuscipes*]; *sp.B* [= *desertorum*]; *forficata* [= *forficata*, *s.s.*]; *sp.C* [= *sp.9* (ANIC)]; *brevinoda* Forel [= *brevinoda*, *s.s.*]; ?*decipiens* Clark [= *decipiens*]; and *hirsuta* Clark.

TABLE 3 Comparison of various indices (described in Chapter 2) in different *Myrmecia* species groups (ranges determined from indices presented in Appendices 5 and 6).

Species group (number of individuals measured)	Indices (range)						
	CI	MI	MI2	SI	PNI	PNI2	MeI
forceps group (N = 3)	99-103	111-121	107-122	113-122	48-52	51-53	34-37
forficata group (N = 18)	94-115	96-122	95-119	94-115	44-77	49-73	33-42
mjobergi group (N = 2)	80-86	121	142-152	118-121	49-50	53-54	32-33
nigriscapa group (N = 3)	98-104	105-109	102-111	112-117	58-62	63-66	36-38
tarsata group (N = 2)	99-101	103-105	102-107	106-107	62-71	69-76	37-42
auriventris group (N = 2)	101-108	99	91-98	94-98	62-70	63-82	39-41
flavicoma group (N = 3)	101-103	100-106	99-103	96-112	61-73	57-62	34-38
gulosa group (N = 2)	95-107	107-110	103-113	118-120	47-63	52-59	31-38
simillima group (N = 10)	95-106	98-114	96-115	94-129	43-63	45-63	33-42
vindex group* (N = 25)	91-102	92-115	99-128	111-127	41-56	42-61	32-37
esuriens group (N = 7)	97-112	93-108	86-111	87-106	57-92	63-97	35-43
nigrocincta group (N = 5)	93-105	107-115	102-116	91-105	49-52	46-56	37-47
harderi group (N = 5)	103-117	96-110	91-104	73-88	72-88	68-85	43-48
pilosula group (N = 39)	99-121	76-114	68-114	67-102	63-106	64-107	41-59
mandibularis group (N = 10)	101-113	94-116	86-107	69-85	75-86	72-98	44-51

TABLE 3 (cont.)

Species group	Indices (range) CI	MI	MI2	SI	PNI	PNI2	MeI
picta group (N = 1)	101	87	87	71	74	78	42
_sp.15_ group (N = 1)	103	88	85	80	65	78	37
fucosa group (N = 2)	96-97	95	98-99	73-78	63-67	68-71	39
urens group (N = 7)	96-104	88-102	87-106	59-82	59-79	60-77	37-44

* Excluding _rowlandi_ which is somewhat doubtfully placed in the _vindex_ group. _M. rowlandi_ has indices which fall within the range for the _vindex_ group except for two (SI = 85, MeI = 43).

Of the above species _nigrocincta_ and _dispar_ are jumpers, while the others are all larger, walking species.

The male terminalia of 50 _Myrmecia_ species, including 21 jumpers, are described and illustrated below. Of these, 31 are newly described, but those that were already known have also been included for purposes of comparison. All species dealt with by Browning (1979) have been re-described and many of the illustrations re-drawn.

3.1.3 Karyotypes

Apart from this study, karyotypes of 13 _Myrmecia_ species have been published (Imai et al., 1977; Crosland and Crozier, 1986; Imai and Taylor, 1986) and those of two others are known (A.D. Bishop, pers. comm.). Each of the 15 species has a different chromosome number, the range being 2n = 2-88 (Table 4). Three nominal species (_pilosula_, _fulvipes_ Roger and _piliventris_ Smith) were found to contain siblings

TABLE 4. Chromosome numbers of 15 *Myrmecia* species known apart from this study.

SPECIES GROUP Species (name used by source)	Locality	(n) 2n	Features of interest	Source
FORFICATA GROUP				
forficata, *s.s.* (*forficata*)	Jenolan Caves (N.S.W.)	50-51	Robertsonian polymorhpism	Imai et al. (1977)
	Honeysuckle Creek (N.S.W.)	49-50	Robertsonian polymorphism	A.D.Bishop (pers. comm.)
pyriformis	Leumeah (N.S.W.)	(41) 81	Robertsonian polymorphism & slight growth of heterochromatin	Imai et al. (1977)
	Tharwa (A.C.T.)	(41) 82		A.D.Bishop (pers. comm.)
	Belair (S.A.)	82		A.D.Bishop (pers. comm.)
brevinoda, *s.s.* (*brevinoda*)	Leumeah (N.S.W.)	84	Substantial heterochromatic growth	Imai et al. (1977)
	Milperra (N.S.W.)	84	Substantial heterochromatic growth	A.D.Bishop (pers. comm.)
decipiens	Bungwahl (N.S.W.)	86-88	Robertsonian polymorphism & substantial heterochromatic growth	A.D.Bishop (pers. comm.)
regularis	Karridale (W.A.)	40		A.D.Bishop (pers. comm.)
GULOSA GROUP				
gulosa	Leumeah (N.S.W.)	38		Imai et al. (1977)
NIGROCINCTA GROUP				
nigrocincta	Leumeah (N.S.W.)	22		Imai et al. (1977)

TABLE 4 (continued).

Species (name used by source)	Locality	(n) 2n	Features of interest	Source
PILOSULA GROUP				
pilosula, *s.l.* (*pilosula*)	Tidbinbilla (A.C.T.)	(1) 2		Crosland and Crozier (1986)
(*ruginoda*)	Victoria	(15)		Crozier (1966)
(*pilosula*)	Picadilly Circus (A.C.T.)	31-32	Chromosome deletion & substantial heterochromatic growth	Imai et al. (1977)
(*pilosula* = *ruginoda*)	Leumeah (N.S.W.)	9-10	Pericentric inversion Complex translocation	Imai et al. (1977)
cephalotes (*cephalotes*)	12 km S of Coombah (N.S.W.)	66		Imai et al. (1977)
MANDIBULARIS GROUP				
fulvipes, *s.l.* (*fulvipes*)	Picadilly Circus A.C.T.	60		Imai et al. (1977)
(*sp.* *cf.* *fulvipes*)	Leumeah (N.S.W.)	12		Imai et al. (1977)
piliventris, *s.l.* (*piliventris*)	Black Mountain (A.C.T.)	(2) 4		Imai and Taylor (1986)
	Jerrabomberra Hill (N.S.W.)	(2)		Imai and Taylor (1986)
	Nelligen Creek Bridge (N.S.W.)	(2)		Imai and Taylor (1986)
(*piliventris*)	Black Mountain (A.C.T.)	(34)		Imai and Taylor (1986)

with marked karyotypic differences (Imai et al., 1977; Imai and Taylor, 1986). Small differences in worker morphology were noted between the *fulvipes* siblings (2n = 60 and 2n = 12) but none between the *pilosula* (n = 1, 2n = 2, 2n = 9,10 and 2n = 31,32) or *piliventris* (n = 2, 2n = 4 and n = 34) siblings. The nominal species *brevinoda* was also found to contain two siblings (2n = 84 and 2n = 86-88; A.D. Bishop, pers. comm.; Crozier, 1980) with indistinguishable workers. However, I have examined the terminalia of males associated with each of the *brevinoda* cytotypes and found quite marked differences between them (see below).

Karyotypes of a number of these species exhibit chromosome polymorphisms. Robertsonian polymorphisms have been reported in three species: (1) *forficata* (2n = 49-50, A.D. Bishop, pers. comm.; 2n = 50-51, Imai et al., 1977); (2) *pyriformis* (n = 41, 2n = 81, Imai et al., 1977); and (3) *decipiens* (2n = 86-88, A.D. Bishop, pers. comm.). A pericentric inversion polymorphism and a complex translocation polymorphism were found in one *pilosula* cytotype (2n = 9-10, Imai et al., 1977). In another *pilosula* cytotype a deletion polymorphism involving loss of one chromosome was detected (2n = 31-32, Imai et al., 1977). And in three species substantial heterochromatic growth in most chromosomes has been reported: (1) *brevinoda* (Imai et al., 1977; A.D. Bishop, pers. comm.); (2) *decipiens* (A.D. Bishop, pers. comm.); and (3) *pilosula* (2n = 31-32; Imai et al., 1977). In addition, *pyriformis* appears to have one or two chromosomes with considerable heterochromatic growth (Imai et al., 1977).

In this study I have karyotyped 22 species of which only two had been karyotyped before. Chromosome numbers (n, 2n) and *nombres fondamentaux* (N.F.) for each colony karyotyped in this study are presented in Table 5. The *nombre fondamental*, or number of major

TABLE 5. Chromosome numbers of 22 *Myrmecia* species determined during this study.

SPECIES GROUP Species (colour form)	Colony number	(n) 2n	N.F.	Features of interest
FORCEPS GROUP				
forceps				
(singularis)	140	62	62	Heterochromatic growth
(obscuriceps)	281	62	62	Heterochromatic growth
FORFICATA GROUP				
forficata, *s.l.* *sp.7*	177	c.66	c.84	
pyriformis	259	82	84	Heterochromatic growth
	259	(41)(?)	84(?)	Heterochromatic growth
	495	82	82	Heterochromatic growth & pericentric inversion
SIMILLIMA GROUP				
arnoldi	437	14	26	
rufinodis	269	10	18	
VINDEX GROUP				
atrata	240	76	77	Robertsonian polymorphism & chromosome deletion
	226	78	78	
	227	(39)	78	
fulgida	431	40	78	
fuscipes	247	(37)	80	
	413	76	76	
	430	76	78	
	468	76	78	
	471	76	78	
	156	76	76	
	155	76	76	
	159	75	76	Robertsonian polymorphism

TABLE 5 (cont.).

SPECIES GROUP Species (colour form)	Colony number	(n) 2n	N.F.	Features of interest
nigriceps, *s.l.*				
sp.11	171	36	68	
sp.13	412	40	80	
	279	(21)	80	
desertorum	147	(32)	80	
nigriceps, *s.s.*	451	70	80	
	453	(36)	78	
	459	74	78	
	443	74	78	
	466	74	78	
	353	74	78	
	486	74	78	
	339	74	80	
	272	74	80	
	272	(37)	80	
	441	74(?)	78(?)	
	453	75	78	
	461	78	80	
	470	78	80	
	464	(39)	80	
princeps	487	30	50	
	161	40	56	
vindex	418	47	76	Robertsonian polymorphism
(*vindex*, *s.s.*)	420	47	76	Robertsonian polymorphism
	463	47	76	Robertsonian polymorphism
	417	52	76	
	465	58	78	
sp.12	306	74	78	
	476	74	78	
	478	74	78	
sp.14	218	56	76	
	202	(31)	76	
	202	62(?)	76(?)	
sp.16	416	67	76	Robertsonian polymorphism
	432	67	76	Robertsonian polymorphism
sp.17	493	34	68	

TABLE 5 (cont.).

SPECIES GROUP Species (colour form)	Colony number	(n) 2n	N.F.	Features of interest
PILOSULA GROUP				
michaelseni	287	c.64	c.70	
pilosula, s.l.	503	16	19	Complex translocation & pericentric inversion
	324	24	32	Complex translocation & pericentric inversion
swalei (dixoni)	297	52	60	
tepperi	271	70	70	
	301	70(?)	70(?)	

chromosome arms, does not include the very short arms of acrocentrics, which are probably totally heterochromatic. Nor does it include longer chromosome arms if they appear to be totally heterochromatic.

3.1.4 Other data

Accompanying the SE micrographs and descriptions of male terminalia and karyotypes are literature synonymies, lists of types, lists of material examined, distribution maps and descriptions of nest structure for each species.

3.2 Genus description

3.2.1 Workers

Mandibles almost as long or longer than head, fully or partly serially dentate; antennae 12-segmented; ocelli present; eyes large; gaster attached to mesosoma by waist consisting of petiole and postpetiole; tarsal claws with free-standing median tooth; sting long, fully functional.

3.2.2 Male terminalia

Male genitalia (e.g. fig. 61a-c) composed of three pairs of valves surrounded anteriorly by basal ring (BR); outer valves (OV) large, convex laterally, almost encompassing middle and inner valves; middle valves (MV) small, attached basally to ventral median region of outer valve; inner valves (IV) medium-sized, laterally compressed, united dorsally by membranous spatha; whole complex retracted into genital cavity at posterior end of gaster. Genital cavity formed dorsally by anal segment consisting of fused ninth and tenth tergites and bearing pygostyles; ventrally by subgenital plate (ninth sternite). Anal segment completely covered by last external dorsal segment (eighth tergite), only pygostyles projecting from beneath. Posterior end of subgenital plate extending beyond margin of last, external ventral segment (seventh sternite). Eighth sternite lies between seventh and ninth sternites, covering anterior end of ninth sternite, entirely covered by seventh sternite.

Ninth and tenth tergites (e.g. fig. 62a) weakly sclerotized throughout; posterior margin with median lobe (ML) separated from pygostyles (Py) by lateral indentations (LI); anterior margin (AM) indented. Sensory pits (SP) distributed around margins of lateral indentations, sparse on median lobe, often with short setae. Pygostyles moderately sclerotized, set with long sensory setae.

Eighth sternite (e.g. fig. 62b) usually weakly sclerotized throughout; angular, trapezoidal or rectangular; posteriorly as wide or wider than anteriorly; posterior (PM) and anterior margins (AM) indented, posterior usually more so. Serrate longitudinal sculpturing (SLS) usually present in posterior quarter, often with associated short setae. Many fine, medium-length setae in middle of segment, sometimes in two distinct regions.

Ninth sternite (e.g. fig. 62c) heavily sclerotized posteriorly; roughly shield-shaped; anterior margin with slender *anterior apodeme* (AA) usually flanked by shorter *antero-lateral lobes* (ALL); *lateral lobes* (LL) sometimes projecting at about middle of segment. Long sensory setae around *posterior margin* (PM); short setae in posterior half. One species (*flavicoma* Roger) with numerous spines dorsally at posterior end.

Basal ring (see fig. 61a-c) more sclerotized laterally, ring-shaped, wider than long, more or less obviously tapered anteriorly; antero-ventral, antero-dorsal and postero-ventral margins broadly indented; postero-dorsal margin slightly indented in middle. Ventral surface with semi-circular membranous flap folded anteriorly at posterior margin.

Outer valve (e.g. fig. 62d) heavily sclerotized posteriorly; dorsal surface curved ventrally, continuing to *posterior end* (PE), which turns medially; shape of posterior end variable; usually with *dorsal median projection* (DMP) arising from around middle of segment. Long sensory setae along posterior margins, short setae on mid-region of lateral surface. Rarely, a cluster of sensilla on ventral surface of posterior end (*esuriens* group). One species with spines on inner postero-ventral surface (*flavicoma*).

Middle valve (e.g. fig. 62e) heavily sclerotized; lateral lobe (*cuspis*; Cu) finger-shaped and short; median lobe (*digitus*; Di) broad, flat, curved distally. Few short setae on postero-ventral end of basal portion. Numerous small sensory pegs (*sensilla basiconica*; SB) on lateral surface of digitus and median surface of cuspis.

Inner valve (e.g. fig. 62f) moderately sclerotized; with rod-like *antero-lateral extension* (ALE) of *anterior apodeme* (AA); *postero-dorsal* *margin* (PDM) usually rounded; *postero-ventral* margin often forming a *lobe* (PVL), usually with *serrations* (Se). Lateral surface often with sharp tooth-like *spines* (Sp)

3.2.3 Karyotypes

Myrmecia karyotypes have chromosome numbers of n = 1-44 and *nombres fondamentaux* of N.F. = 4-88.

3.3 Keys to *Myrmecia*

3.3.1 Key to subgenera, species groups and species (including colour forms) based on workers

This key, based on workers, does not include *inquilina* (a workerless social parasite) or species known only from males (*sp.M1* and *sp.M2*). It also cannot be used to separate biological species whose workers are identical.

1\. Maximum length greater than 17mm; non-jumping species; * usually SI ⩾ 0·94 ....
.... subgenus *Myrmecia*, *s.s.* 2
------- Maximum length less than 15mm; "jumpers"; * usually SI < 0·94 ....
.... subgenus *Promyrmecia* 45

2(1). Outer border of mandibles strongly convex ....
.... *forceps* group ...... 1. *forceps* 3
------- Outer border of mandibles straight or slightly concave 7

3(2). Head red 4
------- Head black 5

4(3). Gaster black .... 1(5). *forceps* (*forceps*, *s.s.* colour form)
------- Gaster red and black ....
.... 1(4). *forceps* (unnamed red and black colour form)

---

* Use only when the first two characters cannot be assessed. See p.16 and appendices 5-6.

5(3). Mesosoma yellow .... 1(1). *forceps* (*obscuriceps* colour form)
------- Mesosoma mainly or entirely dark brown to black 6

6(5). Petiole and postpetiole red .... 1(2). *forceps* (*singularis* colour form)
------- Petiole and postpetiole dark brown to black .... 1(3). *forceps* (unnamed black colour form)

7(2). Mandibles uniformly red-brown to brown, always with strong angulate broadening at base of inner border ..... *forficata* group 8
------- Mandibles yellow to brownish yellow, often with slight angulate broadening at base of inner border, sometimes with dark infuscations 13

8(7). Apex of gaster yellow* 9
------- Apex of gaster black 10

9(8). Maximum length less than 21mm; restricted to south-west Western Australia .... 7. *regularis*
------- Maximum length greater than 23mm; restricted to Kangaroo Island (South Australia) 9. *sp.9*

10(8). Head, mesosoma, petiole and postpetiole dark brown or black .... 6. *pyriformis*
------- Head, mesosoma, petiole and postpetiole red or brownish red 11

11(10). Mandibles with at least some teeth directed posteriorly [see Clark (1951, fig. 2)] 12
------- Mandibles with all teeth erect .... 4. *forficata, s.l.*

12(11). Node four times as long as stalk [see Clark (1951, fig. 1)] .... 5. *hirsuta*
------- Node one and a half times as long as stalk .... 3. *brevinoda, s.l.*

13(7). Apex of gaster yellow 14
------- Apex of gaster brown or black 16

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* Brown (1953b) mentions *forficata* specimens from the eastern states with light-tipped gasters but I have not seen such specimens and therefore exclude them from the key.

14(13). Mesosoma black .... *tarsata* group ...... 12. *tarsata*
------- Mesosoma red ....
.... *nigriscapa* group ...... 11. *nigriscapa* 15

15(14). First segment of gaster black ....
.... 11(1). *nigriscapa* (*analis* colour form)
------- First segment of gaster red and black ....
.... 11(2). *nigriscapa* (*nigriscapa*, *s.s.* colour form)

16(13). Petiole with stalk less than half as long as node 17
------- Petiole with stalk more than two-thirds as long as node 24

17(16). Petiole with stalk almost half as long as node ....
.... *esuriens* group 18
------- Petiole with stalk less than one-third as long as node 23

18(17). Gaster entirely black .... 34. *pulchra* 19
------- Gaster with apex yellow or ferruginous 22

19(18). Petiole and postpetiole brownish red 20
------- Petiole and postpetiole black 21

20(19). Head black .... 34(2). *pulchra* (*pulchra*, *s.s.* colour form)
------- Head mainly brownish red but with black in middle of forehead
between frontal carinae and ocelli ....
.... 34(1). *pulchra* (*crassinoda* colour form)

21(19). Mesosoma black .... 34(4). *pulchra* (*murina* colour form)
------- Mesosoma mainly black except mesonotum and small area on
pronotum brown .... 34(3). *pulchra* (*fallax* colour form)

22(18). Apex of gaster yellow; head red .... 33. *midas*
------- Apex of gaster ferruginous; head black .... 32. *esuriens*

23(17). Head black .... *auriventris* group ...... 13. *auriventris*
------- Head red .... *flavicoma* group ...... 14. *flavicoma*

24(16). Head longer than broad .... *mjobergi* group ...... 10. *mjobergi*
------- Head slightly shorter than broad 25

25(24). Mandibles with slight angulate broadening at base of inner
border .... *vindex* group (part) 26
------- Mandibles without angulate broadening at base of inner border ...
.... 39

26(25). Mesosoma dark brown to black (rarely mesosoma yellow except for
dark brown to black mesonotum) 27
------- Mesosoma yellow, red or reddish brown 30

27(26). Scapes exceed occipital border by less than one-fifth their
length .... 26. *rowlandi*
------- Scapes exceed occipital border by at least one-third their length
.... 28

28(27). Restricted to South Australia 28. *sp.12*
------- Restricted to Western Australia 29

29(28). Mesosoma dark brown to black ....
.... 19. *atrata* or 30. *sp.16* (part)
------- Mesosoma yellow except for dark brown to black mesonotum ....
.... 30. *sp.16* (part)

30(26). Mesosoma yellow 31
------- Mesosoma red or reddish brown 32

31(30). Legs yellow (occasionally light brown) ...... 24. *nigriceps*, *s.l.*
------- Legs dark brown to black .... 22. *fuscipes*

32(30). Epinotum with coarse, transversely striate sculpturing ....
.... 21. *fulgida*
------- Epinotum with medium striate-rugose sculpturing 33

33(32). Restricted to Western Australia 34
------- Restricted to the eastern states (Victoria, New South Wales and
Queensland) 36

34(33). Head red .... 27. *vindex* 35
------- Head dark brown 29. *sp.14*

35(34). First segment of gaster black ....
.... 27(1). *vindex* (*vindex*, *s.s.* colour form)
------- First segment of gaster red and black ....
.... 27(2). *vindex* (*basirufa* colour form)

36(33). Head red .... 20. *ferruginea* 37
------- Head brown 31. *sp.17*

37(36). First segment of gaster black 38
------- First segment of gaster red and black ....
.... 20(3). *ferruginea* (*dimidiata* colour form)

38(37). Head red .... 20(1). *ferruginea* (*ferruginea*, *s.s.* colour form)
------- Head red with dark brown band across middle ....
.... 20(2). *ferruginea* (*fasciata* colour form)

39(25). Gaster red and black .... *gulosa* group ...... 15. *gulosa*
------- Gaster black 40

40(39). Mesosoma yellow .... *vindex* group (part) ...... 25. *princeps*
------- Mesosoma black .... *simillima* group 41

41(40). Petiole with stalk about two-thirds as long as node ....
.... 18. *simillima* 42
------- Petiole with stalk longer than node 44

42(41). Petiole and postpetiole black ....
.... 18(1). *simillima* (*simillima*, *s.s.* colour form)
------- Petiole and postpetiole brownish red 43

43(42). Mesosoma brownish red ....
.... 18(3). *simillima* (*nigriventris* colour form)
------- Mesosoma black except for brownish red epinotal declivity ....
.... 18(2). *simillima* (*tricolor* colour form)

44(41). Restricted to Western Australia; always with black petiole and
postpetiole .... 16. *arnoldi*
------- Restricted to South Australia and Victoria; usually with red petiole and
postpetiole .... 17. *rufinodis*

45(1). Postpetiole smooth 49
------- Postpetiole sculptured 46

46(45). Mandibles reddish brown ....
.... *pilosula* group (part) ...... 50. *rugosa*
------- Mandibles yellow ....
.... *harderi* group ...... 40. *harderi* 47

47(46). Mesosoma red .... 40(1). *harderi* (*harderi*, *s.s.* colour form)
------- Mesosoma mainly black 48

48(47). Petiole red .... 40(2). *harderi* (*scabra* colour form)
------- Petiole black .... 40(3). *harderi* (*celaena* colour form)

49(45). Petiole smooth (covered with pilosity) 50
------- Petiole sculptured 55

50(49). Scapes exceed occipital border by less than their thickness .....
.... *sp.15* group 63. *sp.15*
------- Scapes exceed occipital border by at least one-quarter their
length .... *nigrocincta* group 51

51(50). Pronotum brown or black 52
------- Pronotum yellow or orange-red 54

52(51). Gaster heart-shaped .... 36. *cardigaster*
------- Gaster normal (egg-shaped) 53

53(52).. Restricted to New Caledonia .... 35. *apicalis*
------- Restricted to Queensland .... 39. *petiolata*

54(51). Petiole yellow .... 38. *nigrocincta*
------- Petiole black .... 37. *flammicollis*

55(49). Mandibles with basal teeth reduced 56
------- Mandibles with basal and apical teeth of similar size 61

56(55). Mandibles concave or barely straight along outer border ....
.... *pilosula* group (part) 85
------- Mandibles more or less convex along outer border ....
.... *mandibularis* group 57

57(56). Legs yellow 58
------- Legs black or brown 59

58(57). Apex of gaster yellow .... 57. *fulviculis*
------- Apex of gaster black .... 58. *fulvipes*, *s.l.*

59(57). Mandibles yellow .... 59. *luteiforceps*
------- Mandibles black or brown 60

60(59). Gastric pubescence reddish-yellow .... 60. *mandibularis*
------- Gastric pubescence greenish-yellow .... 61. *piliventris*, *s.l.*

61(55). Mandibles shorter than head 62
------- Mandibles longer than head 69

62(61). Head longitudinally striate; mandibles with large, chunky teeth
.... *pilosula* group (part) ...... 41. *aberrans* 63
------- Head irregularly rugose; mandibles with normal teeth 68

63(62). Head black 64
------- Head red or red and black 65

64(63). Mesosoma black .... 41(6). *aberrans* (*maura* colour form)
------- Mesosoma red except for some black on sides ....
.... 41(5). *aberrans* (*aberrans, s.s.* colour form)

65(63). Head red .... 41(1). *aberrans* (*greavesi* colour form)
------- Head red and black 66

66(65). Head mainly red except for a small amount of black ....
.... 41(2). *aberrans* (*eupoecila* colour form)
------- Head with front half black, rest red 67

67(66). Mesosoma red .... 41(3). *aberrans* (*froggatti* colour form)
------- Mesosoma red except for some black on sides ....
.... 41(4). *aberrans* (*formosa* colour form)

68(62). Gaster black .... *picta* group ...... 62. *picta*
------- Gaster red and black .... *fucosa* group ...... 64. *fucosa*

69(61). Maximum length 9mm; pronotal width less than two-fifths
mesosomal length .... *urens* group ...... 65. *urens*
------- Maximum length greater than 11mm; pronotal width more than
two-fifths mesosomal length ..... *pilosula* group (part) 70

70(69). Gaster densely clothed with gold pubescence 71
------- Gaster without gold pubescence 74

71(70). Petiole red 54. *sp.8*
------- Petiole black 72

72(71). Legs yellow .... 44. *chrysogaster*
------- Legs black 73

73(72). Gastric pubescence greenish-gold .... 49. *queenslandica*
------- Gastric pubescence reddish-gold .... 47. *michaelseni*

74(70). Mandibles with teeth directed posteriorly ....
.... 53. *varians* 75
------- Mandibles with teeth erect 80

75(74). Mesosoma black 76
------- Mesosoma yellowish red 77

76(75). Postpetiole black .... 53(6). *varians* (*goudiei* colour form)
------- Postpetiole yellowish red ....
.... 53(5). *varians* (*varians*, *s.s.* colour form)

77(75). Postpetiole black .... 53(4). *varians* (*elegans* colour form)
------- Postpetiole yellowish red 78

78(77). Mesonotum and metanotum black ....
.... 53(3). *varians* (*occidentalis* colour form)
------- Mesonotum and metanotum yellowish red 79

79(78). Pronotum brown .... 53(2). *varians* (*shepherdi* colour form)
------- Pronotum yellowish red ....
.... 53(1). *varians* (*wilsoni* colour form)

80(74). Mesosoma mainly red 81
------- Mesosoma entirely black 84

81(80). Legs red .... 42. *cephalotes* 82
------- Legs black or brown .... 43. *chasei*

82(81). First two segments of gaster black ....
.... 42(1). *cephalotes* (*cephalotes*, *s.s.* colour form)
------- First two segments of gaster yellowish red 83

83(82). Gaster yellowish red ....
.... 42(3). *cephalotes* (*callima* colour form)
------- Gaster yellowish red and black ....
.... 42(2). *cephalotes* (*hilli* colour form)

84(80). Head, mesosoma, petiole and postpetiole black ....
.... 48. pilosula, s.l.

------- Head and postpetiole brown; mesosoma and petiole reddish brown ..
.... 46. dispar

85(56). Mesosoma black 87

------- Mesosoma red .... 51. swalei 86

86(85). Postpetiole black ...... 51(2). swalei (swalei, s.s. colour form)

------- Postpetiole red .... 51(1). swalei (dixoni colour form)

87(85). Gaster with apex densely clothed with gold pubescence ....
.... 52. tepperi

------- Gaster without gold pubescence .... 45. clarki

3.3.2 Key to species groups and species based on male terminalia

The following key, to species groups and species of Myrmecia based on male terminalia, includes only those species for which males have been dissected in this study and by Browning (1979). Although only 50 Myrmecia species are included it is thought that, when males are examined for the remaining 19 or so species, they will mostly be placeable in one or other of the existing species groups. The key is limited to identifying those species with morphologically distinguishable terminalia, because in some species groups (e.g. the pilosula and vindex groups) species are known with very similar terminalia but divergent karyotypes. Couplets which distinguish the two subgenera have not been indicated because there are no clear-cut diagnostic features of the male terminalia suitable for this purpose.

1. Inner valve with spines on lateral surface 2

------- Inner valve without spines (may have serrations) 35

2(1). Inner valve with large serrations along posterior margin;
postero-ventral lobe absent ....
.... *nigriscapa* group ...... 11. *nigriscapa*
------- Inner valve without large serrations; usually with postero-
ventral lobe 3

3(2). Inner valve with deeply indented posterior margin 4
------- Inner valve with posterior margin not deeply indented 5

4(3). Inner valve with no serrations on posterior margin ....
.... *forceps* group ...... 1. *forceps*
------- Inner valve with serrations along posterior margin ....
.... *pilosula* group (part) 55. *sp.M1*

5(3). Inner valve with 1-5 large spines in postero-dorsal region ......
.... *forficata* group (part) 6
------- Inner valve with small and usually many more spines 10

6(5). Ninth sternite with posterior extension of posterior margin
less than 0.04 times maximum width of segment ....
.... 4(1). *forficata*, *s.s.*
------- Ninth sternite with posterior extension of posterior margin more
than 0.08 times maximum width of segment 7

7(6). Ninth sternite with posterior extension of posterior margin
triangular in cross-section 8
------- Ninth sternite with posterior extension of posterior margin oval
in cross-section 9

8(7). Ninth sternite with large, protruding lateral lobes ....
.... 6. *pyriformis*
------- Ninth sternite with lateral lobes almost absent 9. *sp.9*

9(7). Ninth sternite with posterior extension of posterior margin
expanded posteriorly .... 3(1). *brevinoda*, *s.s.*
------- Ninth sternite with posterior extension of posterior margin
narrowest posteriorly 10

10(9). Ninth sternite less than three-quarters as wide as long ....
.... 5. hirsuta

------- Ninth sternite about five-sixths as wide as long ....
.... 3(2). decipiens

11(5). Inner valve with spines along posterior margin only 12

------- Inner valve with spines in middle of segment and along posterior margin 24

12(11). Ninth sternite with numerous spines ....
.... flavicoma group ...... 14. flavicoma

------- Ninth sternite without spines 13

13(12). Ninth sternite with very narrow posterior extension of posterior margin .... forficata group (part) ...... 7. regularis

------- Ninth sternite with broader posterior extension of posterior margin 14

14(13). Inner valve with postero-ventral lobe reduced (almost absent) ...
.... harderi group ...... 40. harderi

------- Inner valve with postero-ventral lobe not reduced 15

15(14). Inner valve with postero-dorsal margin extending posteriad to postero-ventral lobe ....
.... fucosa group ...... 64. fucosa

------- Inner valve with posterior margin more or less straight 16

16(15). Ninth sternite with broad, indented posterior margin 17

------- Ninth sternite with posterior margin neither broad nor indented
.... 19

17(16). Inner valve with spines only on the postero-ventral lobe ....
.... sp.15 group 63. sp.15

------- Inner valve with spines on postero-ventral lobe and near postero-dorsal margin 18

18(17). Inner valve (excluding anterior apodeme) more than 1.5 times longer than deep .... *picta* group ...... 62. *picta*

------- Inner valve (excluding anterior apodeme) slightly longer than deep .... *urens* group ...... 65. *urens*

19(16). Ninth sternite tapering from anterior half 20

------- Ninth sternite narrowing mainly in posterior quarter .... *mandibularis* group 21

20(19). Ninth sternite with rounded apex .... *nigrocincta* group ...... 38. *nigrocincta*

------- Ninth sternite with parallel-sided apex .... *tarsata* group ...... 12. *tarsata*

21(19). Ninth sternite with numerous short setae in anterior half 22

------- Ninth sternite without setae in anterior half 23

22(21). Ninth sternite with posterior extension of posterior margin about 0.05 times as wide as maximum width of segment .... 60. *mandibularis*

------- Ninth sternite with posterior extension of posterior margin about 0.10 times as wide as maximum width of segment .... 61(2). *gilberti*

23(21). Ninth sternite slightly indented laterally; posterior extension of posterior margin narrowest posteriorly .... 61(1). *piliventris*, *s.s.*

------- Ninth sternite rounded laterally; posterior extension of posterior margin expanded posteriormost .... 58. *fulvipes*, *s.l.*

24(11). Inner valve with spines in middle of segment arranged in a dorsoventral line .... *simillima* group 25

------- Inner valve with spines in middle of segment scattered or in a tight cluster 27

25(24). Ninth sternite with indented posterior margin .... 18. *simillima*

------- Ninth sternite with rounded posterior margin 26

26(25). Ninth and tenth tergites with median lobe of posterior margin extending beyond tips of pygostyles .... 17. *rufinodis*

------- Ninth and tenth tergites with median lobe of posterior margin extending almost to tips of pygostyles .... 16. *arnoldi*

27(24). Ninth sternite with narrow, indented posterior margin .... *gulosa* group ...... 15. *gulosa*

------- Ninth sternite with broad, usually rounded posterior margin .... *vindex* group 28

28(27). Inner valve with middle region of spines in a tight cluster 29

------- Inner valve with middle region of spines not tightly clustered 33

29(28). Ninth sternite with moderately narrow posterior margin 30

------- Ninth sternite with moderately broad posterior margin 31

30(29). Inner valve with about 10 small spines near postero-dorsal margin; about 35 others clustered in middle ...... 20. *ferruginea*

------- Inner valve with 2-4 small spines near postero-dorsal margin; 16-22 others clustered in middle 31. *sp.17*

31(29). Ninth sternite with rounded posterior margin .... 24(1). *nigriceps*, *s.s.* or 22. *fuscipes* [inseparable]

------- Ninth sternite with crinkled or indented posterior margin 32

32(31). Ninth sternite with crinkled posterior margin 28. *sp.12*

------- Ninth sternite with posterior margin indented in middle with flanking straight portions of margin .... 24(2). *desertorum*

33(28). Inner valve with middle region containing 2-6 spines .... 24(3). *sp.11*
------- Inner valve with middle region containing 10-15 spines 34

34(33). Ninth sternite with rounded posterior margin 35
------- Ninth sternite with posterior margin indented ...... 25. *princeps*

34(33). Ninth sternite with very broad, lightly sclerotized posterior margin .... 27. *vindex*
------- Ninth sternite with broad, moderately heavily sclerotized posterior margin 29. *sp.14*

36(1). Ninth sternite with posterior extension of posterior margin turned dorsally and expanded posteriorly to form a barbed hook .. .. *pilosula* group 37
------- Ninth sternite without barbed hook 45

37(36). Inner valve with row of serrations on lateral surface 38
------- Inner valve without row of serrations on lateral surface (although a "tooth" may be present) 40

38(37). Inner valve with postero-ventral lobe about half as wide as anterior apodeme 56. *sp.M1*
------- Inner valve with postero-ventral lobe wider than anterior apodeme 39

39(38). Inner valve with row of serrations less than a seventh as long as segment is deep .... 47. *michaelseni*
------- Inner valve with row of serrations more than a third as long as segment is deep .... 41. *aberrans*

40(37). Inner valve with a "tooth" on the posterior margin 41
------- Inner valve without a "tooth" on the posterior margin 44

41(40). Ninth sternite with two "mounds" of setae in anterior half on dorsal surface .... 53. *varians*
------- Ninth sternite without "mounds" of setae 42

42(41). Ninth sternite with numerous short setae in anterior half ....
.... 43. *chasei*
------- Ninth setae without setae in anterior half 43

42(41). Ninth sternite with posterior margin (excluding posterior
extension) rounded .... 42. *cephalotes*
------- Ninth sternite with posterior margin (excluding posterior
extension) angulate .... 52. *tepperi*

44(40). Ninth sternite with short setae over much of the posterior half .
.... 48. *pilosula*, *s.l.*
------- Ninth sternite with short setae on and around posterior
extension of posterior margin only .... 51. *swalei*

45(36). Inner valve with very narrow lobe projecting ventrally ....
.... *esuriens* group 46
------- Inner valve with pointed postero-ventral lobe ....
.... *mjobergi* group ...... 10. *mjobergi*

46(45). Ninth sternite more than 1.1 times longer than wide ....
.... 32. *esuriens*
------- Ninth sternite more than 1.2 times wider than long 47

47(46). Inner valve with posterior margin rounded .... 33. *midas*
------- Inner valve with posterior margin indented to form a postero-
ventral lobe .... 34. *pulchra*

3.4 Species descriptions

3.4.1 Subgenus *Myrmecia* Fabricius, *s.s.*

Diagnosis

Large non-jumping *Myrmecia* (largest workers greater than 17 mm in length), with at least two worker subcastes.

Composition

(1) *forceps* group
(2) *forficata* group
(3) *mjobergi* group

(4) nigriscapa group
(5) tarsata group
(6) auriventris group
(7) flavicoma group
(8) gulosa group
(9) simillima group
(10) vindex group
(11) esuriens group

[Note: Emery (1911) placed all of these groups in subgenus Myrmecia, s.s., but he also included the nigrocincta and pilosula groups. When Wheeler (1922) removed the nigrocincta and pilosula groups to subgenus Halmamyrmecia he left subgenus Myrmecia, s.s. with the same composition as I propose. The same groups were placed in genus Myrmecia by Clark (1951), except he re-included the nigrocincta group.]

Distribution

All Australian states and mainland territories

New Zealand [introduced]

Comments

Subgenus Myrmecia, s.s. is well delimited from Promyrmecia by its worker locomotion, worker size and size division of workers. Otherwise, its worker morphology, male terminalia and karyotypes lack truly diagnostic features. Chromosome numbers range from n = 5-44 (N.F. = 18-88), which overlaps with Promyrmecia considerably (cf. n = 1-35, N.F. = 4-70).

3.4.1.1. The Myrmecia forceps group

Diagnosis

Large Myrmecia with very distinctive workers and male terminalia. Worker mandibles have the outer border strikingly convex and only a few, widely-spaced teeth on the inner border (fig. 8b). Inner valve of the male terminalia has the posterior margin indented to form a posterodorsal lobe with 12-20 spines (fig. 63b).

Composition

forceps Roger (= *obscuriceps* Viehmeyer = *singularis* Clark)

[*Note* - This species has previously been placed in the *tarsata* group of Emery (1911) and *forceps* group of Clark (1951).]

Distribution

A.C.T., N.S.W., Qld, S.A., Vic., W.A.

Comments

The *forceps* group is well delimited from all other species groups by both its workers and male terminalia. Two nests karyotyped both had 2n = 62 (N.F. = 62).

1. *Myrmecia forceps* Roger

(Figs 8a-c, 43a, 63a-f, 102a, 115a)

Myrmecia forceps Roger, 1861a, p. 34 [♀]. Mayr, 1862, p. 724. Emery, 1911, p. 20. Wheeler, 1933, p. 47, fig. 16. Clark, 1951, p. 24, figs 3-4 [♀]. Brown, 1953b, p. 7. Wheeler and Wheeler, 1971, p. 248 [larva]. Taylor and Brown, 1985, p. 9. Taylor, 1987, p. 43.
Myrmecia forceps Roger var. *obscuriceps* Viehmeyer, 1924, p. 222 [♀].
Myrmecia singularis Clark, 1951, p. 26, fig. 5 [♀].

Types

forceps: syntype workers, Australia, in ZMB.

obscuriceps: syntype workers, Liverpool, N.S.W., in ZMB. [Synonymy by Clark, 1951].

singularis: holotype worker, Kangaroo Island, S.A., in ANIC (examined). [Synonymy by Brown, 1953b].

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 8a-c).

Colour very variable, though constant within nests and populations. Combinations include: (1) head and gaster black; mandibles, antennae, mesosoma, petiole, postpetiole and legs yellow (*obscuriceps* colour form;

resembling *nigriceps*, *s.l.*; e.g. Rocky River H.S., S.A.); (2) head and gaster black; most of mesosoma, and femora dark brown to black; mandibles, antennae, tibiae and tarsi yellow; petiole, postpetiole and patches on dorsum of pronotum and epinotal declivity red (*singularis* colour form; resembling *rufinodis*; e.g. Brownlow, S.A.); (3) head and gaster black; mesosoma, petiole, postpetiole and femora dark brown to black; mandibles, antennae, tibiae and tarsi yellow (unnamed black colour form; resembling *arnoldi* Clark or *pyriformis*; e.g. Twertup, W.A. and Belair, S.A. respectively); (4) head, mesosoma, petiole, postpetiole, most of first segment of gaster, and femora red; posterior margin of first segment of gaster and all three apical segments black; mandibles, antennae, tibiae and tarsi yellow (unnamed red and black colour form; resembling *gulosa*; e.g. Stanthorpe, Qld); and (5) head, mesosoma, petiole, postpetiole and femora red; mandibles, antennae, tibiae and tarsi yellow; gaster black (*forceps*, *s.s.* colour form; resembling *brevinoda*, *s.l.* or *forficata*, *s.l.*; e.g. Sydney, N.S.W.).

Material examined (fig. 43a)

Australian Capital Territory: Black Mountain (BBL). *New South Wales*: Apsley (BBL); Berowra Waters (BBL); Central Mangrove (BBL); Cowan (BBL); Maroota (BBL); Menai (JFr); 3 km W of Mudgee (BBL); 5 km NW of Mulbring (BBL); Putty (BBL); Royal N.P. (cu); Sydney (EWFe). *Queensland*: Stanthorpe (BBL). *South Australia*: Aldinga (BBL); Ashbourne (RDR; in SAM); Belair (BBL); Brownlow [140] [*K*, 3 ♀ prepupae]; Ceduna (BBL); 3 km S of Emu Bay [253]; Hanson Bay [404]; Kangaroo Island (cu) [*singularis* holotype]; 16 km N of Kingston, S.E. (BBL); Lake Gilles C.P. [281] [*K*, 4 ♀ prepupae]; Mount Lofty (BBL); Myponga (BBL); Port Lincoln [403]; Rocky River H.S. [31] [*SEM*, ♀ ; *MT*, 2♂♂, 22.iii.1979]; Taylor's Landing [302]; Vivonne Bay [342]; Waitpinga (BBL). *Victoria*: Halls Gap (TW); Melton (JF). *Western Australia*: Narrogin (D&D) [*MT*, ♂, 16.iii.1975]; 6 km S of Narrogin [458]; 59 km E of Perth (GHL, in WAM); 6 km S of Ravensthorpe (BBL); Twertup [230].

[*Note* - Taylor and Brown (1985, p. 10) did not record this species from A.C.T., Qld, Vic. or W.A.]

Male terminalia (fig. 63a-f)

No variation has been observed in the male terminalia of forceps; obscuriceps colour form has been examined but the others have not.

Ninth and tenth tergites (fig. 63a) 1.4 times wider than long; median lobe rounded (with margin straight opposite tips of pygostyles), extending to tips of pygostyles. Pygostyles slender; length 0.5 times width of segment. Eighth sternite (fig. 63b) rectangular; 1.2 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Medium-sized areas of serrate longitudinal sculpturing flanking midline in posterior quarter, with associated short setae. Numerous short setae over much of anterior three-quarters. Ninth sternite (fig. 63c) 1.4 times longer than wide; long anterior apodeme; antero-lateral lobes well-developed; lateral lobes present; posterior margin broadly indented. Short setae scattered over much of posterior two-thirds; numerous medium length undulate setae flanking midline in anterior half. Basal ring 1.4 times wider than long; 1.4 times wider posteriorly than anteriorly. Outer valve (fig. 63d) 2.0 times longer than deep; posterior end dorso-ventrally flattened; dorsal median projection moderately short, digitate. Middle valve (fig. 63e) with cuspis much shorter than digitus; digitus broad, very curved, similar breadth throughout, distal end rounded. Inner valve (fig. 63f), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe long, narrow, serrated distally; postero-dorsal margin forming a moderately long, moderately broad lobe bearing 12-20 spines ($\overline{x}$ = 16.2, N = 6).

Karyotype (figs 102a, 115a)

No variation was observed in karyotypes of *forceps* from two localities; *singularis* and *obscuriceps* colour forms have been examined but the others have not.

2n = 62 (N.F. = 62)

Brownlow, S.A. (figs 102a, 115a): Eleven out of 38 cells had 2n = 62 while in the others I only saw 2n = 54 (X2), 56 (X2), 57 (X1), 58 (X4), 59 (X5), 60 (X5) and 61 (X8). The karyotype consists of 62A chromosomes (i.e. N.F. = 62). One chromosome of the first pair (fig. 102a) has a large amount of heterochromatic growth (heterochromatin/euchromatin = 1.4) while the other has less (heterochromatin/euchromatin = 0.6). All other chromosomes in the karyotype are normal acrocentrics. This karyotype is associated with *singularis* colour form.

Lake Gilles C.P., S.A.: Three out of 34 cells had 2n = 62 while in the others I only saw 2n = 47 (X1), 52 (X2), 53 (X2), 54 (X2), 56 (X5), 57 (X2), 58 (X2), 59 (X9), 60 (X3) and 61 (X3). The karyotype appears identical to that from Brownlow and is associated with *obscuriceps* colour form.

Taxa included

(1) *obscuriceps* colour form

(2) *singularis* colour form

(3) unnamed black colour form

(4) unnamed red and black colour form

(5) *forceps*, *s.s.* colour form

Nest structure

I collected from colonies of *obscuriceps*, *singularis* and the two unnamed colour forms at four localities in South Australia and two in Western Australia. Each colony consisted of a single, moundless nest;

with one or two round entrances (d ≃ 2 cm; a few centimetres apart if two entrances) concealed by twigs and dead leaves. These ants are strictly nocturnal and on no occasion were workers seen on the surface during daylight. Unlike most other large Myrmecia, when a nest of forceps is disturbed, the workers all retreat. Consequently, the nests are quite difficult to locate.

No nests of this species were completely excavated, but several were followed to depths of about a metre. Excavations were incomplete because the nests were constructed either amongst large stones or in loose sand.

The nests consisted of a chamber, just beneath the entrance(s), where pupae were sometimes found, surmounting a single shaft which descended more or less vertically to the limit of my excavations. I presume that the main chambers would have been located only a little below this depth (60 - 100 cm). The internal structure of these nests can be classified as simple (see Gray, 1974a). These observations concur quite well with those of previous authors. All nests of forceps appear to contain relatively small populations (< c.150 workers). Gray (1974a) completely excavated one nest (colour form unknown) at Jannali (N.S.W.) which was 56 cm deep and collected 112 workers while Wheeler (1933) found only 40 workers in another (forceps, s.s. colour form) at Heathcote (N.S.W.). However, Wheeler also noted that his nest had a mound with a diameter of about 30 cm. Barnett (1977) excavated two nests of obscuriceps colour form near Bacchus Marsh (Vic.) and collected 100 and 120 workers.

Biological references (including unpublished theses)

Freeland (1958); Gray (1974a, 1974b); Barnett (1977); Browning (1979)

Comments

M. forceps is a species, or possibly a complex of sibling species, with highly variable colour patterning (as indicated above). Two other names (*obscuriceps* and *singularis*) have been used for different colour forms but at present there is no evidence from worker morphology, chromosomes or male terminalia to support recognition of these as species. Consequently, I have accepted the synonymies proposed by Clark (1951) and Brown (1953b) respectively.

It is interesting that, in each case examined, the colour form found at a given locality resembles closely the colouration of a large, common, sympatric *Myrmecia* (e.g. *nigriceps*, *s.l.*, *rufinodis*, *arnoldi*, *pyriformis*, *gulosa*, *brevinoda*, *s.l.*, *forficata*, *s.l.*).

Brown (1953b) has suggested that Müllerian mimicry is involved while Greenslade (1979, p. 12) believes *forceps* to be a Batesian mimic. However, I suggest that, although coloural convergence between *forceps* and other *Myrmecia* is well established, there will need to be careful study before it can be confirmed that this convergence is based on mimicry.

The aberrant mandible shape of *forceps* workers suggests that their biology may differ significantly from that of other large *Myrmecia*. Although evidence is required to confirm it, for the following reasons I think it likely that these mandibles have evolved because they are more effective for catching large insects:

(1) In laboratory colonies of *forceps*, individual workers were able to kill large cockroaches quickly by gripping them around the prothorax and stinging. Other species observed: (a) required several workers; (b) could only hold such prey by the legs; and (c) often took hours to succeed in killing.

(2) A nest excavated in the Darling Range (W.A.) by G.H. Lowe (pers. comm) contained remains which belonged mainly to a species of Melolonthinae (Coleoptera : Scarabeidae) packed into the subsurface chamber. These beetle remains (formerly 10 - 15 mm in length) often had holes in the elytra as would be expected if they had been seized in curved jaws.

3.4.1.2. The *Myrmecia forficata* group

Diagnosis

Large *Myrmecia* with very distinctive workers and male terminalia. Worker mandibles have a strong angulate broadening at the base of the inner border (figs 9b, 10b) and are red-brown to brown in colour. Male terminalia have: (1) eighth sternite with anterior margin shallowly indented (about 0.2 times length of segment; e.g. fig. 67b); and (2) inner valve with either 1-5 large spines in middle just in from posterior margin (except *regularis*; e.g. fig. 67f), or four small spines in same position and about seven more along ventral half of posterior margin (*regularis* only; fig. 68e).

Composition

(1) *affinis* Mayr, *sp. indet*.

(2) *brevinoda* Forel, *s.l.* (= *gigas* Forel = *eudoxia* Forel = *decipiens* Clark = *longinodis* Clark) [includes *brevinoda*, *s.s.* and *decipiens*]

(3) *forficata* (Fabricius), *s.l.* (= *sanguinea* Smith = *lucida* Forel = *rubra* Forel = *paucidens* Forel) [includes *forficata*, *s.s.* and *sp.7* (ANIC)]

(4) *hirsuta* Clark

(5) *pyriformis* Smith

(6) *regularis* Crawley

(7) *subfasciata* Viehmeyer, *sp. indet*.

(8) *sp.9* (ANIC)

[*Note* - These species have previously been placed in the *forficata* group of Emery (1911), but Clark (1951) divided them amongst the vindex and gigas groups]

Distribution

A.C.T., N.S.W., Qld, S.A., Tas., W.A., Vic.

New Zealand [introduced]

Comments

The forficata group is well delimited from all other species groups by both its workers and male terminalia. Its species all have broadly similar workers which differ slightly in colouration and formation of mandibular teeth. Differences in male terminalia are greater but leave no doubt about the unity of the group. The most distinctive male terminalia are found in regularis, whose inner valve has a number of small spines instead of a few large spines like the other species. Otherwise, its male terminalia are unremarkable for the group.

Although the workers and male terminalia of the forficata and mjobergi groups are very distinct, it should be noted that there are several similarities between them which suggest close phylogenetic relationship. For example, both have: (1) worker mandibles with strong angulate broadening near base of inner border; (2) eighth sternite of male terminalia broadly and shallowly indented, and with long, stout setae in posterior quarter; and (3) outer valve of male terminalia with posterior end abrupt and Y-shaped in cross-section.

Six species of the forficata group have been karyotyped and have chromosome numbers of 2n = 40-88 and nombres fondamentaux of N.F. = c.60-88. M. brevinoda, s.s. and decipiens both have substantial heterochromatic growth (i.e. in most of their chromosomes), and pyriformis has slight heterochromatic growth (i.e. in only a few of its chromosomes). The lowest chromosome number and nombre fondamental is found in *regularis* providing further evidence that it is the most distinctive member of the group. To derive the haploid karyotype of *decipiens* (2n = 88, N.F. = 88) from *regularis* (2n = 40, N.F. = c.60) requires at least 24 Robertsonian rearrangements and about 14 pericentric inversions.

2. *Myrmecia affinis* Mayr, *sp. indet.*

Myrmecia affinis Mayr, 1862, pp 725, 729 [☿].
Myrmecia simillima Smith, *auct.* (*non* Smith, 1858). Clark, 1951, p. 89, *partim*. Taylor and Brown, 1985, p. 16, *partim*. Taylor, 1987, p. 46, *partim*.

Types

affinis: syntype workers, Australia, in NHMW.

Worker diagnosis (see Mayr, 1862, pp 725, 729)

Material examined: None

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *affinis*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

Although no specimens have been seen, I have placed this species in the *forficata* group because Mayr's (1862) key says it has red or brown mandibles. It is almost certainly a synonym of *forficata*, *s.l.*, *pyriformis*, or *brevinoda*, *s.l.*

3. *Myrmecia brevinoda* Forel, *s.l.*

(Figs 43b, 64a-d)

Myrmecia forficata Fabricius var. *brevinoda* Forel, 1910, p. 2 [☿♀]. Emery, 1911, p. 20.
Myrmecia brevinoda Forel. Brown, 1953b, p. 22. Wheeler and Wheeler, 1971, p. 247 [larva]. Imai, Crozier and Taylor, 1977, p. 345, figs

4, 12 [karyotype]. Taylor and Brown, 1985, p. 6. Taylor, 1987, p. 42.

Myrmecia pyriformis Smith race *gigas* Forel, 1913b, p. 310 [♀]. Forel, 1915, p. 7.

Myrmecia gigas Forel. Clark, 1951, p. 104, fig. 83 [♀♂].

Myrmecia forficata Fabricius var. *eudoxia* Forel, 1915, p. 8 [♀].

Myrmecia eudoxia Wheeler, 1933, p. 35.

Myrmecia decipiens Clark, 1951, p. 86, fig. 66, *emend.*, *syn. nov.* [♀] [introduced as *decipians*, incorrect spelling of *decipiens* which is derived from Latin verb *decipio* (to deceive)]. Taylor and Brown, 1985, p. 8. Taylor, 1987, p. 42.

Myrmecia longinodis Clark, 1951, p. 87, fig. 67, *syn. nov.* [♀]. Taylor and Brown, 1985, p. 12. Taylor, 1987, p. 44.

Types

brevinoda: syntype worker, New South Wales (Walcher), in NMV (examined); syntype workers (2), New South Wales (Walcher), in ANIC (examined); syntype worker(s) and female(s), New South Wales (Walcher) and Gisborne, Vic. (W.W. Froggatt), in GMNH. [*Note* - Brown (1953b) states the type locality of *brevinoda* to be Walcha (N.S.W.), but Forel's (1910) description refers to specimens collected in N.S.W. by Walcher (possibly a misspelling of J.J. Walker)].

gigas: syntype workers, Queensland, in GMNH and RIB. [Synonymy by Brown, 1953b].

eudoxia: syntype workers, Atherton, Qld, in GMNH. [Synonymy by Clark, 1951].

decipiens: holotype worker, Quirindi, N.S.W. (6.xii.1936, C.V. Morisset), in ANIC (examined). [NEW SYNONYMY].

longinodis: holotype worker, Kiama, N.S.W. (F.A. Cudmore), in ANIC (examined). [NEW SYNONYMY].

Worker diagnosis (see Clark, 1951, pp 86-88, 104-107)

Material examined (fig. 43b)

New South Wales: Apsley (BBL); Armidale (RJM); 17 km NE of Armidale (RJM); Bellbird [363]; Bilpin (BBL); Blaxland (BBL); Brooklyn (BBL); Bullawa Creek S.F. (BBL); Bungwahl [61, 64] [*MT*, 2♂♂, 2.xii.1978; *K*]; Cairncross S.F. (TG); Casino (TG); 12 km S of Cessnock (BBL); Cessnock S.F. (BBL); Clarencetown (WWF); 20 km S of Coffs Harbour (EFR); 12 km N of Coonabarabran (BBL); Coraki (C&U); Dorrigo (WH); Durras Lake (BBL); Eungella (BBL); Gerroa (BBL); Gilgai (BBL); Gosford (BBL); Grose Valley (BBL); Gwandalan (BBL); Heaton S.F. (BBL); Iluka (BBL); 4 km SE of Kearsley [361]; Kiama (FAC) [*longinodis* holotype]; Kyogle (WWF); Leumeah (C&I) [*K*]; Lismore (CFD); Maitland (cu); Maroota (BBL); 43 km N of McLean (cu); Milperra [63] [*MT*, ♂, 11.ii.1979; *K*]; Mount Arthur (KHLK); Mudgee (BBL); New South Wales (Walcher) [*brevinoda* syntypes]; Pine Creek S.F. (TG); Pymble (BBL); Quirindi (CVM) [*decipiens* holotype]; Round Mountain (BBL); 5 km S of St Albans (BBL); Styx River (EFR); Sydney (BBL); Tamworth (BBL); Trial Bay (BBL); Tumbulgum (BBL); Uralla (BBL); Wellington (BBL); Wongarbon N.R. (BBL). *Queensland*: Binna Burra (RJKo); Blackall Range (CBo); Bunya Mountains (EJD); Burleigh Heads (CPL); Cairns (FPD); Cunningham's Gap (BBL); Emu Vale (JHe); Fletcher (ESu); Fraser Island (cu); Girraween N.P. (BBL); Landsborough (BBL); Marmadua S.F. (BBL); Mount Coot-tha (BBL); Mount Garnet (TG); Mount Tamborine (RWT); 13 km N of Nanango (BBL); 12 km W of Paluma [514]; Ravensbourne N.P. (BBL); Ravenshoe (TG); Stanthorpe (BBL); Toowoomba (WBB); Traveston (RWT); Wandoan (BBL); Warwick (ASm); 10 km N of Yarraman (BBL).

New Zealand [introduced; see Keall (1981)]: Auckland (K&F).

Male terminalia (fig. 64a-d)

The male terminalia examined for *brevinoda*, *s.l.* suggest that it consists of two biological species:

(1) *Myrmecia brevinoda* Forel, *s.s.*

(Fig.64a-b)

Ninth and tenth tergites, *eighth sternite*, *basal ring*, *outer* and *middle valves* very similar to *pyriformis*. *Ninth sternite* (fig. 64a) 1.3 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin moderately narrow, expanded posteriormost. Short setae scattered over much of posterior two-thirds. *Inner valve* (fig. 64b), excluding anterior apodeme, 1.1 times longer than deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe moderately long, moderately narrow, serrated distally; postero-dorsal margin rounded; two large spines ($\bar{x}$ = 2.0, N = 2) in middle, just in from posterior margin.

(2) Myrmecia decipiens Clark

(Fig.64c-d)

Ninth and tenth tergites, eighth sternite, basal ring, outer and middle valves very similar to pyriformis. Ninth sternite (fig. 64c) 1.2 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin narrow, blunt. Short setae scattered over much of posterior half. Inner valve (fig. 64d), excluding anterior apodeme, 0.9 times as long as deep; anterior extension of anterior apodeme 0.8 times length of rest of segment; postero-ventral lobe moderately short, moderately narrow, serrated distally; postero-dorsal margin rounded; 2-3 large spines in middle ($\bar{x}$ = 2.3, N = 4), just in from posterior margin.

Karyotype

The karyotypes of brevinoda, s.l. determined by other researchers suggest that it contains two biological species:

(1) brevinoda, s.s. with 2n = 84 (N.F. = 84; Imai et al., 1977, colony from Leumeah, N.S.W.; A.D. Bishop, pers. comm., colony from Milperra, N.S.W.); and

(2) decipiens with 2n = 86-88 (N.F. = c.86-88; A.D. Bishop, pers. comm., colony from Bungwahl, N.S.W.)

Both karyotypes have many chromosome arms which appear to consist entirely of heterochromatin. A.D. Bishop (pers. comm.) estimated that brevinoda, s.s. contained c.75% heterochromatin and decipiens contained c.40%.

Taxa included

(1) *brevinoda*, *s.s.*

(2) *decipiens*

Nest structure

Colonies of *brevinoda*, *s.l.* were sampled at two localities in New South Wales. Each nest had a conspicuous bare clay mound which was low and roughly circular in outline ($d_{max} \simeq 60$ cm; $h_{max} \simeq 20$ cm). One entrance was located at the top of the mound and another near the edge. Opening these mounds revealed an internal structure of Gray's (1974a) more complex diffuse type. The nests appeared to be extremely populous and deep.

Gray (1974a) completely excavated one nest at Banyabba S.F. (N.S.W.) and collected 789 workers and incompletely excavated another at Miles (Qld) in which he found 850. The two nests went to depths of 113 and 124 cm respectively. Muir (1975) completely excavated 2 nests (which he called *decipiens*) in the Armidale district (N.S.W.) and collected about 2,100 and 2,400 adult ants (these numbers may have included males and queens).

Biological references (including unpublished theses)

MacQueen (1966); Gray (1974a, 1974b); Muir (1975); Browning (1979); Freeland (1985)

Comments

M. brevinoda, *s.l.* contains two biological species which can be distinguished by their karyotypes and male terminalia, but have indistinguishable workers. I tentatively use the name *brevinoda*, *s.s.* for the species with 2n = 84 and call the other *decipiens* (2n = 86-88). Although there is as yet no strong evidence to support the separation of the north Queensland populations, the distribution of *brevinoda*, *s.l.*

(fig. 43b) suggests that a third species may be present.

4. *Myrmecia forficata* (Fabricius), *s.l.*

(Figs 44a, 65a-b)

Formica forficata Fabricius, 1787, p. 310 [♀].

Myrmecia forficata (Fabricius). Smith, 1858, p. 143. Roger, 1861b, p. 170. Mayr, 1862, pp 726, 729; 1876, p. 95 [♀]. Forel, 1910, p. 2; 1913a, p. 173. Emery, 1911, p. 20; 1914, p. 179. Viehmeyer, 1924, p. 221. Clark, 1927, p. 35 [♂]; 1929, p. 120; 1951, p. 93, figs 72-74. Santschi, 1928, p. 465. Wheeler, 1933, p. 31, fig. 9. Brown, 1953b, p. 29, *partim*. Wheeler and Wheeler, 1971, p. 249 [larva]. Imai, Crozier and Taylor, 1977, p. 345, fig. 1 [karyotype]. Taylor and Brown, 1985, p. 10. Taylor, 1987, p. 43.

Myrmecia sanguinea Smith, 1858, p. 148 [♀]. Mayr, 1862, pp 725, 729. Forel, 1910, p. 3; 1915, p. 4. Emery, 1911, p. 20, pl.1, fig. 8. Viehmeyer, 1924, p. 221. Crawley, 1926, p. 378, fig. 5.

Myrmecia lucida Forel, 1893, p. 457 [♀]. Emery, 1911, p. 20. Clark, 1927, p. 35.

Myrmecia forficata (Fabricius) var. *rubra* Forel, 1910, p. 3 [♀]. Emery, 1911, p. 20. Wheeler, 1933, p. 31.

Myrmecia rubra Forel. Clark, 1927, p. 36, [♀]; 1951, p. 98, fig. 77.

Myrmecia paucidens Forel, 1910, p. 5, *syn. nov.* [♀]. Emery, 1911, p. 20. Clark, 1951, p. 117.

Myrmecia forficata (Fabricius) race *simillima* Smith var. *violacea* Forel, 1915, p. 5 [♀]. [Invalid quadranomen; see Taylor, 1986].

Myrmecia simillima Smith var. *violacea* Forel. Clark, 1927, p. 37. Santschi, 1928, p. 465.

Myrmecia forficata (Fabricius) var. *brevinoda* Forel, *auct.* (*non* Forel, 1910). Clark, 1927, p. 36. Wheeler, 1933, p. 31.

Myrmecia brevinoda Forel, *auct.* (*non* Forel, 1910). Clark, 1951, p. 96, figs 75, 76.

Types

forficata: holotype worker, Tasmania, in BMNH.

sanguinea: syntype workers, Tasmania, in BMNH. [Synonymy by Clark, 1951].

lucida: syntype workers, Hobart, Tas., in GMNH. [Synonymy by Clark, 1951].

rubra: syntype workers, Jarra district, Vic. (W.W. Froggatt), in GMNH. [Synonymy by Brown, 1953b].

paucidens: syntype workers, Tasmania (W.W. Froggatt), in GMNH. [NEW SYNONYMY].

Worker diagnosis (see Clark, 1951, pp 93-94)

Material examined (fig. 44a)

Australian Capital Territory: Bendora (EFR); Brindabella Range (BBL); Gibraltar Creek (BBL); Mount Aggie (RWT); Picadilly Circus [70] [MT, ♂, 26.ii.1979]; Smokers Gap [68] [MT, ♂, 19.ii.1979]. New South Wales: Bago Forest (TG); Batlow (WWF); Berry (BBL); Bowral (BBL); Boyd Plateau (KDF); Brown Mountain (BBL); Calga (BBL); Captain's Flat (BBL); Dorrigo (EFR); Durras Lake (TG); 38 km S of Eden (EFR); Gerroa (BBL); Goodradigbee Valley (BBL); Hartley (FHT); Jenolan Caves (BBL); Kanangaroo S.F. (C&I) [K]; Kangaroo Valley (EFR); Katoomba (BBL); Kosciusko N.P. [69, 75] [MT, 2 ♂♂, 12.iii.1979]; Meadow Flat (BBL); Minnamurra Falls (BBL); Mogo S.F. (BBL); Monga (EFR); Mount Canobolas (EFR); Mount Saddleback (BBL); Myrtle Mountain (BBL); New England N.P. (BBL); Nimmitabel (BBL); Perisher Valley (BBL); Rosedale (BBL); Royal N.P. (BBL); Sydney (WWF); Tallaganda S.F. (BBL); 5 km N of Tathra (BBL); Tinderry Mountains (BBL). South Australia: Cambrai (PJMG); Lake Bonney [265]; Lake Gilles C.P. [177] [K, ♀ prepupa]; Mount Lofty (BBL); Parsons Beach [145]; 8 km N of Peebinga (RDR; in SAM); 10 km S of Streaky Bay (BBL). Tasmania: Ansons Bay (AJD; in TM); Bagdad (SS; F64 in TM); Blackmans Bay (LR; F61, F66 in TM); Blythe Siding (TG); Boat Harbour (TG); Cambridge (RD; in TM); 19 km SE of Campbell Town (B&D; in TM); Chigwell (MW; in TM); Cleveland (TG); Copping (TG); Corinna (TGC); 6 km N of Dover (TG); Elizabeth River (DCP; F59 in TM); Flinders Island (JCa); Glebe (WPC; F58 in TM); 3 km W of Hermit Camp (A&B; F239 in TM); Hobart (DCP; F60 in TM); Huon (B; F63 in TM); King Island (KHLK); Lake Pedder (CDK; F68, F418 in TM); Lake St Clair (TG); Launceston (VVH); 11 km E of Launceston (TG); Lindisfarne (APA; in TM); Lion Rock (TH; in QVM); Little Swanport (TB; F65 in TM); Margate (RLR; in TM); Midway Point (SJK; in TM); Mount Cameron (FAC); Mount Field N.P. (TG); 8 km S of Oonah (TG); Orange River Valley (LHea; F1506 in TM); Port Arthur (cu; in TM); Prion Beach (TH; in QVM); Railton (TG); Rosetta (JFT; in TM); Rupert Point (TGC); 7 km SE of Scottsdale (TG); Snowy Mountains (CDK; F381 in TM); Southport (JWE; in TM); Spreyton (SS; F69 in TM); St Helens

(BCM; in TM); Stanley (L; F62 in TM); Steppes (TG); Strathgordan-Pedder N.P. [296]; Taroona (HDB; F220-F224, F235 in TM); Tasmania (cu; 99.303 in BMNH) [MT, ♂ only, du]; Underwood (GDN; in QVM); Variety Bay (RW; F231 in TM); 16 km N of Wilmot (TG); 32 km W of Wynyard (TG). Victoria: Arthurs Seat (BBL); 20 km N of Benambra [371]; Ben Cairn (TG); Bright (TG); East Beach (PMer; in QVM); Emerald (EJ); Ferntree Gully (JCl); Flinders (BBL); Gellibrand (JCl); Grampians (HC); Harrietville (BBL); Kallista (JCl); Kilcunda [141]; Kinglake (BBL); 4 km N of Lorne [138] [MT, ♂, 7.ii.1981]; Macedon (TG); Mansfield (JCl); Mount Dandenong [532] [MT, ♂ only, 7.iii.1985]; Mount Drummer (EFR); Mount Arthur (RHG; in QVM); Mount Morton (BBL); Narbethong (BBL); 27 km NW of Orbost (EFR); Portland (BBL); 80 km E of Portland (BBL); Romsey (EFR); Shoreham [395]; Wallan (JED); Wattle Glen [372]; Woori Yallock (JED).

[Note - Taylor and Brown (1985, p. 10) did not record this species from A.C.T., N.S.W. or S.A.]

Male terminalia (fig. 65a-b)

No variation has been observed in the male terminalia of forficata, s.l.

(1) Myrmecia forficata (Fabricius), s.s.

(Fig.65a-b)

Ninth and tenth tergites, eighth sternite, basal ring, outer and middle valves very similar to pyriformis. Ninth sternite (fig. 65a) 1.2 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin very narrow, turning ventrally. Short setae scattered over much of posterior half. Inner valve (fig. 65b), excluding anterior apodeme, 1.1 times longer than deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe short, moderately narrow, serrated distally; postero-dorsal margin rounded; 2-4 large spines ($\overline{x}$ = 3.2, N = 12) in middle, just in from posterior margin.

(2) sp.7 (see below) has not been examined.

Karyotype

The karyotypes known for forficata, s.l. suggest that it contains two biological species:

(1) forficata, s.s. with 2n = 50, 51 (N.F. = 84; Imai et al., 1977, colony from Kanangaroo S.F., N.S.W.) and 2n = 49, 50 (N.F. = 84; A.D. Bishop, pers. comm., colony from Honeysuckle Creek T.S., A.C.T.); and

(2) Myrmecia sp.7 (ANIC)
2n = c.66 (N.F. = c.84)

Lake Gilles C.P., S.A.: One out of two cells had 2n = 66 while in the other I saw 2n = 64. The karyotype appears to consist of 14M, 4SM and 48A chromosomes (i.e. N.F. = c.84). Although only one poor preparation was made, the two cells examined were spread and fixed sufficiently to determine that sp.7 has more chromosomes than forficata, s.s. (2n = 49-51) and more non-acrocentrics than pyriformis (see below). Thus, the Lake Gilles C.P. population does not belong to either of these species.

Taxa included

(1) forficata, s.s.

(2) sp.7

Nest structure

I observed one nest of forficata, s.s. at 10 km N of Eaglehawk Neck (Tas.) which was constructed in and beneath a large decomposing log. The nest was only found when the log was broken open so it was not clear where the entrances were. The nest could not be excavated because it was constructed in hard clay soil between large tree roots and was vigorously defended by what appeared to be a population of towards or possibly beyond a thousand workers. The internal structure of the nest was of Gray's (1974a) more complex diffuse type.

Observation of nests identified as forficata by Wheeler (1933, p. 33) and Gray (1974a) probably refer to forficata, s.s. because of the high rainfall mainland locations in which they were found. Nests observed by Wheeler at Saw Pit Creek (N.S.W.) were described as populous and 'under large stones, under or in logs, or at times in mounds'. Gray incompletely excavated one nest at Mount Canobolas (N.S.W.), secured 211 workers, and described the internal structure as being of the more complex diffuse type.

I observed one nest of sp.7 at Lake Gilles C.P. (S.A.) which was moundless, with a single entrance (d ≃ 3 cm) next to the stem of a large bush, and constructed in clay soil. The nest was not completely excavated, because the galleries were intertwined amongst large roots, but it was followed to a depth of about 80 cm. The top 60 cm or so had numerous chambers interconnected by galleries which enables me to classify the internal nest structure as of Gray's (1974a) more complex diffuse type. I collected 90 workers and estimate that the total worker population would have been about 200.

Biological references (including unpublished theses)

Forel (1890); Haskins and Haskins (1950); Gray (1974a, 1974b); Browning (1979)

Comments

M. forficata, s.l. consists of two biological species, initially suspected because of observed inconsistencies in distribution. An undescribed species (sp.7) is present in some dry parts of South Australia. M. forficata, s.l. is usually found in very high rainfall areas (greater than 600 mm annual rainfall) but was also found at several South Australian localities (Cambrai, Lake Bonney, Lake Gilles

C.P., 8 km N of Peebinga, 10 km S of Streaky Bay) where the annual rainfall is much less (250-450 mm). Unfortunately male terminalia are not known for any of these populations but the karyotype and nest structure at Lake Gilles C.P. provide support for my suspicions that the second species, adapted to much drier conditions, is present.

I have tentatively accepted synonymy of *sanguinea*, *lucida* and *rubra* as proposed by Clark (1951) and Brown (1953b) because the brief original descriptions do not allow me to distinguish them from the typical form. Although I have not seen the types, I suspect that *paucidens* is a synonym because Forel's (1910) description clearly identifies his specimens as a species of the *forficata* group and *forficata*, *s.l.* is the only species of this group I have recorded from Tasmania.

5. *Myrmecia hirsuta* Clark

(Figs 45a, 66a-f)

Myrmecia hirsuta Clark, 1951, p. 109, fig. 84 [♀]. Taylor and Brown, 1985, p. 11. Taylor, 1987, p.44.

Type

hirsuta: holotype worker (probable), Stawell, Vic. (April 1928, J.A. Hill), in ANIC (examined). [*Note* - Clark (1951) mentions only specimens from '*Victoria*: Stawell (J. Clark, Dec. 1934)' and that the 'holotype worker [is] in [the] Division of Entomology Museum [= ANIC], C.S.I.R.O., Canberra.' However, the ANIC has no specimens which correspond exactly to this information. Instead there is a worker (Stawell, Vic., April 1928, J.A. Hill) with a holotype label in Clark's handwriting which I presume to be the holotype.]

Worker diagnosis (see Clark, 1951, pp 109-110)

Material examined (fig. 45a)

New South Wales: Beecroft Peninsula (T&B); Bungwahl [62] [*MT*, ♂, 13.xii.1978]. *Victoria*: Stawell (JAH) [*hirsuta* holotype].

[*Note* - Taylor and Brown (1985, p. 11) did not record this species from N.S.W.]

Male terminalia (fig. 66a-f)

No variation has been observed in the male terminalia of *hirsuta*.

Ninth and tenth tergites (fig. 66a) 1.3 times wider than long; median lobe rounded, extending just beyond tips of pygostyles. Pygostyles stout; length 0.3 times width of segment. *Eighth sternite* (fig. 66b) trapezoidal; 1.5 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Stout medium length setae flanking midline in posterior third; a few short setae flanking midline in middle third. *Ninth sternite* (fig. 66c) 1.4 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin narrow, blunt. Short setae scattered over posterior two-thirds. *Basal ring* 1.7 times wider than long; 1.7 times wider posteriorly than anteriorly. *Outer valve* (fig. 66d) 1.7 times longer than deep; posterior end abrupt, Y-shaped in cross-section; dorsal median projection bilobed; dorsal lobe moderately short, pointed; ventral lobe long, rounded. *Middle valve* (fig. 66e) with cuspis shorter than digitus; digitus broad, slightly curved, broadest in middle, distal end bluntly pointed. *Inner valve* (fig. 66f), excluding anterior apodeme, 1.1 times longer than deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe moderately narrow, moderately short, serrated distally; postero-dorsal margin rounded; 3-4 large spines ($\bar{x}$ = 3.5, N = 2) in middle, just in from posterior margin.

Karyotype: Unknown

Taxa included: Typical *hirsuta*

Nest structure: Inapplicable (social parasite)

Biological references (including unpublished theses)

Browning (1979)

Comments

M. hirsuta is a well-defined biological species which can be easily recognized by its worker morphology and male terminalia. The species has been found in mixed nests with *pyriformis* and *brevinoda*, *s.l.* and appears to be a social parasite (Taylor and Brown, 1985, p. 11; B.B. Lowery, pers. comm.; A.D. Bishop, pers. comm.). Unlike *inquilina*, which is a workerless social parasite, *hirsuta* does possess a worker caste.

Its mandibles have backwardly directed teeth, which among *Myrmecia*, *s.s.* are otherwise only present in *brevinoda*, *s.l.*

6. *Myrmecia pyriformis* Smith

(Figs 9a-c, 44b, 67a-f, 102b, 115b)

Myrmecia pyriformis Smith, 1858, p. 144 [♀♀♂].

Myrmecia pyriformis Smith. Mayr, 1862, pp 726, 729. Emery, 1911, p. 20, pl.1, fig. 9 [male genitalia]. Forel, 1915, p. 4. Crawley, 1926, p. 377, fig. 4. Clark, 1927, p. 37; 1951, p. 99, figs 78-80. Brown, 1953b, p. 9. Wheeler and Wheeler, 1971, p. 252 [larva]. Imai, Crozier and Taylor, 1977, p. 345, fig. 12 [karyotype]. Taylor and Brown, 1985, p. 15. Taylor, 1987, p. 45.

Myrmecia tarsata [*sic*] [= *pyriformis*] Smith. Clark, 1929, p. 121.

Myrmecia forficata (Fabricius) subsp. *simillima* Smith, *auct*. (*non* Smith, 1858). Forel, 1907, p. 265; 1910, p. 3. Emery, 1911, p. 20.

Myrmecia forficata simillima Smith, *auct*. (*non* Smith, 1858). Viehmeyer, 1924, p. 221.

Myrmecia simillima Smith, *auct*. (*non* Smith, 1858). Clark, 1928, p. 39; 1934b, p. 51; 1951, p. 89, figs 68-69, *partim*. Wheeler, 1933, p. 34.

Myrmecia sanguinea Smith, *auct*. (*non* Smith, 1858). Wheeler and Wheeler, 1952, p. 112 [larva].

Types

pyriformis: syntype male (possible), Sydney, N.S.W. (E. Damel), in

BMNH (examined); syntype worker(s) and female(s), Melbourne, Vic. and Hunter River, N.S.W., in BMNH. [*Note* - Smith (1858) mentions only specimens from 'Australia (Melbourne; Hunter River)' but the only male specimen in the BMNH bearing a *pyriformis* type label (58.124) has its collection locality listed in the accessions book as being 'Maitland "Partinston" Moreton Bay, Wollanggong [*sic*], Paramatta, Sydney'. This specimen was registered by the BMNH in the same year as Smith published the description of *pyriformis* (1858) and may not have been seen by him. There is also another *pyriformis* male in the BMNH (44.105; without a type label) which was collected at Hunter River by Macgillivray, and registered in 1844. Possibly this specimen is the male syntype of *pyriformis*.]

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 9a-c).

Head, mandibles, scapes, mesosoma, femora, petiole and postpetiole dark brown; funiculi, tibiae and tarsi light brown; gaster black.

Material examined (fig. 44b)

Australian Capital Territory: Black Mountain (BBL); Canberra (BBL); Honeysuckle Creek (BBL); Kowen (TG); Smokers Gap (BBL). *New South Wales*: Beecroft Peninsula (BBL); Berowra (BBL); Bomaderry (BBL); 10 km N of Boorowa (BBL); Bowenfels (BBL); Braidwood [74] [*MT*, ♂, 6.iii.1979]; Brisbane Waters N.P. (BBL); Broulee (BBL); Bungonia (BBL); Burrinjuck Dam (BBL); Congo (MSU); Cowan [76]; Cowra (BBL); Galston (WWF); Gerringong (BBL); Goodradigbee Valley (BBL); Grenfell (BBL); Hunter River (MacG; 44.105 in BMNH) [*MT*, ♂ only, du]; Ingalba N.R. (BBL); Kulnura (BBL); Lawson (BBL); Leumeah (HTI) [*K*]; Lyndhurst (WWF); Menai (BBL); 4 km NW of Merrimbula (BBL); Mittagong (BBL); Morton N.P. (BBL); Mount Victoria (BBL); Mudgee (BBL); Orange (RWT); Paddys River (KRN); Pulletop N.R. (BBL); 40 km E of Queanbeyan (BBL); Rosedale (BBL); Shoalhaven River (TG); Sydney (BBL); Sydney area (ED; 58.124 in BMNH) [*pyriformis* syntype; *MT*, ♂ only, du]; 5 km N of Tathra (BBL); 15 km N of Tathra (BBL); Temora (TG); Tinderry Mountains (BBL); Tumut (BBL); Wellington (BBL); Wentworth Falls (WMM); White Munghorn (BBL); Wisemans Ferry (BBL); Woy Woy (BBL). *South Australia*: Adelaide (AML); American River (BBL); 3 km SW of American River [254]; Belair [39-40, 92, 122]; Blackwood [38]; Clare [65] [*MT*, ♂, 10.iii.1957]; Crafers [481]; 3 km S of Emu Bay [248, 537]; Fulham Gardens [402]; Greenhill [37]; 3 km W of Kingscote (BBL); 5 km NW of Kingscote [312, 314, 501]; Kundaten [382]; Lockleys [401]; Marble Hill [1, 95]; Monarto (BBL); Montacute C.P. [410]; 16 km S of Mount Gambier (BBL); Mount Lofty Range (EFR); Parsons Beach [144] [*MT*, ♂, 29.iv.1981]; Spring Gully C.P. [118]; Stenhouse Bay (BBL); Surrey Downs [351]; Tanunda [400]; Taratap (RDR; in SAM); Upper Hermitage [36] [*SEM*, ♀; *MT*, ♂, 29.iii.1979]; Uraidla [41-44, 259, 530] [*K*, ♂ & 3 ♀ prepupae]; Vivonne Bay [341]; Waitpinga [143] [*MT*, 2♂♂, 29.iv.1981]; Wattle Park [542]. *Victoria*: Aireys Inlet (JMcA); Ararat (GFH); 4 km NW of Ararat [495] [*K*, ♀ prepupa]; Arthurs Seat (BBL); 6 km NE of Bacchus Marsh [357]; Belgrave (JCl); Brisbane Ranges (JF); Broadmeadows (APS); Clayton [399]; Eltham (JED); Ferntree Gully (TG); Flinders (BBL); Harrietville (BBL); Kallista (JCl); Kiata (JCl); Kilmore (BBL); Kinglake N.P. [373]; Melton (JF); Phillip Island (MJ); Riddell (cu); Ringwood (cu); Spring Vale (TG); Stawell (JAH); Victoria (FDB; 85.108 in BMNH) [*MT*, ♂ only, du]; Wallan (BBL); Wedderburn (EFR).

[*Notes* - (1) Taylor and Brown (1985, p. 15) did not record this species from A.C.T. or S.A., and incorrectly recorded it from Tas.

(2) I observed one nest in Lincoln N.P. (S.A.) in January 1983 but was unable to collect any specimens because I had no forceps or jars. This observation supports Clark's (1951) record of *pyriformis* (which he called *simillima*) from southern Eyre Peninsula.]

Male Terminalia (fig. 67a-f)

No variation has been observed in the male terminalia of *pyriformis*.

Ninth and tenth tergites (fig. 67a) 1.3 times wider than long; median lobe rounded, extending just beyond tips of pygostyles. Pygostyles moderately slender; length 0.5 times width of segment. *Eighth sternite* (fig. 67b) trapezoidal; 1.4 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Numerous stout, medium length setae flanking midline in posterior half; numerous short setae in areas near antero-lateral corners. Ninth sternite (fig. 67c) 1.1 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin narrow, indented, triangular in cross-section. Short setae scattered over much of posterior half. Basal ring 1.4 times wider than long; 1.4 times wider posteriorly than anteriorly. Outer valve (fig. 67d) 1.7 times longer than deep; posterior end abrupt, Y-shaped in cross-section; dorsal median projection bilobed; dorsal lobe (DL) moderately long, pointed; ventral lobe (VL) long, rounded. Middle valve (fig. 67e) with cuspis much shorter than digitus; digitus broad, curved, broadest in middle, distal end bluntly pointed. Inner valve (fig. 67f), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe moderately long, narrow, serrated distally; postero-dorsal margin rounded; 2-5 large spines ($\overline{x}$ = 3.5, N = 13) in middle, just in from posterior margin.

Karyotype (figs 102b, 115b)

The karyotypes of pyriformis determined by other researchers and in this study are consistent with intraspecific variation:

n = 41, 2n = 81 (N.F. = 84; Imai et al., 1977, colony from Leumeah, N.S.W.);

n = 41, 2n = 82 (N.F. = 84; A.D. Bishop, pers. comm., colony from 4 km S of Tharwa, A.C.T.);

2n = 82 (N.F. = 84; A.D. Bishop, pers. comm., colony from Belair, S.A.); and

n = 41(?), 2n = 82 (N.F. = 82,84)

Uraidla, S.A.: Three out of 13 cells from worker prepupae had 2n = 82 while in the others I saw 2n = 62 (X1), 73 (X1), 74 (X1), 76 (X1), 77 (X1), 79 (X1), 80 (X2) and 81 (X2). The chromosome number of a male prepupa may have been n = 41 because in six cells I saw n = 39 (X2), 40 (X3) and 42 (X1). The diploid karyotype consists of 2SM and 80A chromosomes (i.e. N.F. = 84) and the haploid karyotype appears to consist of 1SM and 40A (i.e. N.F. = 84). A few of the chromosomes appear to have a small amount of heterochromatic growth.

4 km NW of Ararat, Vic. (figs 102b, 115b): Ten out of 23 cells had 2n = 82 while in the others I only saw 2n = 78(X3), 79 (X3), 80 (X2) and 81 (X5). The karyotype consists of 82A chromosomes (i.e. N.F. = 82). One chromosome of the twelfth pair has a considerable amount of heterochromatic growth (heterochromatin/euchromatin = 1.2) but the other appears to have none. All other chromosomes are normal acrocentrics.

Two populations of pyriformis were karyotyped and both had 2n = 82. However, the number of major chromosome arms in the South Australian population (N.F. = 84) was more than in Victoria (N.F. = 82). The karyotypes from South Australia appeared to be identical to those reported for pyriformis by Imai et al. (1977) and A.D. Bishop (pers. comm.) from colonies collected in New South Wales, Australian Capital Territory and South Australia. To derive the Victorian karyotype from those found in the other states requires one pericentric inversion in the haploid condition.

Taxa included: Typical pyriformis

Nest structure

I collected from colonies of pyriformis at a number of localities in South Australia and two in Victoria. Each nest had a conspicuous clay mound, which was usually bare (sometimes decorated with small twigs), and never had entrances near the top. The mound was high and roughly circular in outline ($d_{max} \simeq 60$ cm, $h_{max} \simeq 30$ cm). A single entrance was located to one side of the mound, usually concealed by leaves. These ants are nocturnal foragers and are not seen on the mound during daylight unless the nest is disturbed. In this case they are very active in defending the nest and impart one of the most painful *Myrmecia* stings I have experienced.

The excavation of an entire *pyriformis* nest is exceedingly difficult because of the large populations they contain and the hard clay soils in which they are constructed. From my incomplete excavations I am able to say that the mound contains several chambers, which usually housed brood during spring, summer and autumn but were empty in winter, and below them a nest of Gray's (1974a) more complex diffuse type (with several main shafts). Gray (1974a) completely excavated two nests at Dee Why (N.S.W.) and Mount Canobolas (N.S.W.) which contained 1,456 and 1,266 workers, and extended to depths of 93 and 77 cm respectively. Barnett (1977) excavated 7 nests at Bacchus Marsh (Vic.) and found somewhat smaller populations of about 200, 230, 250, 300, 320, 350 and 400 workers.

Biological references (including unpublished theses)

Wheeler (1916) [as *sanguinea*]; Freeland (1958; 1985); Gray (1974a, 1974b); Barnett (1977); Browning (1979)

Comments

M. pyriformis is a well-defined biological species, which can be easily distinguished by its male terminalia and karyotype.

7. *Myrmecia regularis* Crawley

(Figs 45a, 68a-e)

Myrmecia regularis Crawley, 1925, p. 579 [♀].

Myrmecia regularis Crawley. Wheeler, 1933, p. 25, fig. 6, [♀]. Clark, 1951, p. 91, figs 70-71 [♂]. Taylor and Brown, 1985, p. 15. Taylor, 1987, p. 45.

Myrmecia sanguinea Smith, *auct*. (*non* Smith, 1858). Forel, 1907, p. 267.
Myrmecia lucida Forel, *auct*. (*non* Forel, 1893). Wheeler and Wheeler, 1971, p. 250 [larva].

Types

regularis: syntype workers, Albany, W.A. (J. Clark), in OUM.

Worker diagnosis (see Clark, 1951, pp 91-92)

Material examined (fig. 45a)

Western Australia: Albany (JCl); Augusta (BBL); 19 km N of Augusta (EFR); Beedelup N.P. (BBL), (WLB; in MCZ) [*MT*, ♂ only, 10.iii.1977]; Denmark (GAC); 10 km N of Denmark [220]; 12 km N of Denmark [222]; Glenoran (EFR); Kenton (RWT); Nornalup (JCl); Pemberton (EFR); 24 km W of Pemberton (EFR); Quinnup (RWT); Walpole [449].

[*Note* - Clark (1951) also records *regularis* from '*South Australia*: Kangaroo Island. *Victoria*: Portland.' but I believe both records to be incorrect. The specimens from Kangaroo Island undoubtedly belong to *sp.9* while the Portland specimens are probably *forficata*, *s.l.* because both species are superficially very similar to *regularis* and are the only species in these areas likely to cause confusion.]

Male terminalia (fig. 68a-e)

No variation has been observed in the male terminalia of *regularis*.

Ninth and tenth tergites unknown. *Eighth sternite* (fig. 68a) trapezoidal; 1.8 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Numerous stout, medium length setae flanking midline in posterior two-thirds. *Ninth sternite* (fig. 68b) 1.1 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin very narrow, turning ventrally. A few short setae scattered over posterior third. *Basal ring* 1.6 times wider than long; 1.8 times wider posteriorly than anteriorly. *Outer valve* (fig. 68c) 1.4 times longer than deep;

posterior end abrupt, Y-shaped in cross-section; dorsal median projection bilobed; dorsal lobe very short, almost absent; ventral lobe long, rounded. Middle valve (fig. 68d) with cuspis shorter than digitus; digitus broad, slightly curved, broadest in middle, distal end bluntly pointed. Inner valve (fig. 68e), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe short, moderately broad, serrated distally; postero-dorsal margin rounded; four small spines (N = 1) in middle, just in from posterior margin, seven more (N = 1) along ventral half of posterior margin.

Karyotype

No variation has been observed in the karyotype of *regularis*.

2n = 40 (A.D. Bishop, pers. comm., colony from Karridale, W.A.)

Taxa included: Typical *regularis*

Nest structure

I observed two colonies of *regularis* at 10 and 12 km N of Denmark (W.A.). The nests were both located under fallen logs and probably had their entrances alongside the log. I cannot be sure whether they had more than one entrance because it was only after turning the logs that I found the nests. The nests appeared to contain only a few hundred workers. In one nest pupae and workers were found in galleries situated in the wood of the log. The internal structure of the nests was of Gray's (1974a) more complex diffuse type.

Biological references (including unpublished theses)

Barbour and Loveridge (1929); Haskins and Haskins (1950, 1955)

Comments

M. regularis is a well-defined biological species, distinguished from all other species in the *forficata* group by its lower chromosome number (2n = 40) and male terminalia. Its workers are very similar to *sp.9* but are noticeably smaller. The species is confined to the high rainfall area of south-west Western Australia.

8. *Myrmecia subfasciata* Viehmeyer, *sp. indet.*

Myrmecia subfasciata Viehmeyer, 1924, p. 221 [♀]. Clark, 1951, p. 117. Taylor and Brown, 1985, p. 16. Taylor, 1987, p. 46.

Type

subfasciata: holotype worker, Liverpool, N.S.W., in ZMB.

Worker diagnosis (see Viehmeyer, 1924, p. 221)

Material examined: None

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *subfasciata*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

Although no specimens have been seen, I have placed this species in the *forficata* group because Viehmeyer (1924) says it has red-brown mandibles. It is probably a synonym of *forficata*, *s.l.*, *pyriformis*, or *brevinoda*, *s.l.*

9. *Myrmecia sp.9* (ANIC)

(Figs 10a-c, 45a, 65c-d)

Myrmecia forficata (Fabricius), *auct.* (*non* Fabricius, 1787). Brown, 1953b, p. 29, *partim*.

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 10a-c).

Head, mandibles, antennae, mesosoma, legs, petiole and postpetiole reddish brown; last dorsal segment of gaster yellow; rest of gaster black.

Material examined (fig. 45a)

South Australia: Cape Torrens C.P. [539]; Flinders Chase N.P. [500]; Hanson Bay [99, 102-103, 107]; Parndana C.P. [34]; Ravine de Casoars [16]; Rocky River [22, 109, 334, 338] [*MT*, ♂, 21.iii.1979]; Rocky River H.S. [12-14, 17, 25, 28-30, 32-33, 52, 106, 323] [*SEM*, ♀; *MT*, 11♂♂, 20-22.iii.1979]; 4 km W of Rocky River H.S. [18-20] [*MT*, ♂, 21.iii.1979]; 6 km N of Rocky River H.S. [21]; West Bay [326]; Western River C.P. [498].

Male terminalia (fig. 65c-d)

No variation has been observed in the male terminalia of *sp.9*.

Ninth and tenth tergites, *eighth sternite*, *basal ring*, *outer* and *middle valves* very similar to *pyriformis*. *Ninth sternite* (fig. 65c) 1.4 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin narrow, blunt. Short setae scattered over posterior half. *Inner valve* (fig. 65d), excluding anterior apodeme, 1.1 times longer than deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe moderately short, moderately narrow, serrated distally; postero-dorsal margin rounded; 1-5 large spines ($\bar{x}$ = 2.8, N = 23) in middle, just in from posterior margin.

Karyotype: Unknown

Taxa included: Typical *sp.9*

Nest structure

I observed numerous colonies of *sp.9* at several localities on the western end of Kangaroo Island (S.A.). These were usually under fallen logs (sometimes with galleries in the log) or around the bases of shrubs (e.g. *Acacia*, *Xanthorrhea*). The nest consisted of a conspicuous clay mound often more than a metre in diameter. Commonly, one or two entrances were present on the mound and one or two others were concealed amongst the surrounding vegetation. The nests were extremely populous (754 workers removed from the incomplete excavation of colony 12) and could not be excavated easily. The internal structure was of Gray's (1974a) more complex, diffuse type.

Biological references (including unpublished theses)

Browning (1979)

Comments

M. sp.9 is an undescribed species restricted to the western end of Kangaroo Island. Specimens have previously been referred to regularis by Clark (1951) and forficata by Brown (1953b). However, it can be easily distinguished from other species of the forficata group by its male terminalia. Its workers closely resemble regularis but they are noticeably larger - probably it is more closely related to pyriformis (see Chapter 4).

3.4.1.3. The Myrmecia mjobergi group

Diagnosis

Large Myrmecia with very distinctive workers and male terminalia. Workers have long heads (CI $\leqslant$ 86, cf. CI $\geqslant$ 91 for other Myrmecia) and long mandibles (MI2 $\geqslant$ 142, cf. MI2 $\leqslant$ 128 for other Myrmecia; fig. 11b). Inner valve of male terminalia has no spines and a moderately long postero-ventral lobe, which has no serrations and is rounded distally (fig. 69e).

Composition

mjobergi Forel

[Note - This species has previously been placed in the vindex group of Clark (1951).]

Distribution

Qld

Comments

The *mjobergi* group is well delimited from all other species groups by its worker morphology and male terminalia. However, phylogenetic relationship with the *forficata* group is indicated by several similarities in the workers and male terminalia (see above).

10. *Myrmecia mjobergi* Forel

(Figs 11a-c, 45b, 69a-e)

Myrmecia mjobergi Forel, 1915, p. 5 [♀]. Clark, 1951, p. 101, figs 81-82 [♀♂]. Brown, 1953b, p. 11. Taylor and Brown, 1985, p. 13. Taylor, 1987, p. 44.

Types

mjobergi: syntype worker, Malanda, Qld (E. Mjoberg), in ANIC (examined); syntype worker(s) and female(s), Atherton and Malanda, Qld, in GMNH.

Worker diagnosis

Measurements and proportions as given and illustrated (figs 11a-c).

Head, mesosoma, petiole, postpetiole and anterior half of first segment of gaster brownish red; rest of gaster black; mandibles, antennae and legs yellow.

Material examined (fig. 45b)

Queensland: Cardwell Range (RHD); Dirran (RHD); Kuranda (EHB); 2 km E of Kuranda (C&U) [*MT*, ♂ only, 11.iii.1964]; Lake Barrine (RWT) [*SEM*, ♀]; Malanda (EM) [*mjobergi* syntype]; Mount Lewis (RWT); Mount Windsor (RWT).

Male terminalia (fig. 69a-e)

No variation has been observed in the male terminalia of *mjobergi*.

Ninth and tenth tergites badly damaged during dissection. Pygostyles narrow; moderately long. *Eighth sternite* (fig. 69a) trapezoidal; 2.0 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment.

Numerous short setae in middle over much of posterior three-quarters. *Ninth sternite* (fig. 69b) 1.2 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin very narrow, turning ventrally. Short setae scattered over posterior half. *Basal ring* 1.7 times wider than long; 1.3 times wider posteriorly than anteriorly. *Outer valve* (fig. 69c) 1.1 times deeper than long; posterior end abrupt, Y-shaped in cross-section; dorsal median projection moderately long, digitate. *Middle valve* (fig. 69d) with cuspis slightly shorter than digitus; digitus broad, slightly curved, broadest in middle, distal end rounded. *Inner valve* (fig. 69e), excluding anterior apodeme, 0.9 times as long as deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe narrow, moderately long, rounded distally; postero-dorsal margin rounded; without spines.

Karyotype: Unknown

Taxa included: Typical *mjobergi*

Nest structure

No nests of *mjobergi* were seen during this study. However, Brown (1953b) states that it '... nests high in the tops of trees in the "peat" gathered by epiphyte masses, including various ferns, orchids and the like.' This is the only *Myrmecia* which does not nest in the ground.

Biological references (including unpublished theses)

MacQueen (1967)

Comments

M. mjobergi is a well-defined biological species, which can be easily distinguished by its worker morphology and male terminalia. It is found only in the rainforests of north Queensland.

3.4.1.4. The *Myrmecia nigriscapa* group

Diagnosis

Large *Myrmecia* with no distinctive characters of the worker morphology. However, they can be characterized by the following combination: 1) red forebody; 2) black scapes; and 3) yellow gastric apex. Support for recognition of this species group relies on characters of the male terminalia. These are easily recognized by the inner valve which has no postero-ventral lobe, large serrations along the posterior margin and a number of small spines in the postero-dorsal corner (fig. 70f).

Composition

nigriscapa Roger (= *analis* Mayr = *atriscapa* Crawley)

[*Note* - Synonyms of this species have previously been placed in the *gulosa* and *tarsata* groups of Emery (1911), while Clark (1951) included the species in the *tricolor* group.]

Distribution

S.A., Vic., W.A., [? N.S.W.]

Comments

The *nigriscapa* group is well delimited from all other groups by its male terminalia, but its workers are broadly similar to the *tarsata*, *auriventris* and *flavicoma* groups. The similarity is evident in the shape of the petiole and mandibles. However, the male terminalia do not indicate that the *nigriscapa* group is closer to any of them than it is to the *forceps*, *forficata*, *mjobergi*, *gulosa*, *simillima* or *vindex* groups.

11. *Myrmecia nigriscapa* Roger

(Figs 12a-c, 45b, 70a-f)

Myrmecia nigriscapa Roger, 1861a, p. 33 [♀]. Mayr, 1862, pp 723, 727. Forel, 1907, p. 266. Emery, 1911, p. 19. Clark, 1925, p. 141 [♀♂]; 1951, p. 51, figs 29-31. Wheeler, 1933, p. 30. Taylor and Brown, 1985, p. 13. Taylor, 1987, p. 44.

Myrmecia analis Mayr, 1862, pp 725, 728, *syn. nov.* [♀]. Emery, 1911, p. 20. Wheeler, 1933, p. 42. Clark, 1927, p. 34; 1951, p. 53, figs 32-33. Taylor and Brown, 1985, p. 6. Taylor, 1987, p. 41.

Myrmecia atriscapa Crawley, 1925, p. 580, *syn. nov.* [♀].

Types

nigriscapa: syntype workers, Australia, in ZMB.

analis: holotype worker, Australia, in NHMW. [NEW SYNONYMY].

atriscapa: syntype worker, Albany, W.A. (J. Clark), in ANIC (examined); syntype worker(s), Albany, W.A. (J. Clark), in OUM. [NEW SYNONYMY; synonymy with *analis* by Clark, 1927].

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 12a-c).

Head, distal end of scapes, funiculi, mesosoma, legs, petiole and postpetiole red; rest of scapes black; mandibles yellow. Colour of gaster variable, though constant within nests and populations. Two forms are known: (1) first segment and anterior half of second segment black; rest of gaster yellow (most W.A. populations) [*analis* colour form; includes *atriscapa*]; and (2) anterior half of first segment red; posterior half of first segment and anterior half of second segment black; rest of gaster yellow (all S.A. and Vic. populations, and a few W.A. populations) [*nigriscapa*, *s.s.* colour form].

Material examined (fig. 45b)

South Australia: Browns Beach [535]; Cape du Couedic [317]; 3 km NE of Coffin Bay [167]; Cox's Scrub (RDR; in SAM); Hanson Bay [104-105, 115]; 5 km NW of Kingscote [310]; 18 km S of Kingscote [252]; Kundaten [381]; Little Desert (BBL); Little Dip C.P. [262]; Mary Seymour C.P. [391]; Meningie (LHM); 8 km E of Meningie (LJC); Mount Barker [394]; Mount Lofty (BBL); 5 km E of Norwood (BBL); 10 km E of Penneshaw [258]; Point Avoid [305] [*SEM*, ♀]; Point Ellen (K&K); Ravine de Casoars [328, 331]; Robe [392]; Rocky River H.S. [11, 15, 49]; Scott C.P. [479]; Strawbridge Point (K,W&P); Taratap (RDR; in SAM); Victor Harbor (BBL); Vivonne Bay [340]; Waitpinga (BBL) [*MT*, ♂ only, 1.iv.1971]; Western

River C.P. [499]. *Victoria*: 6 km SW of Cranbourne [86] [*MT*, ♂, 29.iii.1974]; Gellibrand (JCl); Halls Gap (TW); Melbourne (HT); Melton (JF); Merrick Beach [393]; Spring Vale (TG); Wilsons Promontory (RJM); You Yangs (BBL). *Western Australia*: Albany (JCl) [*atriscapa* syntype]; Augusta (EBB); Blackwood River (BBL) [*MT*, ♂, 18.xii.1969]; Bunbury (JCl); 9 km N of Busselton [216]; 18 km N of Denmark (RWT); Esperance [424, 426]; Frenchman Bay (LPK); Kenton (RWT); Ludlow (JCl); 2 km S of Ludlow [214]; Margaret River (EFR); 32 km SW of Mount Ragged (RWT); Pemberton (IMD); 24 km W of Pemberton (EFR); Picton (JCl); Point d'Entrecasteaux (KRN); Porongorup (EFR); Thomas River (TG); Walpole (cu); 24 km NW of Walpole (EFR); William Bay (BBL); Yallingup (EFR).

[*Note* - Clark (1951) also records *nigriscapa* from '*New South Wales*: Lismore, Eden. *Queensland*: Beaudesert.' and *analis* from '*New South Wales*: Lismore. *Queensland*: Brisbane.' The record from Eden is close to the known range of *nigriscapa*, but I consider that the other records, from northern N.S.W. and southern Qld, are based on misidentified specimens of *gulosa* or *ferruginea* Mayr (*dimidiata* colour form). Taylor and Brown (1985, pp 6, 13) also recorded *nigriscapa* and *analis* from Qld and N.S.W., probably based on the same records]

Male terminalia (fig. 70a-f)

No variation has been observed in the male terminalia of *nigriscapa*; *nigriscapa*, *s.s.* and *analis* colour forms have both been examined.

Ninth and tenth tergites (fig. 70a) 1.6 times wider than long; median lobe angulate, with rounded indentation at apex, extending beyond tips of pygostyles. Pygostyles moderately slender; length 0.3 times width of segment. *Eighth sternite* (fig. 70b) trapezoidal; 1.3 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae in a broad band across middle; a few others in posterior quarter, associated with longitudinal sculpturing. *Ninth sternite* (fig. 70c) 1.1 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin narrow and blunt or indented. Short setae scattered over posterior extension and in areas flanking midline in posterior two-thirds. Basal ring 1.6 times wider than long; 1.4 times wider posteriorly than anteriorly. Outer valve (fig. 70d) 1.8 times longer than deep; posterior end roundly pointed; dorsal median projection moderately short, blunt. Middle valve (fig. 70e) with cuspis much shorter than digitus; digitus moderately broad, curved, similar breadth throughout, distal end rounded. Inner valve (fig. 70f), excluding anterior apodeme, 1.6 times longer than deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe absent; posterior margin with 7-9 large serrations ($\overline{x} = 8.2$, $N = 6$); 12-20 small spines ($\overline{x} = 17.3$, $N = 6$) in postero-dorsal corner.

Karyotype: Unknown

Taxa included

(1) analis colour form

(2) nigriscapa, s.s. colour form

Nest structure

I observed colonies of nigriscapa at numerous localities in South Australia and two in Western Australia. The nests were always located in sandy soils with one being found beneath a large log, one next to a yacca (Xanthorrhea sp.), another amongst a dead tree stump and its roots, a fourth against the base of a large eucalypt and others in the open. Each nest had one entrance ($d \simeq 2$ cm) in the centre of a low mound ($d_{max} \simeq 1$ m, $h_{max} \simeq 10$ cm). No nests were completely excavated, but my observations of the upper portions of nests which I partially excavated support those of Barnett (1977; see below).

The internal structure of nigriscapa nests was quite different to that of other *Myrmecia*, and did not fit readily into any of the three types observed by Gray (1974a). Around the entrance a number of chambers were present, from which several deep shafts descended. These often forked and, according to Barnett, gave rise to a complex of shafts and galleries in the lower levels of the nests. Remarkably, a few shafts also ascended and terminated in a series of chambers only a few centimetres from the surface. In five out of seven nests excavated by Barnett at Bacchus Marsh (Vic.), the colony queen was located in one of these chambers rather than near the bottom of the nest, as is usual in all other species observed. Somewhat similarly, in one nest [214] , I was astonished to collect the colony queen only a few centimetres inside the entrance to a large nest. Why colony queens of this species should be found in such vulnerable positions is unknown and difficult to speculate upon.

The nests are usually of moderate size (around 200 workers) but can be very populous. Barnett obtained 8, 100, 180, 190, 220, 230, 250 and 1,500 workers from the nests she excavated.

Biological references (including unpublished theses)

Barnett (1977); Browning (1979); Beattie et al. (1986)

Comments

M. nigriscapa appears to be a well-defined biological species with two colour forms. In general the *nigriscapa*, *s.s.* colour form is found east of the Nullarbor Plain and the *analis* colour form to the west. However, an anomalous population of *nigriscapa*, *s.s.* is found along the strip of coastal limestone country occupied by the Tuart forests in south-west Western Australia. The two colour forms are synonymized here because of similarities in male terminalia and their overlapping distributions.

3.4.1.5. The *Myrmecia tarsata* group

Diagnosis

Large *Myrmecia* with no distinctive characters of the worker morphology. However, they can be characterized by the following combination: (1) colouration consisting of a bluish metallescence over a jet-black body with the posterior half of the gaster yellow; and (2) petiolar stalk much shorter than node (fig. 13a). Support for recognition of this species group relies on characters of the male terminalia. These are easily recognized by the outer valve which has a spoon-shaped posterior end (fig. 71d).

Composition

tarsata Smith

[*Note* - This species has previously been placed in the *tarsata* group of Emery (1911) and *tricolor* group of Clark (1951).]

Distribution

A.C.T., N.S.W., Qld, Vic.

Comments

The *tarsata* group is well delimited from all other species groups by its male terminalia but its workers are broadly similar to the *nigriscapa*, *auriventris* and *flavicoma* groups. However, the male terminalia do not indicate that the *tarsata* group is closer to any of them than it is to the *forceps*, *forficata*, *mjobergi*, *gulosa*, *simillima* or *vindex* groups.

12. *Myrmecia tarsata* Smith

(Figs 13a-c, 46a, 71a-f)

Myrmecia tarsata Smith, 1858, p. 145 [♀]. Roger, 1861a, p. 33 [♀]. Mayr, 1862, pp 726, 729; 1876, p. 96. Froggatt, 1905, p. 865. Forel, 1910, p. 4. Emery, 1911, p. 20. Viehmeyer, 1924, p. 221. Crawley, 1926, p. 379, fig. 6. Clark, 1927, p. 34; 1929, p. 121;

1951, p. 28, figs 6-9 [♂]. Wheeler, 1933, p. 45, fig. 14. Forbes, 1967, p. 37, figs 1-7 [male terminalia]. Taylor and Brown, 1985, p. 16. Taylor, 1987, p. 46.

Myrmecia ?gulosa (Fabricius), auct. (non Fabricius, 1775). Guérin-Méneville, 1831, p. 207.

Types

tarsata: syntype workers, Hunter River, N.S.W., in BMNH. [Note - Smith's (1858) description mentions material from 'Australia (Hunter River, &c) ', but because he did not elaborate about which localities he included in '&c', I have restricted the type locality to Hunter River.]

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 13a-c).

Head, mesosoma, femora, tibiae, petiole, postpetiole, and first and second segments (except posterior margins) of gaster bluish black; mandibles, antennae, tarsi and rest of gaster yellow.

Material examined (fig. 46a)

Australia: Australia (CPH) [MT, 2♂♂ only, du] [specimens examined by Forbes (1967)]. Australian Capital Territory: Brindabella (TG); Uriarra (TG). New South Wales: Armidale (BBL); Asquith (HPS); 6 km N of Batemans Bay (EFR); Bathurst (BBL); 24 km S of Bega (EFR); 20 km NW of Braidwood [78] [SEM, ♀; MT, ♂, 6.iii.1979]; Broulee (BBL); Campbelltown (EGK) [MT, ♂, 20.ii.1966]; Collaroy (KRN); Crookwell (EFR); Dharug N.P. (BBL); Dorrigo (WWF); Durras Lake (TG); 6 km N of Eden (EFR); Farmer's Creek (BBL); Guyra (EFR); Hanging Rock (EFR); Hornsby (HPS); Kangaroo Valley (EFR); Mittagong (BBL); Mount Kaputar (RJM); Myrtle Mountain (BBL); Narrabeen (cu); Nerriga (TG); Port Hacking (NBT); Rosedale (BBL); Rydalmere (cu); Styx River (EFR); 6 km S of Swansea (BBL); Sydney (BBL); Tinderry Mountains (EFR); Tumut (BBL); Uralla (WMW); Wauchope (B&M); Woy Woy (BBL); Wyong (BBL). Queensland: Brisbane (SHP). Victoria: Cann River (JCl); Orbost (BBL).

Male terminalia (fig. 71a-f)

No variation has been observed in the male terminalia of tarsata.

Ninth and tenth tergites (fig. 71a) 2.2 times wider than long;

median lobe rounded, extending beyond tips of pygostyles. Pygostyles moderately stout; length 0.3 times width of segment. Eighth sternite (fig. 71b) almost rectangular; 1.1 times wider than long; 1.1 times wider anteriorly than posteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae in two large areas flanking midline in anterior two-thirds; a few flanking midline in posterior quarter, associated with longitudinal sculpturing. Ninth sternite (fig. 71c) 1.3 times longer than wide; moderately short anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior extension of posterior margin moderately narrow, blunt, with parallel sides. Numerous short setae scattered over much of posterior half; a few short, fine, undulate setae flanking midline in anterior third; long sensory setae around posterior extension. Basal ring 1.6 times wider than long; 1.6 times wider posteriorly than anteriorly. Outer valve (fig. 71d) 1.9 times longer than deep; posterior end spoon-shaped, with lateral wall higher than median wall; median wall with tooth-like projection; dorsal median projection blunt, dorso-ventrally flattened. Middle valve (fig. 71e) with cuspis much shorter than digitus; digitus broad, very curved, broadest in middle, distal end rounded. Inner valve (fig. 71f), excluding anterior apodeme, 0.9 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe moderately broad, moderately long, serrated distally; postero-dorsal margin rounded; 6-12 small spines ($\overline{x}$ = 8.9, N = 7) in middle, just in from posterior margin.

Karyotype: Unknown

Taxa included: Typical tarsata

Nest structure

No nests of tarsata were seen during this study. However, Wheeler (1933, p. 45) observed that 'colonies ... were nesting in rather large mounds'. Gray (1974a) recorded 1,125 workers from a single nest at Dee Why (N.S.W.) and described the internal structure as being of the less complex diffuse type. Muir (1975) also excavated two large nests in the Armidale district (N.S.W.) and found populations of about 1,300 and 1,900 workers.

Biological references (including unpublished theses)

McAreavey (1948); Haskins and Haskins (1950); Gray (1974a); Muir (1975); Browning (1979); Freeland (1985)

Comments

M. tarsata is a well-defined biological species, which can be easily distinguished by its worker morphology and male terminalia. Wheeler (1933, p. 45) agreed with Froggatt (1905) that the species is quite timid and 'if one or two are captured the other ants retreat into the nest and do not show fight'. The species is found along the east coast of Australia from eastern Victoria to southern Queensland.

3.4.1.6. The Myrmecia auriventris group

Diagnosis

Large Myrmecia with no distinctive characters of the worker morphology. However, they can be characterized by the following combination: 1) yellow mandibles; 2) black and red body, 3) gaster densely clothed with gold pubescence; and 4) petiolar stalk much shorter than node (fig. 14a).

Composition

auriventris Mayr (= athertonensis Forel)

[*Note* - This species has previously been placed in the *tarsata* group of Emery (1911) and *tricolor* group of Clark (1951).]

Distribution

Qld

Comments

The *auriventris* group has workers which are broadly similar to the *nigriscapa*, *tarsata* and *flavicoma* groups. Although its male terminalia are unknown, the dissimilar male terminalia of the *nigriscapa*, *tarsata* and *flavicoma* groups mean that the *auriventris* group cannot be assumed to be closer to any of them than it is to the *forceps*, *forficata*, *mjobergi*, *gulosa*, *simillima* or *vindex* groups.

13. *Myrmecia auriventris* Mayr

(Figs 14a-c, 46a)

Myrmecia auriventris Mayr, 1870, p. 968 [♀]; 1876, p. 95. Emery, 1911, p. 20. Wheeler, 1933, p. 46. Clark, 1951, p. 40, figs 17, 18 [♂]. Brown, 1953b, p. 10. Taylor and Brown, 1985, p. 6. Taylor, 1987, p. 41.

Myrmecia auriventris Mayr var. *athertonensis* Forel, 1915, p. 8 [♀♂]. Clark, 1951, p. 42.

Types

auriventris: syntype workers, Port Mackay and Cape York, Qld, in NHMW.

athertonensis: syntype worker, Atherton, Qld (E. Mjoberg), in ANIC (examined); syntype worker(s) and male(s), Atherton, Qld, in GMNH. [Synonymy by Brown, 1953b].

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 14a-c).

Head, antennae, pronotum, mesonotum, metanotum, femora, tibiae and gaster black; epinotum and petiole red; mandibles and tarsi yellow. Gaster densely clothed with gold pubescence.

Material examined (fig. 46a)

Queensland: Atherton (EM) [*athertonensis* syntype]; Bowen (ASi; in SAM); Byfield (HJC; in SAM); Eungella N.P. (BBL); Kuranda (WMW); Lankelly Creek (PJD); Mareeba (HEH); Maryborough (EWFi); McIlwraith Range (PAM); Mount Spec (Ds); 12 km W of Paluma [510] [*SEM*, ♀]; Palm Island (AML; in SAM); Ravenshoe (Ds).

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *auriventris*

Nest structure

No nests of *auriventris* were seen during this study, but Wheeler (1933, p. 46) says that 'the nests are compact earthen mounds less than a foot in diameter, with eccentric entrance and therefore somewhat oven-shaped. Not more than a dozen workers were found in a colony, and they were very timid compared with many species in the genus. When disturbed they usually retreated into the entrance and remained concealed. They were sometimes found foraging on the trunks and branches of eucalypts.'

Biological references (including unpublished theses)

Turner (1897)

Comments

M. auriventris is a well-defined biological species which is easily recognized by its worker morphology. I have not examined any specimens of Forel's (1915) *athertonensis* colour form but it appears to be a slight colour variant and I have accepted Brown's (1953b) synonymy. The colour variation seems insufficient for me to recognize it here as a distinct colour form.

3.4.1.7. The *Myrmecia flavicoma* group

Diagnosis

Large *Myrmecia* with no distinctive characters of the worker morphology. However, they can be characterized by the following combination: 1) yellow mandibles; 2) red body; and 3) petiolar stalk much shorter than node (fig. 15a). Support for recognition of this species group relies upon characters of the male terminalia. These are easily recognized by the presence of spines on the ninth sternite (fig. 72b) and outer valve (fig. 72d).

Composition

flavicoma Roger (= *minuscula* Forel = *comata* Clark)

[*Note* - This species has previously been included in the *tarsata* group of Emery (1911), while Clark (1951) placed its synonyms in the *tricolor* and *vindex* groups.]

Distribution

N.S.W., Qld

Comments

The *flavicoma* group is well delimited from all other species groups by its male terminalia but its workers are broadly similar to the *nigriscapa*, *tarsata* and *auriventris* groups. However, the male terminalia do not indicate that the *flavicoma* group is closer to any of them than it is to the *forceps*, *forficata*, *mjobergi*, *gulosa*, *simillima* or *vindex* groups.

14. *Myrmecia flavicoma* Roger

(Figs 15a-c, 46b, 72a-f)

Myrmecia flavicoma Roger, 1861b, p. 171 [♀]. Mayr, 1862, p. 725. Emery, 1911, p. 20. Viehmeyer, 1924, p. 221. Clark, 1951, p. 74, fig. 53.

Myrmecia flavicoma flavicoma Roger. Taylor and Brown, 1985, p. 9.

Taylor, 1987, p. 43.

Myrmecia flavicoma Roger var. *minuscula* Forel, 1915, p. 8, *syn. nov.* [♀]. Clark, 1951, p. 76.

Myrmecia flavicoma minuscula Forel. Taylor and Brown, 1985, p. 9. Taylor, 1987, p. 43.

Myrmecia comata Clark, 1951, p. 43, fig. 19, *syn. nov.* [♀]. Wheeler and Wheeler, 1971, p. 247 [larva]. Taylor and Brown, 1985, p. 7. Taylor, 1987, p. 42.

Types

flavicoma: syntype workers, Australia, in MNHP.

minuscula: syntype worker, Cedar Creek (= Ravenshoe), Qld (E. Mjoberg), in ANIC (examined); syntype workers, Malanda and Cedar Creek (= Ravenshoe), Qld, in GMNH. [NEW SYNONYMY].

comata: holotype worker, Bunya Mountains, Qld (E.J. Dumigan), in ANIC (examined). [NEW SYNONYMY].

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 15a-c).

Head, mesosoma, petiole and postpetiole red; mandibles yellow; antennae and legs reddish yellow; gaster black.

Material examined (fig. 46b)

New South Wales: Clarence River (Z&Z; in SAM); Tumbulgum (BBL). *Queensland*: Beaudesert (SHP); Bunya Mountains (EJD) [*comata* holotype]; 6 km N of Cooyar (BBL) [*SEM*, ♀]; Cunningham's Gap (BBL); Emu Vale (JHe); Girraween N.P. (BBL); Goodna (BBL); 30 km W of Kilcoy (BBL); Mount Coot-tha (BBL); Mount Jacob (*Ds*; in MCZ) [*MT*, ♂, March 1958]; Nanango (FAC); Ravenshoe (EM) [*minuscula* syntype]; Toowoomba (TG).

[*Note* - Taylor and Brown (1985, pp 8-9) did not record this species from N.S.W.]

Male terminalia (fig. 72a-f)

No variation has been observed in the male terminalia of *flavicoma*.

Ninth and tenth tergites (fig. 72a) 1.8 times wider than long; median lobe rounded, extending to tips of pygostyles. Pygostyles slender; length 0.3 times width of segment. *Eighth sternite* (fig. 72b) trapezoidal; 1.4 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Small areas of serrate longitudinal sculpturing flanking midline in posterior quarter, with associated short setae. Large contiguous areas of short setae flanking midline in anterior three-quarters. Ninth sternite (fig. 72c) 1.5 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin narrow, rounded. Short setae scattered over much of posterior half; numerous short, fine undulate setae flanking midline in anterior half. Numerous spines (Sp) dorsally in posterior half. Basal ring 1.4 times wider than long; 1.4 times wider posteriorly than anteriorly. Outer valve (fig. 72d) 1.8 times longer than deep; posterior end expanded to form two lobes; ventral lobe narrow, pointed, bearing spines (Sp) on medial surface; dorsal lobe rounded; dorsal median projection blunt. Middle valve (fig. 72e) with cuspis extending just beyond end of digitus; digitus moderately broad, curved slightly, widest in middle, distal end rounded. Inner valve (fig. 72f), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.5 times length of rest of segment; postero-ventral lobe moderately long, moderately narrow, serrated; postero-dorsal lobe rounded; two small spines ($\bar{x} = 2.0$, N = 2) near postero-dorsal margin.

Karyotype: Unknown

Taxa included: Typical flavicoma

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. flavicoma is a well-defined biological species, which can be easily distinguished by its male terminalia and worker morphology. Type specimens of both *minuscula* and *comata* were examined, and neither could be distinguished from specimens in the ANIC identified as *flavicoma* by J. Clark. Consequently, I have recognized only a single species.

3.4.1.8. The *Myrmecia gulosa* group

Diagnosis

Large *Myrmecia* with no distinctive characters of the worker morphology. However, they can be recognised by the following combination: (1) red forebody (including scapes); (2) posterior half of gaster black; and (3) inner border of mandible without angulate broadening at the base (fig. 28b). Support for the recognition of this species group relies on characters of the male terminalia. These are easily recognized by the outer valve which has its dorsal median projection lengthened antero-posteriorly (fig. 73a).

Composition

gulosa (Fabricius) (= *obscurior* Forel)

[*Note* - This species has previously been placed in the *gulosa* group of Emery (1911) and *tricolor* group of Clark (1951).]

Distribution

A.C.T., N.S.W., Qld

Comments

The *gulosa* group has workers with long petioles like the *forceps*, *mjobergi*, *simillima* and *vindex* groups, and mandibles which are closest to the *nigriscapa*, *tarsata*, *auriventris*, *flavicoma* and *simillima* groups. The male terminalia are most similar to the *simillima* and *vindex* groups - particularly the inner valves. Overall, I consider that the *gulosa* group is closest to the *simillima* and *vindex* groups.

One nest karyotyped by Imai et al. (1977) had $2n = 38$ (N.F. = 76).

This is similar to the *vindex* group (2n = 30-78; N.F. = 50-80), but much higher than the *simillima* group (2n = 10-14, N.F. = 18-26).

15. *Myrmecia gulosa* (Fabricius)

(Figs 16a-c, 47a, 73a-f)

Formica gulosa Fabricius, 1775, p. 395 [♀]. Latreille, 1802, p. 215.

Myrmecia gulosa (Fabricius). Fabricius, 1804, p. 424. Smith, 1858, p. 143 [♂]. Roger, 1861a, p. 33. Mayr, 1862, pp 723, 727. Emery, 1911, p. 19. Viehmeyer, 1924, p. 221. Clark, 1925, p. 141; 1951, p. 49, figs 26-28 [♀]. Wheeler, 1933, p. 29, fig. 7. Wheeler and Wheeler, 1952, p. 111 [larva]; 1971, p. 246 [larva]. Imai, Crozier and Taylor, 1977, p. 345, fig. 12 [karyotype]. Taylor and Brown, 1985, p. 11. Taylor, 1987, p. 43.

Eciton gulosa (Fabricius). Latreille, 1805, p. 258.

Ponera gulosa (Fabricius). Illiger, 1807, p. 194.

Myrmecia gulosa (Fabricius) var. *obscurior* Forel, 1922, p. 87 [♀].

Types

gulosa: syntype workers, Australia, in BMNH.

obscurior: syntype workers, Australia, in GMNH. [Synonymy by Clark, 1951].

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 16a-c).

Head, antennae, mesosoma, legs, petiole, postpetiole and anterior three-quarters of first segment of gaster red; rest of gaster black; mandibles yellow.

Material examined (fig. 47a)

Australian Capital Territory: Black Mountain (TG); Jervis Bay (EFR). *New South Wales*: Bellbird [364] [*SEM*, ♀]; Berowra Waters (BBL); Botany Bay (HPS); Brooklyn (BBL); Brookvale (TG); Bucketty (BBL); Cessnock S.F. (BBL); 10 km N of Coonabarabran (BBL); 16 km ENE of Coonabarabran (KHLK); 30 km N of Coonabarabran (BBL); Gilgai (BBL); Glenungie S.F. (BBL); 19 km S of Grafton (EFR); Iluka (BBL); 4 km SE of Kearsley [362]; Ku-ring-gai Chase N.P. [407]; Leumeah (C&I) [*K*]; Lismore (CFD); Liverpool (AML); Minnie Water (PT); Mudgee (BBL); Sutherland (WMW); 6 km

S of Swansea (BBL); Sydney [79] [MT, ♂, 25.ii.1966]; Taree (TG); White Munghorn (BBL); Wisemans Ferry (BBL). Queensland: Brisbane (TG); Fraser Island (KHLK); 10 km S of Girraween N.P. [374]; Nanango (BBL); Stanthorpe (BBL); St George (RS); Wacol (BBL); 10 km S of Warwick [366-367].

[Note - Taylor and Brown (1985, p. 11) did not record this species from A.C.T.].

Male terminalia (fig. 73a-f)

No variation has been observed in the male terminalia of *gulosa*.

Ninth and tenth tergites (fig. 73a) 1.9 times wider than long; median lobe angulate, with rounded apex, extending beyond tips of pygostyles. Pygostyles moderately slender; length 0.2 times width of segment. Eighth sternite (fig. 73b) trapezoidal; 1.3 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae scattered over much of anterior three-quarters. Ninth sternite (fig. 73c) 1.4 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin moderately narrow, indented posteriorly. Short setae scattered over much of posterior half; few short, undulate setae in anterior half. Basal ring 1.6 times wider than long; 1.7 times wider posteriorly than anteriorly. Outer valve (fig. 73d) 1.7 times longer than deep; posterior end lengthened antero-posteriorly; dorsal median projection laterally flattened, dorsal end bluntly pointed, ventral end angulate. Middle valve (fig. 73e) with cuspis much shorter than digitus; digitus moderately broad, very curved, similar breadth throughout, distal end bluntly pointed. Inner valve (fig. 73f), excluding anterior apodeme, 1.1 times longer than deep; anterior extension of anterior apodeme 0.5 times as long as rest of segment; postero-ventral lobe narrow, long, serrated distally; about

13-16 small spines ($\bar{x} = 14.5$, N = 2) scattered in middle and posterodorsal corner.

Karyotype

No variation has been observed in the karyotype of gulosa.

2n = 38 (Imai et al., 1977, 2 colonies from Leumeah, N.S.W.)

Taxa included: Typical gulosa

Nest structure

Colonies of gulosa were observed at two localities in New South Wales and one in southern Queensland. Each colony had a single nest with a large, low, bare mound ($d_{max} \simeq 70$-90 cm, $h_{max} \simeq 10$-40 cm). The mound had 1 or 2 entrances (d ≃ 2 cm) near the top. The internal nest structure was of Gray's (1974a) more complex diffuse type. Nest populations can be extremely large - one nest, incompletely excavated to a depth of 93 cm by Gray (1974a) at Jannali (N.S.W.), yielded 2,284 workers, and another excavated by Haskins and Haskins (1950) near Sutherland (N.S.W.) contained 1,586 workers. Gray (1974a) also completely excavated two smaller colonies at Banyabba S.F. (N.S.W.) which contained 251 and 11 workers and went to depths of 77 and 65 cm respectively.

Biological references (including unpublished theses)

Haskins and Haskins (1950); Freeland (1958; 1985); Robertson et al. (1964); MacQueen (1966); Robertson (1971); Haskins et al. (1973); Gray (1974a, 1974b); Sisson (1974); Browning (1979)

Comments

M. gulosa is a well-defined biological species which can be easily recognized by its worker morphology, male terminalia and karyotype. Superficially its workers are similar to nigriscapa (nigriscapa, s.s. colour form) and ferruginea (dimidiata colour form; which is often sympatric), but they can be separated from nigriscapa by the absence of black scapes and yellow gastric apex and from ferruginea by the mandibles, which do not have even slight angulate broadening near the base of the inner border.

3.4.1.9. The Myrmecia simillima group

Diagnosis

Large Myrmecia with no distinctive characters of the worker morphology. However, they can be characterized by the following combination: (1) forebody predominantly, or entirely, black or dark brown; (2) yellow to brownish yellow mandibles with straight inner border; and (3) long petiolar stalk (figs 17a, 18a). Support for recognition of this species group relies on characters of the male terminalia. These are most easily recognized by the inner valve which has a group of spines in the middle spread dorso-ventrally (e.g. fig. 76f).

Composition

(1) arnoldi Clark (= rubripes Clark)
(2) rufinodis Smith (= crudelis Smith = gracilis Emery)
(3) simillima Smith (= nigriventris Mayr = tricolor Mayr = spadicea Mayr = rogeri Emery)

[Note - These species have previously been placed in the vindex, forficata and tarsata groups of Emery (1911), and the tricolor group of Clark (1951).]

Distribution

A.C.T., N.S.W., Qld, S.A., Vic, W.A.

Comments

The simillima group has workers with long petioles like the forceps, mjobergi, gulosa and vindex groups, and mandibles which are closest to the *nigriscapa*, *tarsata*, *auriventris*, *flavicoma* and *gulosa* groups. The male terminalia are most similar to the *gulosa* and *vindex* groups. Overall, I consider that it is closest to the *gulosa* and *vindex* groups.

However, the karyotypes known for the *simillima* group (2n = 10-14, N.F. = 18-26) are much lower than those for the *gulosa* (2n = 38, N.F. = 76) and *vindex* (2n = 30-78, N.F. = 50-80) groups.

Within the *simillima* group, workers of *arnoldi*, *rufinodis* and *simillima* are quite similar, but male terminalia indicate that *arnoldi* and *rufinodis* are much closer to each other than they are to *simillima*. This similarity is supported by my field observations of the nest structure and behaviour of each species.

The karyotypes of *arnoldi* (2n = 14, N.F. = 26) and *rufinodis* (2n = 10, N.F. = 18) are quite similar and can be derived from one another by two Robertsonian rearrangements and two pericentric inversions in the haploid condition. *M. simillima* is yet to be karyotyped, but is expected to be similarly low-numbered.

16. *Myrmecia arnoldi* Clark

(Figs 17a-c, 46b, 75a-f, 103a, 115c)

Myrmecia arnoldi Clark, 1951, p. 36, fig. 14 [♀]. Wheeler and Wheeler, 1971, p. 246 [larva]. Taylor and Brown, 1985, p. 6. Taylor, 1987, p. 41.

Myrmecia rubripes Clark, 1951, p. 34, fig. 12, *syn. nov.* [♀]. Taylor and Brown, 1985, p. 15. Taylor, 1987, p. 45.

Types

arnoldi: holotype worker (probable), Emu Rock, W.A. (H. Reynolds), in ANIC (examined). [*Note* - Clark (1951) mentions specimens from '*Western Australia*: Emu Rock (A. Arnold, May 1926), Ravensthorpe (T. Greaves, Dec. 1947)' and that the holotype worker is in the ANIC. The ANIC has no specimens which correspond exactly to this information. Instead there is a worker (Emu Rock, W.A., H. Reynolds) which has a holotype label in Clark's handwriting and is presumed to be the holotype.]

rubripes: syntype workers (15) (probable), Ongerup, W.A. (4.xi.1947, T. Greaves), in ANIC (examined). [*Note* - Clark (1951) mentions only specimens from '*Western Australia*: Ongerup (T. Greaves, November 4, 1947)' and that the holotype worker is in the ANIC. The ANIC has 15 workers which correspond to this information but none have type labels. I therefore presume that these specimens are syntypes and a lectotype will need to chosen from amongst them.] [NEW SYNONYMY].

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 17a-c).

Head, mesosoma, femora, petiole, postpetiole and gaster black; antennae, tibiae and tarsi red; mandibles yellow.

Material examined (fig. 46b)

Western Australia: East Mount Barron (D&D, in WAM); Emu Rock (HR) [*arnoldi* holotype]; Esperance [423]; Fitzgerald River (cu; in WAM); 32 km W of Hopetoun (BC, in WAM); Jerramungup [233, 437] [SEM, ♀; *K*, 4 ♀ prepupae]; Kellerberin (WC); Kundip (cu; in WAM); Mount Ragged (TG); 32 km S of Mount Ragged (BBL); Ongerup (TG) [*arnoldi* syntypes]; Pink Lake (BBL); 22 km SW of Tambellup [354] [*MT*, ♂, 17.vi.1982]; Twertup [229].

Male terminalia (fig. 76a-f)

No variation has been observed in the male terminalia of *arnoldi*.

Ninth and tenth tergites (fig. 76a) 1.7 times wider than long; median lobe rounded, extending almost to tips of pygostyles. Pygostyles moderately slender; length 0.5 times width of segment. *Eighth sternite* (fig. 76b) trapezoidal; 1.4 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae scattered in two large areas flanking midline in middle half; a few others in posterior quarter, associated with longitudinal sculpturing. *Ninth sternite* (fig. 76c) 1.4 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin moderately narrow, rounded. Short setae scattered over much of posterior two-thirds; a few short undulate setae flanking midline in anterior half; long sensory setae around posterior margin. Basal ring 1.6 times wider than long; 1.7 times wider posteriorly than anteriorly. Outer valve (fig. 76d) 1.9 times longer than deep; posterior end dorso-ventrally flattened; dorsal median projection bluntly pointed. Middle valve (fig. 76e) with cuspis shorter than digitus; digitus broad, curved, broadest in middle, distal end blunt. Inner valve (fig. 76f), excluding anterior apodeme, 0.8 times as long as deep; anterior extension of anterior apodeme 0.6 times as long as rest of segment; postero-ventral lobe narrow, moderately long, serrated distally; postero-dorsal margin rounded; about 16 small spines (N = 1) near postero-dorsal margin; about 23 others (N = 1) in middle, spread dorso-ventrally.

Karyotype (figs 103a, 115c)

No variation has been observed in the karyotype of arnoldi.

2n = 14 (N.F. = 26)

Jerramungup, W.A.: Forty-three out of 53 cells had 2n = 14 while in the others I saw 2n = 12 (X2), 13 (X6), 15 (X1) and 28 (X1). The karyotype consists of 8SM, 4ST and 2A chromosomes (i.e. N.F. = 26).

Taxa included: Typical arnoldi

Nest structure

Colonies of arnoldi were observed at three localities in Western Australia. The nests were very similar to rufinodis (described below), and were located in similar soil types. However, on average, they appeared to be slightly larger than those of rufinodis.

Biological references (including unpublished theses): None

Comments

M. arnoldi is a well-defined biological species which can be easily distinguished from all other species (except *rufinodis*) by its worker morphology and male terminalia. It can be distinguished from *rufinodis* by its black petiole and postpetiole, and karyotype. *M. arnoldi* is found west of the Nullarbor Plain only, and *rufinodis* only to the east.

17. *Myrmecia rufinodis* Smith

(Figs 46b, 76a-f, 103b, 115d)

Myrmecia rufinodis Smith, 1858, p. 145 [☿]. Mayr, 1862, p. 727; 1876, p. 96. Emery, 1911, p. 20. Clark, 1951, p. 37, fig. 15 [♀♂]. Brown, 1953b, p. 8. Taylor and Brown, 1985, p. 15. Taylor, 1987, p. 45.

Myrmecia crudelis Smith, 1858, p. 147, *syn. nov.* [☿♀]. Mayr, 1862, pp 725, 728; 1876, p. 96. Forel, 1910, p. 3. Emery, 1911, p. 19. Crawley, 1926, p. 374, fig. 1. Clark, 1934b, p. 51; 1951, p. 35, fig. 13.

Myrmecia gracilis Emery, 1898, p. 232 [☿]. Clark, 1938, p. 357; 1951, p. 39, fig. 16 [♀♂].

Myrmecia crudelis Smith var. *gracilis* Emery. Emery, 1911, p. 19.

Types

rufinodis: syntype workers, Adelaide, S.A., in BMNH.

crudelis: syntype worker(s) and female(s), Adelaide, S.A., in BMNH. [NEW SYNONYMY].

gracilis: holotype worker, Kingskate (= Kingscote), S.A. (J.G.O. Tepper), in MCSN. [Synonymy by Brown, 1953b].

Worker diagnosis

Identical to *arnoldi*, except patches on dorsum of pronotum and epinotal declivity, petiole and postpetiole red. All specimens I examined were coloured thus, but B.B. Lowery (pers. comm.) says some populations have those parts black, and Clark (1951) implies that not all specimens have red on the mesosoma.

Material examined (fig. 46b)

South Australia: 5 km SW of American River (K,W&p); 14 km SW of American River (K,W&p); Ballast Head (K,W&p); 2 km S of Browns Beach

[536]; 4 km NE of Browns Beach [386]; Coonalpyn (BBL); 3 km S of Emu Bay [250-251, 255, 538]; Foul Bay [268]; Innes N.P. (BBL); Kingscote (WLB); 3 km W of Kingscote (BBL); 5 km NW of Kingscote [309, 502]; 7 km S of Kingscote [35]; 5 km SE of Kingscote Aerodrome [348] [MT, 2♂♂, 5.iv.1983]; Klemzig (ETG; in SAM); 20 km S of Lameroo (RDR; in SAM); 24 km S of Lameroo (PA; in SAM); Lincoln N.P. [119, 299-300] [K, 2 ♀ prepupae]; Little Sahara [256]; Malinong (RDR; in SAM); Marion Bay [269] [K, ♀ prepupa]; Mount Lofty (AHE); Nepean Bay (BBL); Peake (BBL); Phillips Hill (KHLK); Proper Bay [515]; Stansbury (JWM; in SAM); Stenhouse Bay [387]; Taylor's Landing [304]; Vivonne Bay [497]; 19 km SW of Warooka (BBL); Warrenben C.P. [60, 90-91] [MT, 3♂♂, 14.iv.1979 & 19.iv.1980]; 3 km NW of Woods Well (H,G&G; in SAM). *Victoria*: Kaniva (BBL); Kiata (BBL).

[*Note* - Taylor and Brown (1985, p. 15) did not record this species from Vic.]

Male terminalia (fig. 76a-f)

No variation has been observed in the male terminalia of *rufinodis*.

Ninth and tenth tergites (fig. 76a) 1.4 times wider than long; median lobe rounded, extending beyond tips of pygostyles. Pygostyles moderately slender; length 0.3 times width of segment. *Eighth sternite* (fig. 76b) trapezoidal; 1.3 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae scattered in two large areas flanking midline in middle half. *Ninth sternite* (fig. 76c) 1.3 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin moderately narrow, rounded. Short setae scattered over much of posterior three-quarters; a few short undulate setae flanking midline in anterior half; long sensory setae around posterior margin. *Basal ring* 1.7 times wider than long; 1.7 times wider posteriorly than anteriorly. *Outer valve* (fig. 76d) 1.7 times longer than deep; posterior end dorso-ventrally flattened; dorsal median projection bluntly pointed. Middle valve (fig. 76e) with cuspis shorter than digitus; digitus broad, curved, similar breadth throughout, distal end blunt. Inner valve (fig. 76f), excluding anterior apodeme, 0.8 times as long as deep; anterior extension of anterior apodeme 0.7 times as long as rest of segment; postero-ventral lobe narrow, moderately long, serrated distally; postero-dorsal margin rounded; 12-21 small spines ($\bar{x}$ = 15.9, N = 10) near postero-dorsal margin; 11-18 others ($\bar{x}$ = 15.3, N = 10) in middle, spread dorso- ventrally.

Karyotype (figs 103b, 115d)

No variation has been observed in the karyotype of rufinodis.

$$2n = 10\ (N.F. = 18)$$

Marion Bay, S.A. (figs. 113b, 115a): Thirty-two out of 37 cells had 2n = 10 while in the others I saw 2n = 9 (X5). The karyotype consists of 4SM, 4ST and 2A chromosomes (i.e. N.F. = 18).

Lincoln N.P., S.A.: Twenty-two out of 24 cells had 2n = 10 while in the others I saw 2n = 9 (X2). The karyotype was identical to that found at Marion Bay.

Taxa included: Typical rufinodis

Nest structure

Colonies of rufinodis were observed at numerous localities in South Australia. Each nest had a volcano-shaped mound ($d_{max} \simeq 1$ m, $h_{max} \simeq 40$ cm), with the surface usually decorated by gravel and twigs. Several entrances ($d \simeq 5$ cm) were located inside the 'mouth of the crater' at the top of the nest.

No nests were completely excavated because they were very populous and always located amongst limestone. Furthermore, the workers were extremely aggressive and imparted one of the most painful Myrmecia stings I have experienced.

I collected more than 1300 workers from a nest at Warrenben C.P. (S.A.) [90], which I excavated to a depth of about 90 cm, but I would estimate, from the small number of nanitics collected, that this number was probably less than two-thirds the full nest complement.

Biological references (including unpublished theses)

Browning (1979) [as ?*gracilis*]

Comments

M. rufinodis is a well-defined biological species which can be easily distinguished from all other species (except *arnoldi*) by its worker morphology and male terminalia. It can be distinguished from *arnoldi* by its red petiole and postpetiole, and karyotype. *M. rufinodis* is found only to the east of the Nullarbor Plain.

I have accepted Brown's (1953b) synonymy of *gracilis* without examining the type because I have searched extensively around Kingscote (the type locality) and have been unable to find any ants, other than *rufinodis*, which fit Emery's (1898) description. There is a species of the *vindex* group (*sp.12*) which can be confused with *rufinodis*, and which I thought could be the form Emery had seen but, while *sp.12* is common in the southern parts of Eyre, Yorke and Fleurieu Peninsulas, I have yet to find it on Kangaroo Island. If it were to be found there I would reconsider the possibility that *sp.12* and *gracilis* are the same species. This nomenclatural problem could be resolved easily by examining the holotype of *gracilis*, because the mandibles of *sp.12* can be distinguished from *rufinodis* by a slight angulate broadening near the base of the inner border.

A similar problem exists in deciding the identity of *crudelis*. The two candidates are once again *rufinodis* and *sp.12*, but Crawley's (1926) illustration of the head (particularly the mandibles) of the syntype female, leads me to conclude that it too is a synonym of the former.

18. *Myrmecia simillima* Smith

(Figs 18a-c, 47b, 74a-f)

Myrmecia simillima Smith, 1858, p. 144 [♀]. Roger, 1861a, p. 34. Mayr, 1862, pp 726, 729; 1876, p. 96. Crawley, 1926, p. 376, fig. 3. Brown, 1953b, p. 12. Wheeler and Wheeler, 1971, p. 253 [larva]. Taylor and Brown, 1985, p. 16, *partim*. Taylor, 1987, p. 46, *partim*.

Myrmecia tricolor Mayr, 1862, pp 724, 728 [♀]; 1865, p. 85. Emery, 1911, p. 20; 1914, p. 179. Wheeler, 1933, p. 44. Clark, 1951, p. 44, figs 20-21 [♀].

Myrmecia nigriventris Mayr, 1862, pp 724, 727 [♀].

Myrmecia tricolor Mayr var. *nigriventris* Mayr. Emery, 1900, p. 110 [♀]; 1911, p. 20. Forel, 1910, p. 7. Wheeler, 1933, p. 44.

Myrmecia tricolor nigriventris Mayr. Clark, 1951, p. 45, figs 22-23.

Myrmecia spadicea Mayr, 1862, pp 724, 728 [♀]; 1865, p. 86. Emery, 1900, p. 110 [♀]. Forel, 1910, p. 7.

Myrmecia tricolor Mayr var. *rogeri* Emery, 1914, p. 181 [♀]. Viehmeyer, 1924, p. 222. Wheeler, 1933, p. 44.

Myrmecia rogeri Mayr. Clark, 1951, p. 32, figs 10-11.

Types

simillima: syntype workers, Australia, in BMNH.

tricolor: syntype workers, Sydney, N.S.W., in NHMW. [Synonymy by Brown, 1953b].

nigriventris: holotype worker, Australia, in NHMW. [Synonymy by Brown, 1953b].

spadicea: syntype workers, Sydney, N.S.W., in NHMW. [*Note* - Mayr's (1862) description also mentions material from Adelaide, S.A., but this has not been located and, assuming the locality is correct, is extremely unlikely to be conspecific with the Sydney syntypes. I have therefore restricted the type locality to Sydney.] [Synonymy by Clark, 1951].

rogeri: syntype workers, Sydney, N.S.W., in MCSN. [Synonymy by Brown, 1953b].

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 18a-c).

Colour variable and appears to intergrade between populations from:

(1) head, mesosoma, femora, tibiae, petiole, postpetiole and gaster black; mandibles, antennae and tarsi brownish yellow [*similima*, *s.s.* colour form; includes *rogeri*]; to (2) head, mesosoma (except epinotal declivity), femora, tibiae and gaster black; epinotal declivity, petiole and postpetiole brownish red; mandibles, antennae and tarsi brownish yellow [*tricolor* colour form]; to (3) head, mesosoma, femora, tibiae, petiole and postpetiole brownish red; gaster black; mandibles, antennae and tarsi yellow [*nigriventris* colour form; includes *spadicea*].

Material examined (fig. 47b)

Australian Capital Territory: Black Mountain (RYB); Blundells (EFR); Canberra (GW); Gibraltar Creek (BBL); Mount Ainslie (BBL); Mount Majura (BBL); Tidbinbilla N.R. (BBL). *New South Wales*: Armidale (RJM); Batemans Bay (cu); 6 km N of Batemans Bay (EFR); Bega (BBL); 24 km S of Bega (EFR); Bermagui (BBL); Berowra (BBL); 3 km E of Berry (BBL); Blackheath (BBL); Bomaderry (BBL); 10 km N of Boorowa (BBL); Bournda N.R. (BBL); Bowral (BBL); Brisbane Water N.P. (BBL); Bucketty (BBL); 10 km NW of Bungendore (BBL); Burrinjuck Dam (BBL); Central Mangrove (BBL); 12 km S of Cessnock (BBL); Cessnock S.F. (BBL); Currowan S.F. (BBL); Durras Lake (TG); Ebor (EFR); Fassifern (BBL); Fitzgerald's Mountain [509] [SEM, ♀]; Gerroa (BBL); Glen Innes (FAC); Guyra (EFR); Heaton S.F. (BBL); Helensburg [543] [*MT*, 2♂♂, collected as pupae, 23.xii.1984]; Kanangra Walls N.P. (BBL); 6 km N of Karuah (BBL); Katoomba (BBL); Kulnura (BBL); 20 km N of Kulnura (BBL); Lawson (BBL); Leumeah (BBL); Lithgow (BBL); Loftus (cu); Manar (TG); 10 km S of Mangrove Mountain (BBL); Martinsville (BBL); Meadow Flat (BBL); 4 km NW of Merrimbula (BBL); Mittagong (WWF); Mount Victoria (BBL); Mudgee (BBL); Myrtle Mountain (BBL); Nerriga (TG); 8 km S of Nowra (RJB); 3 km N of Peats Ridge [360]; Pymble (BBL); 40 km E of Queanbeyan (BBL); Rosedale (BBL); 5 km S of St Albans (BBL); Strickland S.F. (BBL); Sydney (WWF); Tallaganda S.F. (BBL); 5 km N of Tathra (BBL); 6 km N of The Entrance (BBL); Tinderry Mountains (BBL); Wentworth Falls (CVM); Woy Woy (BBL); Wyong (BBL). *Queensland*: Nanango (FAC). *Victoria*: Altona (AN); Ballarat (HWD); Elphinstone (BBL); Gellibrand (JC1); Halls Gap (BBL); Harrietville (BBL); Lakes Entrance (BBL); Lerderberg Gorge (BBL); Marlo

(BBL); Nowa Nowa (BBL); Riddell (GFH); Spring Vale (TG); Watsonia (BBL); Wilsons Promontory (cu).

[Note - Taylor and Brown (1985, p. 16) did not record this species from A.C.T. or Qld and incorrectly recorded it from S.A. (probably confusing it with rufinodis).]

Male terminalia (fig. 74a-f)

No variation has been observed in the male terminalia of simillima; simillima, s.s. colour form has been examined but the others have not.

Ninth and tenth tergites (fig. 74a) 1.9 times wider than long; median lobe rounded, extending beyond tips of pygostyles. Pygostyles slender; length 0.4 times width of segment. Eighth sternite (fig. 74b) trapezoidal; 1.3 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae scattered in a broad band across anterior two-thirds. Ninth sternite (fig. 74c) 1.3 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin moderately narrow, indented posteriorly. Short setae scattered over much of posterior half. Basal ring 1.6 times wider than long; 1.4 times wider posteriorly than anteriorly. Outer valve (fig. 74d) 1.7 times longer than deep; posterior end dorso-ventrally flattened; dorsal median projection bluntly pointed, with a slight shoulder on the dorsal side. Middle valve (fig. 74e) with cuspis much shorter than digitus; digitus moderately broad, curved, similar breadth throughout, distal end blunt. Inner valve (fig. 74f), excluding anterior apodeme, 0.8 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe narrow, long, serrated distally; postero-dorsal margin rounded; 5-7 small spines ($\overline{x} = 6.0$, N = 2) near postero-dorsal margin; about 13 others ($\overline{x} = 13.0$, N = 2) in middle, spread dorso-ventrally.

Karyotype: Unknown

Taxa included

(1) *similima*, *s.s.* colour form

(2) *tricolor* colour form

(3) *nigriventris* colour form

Nest structure

I observed only one nest of *simillima* (*simillima*, *s.s.* colour form) in New South Wales, on a very cold day (temperature ≃ 10°C). The nest had a low mound ($d_{max} \simeq 45$ cm, $h_{max} \simeq 20$ cm), was decorated with twigs and had no apparent entrances. When I opened the mound, only a single worker was collected and the internal structure appeared to be of Gray's (1974a) less complex diffuse type. Gray (1973, 1974a) completely excavated four nests of *simillima*, *s.s.* colour form at Waterfall, Wyong, Kanangra Walls, Bowral and one of *tricolor* form at Woodford (all N.S.W.). The colonies contained 136, 260, 67, 200 and 144 workers and were 62, 69, 98, 77 and 72 cm deep respectively. Muir (1975) obtained similar numbers from two nests of *simillima*, *s.s.* colour form in the Armidale district (N.S.W.) (about 120 and 190 workers), but a third contained significantly more (about 700 workers).

Biological references (including unpublished theses)

Gray (1973, 1974a, 1974b); Muir (1975)

Comments

M. simillima is a single species, or possibly a complex of sibling species, with variable colouration, which intergrades between two extremes as described above. Unfortunately, male terminalia of only one colour form have been examined and no karyotypes are known so, in the absence of any evidence to support species status for any of the colour forms, I have included all under one name and tentatively accepted Clark's (1951) and Brown's (1953b) synonymies of *tricolor*, *nigriventris*, *spadicea* and *rogeri*. However, I cannot accept Brown's (1953b) synonymy of *paucidens* (type locality: Tasmania) because: (1) I have not seen any specimens from Tasmania referable to *simillima*; and (2) Forel's description states that *paucidens* has red-brown mandibles.

Clark (1951) used the name *simillima* for *pyriformis* as stated by Brown (1953b), but the two are only superficially similar and can be easily separated by mandible shape and colour.

3.4.1.10. The *Myrmecia vindex* group

Diagnosis

Large *Myrmecia* with no distinctive characters of the worker morphology. However, except for *princeps* Clark, they can be characterized by the following combination: (1) yellow mandibles with slight angulate broadening at the base of the inner border; and (2) long petiolar stalk (e.g. fig. 19a). *M. princeps* also has a long petiolar stalk (fig. 28a), but its mandibles have a straight inner border and are very long (fig. 28b). Support for recognition of this species group relies upon characters of the male terminalia. These can be recognized by the inner valve which has spines in the middle near the dorsal margin, often forming a tight cluster (e.g. fig. 62f).

Composition

(1) *atrata* Clark (= *pavida* Clark)

(2) *ferruginea* Mayr (= *fasciata* Clark = *dimidiata* Clark = *suttoni* Clark)

(3) *fulgida* Clark

(4) *fuscipes* Clark

(5) *inquilina* Douglas and Brown

(6) *nigriceps* Mayr, *s.l.* (= *desertorum* Wheeler = *lutea* Crawley) [includes *nigriceps*, *s.s.*, *desertorum*, *sp.11* (ANIC), *sp. nov.* and *sp.13* (ANIC), *sp. nov.*]

(7) *princeps* Clark

(8) *rowlandi* Forel (= *malandensis* Forel)

(9) *vindex* Smith (= *basirufa* Forel = *gratiosa* Clark)

(10) *sp.12* (ANIC), *sp. nov.*

(11) *sp.14* (ANIC), *sp. nov.*

(12) *sp.16* (ANIC), *sp. nov.*

(13) *sp.17* (ANIC), *sp. nov.*

[*Note* - These species have previously been placed in the *vindex* and *tarsata* groups of Emery (1911), and the *tricolor* and *vindex* groups of Clark (1951).]

Distribution

All Australian mainland states and territories

Comments

The *vindex* group has workers with long petioles like the *forceps*, *mjobergi*, *gulosa* and *simillima* groups, but mandibles which are distinctive. The male terminalia are most similar to the *gulosa* and *simillima* groups, so that overall I consider it to be closer to them than the other groups.

The range of karyotypes known (2n = 30-78, N.F. = 50-80) encompasses the *gulosa* group (2n = 38, N.F. = 76), but is much higher than the *simillima* group (2n = 10-14, N.F. = 18-26).

The most distinctive species of the *vindex* group are *inquilina* (a workerless social parasite with small queens) and *rowlandi* (whose workers have several measurement indices outside the normal range for the group; see Table 4). Male terminalia and karyotypes for both species are unknown, and I include them in this species group somewhat tentatively, pending investigation of those characters. Workers of the remaining species in the group differ mainly in colour, except for *princeps* which has noticeably longer mandibles that lack slight angulate broadening near the base of the inner border. Male terminalia are broadly similar in all species investigated, but provide some support for recognizing *princeps* as the most distinctive species, particularly the shapes of the ninth and tenth tergites, and outer and middle valves.

The ninth sternites indicate that the other species should be separated into three sub-groups: (1) *ferruginea* and *sp.17*; (2) *desertorum*, *fuscipes*, *nigriceps*, *s.s.*, *sp.11* and *sp.12*; and (3) *vindex* and *sp.14*. However, the inner valves suggest two different sub-groups: (1) *ferruginea*, *sp.17*, *desertorum*, *fuscipes*, *nigriceps*, *s.s.*, and *sp.12*; and (3) *sp.11*, *vindex* and *sp.14*.

Karyotypes also separate *princeps* as the most distinctive species with N.F. = 50-56 while the other species have N.F. = 68-80. The *nombres fondamentaux* of the higher-numbered group suggest two different sub-groups: (1) *sp.17* and *sp.11* (N.F. = 68); and (2) *atrata*, *desertorum*, *fulgida*, *fuscipes*, *nigriceps*, *s.s.*, *vindex*, *sp.12*, *sp.13*, *sp.14* and *sp.16* (N.F. = 76-80).

Overall, the evidence from workers, male terminalia and karyotypes suggests that the *vindex* group contains seven sub-groups: (1) *inquilina*; (2) *rowlandi*; (3) *princeps*; (4) *sp.11*; (5) *ferruginea* and *sp.17*; (6) *atrata*, *desertorum*, *fuscipes*, *nigriceps*, *s.s.*, *sp.12*, *sp.13* and *sp.16*; and (7) *fulgida*, *vindex* and *sp.14*.

The terminal karyotypes in the *vindex* group - n = 15 (N.F. = 50) and n = 39 (N.F. = 80) - are separated by at least 24 Robertsonian rearrangements and 15 pericentric inversions in the haploid condition.

19. *Myrmecia atrata* Clark

(Figs 19a-c, 20a-c, 48a, 103c-d, 116a-b)

Myrmecia atrata Clark, 1951, p. 77, fig. 55 [♀]. Taylor and Brown, 1985, p. 6. Taylor, 1987, p. 41.

Myrmecia pavida Clark, 1951, p. 76, fig. 54 [♀]. Taylor and Brown, 1985, p. 14. Taylor, 1987, p. 45.

Types

atrata: holotype worker, Ravensthorpe, W.A. (10.xi.1947, T. Greaves), in ANIC (examined).

pavida: holotype worker, Mount Barker, W.A. (6.xi.1947, T. Greaves), in ANIC (examined).

Worker diagnosis

Measurements and proportions as given and illustrated (figs 19a-c, 20a-c).

Head, mesosoma, femora, tibiae, petiole, postpetiole and gaster black; mandibles, antennae and tarsi yellow.

Material examined (fig. 48a)

Western Australia: Dalyup River (BBL); Esperance (BBL); 16 km ENE of Esperance (RWT); 48 km N of Esperance (BBL); 64 km W of Esperance (BBL); Israelite Bay (TG); Jacup (EFR); Jerramungup [225-227, 231, 438-439] [SEM, ♀; *K*, ♀ & ♂ prepupae]; 20 km SW of Jerramungup [239]; 24 km W of Jerramungup [442]; Mount Barker (TG) [*pavida* holotype]; Ravensthorpe (TG) [*atrata* holotype], [240-244, 434-436] [SEM, ♀; *K*, 3 ♀ prepupae]; 6 km S of Ravensthorpe (BBL); Stirling Ranges N.P. [445-448]; Thomas River (RWT).

Male terminalia: Unknown

Karyotype (figs 103c-d, 116a-b)

The variation in the karyotype of *atrata* is consistent with intraspecific variation, but it should be noted that the following cytotypes have been observed:

(1) 2n = 76 (N.F. = 77); and

(2) N.F. = 78 (N.F. = 78).

Ravensthorpe, W.A. (figs 103c, 116a): Four out of 17 cells had 2n = 76 while in the others I saw 2n = 49 (X1), 65 (X3), 68 (X1), 69 (X2), 72 (X1), 73 (X1), 74 (X1) and 75 (X3). The karyotype consists of 1M and 75A chromosomes (i.e. N.F. = 77). The karyotype appears to contain a Robertsonian polymorphism and a chromosome deletion.

Jerramungup, W.A. (figs 103d, 116b): Six out of nine cells from a worker prepupa had 2n = 78 while in the others I saw 2n = 74 (X1), 75 (X1) and 76 (X1). Nineteen out of 35 cells from a male prepupa had n = 39 while in the others I saw n = 36 (X3), 37 (X2), 38 (X8) and 40 (X3). The diploid karyotype consists of 78A chromosomes (i.e. N.F. = 78) and the haploid karyotype has 39A chromosomes (i.e. N.F. = 78).

Two populations of atrata were karyotyped and their diploid complements differed by two chromosomes and one chromosome arm. It appears that the diploid karyotypes are related by one Robertsonian rearrangement and that one small chromosome has been lost from the Ravensthorpe karyotype.

Taxa included

(1) N.F. = 77 cytotype

(2) N.F. = 78 cytotype

Nest structure

About 20 nests of atrata were observed at five localities in Western Australia. All nests were moundless, although sometimes a small amount of soil was scattered about the single entrance (d ≃ 2 cm). The nests were impossible to excavate completely, because of the hard soil in which they had been dug, but I collected full nest series (including nest queens) from two nests at Jerramungup [226, 227] by flooding them with water. Partial excavation to a depth of 1 m was possible in the water-softened soil, and revealed an internal structure of Gray's (1974a) less complex diffuse type. The nests contained small numbers of workers with only 25 and 37 being collected from colonies 227 and 226 respectively. Probably all nests of this species have less than 100 workers.

Biological references (including unpublished theses): None

Comments

M. atrata is a well-defined biological species, which can be easily distinguished from all other species of the *vindex* group, except *sp.12* and the dark brown colour variant of *sp.16*, by its worker colouration. It can be separated from *sp.12* by its geographic distribution (*sp.12* only east of Nullarbor Plain, *atrata* only west of Nullarbor Plain), and karyotype (*sp.12* has 2n = 74, *atrata* has 2n = 76,78) but is only distinguishable from the dark brown variant of *sp.16* by its karyotype (*sp.16* has 2n = 67).

Although karyotypes from Jerramungup and Ravensthorpe were slightly different, workers at each location were examined by SEM and appeared identical. One nest was found to be parasitized by a eucharitine wasp (Hymenoptera: Pteromalidae: Eucharitinae).

20. *Myrmecia ferruginea* Mayr

(Figs 48a, 79e-f)

Myrmecia nigriceps Mayr var. *ferruginea* Mayr, 1876, p. 95 [♀].

Myrmecia ferruginea Mayr. Brown, 1953b, p. 22. Taylor and Brown, 1985, p. 9. Taylor, 1987, p. 43.

Myrmecia fasciata Clark, 1951, p. 63, fig. 40, *syn. nov.* [♀]. Taylor and Brown, 1985, p. 9. Taylor, 1987, p. 43.

Myrmecia dimidiata Clark, 1951, p. 71, fig. 49, *syn*. *nov*. [⚲]. Taylor and Brown, 1985, p. 8. Taylor, 1987, p. 42.

Myrmecia suttoni Clark, 1951, p. 72, figs 50-51, *syn*. *nov*. [⚲ ♀]. Taylor and Brown, 1985, p. 16. Taylor, 1987, p. 46.

Myrmecia vindex Smith, *auct*. (*non* Smith, 1858). Emery, 1911, p. 19, *partim*.

Types

ferruginea: syntype workers, Peak Downs, Qld, in NHMW.

fasciata: holotype worker (probable), Pilliga, N.S.W. (W.W. Froggatt), in ANIC (examined). [*Note* - Clark (1951) mentions specimens from '*New South Wales*: Pilliga (W.W. Froggatt), Barraba (T. Greaves)' and that the holotype worker is in the ANIC. The ANIC has a worker (Pilliga Scrub, N.S.W., W.W. Froggatt) with a holotype label in Clark's handwriting which is presumed to be the holotype.] [NEW SYNONYMY].

dimidiata: holotype worker (probable), Stanthorpe, Qld (Jan. 1928, H.J. Carter), in ANIC (examined). [*Note* - Clark (1951) mentions only specimens from '*Queensland*: Stanthorpe (E.E. Sutton)' and that the holotype worker is in the ANIC. The ANIC has no specimens which correspond to this information exactly. Instead there is a worker (Stanthorpe, Qld, Jan. 1928, H.J. Carter) with a holotype label in Clark's handwriting which is presumed to be the holotype.] [NEW SYNONYMY].

suttoni: holotype worker, Fletcher, Qld (E. Sutton), in ANIC (examined). [NEW SYNONYMY].

Worker diagnosis

Antennae, mesosoma, legs, petiole and postpetiole red; mandibles yellow. Colour of head and gaster variable, though constant within nests and populations. Three forms are known: (1) head red, gaster black [*ferruginea*, *s*.*s*. colour form; includes *suttoni*]; (2) head with dark brown band across middle, gaster black [*fasciata* colour form]; and (3) head red, gaster with anterior two-thirds of first segment red and rest black [*dimidiata* colour form].

Material examined (fig. 48a)

New South Wales: Barraba (TG); Gilgai (BBL); Pilliga [521], (WWF) [*fasciata* holotype]; Tamworth (BBL). *Queensland*: 32 km SE of Biloela (BBL); Dalby (NG; in QM) [*MT*, ♂, March 1936]; Fletcher (ESu) [*suttoni* holotype]; Leyburn (BBL); 13 km N of Nanango (BBL); 16 km S of Nanango (BBL); 20 km N of Nanango (BBL); Stanthorpe [369], (HJC) [*dimidiata* holotype]; 48 km N of Tambo (BBL); Taroom (BBL); Wacol (BBL).

Male terminalia (fig. 79e-f)

No variation has been observed in the male terminalia of *ferruginea*; *ferruginea*, *s.s.* colour form has been examined but the others have not.

Ninth and tenth tergites, *eighth sternite*, *basal ring*, *outer valve* and *middle valve* similar to *sp.17*. *Ninth sternite* (fig. 79e) 1.2 times longer than wide; moderately long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin moderately narrow, rounded. Moderately short setae over much of posterior third; long sensory setae around posterior margin. *Inner valve* (fig. 79f), excluding anterior apodeme, 0.8 times as long as deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe moderately narrow, moderately long, serrated distally; postero-dorsal margin rounded; about 10 small spines (N = 1) near postero-dorsal margin; about 35 others (N = 1) in a tight cluster in middle near posterior margin.

Karyotype: Unknown

Taxa included

(1) *ferruginea*, *s.s.* colour form

(2) *fasciata* colour form

(3) *dimidiata* colour form

Nest structure

One nest of *ferruginea* (*dimidiata* colour form) was observed at Stanthorpe (Qld) [369]. The nest had a medium-sized mound (d ≃ 60 cm, h ≈ 20 cm), with 2 entrances near the top, constructed around a small bush. It was not completely excavated, but about 250 workers were collected and probably less than 50 more would have been present. The internal structure was of Gray's (1974a) less complex, diffuse type and was about 1 m deep.

Biological references (including unpublished theses): None

Comments

M. ferruginea is a single species, or possibly a complex of sibling species, with variable colouration. It can be distinguished from all other species (except *sp.17*) by its male terminalia. The only consistent differences noted between *sp.17* and *ferruginea* are head colour and nest structure. Karyotype analysis should be of considerable value for deciding the status of these taxa.

21. *Myrmecia fulgida* Clark

(Figs 21a-c, 48b, 104a, 116c)

Myrmecia fulgida Clark, 1951, p. 73, fig. 52 [♀]. Taylor and Brown, 1985, p. 10. Taylor, 1987, p. 43.

Type

fulgida: holotype worker, Parker's Range, W.A. (3.xi.1947, T. Greaves), in ANIC (examined).

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 21a-c).

Head, antennae, mesosoma, legs, petiole and postpetiole brownish red; mandibles yellow; gaster black.

Material examined (fig. 48b)

Western Australia: Middle Ironcap [188]; Parker's Range (TG) [*fulgida* holotype]; South Ironcap [431] [SEM, ♀; *K*, 2 ♀ prepupae].

Male terminalia: Unknown

Karyotype (figs 104a, 116c)

No variation has been observed in the karyotype of fulgida.

$$2n = 40 \ (N.F. = 78)$$

South Ironcap, W.A.: Twenty-four out of 59 cells had $2n = 40$ while in the others I saw $2n = 34$ (X2), 36 (X2), 37 (X5), 38 (X8) and 39 (X18). The diploid karyotype consists of 18M, 20SM and 2A chromosomes (i.e. N.F. = 78).

Taxa included: Typical fulgida

Nest structure (previously unknown)

One nest of fulgida, at South Ironcap (W.A.), had a very large mound ($d \simeq 1$ m, $h \simeq 40$ cm), with 6 entrances located at the top. It was near a 3 m high Casuarina sp. in a dense thicket, composed mainly of 1 - 2 m high Melaleuca sp. and Dryandra sp., situated on ironstone soil. The workers were very aggressive and at least 1,000 were seen on the surface after the mound was opened. I estimate that the nest had a population of at least twice this number. Although excavation of the nest was impracticable, the internal structure appeared to be of Gray's (1974a) less complex, diffuse type.

Biological references (including unpublished theses): None

Comments

M. fulgida is a well-defined biological species, apparently confined to an ironstone area in and about the Parker Range, which can be distinguished by its worker morphology. I expect that when male terminalia are known it will be found to be closest to vindex (which it resembles more closely) or possibly nigriceps, s.l. The species was described by Clark (1951) on the basis of six workers collected in 1947 and has only now been recollected.

22. *Myrmecia fuscipes* Clark

(Figs 22a-c, 23a-c, 24a-c, 25a-c, 48b, 61a-c, 62a-f, 102b-c, 105a-b, 106a, 117a-c)

Myrmecia fuscipes Clark, 1951, p. 62, fig. 39 [♀].
Myrmecia desertorum Wheeler, *auct*. (*non* Wheeler, 1915). Brown, 1953b, p. 25, *partim*.

Type

fuscipes: holotype worker, Port Lincoln, S.A. (Dec. 1936, J. Clark), in ANIC (examined).

Worker diagnosis

Measurements and proportions as given and illustrated (figs 22a-c, 23a-c, 24a-c, 25a-c).

Head and gaster black; mandibles, antennae, mesosoma, tarsi, petiole and postpetiole yellow; femora and tibiae dark brown.

Material examined (fig. 48b)

South Australia: Berri (JT; in SAM); Ceduna (BBL); 56 km E of Ceduna (EFR); Crystal Brook (BBL); Elliston [120, 174] [*MT*, ♂, reared in captivity]; 6 km NW of Kadina [267, 475]; 24 km E of Kimba (EFR); Lake Hart [152-153, 280, 490-491]; Laura Bay C.P. [131-132, 175-176]; 13 km W of Nonning H.S. [189]; 4 km W of Nullarbor [294, 471] [SEM, ♀; *K*, 2 ♀ prepupae]; 160 km W of Penong (EFR); 192 km W of Penong (EFR); Port Augusta (TG); Port Germein [121, 134, 155] [*K*, ♀ prepupa]; Port Kenny [130]; Port Lincoln (JCl) [*fuscipes* holotype]; Port Parham [2-6, 88, 156-159] [*SEM*, 2♀♀; *MT*, 99♂♂, 27.ii.1979 & 3.iii.1979; *K*, 2 ♀ prepupae]; Port Prime [7, 96-98, 137, 356]; Reevesby Island [540-541]; 46 km N of Renmark [58-59, 93, 146, 247] [*K*, 5 ♂ prepupae; Ridley C.P. [57]; Roopena [275]; Streaky Bay (BBL). *Western Australia*: 128 km S of Balladonia [413] [*K*, ♀ prepupa]; Breeborinia Rocks [293] [*MT*, ♂, 1.iii.1983]; 7 km SE of Coolgardie [468] [*K*, ♀ prepupa]; 33 km WNW of Fraser Range H.S. (RWT); 22 km SW of Fraser Range H.S. (RWT); Israelite Bay [414]; 4 km SW of Kalgoorlie [192]; 8 km SW of Kalgoorlie [193]; Madura (TG; in QM); Norseman (BBL); 16 km E of Norseman (BBL); 26 km E of Norseman [292] [*MT*, ♂, 28.ii.1983]; 52 km N of Norseman [191]; 66 km E of Norseman [469]; 2 km S of Peak Charles [430] [SEM, ♀; *K*, 2 ♀

prepupae]; Salmon Gums (BBL); 34 km N of Salmon Gums [290].

[Note - Clark (1951) also records fuscipes from 'Victoria: Dimboola.' Although I have not seen any specimens of fuscipes from Vic., this record appears likely because it is not far outside the known range. The species also undoubtedly occurs in N.S.W., because the population at 46 km N of Renmark is situated only 100 metres from the S.A. - N.S.W. state border.]

Male terminalia (figs 61a-c, 62a-f)

No variation has been observed in the male terminalia of fuscipes.

Ninth and tenth tergites (fig. 62a) 1.4 times wider than long; median lobe rounded, extending beyond tips of pygostyles. Pygostyles moderately slender; length 0.4 times width of segment. Eighth sternite (fig. 62b) trapezoidal; 1.3 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae concentrated in two large areas flanking midline in middle half; a few others in posterior quarter associated with longitudinal sculpturing. Ninth sternite (fig. 62c) 1.3 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin broad, rounded. Short setae scattered over much of posterior half; moderately few short undulate setae flanking midline in middle; long sensory setae around posterior margin. Basal ring 1.5 times wider than long; 1.6 times wider posteriorly than anteriorly. Outer valve (fig. 62d) 1.6 times longer than deep; posterior end dorso-ventrally flattened; dorsal median projection triangulate, sharply pointed. Middle valve (fig. 62e) with cuspis shorter than digitus; digitus moderately broad, very curved, similar breadth throughout, distal end blunt. Inner valve (fig. 62f), excluding anterior apodeme, 0.9 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe moderately narrow, moderately long, serrated distally; postero-dorsal margin rounded; 5-20 small spines ($\overline{x}$ = 12.5, N = 181) near postero-dorsal margin; 13-29 others ($\overline{x}$ = 22.3, N = 183) in a tight cluster in middle near dorsal margin.

Karyotype (figs 104b-c, 105a-b, 106a, 117a-c)

Variation in the karyotype of fuscipes is consistent with being intraspecific, but it should be noted that three cytotypes have been observed:

(1) 2n = 75,76 (N.F. = 76);

(2) 2n = 76 (N.F. = 78); and

(3) n = 37 (N.F. = 80).

Port Germein, S.A.: One out of four cells had 2n = 76 while in the others I saw 2n = 65 (X1), 71 (X1) and 74 (X1). The karyotype consists of 76A chromosomes (i.e. N.F. = 76).

Port Parham, S.A. (figs 104b,c, 117a): Five out of nine cells from colony 156 had 2n = 76 while in the others I saw 2n = 68 (X1), 71 (X1), 73 (X1) and 74 (X1). The karyotype consists of 76A chromosomes (i.e. N.F. = 76).

One out of six cells from colony 159 had 2n = 75 while in the others I saw 2n = 49 (X1), 57(X1), 69(X1), 71(X1) and 73(X1). A large metacentric chromosome was evident in each of the six cells. This was interpreted as evidence for a Robertsonian polymorphism. The karyotype consists of 1M and 74A chromosomes (i.e. N.F. = 76).

128 km S of Balladonia, W.A. (fig. 105a): Two out of 12 cells had 2n = 76 while in the others I saw 2n = 58 (X1), 64 (X1), 65 (X1), 66 (X1), 67 (X2), 70 (X2), 72 (X1) and 74 (X1). The karyotype consists of 76A chromosomes (i.e. N.F. = 76).

2 km S of Peak Charles, W.A. (figs 105b, 117b): Fifteen out of 43 cells had 2n = 76 while in the others I saw 2n = 63 (X2), 69 (X2), 70 (X1), 71 (X2), 72 (X1), 73 (X1), 74 (X5), 75 (X13) and 77 (X1). The karyotype consists of 2SM and 74A chromosomes (i.e. N.F. = 78).

7 km SE of Coolgardie, W.A.: Fourteen out of 23 cells had 2n = 76 while in the others I saw 2n = 67 (X1), 73 (X2), 74 (X1) and 75 (X5). The karyotype consists of 2SM and 74A chromosomes (i.e. N.F. = 78).

4 km W of Nullarbor, S.A.: Twelve out of 30 cells had 2n = 76 while in the others I saw 2n = 68 (X1), 69 (X2), 70 (X2), 72 (X1), 73 (X2), 74 (X4), 75 (X5) and 77 (X1). The karyotype consists of 2SM and 74A chromosomes (i.e. N.F. = 78).

46 km N of Renmark, S.A. (figs 106a, 117c): Twenty-eight out of 42 cells had n = 37 while in the others I saw n = 31 (X1), 34 (X2), 35 (X4) and 36 (X7). The karyotype consists of 2SM, 1ST and 34A chromosomes (i.e. N.F. = 80).

Seven populations of fuscipes were karyotyped and had chromosome numbers of n = 37,38 (N.F. = 76,78,80). The karyotypes with N.F. = 76 and 78 appear to be related by one pericentric inversion in the haploid condition but that from 46 km N of Renmark is slightly more distinctive. To derive that karyotype (n = 2SM + 1ST + 34A) from the nearest one (n = 1SM + 37A) requires at least one Robertsonian rearrangement and one pericentric inversion in the haploid condition.

Taxa included

(1) N.F. = 76 cytotype

(2) N.F. = 78 cytotype

(3) N.F. = 80 cytotype

Nest structure

Colonies of fuscipes were observed at numerous localities in South

Australia and Western Australia. The species forms very distinctive polydomous (multi-nest) colonies of 2 - 20 nests which were first described by Thomas (1972). The main nest has a mound like a flattened volcano ($d_{max} \simeq 60$ cm, $h_{max} \simeq 20$ cm) with a large, gaping entrance at the top ($d \simeq 5$ cm). The satellite nests are similarly shaped and may be as large as the main nest, but usually are quite small ($d \simeq 15$ cm, $h \simeq 5$ cm). The main nest contains most of the workers, while the satellite nests together contain less than 5% of the total worker population. Satellite nests always contained less than 20 workers and generally less than 5. Usually the main nest contained all the brood, but I once collected three larvae from one of the satellites. The depths of the main nests at Port Parham and other coastal localities were less than 60 cm but inland much deeper nests were found. Excavation of the main nest in colony 59 at 46 km N of Renmark (S.A.) was abandoned at a depth of 2.2 m, while at Lake Hart (S.A.) the incomplete excavation of colony 152 had already produced a hole 1.5 m deep.

To gain a better understanding of how such polydomous colonies might function I wax-cast three nests of colony 146, and analysed the sizes of workers found in various parts. This analysis is presented in Chapter 4.

Seven nests were excavated completely and the numbers of workers collected from nests at different localities were: (a) Laura Bay (188 [131], 286 [132]); (b) Port Germein (38 [155]); (c) Port Parham (132 [2], 284 [3], 209 [156]); and (d) 46 km N of Renmark (452 [146]).

Thomas (1972) excavated 7 nests at Port Parham (S.A.) and collected 40, c.400, 402, 412, 529, c.800 and c.800 workers.

Biological references (including unpublished theses)

Thomas (1972); Browning (1979)

Comments

M. fuscipes is a well-defined biological species, which can be distinguished from all other *Myrmecia* (except *nigriceps*, *s.l.* (*nigriceps*, *s.s.*) and *sp.12*) by its male terminalia. It can be distinguished from *nigriceps*, *s.l.* and *sp.12* by its worker morphology, karyotype and nest structure. The species is typically found in coastal samphire swamps where it may even nest in pure shellgrit, but some populations occur far inland (e.g. Lake Hart, 46 km N of Renmark).

Four workers from three populations (one in S.A. and two in W.A.), including large and small workers from Port Parham were examined by SEM. All were virtually identical, except that the South Australian specimens had pronotal sculpture with typical arched striations, while the Western Australian specimens tended towards being longitudinally striate in the middle.

23. *Myrmecia inquilina* Douglas and Brown

(Fig. 49a)

Myrmecia inquilina Douglas and Brown, 1959, p. 13 [♀]. Taylor and Brown, 1985, p. 11. Taylor, 1987, p. 44.

Type

inquilina: holotype female, Badjanning Rocks, 6 km NW of Wagin, W.A. (23.iii.1955, A. Douglas), in WAM (examined).

Worker diagnosis: Inapplicable (workerless species)

Material examined (fig. 49a)

New South Wales: 12 km N of Coonabarabran (BBL). *Western Australia*: Badjanning Rocks (AMD; in WAM) [*inquilina* holotype]; Boddington (AMD).

[*Note* - Taylor and Brown (1985, p. 11) did not record this species from N.S.W.]

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *inquilina*

Nest structure: Inapplicable (social parasite)

Biological references (including unpublished theses)

Douglas (1956); Haskins and Haskins (1964)

Comments

M. inquilina is a well-defined biological species which is socially parasitic on at least two species of the *vindex* group (*vindex* and *nigriceps*, *s.l.*; Douglas and Brown, 1959; Haskins and Haskins, 1964; B.B. Lowery, pers. comm.). The species lacks a worker caste and several queens may be found per nest. These queens are much smaller than those of other species of the *vindex* group. I have tentatively included the species in the *vindex* group, but do not believe I have yet examined its male terminalia. Douglas and Brown (1959) reported collecting males, which they presumed to be of *inquilina*, but I have examined the terminalia of one of these and found them to be identical to *vindex* (the host). It remains possible that the male terminalia of *inquilina* and *vindex* are identical, but I think that is unlikely.

24. *Myrmecia nigriceps* Mayr, *s.l.*

(Figs 26a-c, 27a-c, 49b, 78c-f, 79c-d, 106b-c, 107a-c,
108a-c, 109a-b, 118a-d, 119a-c, 120a-c)

Myrmecia nigriceps Mayr, 1862, pp 725, 728 [♀]; 1876, p. 95. Kirby, 1896, p. 206. Clark, 1930, p. 22; 1951, p. 64, figs 41-43 [♂]. Wheeler, 1933, p. 38. Taylor and Brown, 1985, p. 13. Taylor, 1987, p. 44.

Myrmecia vindex Smith var. *nigriceps* Mayr. Forel, 1907, p. 264; 1910, p. 3 [♀]. Emery, 1911, p. 19. Viehmeyer, 1924, p. 221. Clark, 1925, p. 144.

Myrmecia vindex Smith var. *desertorum* Wheeler, 1915, p. 805, *syn. nov.* [♀]. Clark, 1925, p. 143 [♀♂].

Myrmecia desertorum Wheeler. Clark, 1928, p. 39; 1951, p. 59, figs 36-37. Wheeler, 1933, p. 40. Brown, 1953b, p. 25, *partim*. Taylor and

Brown, 1985, p. 8, *partim*. Taylor, 1987, p. 42, *partim*.

Myrmecia lutea Crawley, 1922a, p. 429, *syn*. *nov*. [♀]. Clark, 1951, p. 61, fig. 38.

Myrmecia vindex Smith, *auct*. (*non* Smith, 1858). Froggatt, 1914, p. 459. Clark, 1925 , p. 143.

Types

nigriceps: syntype workers, Australia, in NHMW.

desertorum: syntype workers (2), Todmorden, S.A. (S.A. White), in SAM (examined); syntype workers, Todmorden, S.A. (S.A. White), in MCZ. [NEW SYNONYMY].

lutea: syntype workers (2), Ludlow, W.A. (J. Clark), in ANIC (examined); syntype workers, Ludlow, W.A., in OUM. [NEW SYNONYMY; synonymy with *desertorum* by Brown, 1953b].

Worker diagnosis

Measurements and proportions as given and illustrated (figs 26a-c, 27a-c).

Head and gaster black; mandibles, antennae, mesosoma, legs, petiole and postpetiole yellow. The yellow varies from light to almost brownish yellow but is constant within nests and populations.

Material examined (fig. 49b)

Australia: Australia (CPH) [*MT*, ♂ only, du] [*nigriceps*, *s.s.*] [specimen examined by Forbes (1967)]. *Australian Capital Territory*: Black Mountain (TG); Canberra (GAC); Kowen (TG); Mount Ainslie (BBL). *New South Wales*: Abington (TG); Apsley (BBL); Ardlethan (BBL); Barellan (BBL); 5 km N of Barmedman (BBL); Berrigan S.F. (BBL); Bourke (WWF); Broken Hill (BBL); Burrinjuck Dam (BBL); 12 km S of Cessnock (BBL); Cessnock S.F. (BBL); Cobar (HMit); Condobolin (BBL); 6 km N of Condobolin (BBL); 12 km N of Coonabarabran (BBL); Cowan (BBL); 18 km NW of Deniliquin (BBL); Eumungerie S.F. (BBL); 29 km W of Euston (MJDW); Glen Emu (BBL); 30 km N of Grenfell (BBL); Grenfell Weddin Mountain N.P. (BBL); 10 km S of Gunning (BBL); Hay (BBL); Heathcote (WMW); Ingalba N.R. (BBL); Jindalee S.F. (BBL); Lake Menindee [81] [*MT*, ♂, 5.vi.1960] [*nigriceps*, *s.s.*]; Mairjimmy S.F. (BBL); 5 km W of Merriwagga (BBL); Moulamein (BBL); Mount Ku-ring-gai (TW); Mudgee (BBL); Mungindi (BBL);

Narrabri (BBL); Nyngan (BBL); Pulletop N.R. (BBL); 19 km W of Rankin Springs; Sydney (BBL); Tabbita (BBL); Trundle (BBL); 20 km W of Urana (BBL); Walbundrie (BBL); Wallacia (H&T; in SAM) [*MT*, ♂, March 1927] [*nigriceps*, *s.s.*]; Warrumbungles N.P. (BBL); Wellington (BBL); Wilcannia (BBL); Wilton (JCl); Yarramundi (BBL); Yiddah (BBL). *Northern Territory*: Amadeus Basin (PR); Ayers Rock (Dielli); 21 km SW of Barrow Creek (MSU); 60 km W of Erldunda [522]; Mount Olga (cu); Napperby Creek (McI&D); 21 km ENE of Narwietooma H.S. (McI&D); Standley Chasm (U&B); Tennant Creek (JFF); The Granites (McI&D); 59 km W of Victory Downs (McI&D). *Queensland*: Cunnamulla (TC); 24 km N of Cunnamulla (BBL); St George (BBL); Winton (SHP). *South Australia*: Aldinga (BBL); 6 km SW of American River [257]; Andrewilla W.H. [264]; Anna Creek R.S. (RSMcI); Aroona Valley [117]; Blanchetown [179]; Blewitt Springs [8-10, 50, 135-136, 160] [*MT*, ♂, 4.ii.1981] [*nigriceps*, *s.s.*]; Bundaleer Reservoir [283]; Castle's Landing [116]; Chillimookoo W.H. [507]; Cleve (AML); Coorong N.P. (BBL); Cuttapirie Corner W.H. [508]; Devlin Pound [412] [*K*, 4 ♀ prepupae] [*sp.13*]; Elliston [66, 126-129, 170-173, 308] [*SEM*, ♀; *MT*, 2♂♂, 20.i.1981; *K*, 2 ♀ prepupae] [*sp.11*]; 58 km WSW of Ernabella Mission (McI&D); 32 km ENE of Everard Park H.S. (McI&D); 11 km N of Farina [370]; Farina Creek [523]; Gammon Ranges N.P. [504]; Hanson Bay [101, 113, 180, 182-185, 339] [*K*, 2 ♀ prepupae] [*nigriceps*, *s.s.*]; Hesso (BBL); Inneston [270, 272] [*MT*, ♂, 13.i.1983; *K*, ♂ & 3 ♀ prepupae] [*nigriceps*, *s.s.*]; Katarapko Island [516]; 27 km SSE of Kenmore (McI&D); Kingoonya (RSMcI); Lake Albert (BBL); Lake Bonney [94]; Lake Gilles C.P. [133] [*MT*, ♂, 23.i.1981] [*nigriceps*, *s.s.*]; Lake Merreti [375]; Lake Palankarinna (JT; in SAM); Mambray Creek (EFR); Mannum [505-506]; Melrose (BBL); 59 km E of Mount Davies (McI&D); 24 km W of Mount Morris (McI&D); Mount Remarkable N.P. [353] [*K*, 2 ♀ prepupae] [*nigriceps*, *s.s.*]; 13 km S of Morgan (BBL); Musgrave Ranges (BBL); Naracoorte [385]; 50 km SSW of Observatory Hill (McI&D); 12 km SW of Olympic Dam [279] [*K*, ♂ prepupa] [*sp.13*], [484-486] [*K*, 3 ♀ prepupae] [*nigriceps*, *s.s.*]; Overland Corner [411]; Pennington Bay (BBL); 15 km NW of Pimba [489]; 41 km S of Pimba [154, 276]; Poochera (BBL); 16 km E of Port Augusta (BBL); Rocky River H.S. [24, 26-27, 108, 110-112, 181, 186-187] [*MT*, 2♂♂, 21.iii.1979] [*nigriceps*, *s.s.*]; Seal Bay [344]; Sellicks Hill [496]; St Mary Pool [384]; 32 km S of Tailem Bend (BBL); Tirrawarra W.H. [246]; Todmorden (SAW; in SAM) [*desertorum* syntypes], [147-151] [*SEM*, ♀; *MT*, 2♂♂, reared in captivity; *K*, 4 ♂

prepupae] [desertorum]; Warrenben C.P. (BBL); West Bay [327]; 21 km WNW of William Creek (JEF); Wilpena H.S. [349]; Wilpena Pound [350]; Wirraminna H.S. (cu); 24 km N of Wirrulla (K,U&B); 16 km WNW of Wooltarlinna (McI&D); Yudnamutana (BBL). Victoria: 6 km NE of Bacchus Marsh [89] [MT, ♂, collected as pupa, 1.iii.1975] [nigriceps, s.s.]; Chiltern S.F. (BBL); Echuca (BBL); Heathcote (BBL); Lake Hattah (JED); Stawell (JAH); Wedderburn (EFR); Werribee Gorge (BBL). Western Australia: Arthur River [84, 517] [MT, ♂, 17.vi.1962] [nigriceps, s.s.]; 44 km W of Balladonia [470] [K, ♀ prepupa] [nigriceps, s.s.]; 12 km E of Boddington [203]; 13 km N of Broad Arrow [195]; 24 km ENE of Cardawan H.S. (McI&D); 54 km NE of Cardawan H.S. (McI&D); Cataby Brook [461] [K, ♀ prepupa] [nigriceps, s.s.]; 49 km E of Collie [213]; 5 km ENE of Coolawanyah H.S. (McI&D); 27 km SW of Coolawanyah H.S. (McI&D); 43 km WNW of Coolawanyah H.S. (McI&D); 13 km SW of Coolgardie (RWT); Cranbrook [80] [MT, ♂, 25.ii.1962] [nigriceps, s.s.]; Crossman [459] [K, ♀ prepupa] [nigriceps, s.s.]; 18 km N of Denmark (RWT); Fortescue River (McI&D); Geraldton (EFR); 16 km S of Geraldton (EFR); 29 km W of Giles (McI&D); 58 km ENE of Giles (McI&D); Gum Creek (McI&D); Hines Hill [466-467] [K, ♀ prepupa] [nigriceps, s.s.]; 6 km W of Jerramungup [232]; 9 km W of Jerramungup [234-236, 441] [MT, ♂, reared in captivity; K, ♀ prepupa] [nigriceps, s.s.]; Jigalong (JHi); John Forrest N.P. [409]; 15 km N of Kalgoorlie [194]; 13 km NW of Leonora [197-198]; Ludlow (JCl) [lutea syntypes]; Meekatharra [82], (CTM) [MT, 2 ♂♂, 19.v.1967] [nigriceps, s.s.]; 64 km N of Menzies [196]; Millstream (JEF); Moora [464] [K, ♂ prepupa] [nigriceps, s.s.]; Morgan Falls (C&U); 16 km NE of Mount Cooper (McI&D); 27 km WNW of Mount Cooper (McI&D); 32 km SW of Mundiwindi (McI&D); Murchison River (TG); 7 km S of Narrogin [205]; 72 km E of Norseman (BBL); 24 km WNW of Norseman (RWT); Ongerup [443] [K, 3 ♀ prepupae] [nigriceps, s.s.]; Perth (JCl); Pingrup (TG); Porongorup N.P. [223]; Ravensthorpe (TG); Sandstone [85, 512] [MT, 2 ♂♂, 29.iii.1975] [desertorum]; 35 km W of Sandstone [519]; 110 km SW of Sandy Blight (McI&D); Swan View (JCl); Tambellup (TG); 13 km SW of Terhans R.H. (McI&D); Wagin [83, 518] [MT, 2 ♂♂, 17.ii.1962] [nigriceps, s.s.]; 4 km W of Wagin [453] [K, ♀ & 2 ♂ prepupae] [nigriceps, s.s.]; 5 km W of Wagin [208-211, 451-452] [K, ♀ prepupa] [nigriceps, s.s.]; 43 km W of Wagin [212]; 26 km SSE of Widgiemooltha (RWT); 30 km NNW of Widgiemooltha (RWT); 24 km ESE of Wittenoom (McI&D); 66 km SSE of Wittenoom (McI&D).

[*Note* - Taylor and Brown (1985, pp 3, 8) did not record this species from N.T. or Qld.]

Male terminalia (figs 78c-f, 79c-d)

The male terminalia examined for *nigiceps*, *s.l.* suggest that the following three are distinct biological species, but karyotype analysis (as shown below) suggests that a fourth (whose males are unknown) is also present:

(1) *Myrmecia nigriceps* Mayr, *s.s.*

(Fig. 78c,d)

Ninth and tenth tergites, *eighth sternite*, *basal ring*, *outer valve* and *middle valve* similar to *fuscipes*. *Ninth sternite* (fig. 78c) 1.2 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin broad, rounded. Short setae scattered over much of posterior half; a few short undulate setae flanking midline in middle; long sensory setae around posterior margin. *Inner valve* (fig. 78d), excluding anterior apodeme, 0.9 times as long as deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe moderately narrow, moderately long, serrated distally; postero-dorsal margin rounded; 6-7 small spines ($\bar{x}$ = 11.8, N = 30) near postero-dorsal margin; 16-30 others ($\bar{x}$ = 22.8, N = 29) in middle near dorsal margin.

(2) *Myrmecia desertorum* Wheeler

(Fig. 78e,f)

Ninth and tenth tergites, *eighth sternite*, *basal ring*, *outer valve* and *middle valve* similar to *fuscipes*. *Ninth sternite* (fig. 78e) 1.1 times longer than wide; moderately long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin broad, slightly indented in middle, indentation flanked by straight portions of margin. Short setae scattered over posterior sixth; a few short undulate setae flanking midline in anterior half; long sensory setae around posterior margin. *Inner valve* (fig. 78f), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.5 times as long as rest of segment; postero-ventral lobe moderately broad, moderately short, serrated distally; postero-dorsal margin rounded; 8-15 small spines ($\bar{x}$ = 11.6, N = 8) near postero-dorsal margin; 17-23 others ($\bar{x}$ = 19.4, N = 8) tightly clustered in middle near dorsal margin.

(3) *Myrmecia sp.11* (ANIC), *sp. nov.*

(Fig. 79c-d)

Ninth and tenth tergites, *eighth sternite*, *basal ring*, *outer valve* and *middle valve* similar *fuscipes*. *Ninth sternite* (fig. 79c) 1.1 times longer than wide; moderately long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin broad, more or less rounded with a corrugated margin. Short setae scattered over posterior third; a few short undulate setae in middle and flanking midline in anterior half; long sensory setae around posterior margin. *Inner valve* (fig. 79d), excluding anterior apodeme, 0.8 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe moderately long, moderately narrow, serrated distally; postero-dorsal margin rounded; 7-11 small spines ($\bar{x}$ = 8.8, N = 4) near postero-dorsal margin; 5-9 others ($\bar{x}$ = 6.8, N = 4) clustered in middle near dorsal margin.

Karyotype (figs 106b-c, 107a-c, 108a-c, 109a-b, 118a-d, 119a-c, 120a-c)

The karyotypes examined for *nigriceps*, *s.l.* provide evidence for the existence of four biological species:

(1) Myrmecia nigriceps Mayr, s.s.

(Figs 107c, 108a-c, 109a-b, 119a-c, 120a-c)

The variation in the karyotype of nigriceps, s.s. is consistent with intraspecific variation but it should be noted that nine cytotypes have been observed:

(a) n = 36 (N.F. = 78);

(b) 2n = 75 (N.F. = 78);

(c) 2n = 74 (N.F. = 78) [2n = 2SM + 2ST + 70A];

(d) 2n = 74 (N.F. = 78) [2n = 2M + 2ST + 70A];

(e) 2n = 74 (N.F. = 78) [2n = 1M + 1SM + 2ST + 70A];

(f) 2n = 74 (N.F. = 78) [2n = 4SM + 70 A];

(g) 2n = 70 (N.F. = 80);

(h) 2n = 74 (N.F. = 80); and

(i) 2n = 78 (N.F. = 80).

4 km W of Wagin, W.A. (figs 108a,b, 119b,c): Ten out of 13 cells from the male prepupae had n = 36 while in the others I saw n = 34 (X1), 35 (X1) and 37 (X1). The haploid karyotype consists of 1SM, 2ST and 33A chromosomes (i.e. N.F. = 78).

Six out of 19 cells from the worker prepupa had 2n = 75 while in the others I saw 2n = 68 (X1), 70 (X1), 71 (X1), 72 (X2), 73 (X2), 74 (X5) and 77 (X1). The diploid karyotype consists of 3SM and 72A chromosomes (i.e. N.F. = 78).

Crossman, W.A.: Five out of 10 cells had 2n = 74 while in the others I saw 2n = 65 (X2), 72 (X2) and 73 (X1). The karyotype consists of 2SM, 2ST and 70A chromosomes (i.e. N.F. = 78).

Hines Hill, W.A. (figs 107c, 120a): Eighteen out of 30 cells had 2n = 74 while in the others I saw 2n = 63 (X1), 66 (X1), 68 (X1), 70 (X1), 71 (X2), 72 (X2) and 73 (X4). The karyotype consists of 2M, 2ST and 70A chromosomes (i.e. N.F. = 78).

Ongerup, W.A. (figs 109a, 120b): Seventeen out of 39 cells had 2n = 74 while in the others I saw 2n = 48 (X1), 57 (X1), 63 (X1), 67 (X3), 68 (X1), 69 (X2), 70 (X1), 71 (X2), 72 (X5) and 73 (X5). The karyotype consists of 2SM, 2ST and 70A chromosomes (i.e. N.F. = 78).

9 km W of Jerramungup, W.A.: The chromosome number may have been 2n = 74 because in one cell I saw 2n = 73. The karyotype appears to consist of 2SM, 2ST and 70A (i.e. N.F. = 78).

Mount Remarkable N.P., S.A.: Three out of 16 cells had 2n = 74 while in the others I saw 2n = 53 (X1), 54 (X1), 57 (X1), 63 (X1), 64 (X2), 67 (X1), 68 (X2), 72 (X1), 73 (X2) and 75 (X1). The karyotype consists of 1M, 1SM, 2ST and 70A chromosomes (i.e. N.F. = 78).

12 km SW of Olympic Dam, S.A.: Two out of 31 cells had 2n = 74 while in the others I saw 2n = 60 (X1), 61 (X1), 63 (X3), 65 (X1), 66 (X1), 68 (X1), 70 (X2), 71 (X3), 72 (X1), 73 (X4), 74 (X9) and 75 (X2). The karyotype consists of 4SM and 70A chromosomes (i.e. N.F. = 78).

5 km W of Wagin, W.A. (figs 108c, 119a): Five out of nine cells had 2n = 70 while in the others I saw 2n = 60 (X1), 65 (X1), 67 (X1) and 68 (X1). The karyotype consists of 2M, 8SM and 60A chromosomes (N.F. = 80).

Hanson Bay, S.A.: Six out of 12 cells had 2n = 74 while in the others I saw 2n = 63 (X1), 65 (X1), 67 (X1), 68 (X1), 72 (X1) and 73 (X1). The karyotype consists of 4M, 2SM and 68A chromosomes (i.e. N.F. = 80).

Inneston, S.A.: Eight out of 28 cells from the worker prepupae had 2n = 74 while in the others I saw 2n = 60 (X1), 62 (X1), 64 (X2), 65 (X4), 66 (X1), 67 (X2), 68 (X1), 69 (X2), 70 (X3), 73 (X2) and 75 (X1). The diploid karyotype consists of 4M, 2SM and 68A chromosomes (i.e. N.F. = 80).

Four out of 5 cells from the male prepupa had n = 37 while in the other I saw n = 36. The haploid karyotype consists of 2M, 1SM and 34A (i.e. N.F. = 80).

44 km W of Balladonia, W.A. (figs 109b, 120c): Thirteen out of 36 cells had 2n = 78 while in the others I saw 2n = 59 (X1), 72 (X3), 73 (X1), 74 (X1), 75 (X4), 76 (X4), 77 (X7) and 79 (X2). The karyotype consists of 2M and 76A chromosomes (i.e. N.F. = 80).

Cataby Brook, W.A.: One out of two cells had 2n = 78 while in the other I saw 2n = 77. The karyotype consists of 2M and 76A chromosomes (i.e. N.F. = 80).

Moora, W.A.: One out of four cells had n = 39 while in the others I saw n = 37 (X3). The karyotype consists of 1M and 38A chromosomes (i.e. N.F. = 80).

Thirteen populations of nigriceps, s.s. were karyotyped and had haploid chromosome numbers ranging from 35 to 39 (N.F. = 78,80). To relate the terminal karyotypes in this series - n = 35 (N.F. = 78) and n = 39 (N.F. = 80) - requires at least four Robertsonian rearrangements and one pericentric inversion in the haploid condition.

(2) Myrmecia desertorum Wheeler

(Figs 106c, 118d)

n = 32 (N.F. = 80)

Todmorden, S.A.: Eleven out of 38 cells had n = 32 while in the others I saw n = 21 (X1), 23 (X1), 24 (X1), 25 (X1), 26 (X1), 27 (X2), 28 (X4), 29 (X5), 30 (X7) and 31 (X4). The haploid karyotype consists of 3M, 4SM, 1ST and 24A chromosomes (i.e. N.F. = 80).

(3) Myrmecia sp.11 (ANIC), sp. nov.

(Figs 106b, 118a)

2n = 36 (N.F. = 68)

Elliston, S.A.: Seventeen out of 25 cells had 2n = 36 while in the others I saw 2n = 23 (X1), 29 (X1), 31 (X1) and 35 (X5). The diploid karyotype consists of 4M, 26SM, 2ST and 4A chromosomes (i.e. N.F. = 68).

(4) Myrmecia sp.13 (ANIC), sp. nov.

(Figs 107a-b, 118b-c)

The variation in the karyotype of sp.13 is consistent with intraspecific variation but it should be noted that two cytotypes have been observed:

(a) 2n = 40 (N.F. = 80); and

(b) n = 21 (N.F. = 80).

Devlin Pound, S.A. (figs 107a, 118b): Thirty-six out of 43 cells had 2n = 40 while in the others I saw 2n = 37 (X1) and 39 (X6). The karyotype consists of 26M and 14SM chromosomes (i.e. N.F. = 80).

12 km SW of Olympic Dam, S.A. (figs 107b, 118c): Twenty-two out of 31 cells had n = 21 while in the others I saw n = 16 (X1), 17 (X1), 19 (X3) and 20 (X4). The karyotype consists of 9M, 8SM, 2ST and 2A chromosomes (i.e. N.F. = 80).

Karyotypes from Devlin Pound and 12 km SW of Olympic Dam are separated by at least one Robertsonian rearrangement in the haploid condition.

Taxa included

(1) nigriceps, s.s.
    (a) n = 36 (N.F. = 78) cytotype
    (b) 2n = 75 (N.F. = 78) cytotype
    (c) 2n = 74 (N.F. = 78) [2n = 2SM + 2ST + 70A] cytotype

(d) $2n = 74$ (N.F. = 78) [$2n = 2M + 2ST + 70A$] cytotype

(e) $2n = 74$ (N.F. = 78) [$2n = 1M + 1SM + 2ST + 70A$] cytotype

(f) $2n = 74$ (N.F. = 78) [$2n = 4SM + 70 A$] cytotype

(g) $2n =70$ (N.F. = 80) cytotype

(h) $2n = 74$ (N.F. = 80) cytotype

(i) $2n = 78$ (N.F. = 80) cytotype

(2) desertorum

(3) sp.11

(4) sp.13

(a) $2n = 40$ (N.F. = 80) cytotype

(b) $n = 21$ (N.F. = 80) cytotype

Nest structure

I observed colonies of nigriceps, s.l. at about 15 localities in South Australia and 15 more in Western Australia. The nests had a variety of structures at different localities and these are summarized below:-

(1) At Elliston (S.A.) many nests of sp.11 were found with large flat mounds ($d_{max} \simeq 90$ cm, $h_{max} \simeq 5$ cm) and up to 5 entrances. These colonies were nesting in pure white coastal sandhills beneath Eucalyptus sp. and amongst pigface (Carpobrotus sp.). No established nests could be completely excavated because of the extremely loose sand in which they were constructed, but several were excavated to depths of about 1.5 m. The internal nest structure was of Gray's (1974a) less complex diffuse type. Mature colonies probably contained between 500 and 1,000 workers. One incipient nest was completely excavated and found to contain seven dealate queens and one worker. The nest had no mound and only a single inconspicuous entrance ($d \simeq 2$ cm). It had one chamber only and was 5 cm deep. Another incipient nest contained two

queens and two larvae. These were two of only three nests of large Myrmecia which I have found with more than one dealate queen, and demonstrates that this species is sometimes pleometric (i.e. founds its colonies with more than one queen).

(2) At Todmorden (S.A.) and many localities in W.A. (44 km W of Balladonia, 12 km E of Boddington, 13 km N of Broad Arrow, Cataby Brook, 49 km E of Collie, Crossman, Hines Hill, 6 and 9 km W of Jerramungup, 15 km N of Kalgoorlie, 13 km N of Leonora, Moora, 7 km S of Narrogin, Ongerup, 4 km W of Wagin) nests of desertorum and nigriceps, s.s. with very large mounds were observed. These were shaped like flattened volcanoes ($d_{max} \simeq 70$ cm, $h_{max} \simeq 40$ cm), had one or a few entrances at the top ($d_{max} \simeq 5$ cm), and usually were decorated with dead leaves, twigs and gum nuts. The nests were mainly found beneath Eucalyptus spp either in roadside vegetation (in wetter areas) or along river courses (in drier areas). None of these nests were excavated completely but one at Todmorden was followed to a depth of almost 2 m. The internal nest structure was of Gray's (1974a) less complex diffuse type. The nests appeared to be very populous and probably contained 500 - 1000 workers.

(3) At three South Australian localities (15 km NW and 41 km S of Pimba, 12 km SW of Olympic Dam) and at 64 km N of Menzies (W.A.) highly characteristic mounds of sp.13 and nigriceps, s.s. were observed. These mounds were somewhat pudding-shaped ($d_{max} \simeq 30$ cm, $h_{max} \simeq 20$ cm), included numerous interwoven Acacia leaves, and had a single large entrance ($d \simeq 5$ cm) at the top, giving them an appearance much like a bird's nest. Such mounds were invariably found in red-brown sandy soils. Although no nests were excavated completely one was followed to a depth of 2.4 m before the excavation was abandoned. The internal

structure of the nest was of Gray's (1974a) less complex diffuse type and the populations of these nests seemed to be relatively small (probably less than 300 workers).

[Note - Two colonies with this nest type were karyotyped, both from 12 km SW of Olympic Dam, S.A. [279 & 486], and had quite dissimilar karyotypes. I consider that the two karyotypes belong to different species (see above). Consequently, I must assume that either (1) sp.13 and nigriceps, s.s. can both construct the same very distinctive type of nest, or (2) one of the karyotypes has been incorrectly associated with this nest type. The 2n = 74 karyotype came from prepupae collected only a few days before slides were prepared so it is unlikely that any confusion could have arisen. However, the n = 21 karyotype [279] came from a male prepupa, which developed from an egg laid by a worker I collected about a year before. The worker had been alone in a container for several months before producing a batch of eggs. While it is unlikely that the worker could have come from a colony other than colony 279, it is not impossible as occasionally workers did escape from my laboratory colonies. Therefore, I believe that the distinctive bird nest structure is more strongly associated with nigriceps, s.s. (2n = 74) than it is with sp.13 (n = 21).]

(4) At several South Australian localities (Blewitt Springs, Hanson Bay, Lake Bonney, Rocky River) and at 5 and 43 km W of Wagin (W.A.) nests of nigriceps, s.s. were observed with only very small mounds. These were all in sandy soils and relatively easy to excavate. The nests were like flattened volcanoes ($d_{max} \simeq 30$ cm, $h_{max} \simeq 5$ cm) with a single entrance at the top ($d \simeq 3$ cm). They were quite shallow and never exceeded 50 cm deep. The internal structure of the nests was of the less complex diffuse type. The populations contained in the

nests were modest in size, with the numbers of workers collected from nests at the different localities being: (a) Blewitt Springs (200 [9], 95 [10], 46 [135], 72 [136], 41 [160]); (b) Hanson Bay (63 [180], 93 [339]); (c) Rocky River (31 [108], 102 [111]); and (d) 4 km W of Wagin (52 [209], 47 [211]).

(5) At Inneston, Seal Bay and West Bay (all S.A.) nests of nigriceps, s.s. were observed which were located in sandy soil beneath stones (or in one case a piece of rusty tin). None of these were completely excavated, but one was followed to a depth of about 1.0 m. The internal structure was of the less complex diffuse type.

(6) At Lake Gilles C.P. (S.A.) one nest of nigriceps, s.l. [133] was observed which had no trace of a mound. The nest was in hard clay soil and had a single entrance (d ≃ 3 cm) surrounded by dead leaves and twigs. The entire nest was excavated and found to contain 48 workers. The internal structure was of the less complex diffuse type and went to a depth of 60 cm.

(7) At Porongorup N.P. (W.A.) one nest of nigriceps, s.l. [223] was observed which had no mound and was in very stony clay soil. Although no queen was collected it appeared that the entire nest was collected. It was 50 cm deep and contained 101 workers. The internal structure was of the less complex diffuse type.

Gray (1974a) completely excavated three nests of nigriceps at Ingleburn, Mudgee and Bulgadie (all N.S.W.), which contained 134, 189 and 130 workers and were 98, 33 and 36 cm deep respectively. He also completely excavated three other nests of desertorum at Hillston, Nyngan and Box Tank (all N.S.W.) which contained 292, 489 and 246 workers and were 77, 100 and 77 cm deep respectively. Barnett (1977) excavated one nest of nigriceps at Bacchus Marsh (Vic.) which contained 250 workers.

The variety of nest structures observed for *nigriceps*, *s.l.* is not surprising, considering that four biological species are present, and suggests that others may be found.

Biological references (including unpublished theses)

Gray (1971b, 1974a, 1974b); Barnett (1977); Browning (1979)

Comments

M. nigriceps, *s.l.* contains at least four biological species which vary markedly in nest structure, karyotype and male terminalia, and have slight variation in worker colouration. Karyotypes are known for all four species and male terminalia are only unknown for *sp.13*.

M. sp.11 is the most distinctive species because its karyotype has fewer chromosome arms (i.e. N.F. = 68; cf. N.F. = 76-80 for others) and its male terminalia do not have a cluster of spines in the middle of the inner valve. The male terminalia of *desertorum* are distinguished from *nigriceps*, *s.s.* by their ninth sternite which has its posterior margin with straight portions flanking the middle. The karyotypes of *sp.13*, *desertorum* and *nigriceps*, *s.s.* are distinguished by their chromosome numbers which are n = 20-21, n = 32 and n = 35-39 respectively.

The species included in *nigriceps*, *s.l.* vary in the darkness of their yellow colouring, with *nigriceps*, *s.s.* being the darkest and *desertorum* the lightest. The four species appear to be closely related to several other species, (i.e. *atrata*, *fuscipes*, *sp.12* and *sp.16*) which differ mainly in having some or most parts darker.

On several occasions nests of *nigriceps*, *s.l.* were found to be parasitized by eucharitine wasps [Hymenoptera: Pteromalidae: Eucharitinae].

25. *Myrmecia princeps* Clark

(Figs 28a-c, 50a, 81a-f, 110a-b, 121a-b)

Myrmecia princeps Clark, 1951, p. 46, fig. 24 [♀].
Myrmecia desertorum Wheeler, *auct*. (*non* Wheeler, 1915). Brown, 1953b, p. 25, *partim*.

Type

princeps: holotype worker, Tarcoola, S.A. (7.v.1925, K. Millar), in ANIC (examined).

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 28a-c).

Head and gaster black; mandibles, antennae, mesosoma, legs, petiole and postpetiole yellow.

Material examined (fig. 50a)

South Australia: Bungunnia (RDR; in SAM); Calperum [161, 377] [SEM, ♀; *MT*, ♂, reared in captivity; *K*, 2 ♀ prepupae]; Danggali C.P. [355, 376]; Kychering Soak (RCC); Muckera R.H. [524]; 12 km SW of Olympic Dam [278, 487-488] [*K*, 2 ♀ prepupae]; 15 km S of Olympic Dam [483]; 20 km S of Olympic Dam [277]; 25 km S of Olympic Dam [482]; Ooldea (EC1); Pinkawillinie [260-261]; Roxby Downs [263]; Tarcoola (KM) [*princeps* holotype]. *Victoria*: Bannerton (ACN).

[*Note* - This species also occurs in south-eastern Western Australia, where specimens have been collected by B.B. Lowery (pers. comm.) and is probably present in south-western New South Wales because specimens have been collected quite close to the S.A. / N.S.W. border.]

Male terminalia (fig. 81a-f)

No variation has been observed in the male terminalia of *princeps*.

Ninth and tenth tergites (fig. 81a) 1.8 times wider than long; median lobe rounded, extending noticeably beyond tips of pygostyles. Pygostyles moderately stout; length 0.2 times width of segment. *Eighth sternite* (fig. 81b) trapezoidal; 1.4 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae concentrated in two large areas flanking midline in anterior two-thirds; a few others in posterior quarter associated with serrate longitudinal sculpturing. Ninth sternite (fig. 81c) 1.0 times longer than wide; moderately long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin broad, broadly indented. Short setae scattered over much of posterior quarter; a few short undulate setae flanking midline in middle; long sensory setae around posterior margin. Basal ring 1.7 times wider than long; 1.6 times wider posteriorly than anteriorly. Outer valve (fig. 81d) 1.9 times longer than deep; posterior end dorso-ventrally flattened; dorsal median projection triangulate, sharply pointed. Middle valve (fig. 81e) with cuspis shorter than digitus; digitus moderately broad, very curved, broadest in middle, distal end bluntly pointed. Inner valve (fig. 81f), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe moderately narrow, moderately long, serrated distally; postero-dorsal margin rounded; about 11 small spines (N = 1) near postero-dorsal margin; about 14 others (N = 1) grouped in middle near dorsal margin.

Karyotype (figs 110a-b, 121a-b)

The variation in the karyotype of princeps is consistent with intraspecific variation but it should be noted that the following cytotypes have been observed:

(1) 2n = 30 (N.F. = 50); and

(2) 2n = 40 (N.F. = 56).

12 km SW of Olympic Dam, S.A. (figs 110b, 121a): Fourteen out of 24 cells had 2n = 30 while in the others I saw 2n = 27 (X1), 29 (X4) and 31 (X5). The karyotype consists of 6M, 10SM, 4ST and 10A chromosomes

(i.e. N.F. = 50).

Calperum, S.A. (figs 110a, 121b): Ten out of 16 cells had $2n = 40$ while in the others I saw $2n = 36$ (X1), 37 (X2), 39 (X2) and 41 (X1). The karyotype consists of 2M, 12SM, 2ST and 24A chromosomes (i.e. N.F. = 56).

Karyotypes from 12 km SW of Olympic Dam and Calperum differ in chromosomes number ($2n = 30$ and 40) and nombre fondamental (N.F. = 50 and 56). Both contain two pairs of very large chromosomes which are undoubtedly homologous. The two cytotypes are separated by at least five Robertsonian rearrangements and three pericentric inversions.

Taxa included

(1) $2n = 30$ cytotype

(2) $2n = 40$ cytotype

Nest structure

Nests of princeps were observed at Calperum and several localities south of Olympic Dam (all S.A.). All were large, with a crater-shaped mound ($d_{max} \simeq 1$ m, $h_{max} \simeq 15$ cm), and as many as 11 entrances located inside the mouth of the crater. The mounds were decorated with gum nuts and leaves mainly in the middle of the crater around the entrances. All nests were found in red sandy soil either: (1) amongst Triodia irritans beneath Eucalyptus sp. (at Calperum); or (2) in bare soil beneath Casuarina sp. and Acacia sp. (south of Olympic Dam). No nests were completely excavated because of their large size, but the internal structure appeared to be of the less complex, diffuse type. I collected more than 700 workers from colony 161 which was probably about two-thirds of the total population.

Biological references (including unpublished theses): None

Comments

M. princeps appears to be a single biological species, with two cytotypes, which can be distinguished from other species of the vindex group by its worker morphology, male terminalia and karyotype.

26. Myrmecia rowlandi Forel

(Fig. 49a)

Myrmecia tarsata Smith subsp. rowlandi Forel, 1910, p. 4. Wheeler, 1933, p. 46 [♀].
Myrmecia tarsata Smith var. rowlandi Forel. Emery, 1911, p. 20.
Myrmecia tarsata Smith race rowlandi Forel. Forel, 1915, p. 9.
Myrmecia rowlandi Forel. Clark, 1951, p. 78, fig. 56. Brown, 1953b, p. 10. Taylor and Brown, 1985, p. 15. Taylor, 1987, p. 45.
Myrmecia tarsata Smith race malandensis Forel, 1915, p. 9 [♀♂].
Myrmecia tarsata Smith subsp. malandensis Forel. Wheeler, 1933, p. 46. Clark, 1951, p. 32.

Types

rowlandi: syntype workers, Kuranda and Cairns, Qld (R. Turner), in GMNH.

malandensis: syntype worker, Malanda, Qld (E. Mjoberg), in ANIC (examined); syntype worker(s), Malanda, Qld, in GMNH; syntype males, Cedar Creek (= Ravenshoe) and Atherton, Qld, in GMNH. [Synonymy by Brown, 1953b].

Worker diagnosis (see Clark, 1951, pp 78-79)

Material examined (fig. 49a)

Queensland: Beatrice River (Ds); Cairns (AML; in SAM); Josephine Falls N.P. (BBL); Kuranda (FPD); Malanda (EM) [malandensis syntype]; Mossman Gorge (RWT); Shiptons Flat (Ds).

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical rowlandi

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. rowlandi is a well-defined biological species which can be easily recognized by its worker morphology. It has often been listed as a subspecific category of *tarsata*, but there are too many differences (especially petiolar shape) for them to be included in the same species group. Its mandible shape and long petiolar stalk suggest that it fits best into the *vindex* species group. However, there are several indices from measurements of the workers which suggest that the placement of *rowlandi* in the *vindex* group is doubtful. It differs mainly in having shorter scapes (SI = 85, cf. SI = 111-127 for rest of group) and a broader mesosoma (MeI = 43, cf. MeI = 32-37). Consequently, it is important that this placement is tested by examining the male terminalia.

27. *Myrmecia vindex* Smith

(Figs 29a-c, 50a, 77a-f, 111a-c, 122a-c)

Myrmecia vindex Smith, 1858, p. 144 [♀]. Roger, 1861a, p. 34. Mayr, 1862, p. 725. Forel, 1907, p. 264 [♀]; 1915, p. 5. Crawley, 1922b, p. 119; 1926, p. 376, fig. 2. Wheeler, 1933, p. 36. Clark, 1951, p. 67, figs 45-48 [♂]. Forbes, 1967, p. 40, figs 8-14 [male terminalia]. Wheeler and Wheeler, 1971, p. 254 [larva].

Myrmecia vindex Smith. Emery, 1911, p. 19, *partim*.

Myrmecia vindex vindex Smith. Taylor and Brown, 1985, p. 17. Taylor, 1987, p. 46.

Myrmecia vindex Smith var. *basirufa* Forel, 1907, p. 264, *syn. nov.* [♀]. Emery, 1911, p. 19. Wheeler, 1933, p. 37. Clark, 1951, p. 70 [♀♂].

Myrmecia vindex basirufa Forel. Taylor and Brown, 1985, p. 17. Taylor, 1987, p. 46.

Myrmecia graticosa Clark, 1951, p. 66, fig. 44, *syn. nov.* [♀]. Wheeler and Wheeler, 1971, p. 250 [larva]. Taylor and Brown, 1985, p. 11. Taylor, 1987, p. 43.

Types

vindex: syntype workers, W.A., in BMNH.

basirufa: syntype worker, Subiaco, W.A., in ANIC (examined); syntype workers, Subiaco, W.A., in GMNH. [NEW SYNONYMY].

gratiosa: holotype worker (probable), Bendering, W.A. (Nov. 1925, C.A. Gardner), in ANIC (examined). [*Note*: Clark (1951) mentions specimens from '*Western Australia*: Bendering (C.A. Gardner), Emu Rock (F. Cadd)' and that the holotype worker is in the ANIC. The ANIC has a worker (Bendering, W.A., Nov. 1925, C.A. Gardner) with a holotype label in Clark's handwriting which is therefore presumed to be the holotype. [NEW SYNONYMY].

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 29a-c).

Head, antennae, mesosoma, legs, petiole and postpetiole red; mandibles yellow. Colour of gaster variable, though constant within nests. Two forms are known: (1) gaster black [*vindex*, *s.s.* colour form; includes *gratiosa*]; and (2) gaster with anterior two-thirds of first segment red, rest black [*basirufa* colour form].

Material examined (fig. 50a)

Australia: Australia (CPH) [*MT*, 3♂♂ only, du] [specimens examined by Forbes (1967)]. *Western Australia*: Albany (cu); Bendering (CAG) [*gratiosa* holotype]; Blackwood River (EFR); Bremer Bay [237-238]; 9 km N of Busselton [215]; Canning River [200]; Cape le Grand [291, 417-418, 420] [*K*, 3 ♀ prepupae]; 35 km E of Cervantes [462]; Cranbrook (TG); Darlington [224]; Dwellingup (JCl); Esperance [421-422, 427-429]; Hill River [77, 520] [*MT*, 2♂♂, 9.iv.1955]; John Forrest N.P. [408]; Kalbarri [463] [*K*, 2 ♀ prepupae]; Lake Cronin [474]; Ludlow (JCl); Margaret River (EFR); 16 km S of Margaret River (EFR); Mundaring Weir [199]; 6 km S of Narrogin [204]; 13 km S of Narrogin [206]; 23 km S of Narrogin [456-457]; 35 km S of Narrogin [207]; New Norcia [465] [*K*, 6 ♀ prepupae]; 16 km E of Nornalup (EFR); Ongerup (TG); 8 km W of Ongerup [444]; Perth [139] [*MT*, 2♂♂, 30.xii.1974]; Rockingham [71, 352] [*MT*, 2♂♂, 11.ii.1962]; Stirling Range (EFR); Swan River (JCl; F217 in TM); Thistle Bay [286] [SEM, ♀; *MT*, ♂, 26.ii.1983]; Toodyay (MSU); Waroona (AC).

Male terminalia (fig. 77a-f)

No variation has been observed in the male terminalia of vindex; vindex, s.s. and basirufa colour forms have both been examined.

Ninth and tenth tergites (fig. 77a) 1.9 times wider than long; median lobe rounded, extending beyond tips of pygostyles. Pygostyles slender; length 0.3 times width of segment. Eighth sternite (fig. 77b) trapezoidal; 1.4 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Moderately few short setae scattered in two areas flanking midline in middle third; a few others in posterior quarter associated with longitudinal sculpturing. Ninth sternite (fig. 77c) 1.0 times as long as wide; moderately long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin very broad, rounded. Short setae scattered over much of posterior half; a few short undulate setae flanking midline in anterior half; long sensory setae around posterior margin. Basal ring 1.5 times wider than long; 1.4 times wider posteriorly than anteriorly. Outer valve (fig. 77d) 1.7 times longer than deep; posterior end dorso-ventrally flattened; dorsal median projection triangulate, sharply pointed. Middle valve (fig. 77e) with cuspis shorter than digitus; digitus moderately broad, very curved, similar breadth throughout, distal end blunt. Inner valve (fig. 77f), excluding anterior apodeme, 0.8 times as long as deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe narrow, moderately long, serrated distally; postero-dorsal margin rounded; 7-18 small spines ($\bar{x}$ = 13.1, N = 13) near postero-dorsal margin; 5-18 others ($\bar{x}$ = 11.9, N = 14) scattered in middle near dorsal margin.

Karyotype (figs 111a-c, 122a-c)

Variation in the karyotype of *vindex* is consistent with being intraspecific, but it should be noted that the following cytotypes (all from *vindex*, *s.s.* colour form) have been observed:

(a) 2n = 47 (N.F. = 76);

(b) 2n = 52 (N.F. = 76); and

(c) 2n = 58 (N.F. = 78).

Cape le Grand, W.A. (figs 111a,b, 122a,b): Twenty-five out of 35 cells from colony 418 had 2n = 47 while in the others I saw 2n = 43 (X2), 45 (X4) and 46 (X4). Fourteen out of 15 cells from colony 420 had the same number while in the other I saw 2n = 44. The karyotypes from both colonies consist of 16M, 11SM, 2ST and 18A chromosomes (i.e. N.F. = 76).

Twelve out of 35 cells from colony 417 had 2n = 52 while in the others I saw 2n = 39 (X1), 41 (X2), 42 (X2), 43 (X1), 44 (X3), 46 (X1), 47 (X3), 48 (X3), 50 (X4) and 51 (X3). The karyotype consists of 12M, 10SM, 2ST and 28A chromosomes (i.e. N.F. = 76).

Kalbarri, W.A.: Five out of 15 cells had 2n = 47 while in the others I saw 2n = 43 (X2), 44 (X3), 45 (X1), 46 (X3) and 48 (X1). The karyotype consists of 16M, 11SM, 2ST and 18A chromosomes (i.e. N.F. = 76).

New Norcia, W.A. (figs 111c, 112c): Eight out of 29 cells had 2n = 58 while in the others I saw 2n = 44 (X1), 45 (X1), 47 (X1), 49 (X1), 50 (X1), 52 (X1), 53 (X2), 54 (X5), 55 (X4), 56 (X3) and 57 (X1). The karyotype consists of 6M, 14SM and 28A chromosomes (i.e. N.F. = 78).

Three populations of *vindex* were found to differ markedly in chromosome number (2n = 47,52,58). However, their *nombres fondamentaux* were more uniform (N.F. = 76,78). Terminal members of this group - $2n = 16M + 11SM + 2ST + 18A = 47$ and $2n = 6M + 14SM + 28A = 58$ - are separated by at least 11 Robertsonian rearrangements and two pericentric inversions in the diploid condition. This degree of variation is tentatively assumed to be intraspecific.

The material examined is all associated with the *vindex*, *s.s.* colour form.

Taxa included

(1) *vindex*, *s.s.* colour form
    (a) 2n = 47 cytotype
    (b) 2n = 52 cytotype
    (c) 2n = 58 cytotype
(2) *basirufa* colour form

Nest structure

I observed colonies of *vindex* (*vindex*, *s.s.* colour form) at about 20 localities in Western Australia. The nests had a variety of structures at different localities and these are summarized below:-

(1) At Kalbarri, a very large nest was found which had a crater-shaped mound (d ≃ 70 cm, h ≃ 45 cm) with a large gaping entrance at the top. This nest was only opened, but I would estimate that it probably contained a population of between 1000 and 2000 workers. It was located in sandy soil, next to a gum tree (*Eucalyptus* sp.).

(2) At Thistle Bay and Esperance, smaller nests with similar shaped mounds (d ≃ 40 cm, h ≃ 10 cm) were found. These could not be excavated because they were located amongst limestone, but they appeared to contain modest populations which I estimated at between 300 and 600 workers.

(3) Moderately large colonies were found at New Norcia, 8 km W of Ongerup and at several localities between 6 and 35 km S of Narrogin. These nests had mounds which were flattened domes ($d_{max} \simeq 60$ cm, $h_{max} \simeq 40$ cm), with one or two entrances on the side near the top. They were usually located beneath large trees (Eucalyptus sp. or Casuarina sp.), in clay soils which made them impossible to excavate. The most completely excavated nest [207] was followed to a depth of 70 cm before digging was abandoned and I filled the remaining galleries with water. During the next 10 minutes many workers emerged followed by the colony queen. The total of 109 workers collected probably represents almost the entire nest population.

(4) A colony at Mundaring Weir [199] had a nest with a slight mound, which was detected by its two entrances ($d \simeq 2$ cm, 12 cm apart) and surrounding excavated grey clay soil. The nest was completely excavated and had an internal structure of Gray's (1974a) less complex diffuse type. It contained 56 workers and went to a depth of about 120 cm. A similar nest was found at Canning River in white sandy soil, but this was not completely excavated.

(5) At Cape Le Grand and Bremer Bay, I found six nests which were moundless and had their entrances beneath, or between, large rocks on steep hillsides. Two recently established nests went to depths of less than 10 cm and were completely excavated, but the larger nests could only be opened. The incipient nests, [237] and [420], contained one dealate queen and three workers, and three dealate queens respectively while the larger nests probably had worker populations of a few hundred at most. The unusual finding of more than one queen in a nest was one of only three such observations I have made in large Myrmecia, and demonstrates that vindex may sometimes be pleometric.

No nests of *basirufa* colour form were found during this study.

Haskins and Haskins (1950) completely excavated one nest at Perth (W.A.) and collected 94 workers, while the incomplete excavation of another at Bellevue (W.A.) yielded 268. Douglas and McKenna (1970) also completely excavated a nest at Bellevue, which contained 210 workers and went to a depth of 71 cm.

Biological references (including unpublished theses)

Haskins and Haskins (1950, 1974); Douglas and McKenna (1970); Browning (1979); Billen (1986)

Comments

M. vindex is a single species, or possibly a complex of sibling species, which varies markedly in nest structure and karyotype, and exhibits slight variation in worker colouration.

28. *Myrmecia sp.12* (ANIC), *sp. nov.*

(Figs 50b, 79a-b, 112a, 121c)

Myrmecia gracilis Roger [*sic*] [= Emery], *auct.* (*non* Emery, 1898).
Wheeler and Wheeler, 1971, p. 250 [larva].

Worker diagnosis

Head, mesosoma, femora, tibiae, petiole, postpeticle and gaster black; mandibles antennae and tarsi yellow.

Material examined (fig. 50b)

South Australia: Ashbourne (RDR; in SAM); Belair (BBL); Bundaleer Reservoir [284]; 3 km NE of Coffin Bay [168-169, 306] [*K*, 4 ♀ prepupae]; 16 km N of Coulta (BBL); 83 km S of Elliston [307]; 9 km W of Gladstone [274]; Maitland [380]; 8 km E of Maitland [476-478] [*K*, 2 ♀ prepupae]; Mambray Creek [378]; Melrose (BBL); Port Lincoln [123, 162-163] [*MT*, 2♂♂, collected as pupae, 8.xii.1981]; Scott C.P. [480]; Taylors Landing [303]; Uley-Wanilla P.S. [124-125, 165-166] [*MT*, ♂, 19.i.1981]; Victor Harbor (BBL); Williamstown [383]; Wilpena [379].

Male terminalia (fig. 79a-b)

No variation has been observed in the male terminalia of *sp.12*.

Ninth and tenth tergites, eighth sternite, basal ring, outer valve and middle valve similar to *fuscipes*. Ninth sternite (fig. 79a) 1.2 times longer than wide; moderately long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin moderately broad, crinkled. Short setae scattered over much of posterior third; a few short, undulate setae flanking midline in middle; long, sensory setae around posterior margin. Inner valve (fig. 79b), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe moderately narrow, moderately short, serrated distally; postero-dorsal margin rounded; 4-10 small spines ($\bar{x} = 7.0$, N = 5) near postero-dorsal margin; 13-21 others ($\bar{x} = 16.7$, N = 6) tightly clustered in middle near dorsal margin.

Karyotype (figs 112a, 121c)

No variation has been observed in the karyotype of *sp.12*.

2n = 74 (N.F. = 78)

3 km NE of Coffin Bay, S.A.: Twenty-seven out of 54 cells had 2n = 74 while in the others I saw 2n = 57 (X1), 66 (X3), 67 (X2), 69 (X3), 70 (X2), 71 (X6), 72 (X3) and 73 (X7). The karyotype consists of 4M and 70A chromosomes (i.e. N.F. = 78).

8 km E of Maitland, S.A.: Twenty out of 33 cells from colony 478 had 2n = 74 while in the others I saw 2n = 55 (X1), 64 (X1), 70 (X1), 71 (X2), 72 (X3), 73 (X4) and 76 (X1). Four out of 17 cells from colony 476 also had 2n = 74 while in the others I saw 2n = 68 (X1), 69 (X2), 70 (X1), 72 (X3), 73 (X4) and 75 (X2). The karyotypes also consist of 4M and 70A chromosomes.

Karyotypes from 3 km NE of Coffin Bay and 8 km E of Maitland appear to be identical.

Taxa included: Typical *sp.12*

Nest structure

Nests of *sp.12* were observed at eight localities in South Australia. Each nest had a very small mound ($d_{max} \simeq 30$ cm, $h_{max} \simeq 5$ cm) and 1-4 entrances ($d \simeq 2$ cm). Colonies 162 and 306 were completely excavated. The former was only 30 cm deep and contained 242 workers while the latter was 60 cm deep and contained 50 workers. The internal structure was of Gray's (1974a) less complex diffuse type.

Biological references (including unpublished theses): None

Comments

M. sp.12 appears to be a well defined biological species which is very similar to *atrata*. However, *sp.12* has a chromosome number of $2n = 74$ and is found only in South Australia while *atrata* has $2n = 76$, 78 and is restricted to Western Australia. Although *sp.12* has male terminalia which are very similar to those of *fuscipes* and *nigriceps*, *s.l.* (*nigriceps*, *s.s.*), I am confident of its status as a separate species because its karyotype is slightly different and no intergrading colour forms have been found even though *sp.12* and *nigriceps*, *s.l.* are sometimes closely sympatric.

29. *Myrmecia sp.14* (ANIC), *sp. nov.*

(Figs 50b, 78a-b, 112b-c, 123a-b)

Worker diagnosis

Identical to *vindex*, except head dark brown.

Material examined (fig. 50b)

Western Australia: 2 km S of Margaret River [217-219, 450] [*K*, 4 ♀ prepupae]; 48 km SE of Pinjarra [201-202] [*K*, ♀ & 2 ♂ prepupae; *MT*, ♂, reared in captivity]; 71 km NE of Williams [460].

Male terminalia (fig. 78a-b)

No variation has been observed in the male terminalia of sp.14.

Ninth and tenth tergites, eighth sternite, basal ring, outer valve and middle valve similar to vindex. Ninth sternite (fig. 78a) 1.1 times longer than wide; moderately long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin very broad, rounded. Short setae scattered over much of posterior half; a few short undulate setae flanking midline in anterior half; long sensory setae around posterior margin. Inner valve (fig. 78b), excluding anterior apodeme, 0.9 times as long as deep; anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe moderately narrow, moderately long, serrated distally; postero-dorsal margin rounded; about 12 small spines ($\bar{x}$ = 12.0, N = 2) near postero-dorsal margin; about 12 others ($\bar{x}$ = 12.0, N = 2) scattered in middle near postero-dorsal margin.

Karyotype (figs 112a-b, 123a-b)

The variation in the karyotype of sp.14 is consistent with intraspecific variation but it should be noted that two cytotypes have been observed:

(1) 2n = 56 (N.F. = 76); and

(2) n = 31, 2n = 62(?) (N.F. = 76).

2 km S of Margaret River, W.A. (figs 112a, 123a): Seventeen out of 48 cells had 2n = 56 while in the others I saw 2n = 38 (X2), 42 (X1), 46 (X1), 49 (X1), 51 (X2), 52 (X3), 53 (X5), 54 (X4), 55 (X6), 52 (X3), 58 (X1) and 61 (X2). The karyotype consists of 14M, 4SM, 2ST and 36A chromosomes (i.e. N.F. = 76).

48 km SE of Pinjarra, W.A. (figs 112b, 123b): Thirty-six out of 52 cells from the male prepupae had n = 31 while in the others I saw n = 26 (X1), 27 (X1), 28 (X1), 29 (X7), 30 (X5) and 32 (X1). The

haploid karyotype consists of 4M, 3SM and 24A chromosomes (i.e. N.F. = 76).

The chromosome number of the worker prepupa may have been 2n = 62 because 13 cells had 2n = 55 (X1), 56 (X1), 58 (X3), 59 (X4), 60 (X3) and 61 (X1). The diploid karyotype appears to consist of 8M, 6SM and 48A chromosomes (i.e. N.F. = 76).

Karyotypes from 2 km S of Margaret River and 48 km SE of Pinjarra differ in chromosome number (n = 28 and 31) but have the same nombre fondamental (N.F. = 76). The two appear to be separated by three Robertsonian rearrangements in the haploid condition.

Taxa included

(1) 2n = 56 cytotype

(2) n = 31 cytotype

Nest structure

Near Margaret River and at 48 km SE of Pinjarra, I completely excavated three nests with small populations. These were colonies 201, 218 and 219, which contained 49, 62 and 53 workers respectively. Nest 201 was found under a rock and was only 20 cm deep; nests 218 and 219 were found under logs and were 25 and 35 cm deep respectively. No larger nests were found at either locality but a similar nest which was not excavated was found at 71 km NE of Williams. The internal structure of these nests was of Gray's (1974a) simple type.

Biological references (including unpublished theses): None

Comments

M. sp.14 appears to be a well-defined biological species, with two cytotypes, which can be distinguished from all other Myrmecia, except vindex, by its male terminalia. It can be separated from vindex by its karyotype and brown head.

30. *Myrmecia sp.16* (ANIC), *sp. nov.*

(Figs 50b, 112c, 123c)

Worker diagnosis

Head and gaster black. Colour of mesosoma, legs, petiole and postpetiole variable, even within nests. Two variants are known: (1) antennae, mesosoma, legs, petiole and postpetiole dark brown to black; and (2) metanotum dark brown to black; antennae, pronotum, mesonotum, epinotum, legs, petiole and postpetiole yellow.

Material examined (fig. 50b)

Western Australia: Condingup [289]; Four Mile Beach [432] [*K*, 3 ♀ prepupae]; 105 km W of Israelite Bay [416] [*K*, 2 ♀ prepupae].

Male terminalia: Unknown

Karyotype (figs 112c, 123c)

No variation has been observed in the karyotypes of *sp.16*.

$$2n = 67 \ (N.F. = 76)$$

Four Mile Beach, W.A. (figs 112c, 123c): Twenty-four out of 36 cells had 2n = 67 while in the others I saw 2n = 63 (X1), 64 (X1), 66 (X5), 68 (X2) and 69 (X3). The karyotype consists of 7M, 2SM and 58A chromosomes (i.e. N.F. = 76).

105 km W of Israelite Bay, W.A.: Eleven out of 31 cells had 2n = 67 while in the others I saw 2n = 54 (X1), 55 (X1), 56 (X1), 58 (X1), 61 (X1), 62 (X1), 63 (X3), 64 (X2), 65 (X2), 66 (X6) and 68 (X1). This karyotype also consists of 7M, 2SM and 58A chromosomes.

Karyotypes from Four Mile Beach and 105 km W of Israelite Bay are identical. Both appear to have a Robertsonian polymorphism because their odd-numbered chromosome complement includes two unpaired acrocentrics and one unpaired metacentric.

Taxa included: Typical *sp.16*

Nest structure

Three nests of sp.16 were observed at Condingup, Four Mile Beach and 105 km W of Israelite Bay (all W.A.). The nests were moundless although sometimes a small amount of soil was scattered about the single entrance (d ≃ 2 cm). Two of the nests were impossible to excavate completely, because of the hard soil in which they had been dug but one small nest at Condingup was secured. This nest contained only 18 workers and went to a depth of 20 cm. I estimate that a mature nest at Four Mile Beach contained at least 200 workers.

Biological references (including unpublished theses): None

Comments

M. sp.16 appears to be a well-defined biological species which consists of two colour variants within nests. Although the yellow and black variant is easily distinguished from all other Myrmecia by its colouration, the dark brown variant is impossible to distinguish from atrata and sp.12 on this basis. Consequently, if only dark brown workers are found in a nest it is necessary to examine the karyotype to enable separation from atrata (which may be broadly sympatric) and sp.12.

31. Myrmecia sp.17 (ANIC), sp. nov.

(Figs 30a-c, 50b, 80a-f, 113a, 124a)

Worker diagnosis

Measurements and proportions as given and illustrated (figs 30a-c).

Head dark brown; mandibles yellow; antennae, mesosoma, legs, petiole and postpetiole reddish brown; gaster black.

Material examined (fig. 50b)

New South Wales: Bellbird [365]; 6 km S of Cessnock (BBL); Cessnock S.F. (BBL); 6 km W of Fassifern (BBL); 12 km S of Narrabri (BBL); 6 km N of Raymond Terrace (BBL). Queensland: 80 km N of Goondiwindi (JD); Marmadua S.F. (BBL). Victoria: 5 km NE of Bacchus Marsh [87, 358-359, 493-494] [SEM, ♀; *MT*, 2♂♂, 27.ii.1975 & collected as pupa, 4.ii.1984; *K*, ♀ prepupa]; Melton (BBL).

Male terminalia (fig. 80a-f)

No variation has been observed in the male terminalia of *sp.17*.

Ninth and tenth tergites (fig. 80a) 1.5 times wider than long; median lobe rounded, extending just beyond tips of pygostyles. Pygostyles moderately slender; length 0.3 times width of segment. *Eighth sternite* (fig. 80b) trapezoidal; 1.5 times wider than long; 1.4 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae concentrated in two large contiguous areas flanking midline in middle half; a few others in posterior quarter, associated with serrate longitudinal sculpturing. *Ninth sternite* (fig. 80c) 1.3 times longer than wide; long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin moderately narrow, rounded. Short setae scattered over much of posterior half; long, sensory setae around posterior margin. *Basal ring* 1.4 times wider than long; 1.4 times wider posteriorly than anteriorly. *Outer valve* (fig. 80d) 1.8 times longer than deep; posterior end dorso-ventrally flattened; dorsal median projection triangulate, bluntly pointed. *Middle valve* (fig. 80e) with cuspis much shorter than digitus; digitus moderately broad, very curved, similar breadth throughout, distal end bluntly pointed. *Inner valve* (fig. 80f), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.5 times length of rest of segment; postero-ventral lobe moderately narrow, moderately short, serrated distally; postero-dorsal margin rounded; 2-4 small spines ($\bar{x}$ = 3.3, N = 4) near postero-dorsal margin; 16-22 others ($\bar{x}$ = 17.8, N = 4) tightly clustered in middle near dorsal margin.

Karyotype (figs 113a, 124a)

No variation has been observed in the karyotype of sp.17.

$$2n = 34 \ (N.F. = 68)$$

5 km NE of Bacchus Marsh, Vic.: Forty out of 41 cells had 2n = 34 while in the other I saw 2n = 33. The karyotype consists of 24M, 8SM and 2ST chromosomes (i.e. N.F. = 68).

Taxa included: Typical sp.17

Nest structure

Colonies of sp.17 were observed near Bacchus Marsh (Vic.) and at Bellbird (N.S.W.). The nests have a high and fairly steep mound ($d_{max} \approx 80$ cm, $h_{max} \approx 50$ cm), decorated with small twigs, with about 5-10 entrances located towards the summit. These nests were located in hard clay and were not completely excavated. The internal structure of the nest was similar to that of the other mound-building species in the vindex group. Chambers were located in the mound and only a few shafts descended below. I estimated populations in these nests to be 200-500 workers.

Barnett (1977) excavated three nests at Bacchus Marsh (Vic.) which contained 52, 90 and 1300 workers. The largest population was found in a nest which was incompletely excavated to a depth of 1.25 m.

Biological references (including unpublished theses)

Barnett (1977); Browning (1979)

Comments

M. sp.17 appears to be a well-defined biological species, which is closely related to ferruginea. The male terminalia of these two species are difficult to distinguish and workers can only be separated by head colour. However, all colonies with dark heads correspond to the typical sp.17 nest structure. I expect that when karyotypes of the colour forms of *ferruginea* have been determined this interspecific difference will be confirmed.

This species is undoubtedly the same one that Barnett (1977) called *sp.10*. However, I have refrained from calling it *sp.10* here on the advice of R.W. Taylor (pers. comm.) because, although vouchers for *sp.10* were deposited in the ANIC (J. Barnett, pers. comm.), they cannot be found.

3.4.1.11. The *Myrmecia esuriens* group

Diagnosis

Large *Myrmecia* with no distinctive characters of the worker morphology. However, they can be characterized by the following combination: (1) yellow mandibles with slight or no angulate broadening at the base of the inner border; (2) petiolar stalk much shorter than node; and (3) scapes exceeding the occipital border by less than a quarter of their length. Support for recognition of this species group relies upon characters of the male terminalia. These can be easily recognized by the inner valve which has no spines and a long, narrow ventral lobe (e.g. fig. 82e).

Composition

(1) *esuriens* Fabricius = *tasmaniensis* Smith = *walkeri* Forel

(2) *midas* Clark

(3) *pulchra* Clark = *crassinoda* Clark = *fallax* Clark = *murina* Clark = *picticeps* Clark

[*Note* - These species have previously been placed in the *esuriens* group of Emery (1911) and the *tricolor* and *vindex* groups of Clark (1951).]

Distribution

All Australian states and mainland territories, except N.T.

Comments

The *esuriens* group is well delimited from all other species groups by its workers and male terminalia. Within the group, workers of *esuriens*, *midas* and *pulchra* are quite similar, except for colour. However, the male terminalia, while being broadly similar, are more distinct.

32. *Myrmecia esuriens* Fabricius

(Figs 51a, 82a-e)

Myrmecia esuriens Fabricius, 1804, p. 424 [♀]. Mayr, 1862, pp 727, 729. Emery, 1911, p. 20. Forel, 1913a, p. 173. Clark, 1934a, p. 16 [♀♂]; 1951, p. 84, figs 63-65. Taylor and Brown, 1985, p. 8. Taylor, 1987, p. 42.

Myrmecia tasmaniensis Smith, 1858, p. 147 [♀].

Myrmecia walkeri Forel, 1893, p. 456 [♀].

Types

esuriens: holotype or syntypes, Australia, have not been located (see Roger, 1861a).

tasmaniensis: syntype workers, Tasmania, in BMNH. [Synonymy by Clark, 1934a].

walkeri: syntype workers, Hobart, Tas. (J.J. Walker), in GMNH. [Synonymy by Clark, 1934a].

Worker diagnosis (see Clark, 1951, pp 84-85)

Material examined (fig. 51a)

Tasmania: Bronte (TG); Bruny Island (PWB; in TM); 21 km E of Campbell Town (B,*Bea*; F383 in TM); Cape Pillar N.P. [295]; Corinna (TGC); Erriba (TG); Frankford (AML); Hastings (TG); Hobart (CL); Hobart (AML; in MCZ) [*MT*, ♂ only, du]; Interview River (TGC); Lake St Clair (TG); Mount Barrow (TG); Mount Wellington (CEC); Mount Field National Park (FEW); 11 km S of Parrawe (TG); Port Arthur (EC1); Scottsdale (GFH); Snowy Mountains (CDK; F382 in TM); Snug (JWE; F70 in TM); Waratah (ESm).

Male terminalia (fig. 82a-e)

No variation has been observed in the male terminalia of *esuriens*.

Ninth and tenth tergites damaged. Eighth sternite (fig. 82a) trapezoidal; 1.7 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae concentrated in two moderately small areas flanking midline in anterior half; numerous others in posterior quarter associated with longitudinal sculpturing. Ninth sternite (fig. 82b) 1.1 times longer than wide; moderately short anterior apodeme; antero-lateral lobes slightly developed; lateral lobes absent; posterior margin narrow, tapering to rounded tip. Short setae scattered over much of posterior two-thirds; long sensory setae around tip of posterior margin. Basal ring 1.8 times wider than long; 1.4 times wider posteriorly than anteriorly. Outer valve (fig. 82c) 1.5 times longer than deep; posterior end broadly divided into two lobes; dorsal lobe (DL) bluntly pointed, may be homologous to dorsal median projection of other *Myrmecia*; ventral lobe (VL) blunt, with sensillae (Se) on dorsal surface. Middle valve (fig. 82d) with cuspis much shorter than digitus; digitus moderately narrow, very curved, broadest in middle, distal end very long, blunt. Inner valve (fig. 82e), excluding anterior apodeme, 0.9 times as long as deep; anterior extension of anterior apodeme 0.4 times length of rest of segment; ventral lobe (VL) long, narrow, serrated distally; postero-dorsal margin rounded; posterior margin expanded ventrally to form a postero-ventral lobe lacking serrations and spines.

Karyotype: Unknown

Taxa included: Typical *esuriens*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. esuriens is a well-defined biological species, restricted to Tasmania, which is easily recognized by its worker morphology and male terminalia.

33. *Myrmecia midas* Clark

(Figs 51a, 83a-d)

Myrmecia midas Clark, 1951, p. 55, figs 34-35 [♀♀]. Taylor and Brown, 1985, p. 13. Taylor, 1987, p. 44.

Type

midas: holotype worker (probable), Dorrigo, N.S.W. (W.W. Froggatt), in ANIC (examined). [*Note* - Clark (1951) mentions specimens from '*New South Wales*: Dorrigo (R. Heron [sic]), Brooklana (W.W. Froggatt). *Queensland*: National Park, Mt. Tambourine (H. Hacker)' and that the holotype worker is in the ANIC. The ANIC has a worker (Dorrigo, N.S.W., W.W. Froggatt) with a holotype label in Clark's handwriting and four workers (Dorrigo, N.S.W., W. Heron) with Clark paratype labels. I presume that the specimen with the holotype label is the holotype.]

Worker diagnosis (see Clark, 1951, pp 55-56)

Material examined (fig. 51a)

New South Wales: Dorrigo (WWF) [*midas* holotype], (WH), (WH; in MCZ) [*MT*, ♂ only, du]; Mount Warning (BBL). *Queensland*: Lamington N.P. (BBL).

[*Note* - Taylor and Brown (1985, p. 13) did not record this species from Qld.]

Male terminalia (fig. 83a-d)

No variation has been observed in the male terminalia of *midas*.

Ninth and tenth tergites damaged. *Eighth sternite* (fig. 83a) trapezoidal; 1.8 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.4 times length of segment. Moderately few short setae concentrated in two moderately small areas flanking midline in anterior third; numerous others in posterior third associated with longitudinal sculpturing. *Ninth sternite* (fig. 83b) 1.4 times longer than wide; moderately short anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin moderately narrow, tapering to angulate tip. Short setae scattered over much of posterior three-quarters; long sensory setae around tip of posterior margin. *Basal ring* 2.0 times wider than long; 1.7 times wider posteriorly than anteriorly. *Outer valve* (fig. 83c) 1.5 times longer than deep; posterior end broadly divided into two lobes; dorsal lobe bluntly pointed, may be homologous to dorsal median projection of other *Myrmecia*; ventral lobe blunt, with sensillae on dorsal surface. *Middle valve* similar to *pulchra*. *Inner valve* (fig. 83d), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.4 times length of rest of segment; ventral lobe long, narrow, serrated distally; postero-dorsal margin rounded; posterior margin expanded ventrally to form a postero-ventral lobe lacking spines and serrations.

Karyotype: Unknown

Taxa included: Typical *midas*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. midas is a well-defined biological species, which can be distinguished by its worker morphology and male terminalia. The few specimens available all came from southern Queensland and northern New South Wales.

34. *Myrmecia pulchra* Clark

(Figs 31a-c, 51a, 84a-f)

Myrmecia pulchra Clark, 1929, p. 119 [♀☿]; 1951, p. 82, figs 61-62. Brown, 1953b, p. 27. Taylor and Brown, 1985, p. 14. Taylor, 1987,

p. 45.

Myrmecia crassinoda Clark, 1934b, p. 50 [⚲♀]; 1951, p. 88.

Myrmecia fallax Clark, 1951, p. 79, fig. 57 [⚲].

Myrmecia murina Clark, 1951, p. 80, figs 58-60 [⚲♀♂]. Wheeler and Wheeler, 1971, p. 251 [larva].

Myrmecia picticeps Clark, 1951, p. 47, fig. 25, *syn. nov.* [⚲]. Taylor and Brown, 1985, p. 14. Taylor, 1987, p. 45.

Types

pulchra: syntype workers (4), Cann River, Vic. (Nov. 1928, J. Clark), in NMV (examined); syntype workers (2), Cann River, Vic. (Nov. 1928, J. Clark), in ANIC (examined).

crassinoda: syntype workers (2) and female, Gellibrand, Vic. (19-23.i.1932, J. Clark), in NMV (examined). [Synonymy by Brown, 1953b].

fallax: holotype worker, Kerrie, Vic. (1937, J.E. Dixon), in ANIC (examined). [Synonymy by Brown, 1953b].

murina: holotype worker, Belgrave, Vic. (Dec. 1920, L.B. Thorn), in ANIC (examined). [Synonymy by Brown, 1953b].

picticeps: holotype worker, Albany, W.A. (J. Clark), in ANIC (examined). [NEW SYNONYMY].

Worker diagnosis

Measurements and proportions as given and illustrated (figs 31a-c).

Colour variable, though constant within nests and populations. Combinations intergrade from: (1) Most of head, mesosoma, petiole and postpetiole brownish red; gaster and middle of forehead between frontal carinae and ocelli black; mandibles, antennae, anterior legs, and all tarsi yellow; femora and tibiae of middle and posterior legs brown (*crassinoda* colour form; includes *picticeps*); to (2) Head and gaster black; mesosoma, petiole and postpetiole brownish red; mandibles, antennae, anterior legs, and all tarsi yellow; femora and tibiae of middle and posterior legs brown (*pulchra*, *s.s.* colour form); to (3) Head, most of mesosoma, petiole, postpetiole, gaster, anterior femora, femora and tibiae of middle and posterior legs black; mesonotum and small area on pronotum brown; mandibles, antennae, anterior tibiae, and all tarsi yellow (fallax colour form); to (4) Head, mesosoma, petiole, postpetiole, gaster, anterior femora, femora and tibiae of middle and posterior legs black; mandibles, antennae, anterior tibiae and all tarsi yellow (murina colour form).

Material examined (fig. 51a)

Australian Capital Territory: Brindabella Range (RJKo); Honeysuckle Creek (BBL); Smoker's Gap [72] [MT, ♂, 7.ii.1978]. New South Wales: Barlow (TG); Bowral (BBL); Heaton S.F. (BBL); Mangrove Mountain (BBL); Mittagong (BBL); Mogo S.F. (BBL); Monga (EFR); Mount Canobolas (EFR); Mount Wilson (BBL); Nimmitabel (BBL); 8 km E of Nimmitabel (BBL); 32 km S of Nowra (BBL); Rosedale (BBL); Tallaganda S.F. (BBL); Tantawangalo Mountains (GFH); Tinderry Mountains (BBL). South Australia: Belair [388]; Mount Lofty [73] [SEM, ♀; MT, ♂, 23.iii.1969]; Rocky River [335]. Victoria: Belgrave (LBT; JCl) [murina holotype]; Cann River (JCl; in NMV) [pulchra syntypes]; Gellibrand (JCl; in NMV) [crassinoda syntypes]; Halls Gap (BBL); Kerrie (JED) [fallax holotype]; Mansfield (JCl); Mount Buffalo (TG); Narbethong (BBL); 48 km N of Orbost (EFR); Tambo Crossing (cu); Walhalla (JCG). Western Australia: Albany (JCl) [picticeps holotype]; Booanya (AEB); Porongorups (BBL).

[Note - Taylor and Brown (1985, pp 14-15) did not record this species from A.C.T., N.S.W. or S.A.]

Male terminalia (fig. 84a-f)

No variation has been observed in the male terminalia of pulchra; pulchra, s.s. and murina colour forms have been examined but the others have not.

Ninth and tenth tergites (fig. 84a) 2.8 times wider than long; median lobe angulate, with rounded apex, extending just beyond tips of pygostyles. Pygostyles moderately slender; length 0.3 times width of segment. Eighth sternite (fig. 84b) trapezoidal; 1.6 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae scattered in anterior three-quarters; moderately few others others in posterior quarter, associated with longitudinal sculpturing. Ninth sternite (fig. 84c) 1.2 times longer than wide; moderately short anterior apodeme; antero-lateral lobes barely developed; lateral lobes absent; posterior margin moderately narrow, tapering to rounded tip. Short setae scattered over much of posterior half; long sensory setae around tip of posterior margin. Basal ring 1.7 times wider than long; 1.4 times wider posteriorly than anteriorly. Outer valve (fig. 84d) 1.4 times longer than deep; posterior end broadly divided into two lobes; dorsal lobe bluntly pointed, may be homologous to dorsal median projection of other *Myrmecia*; ventral lobe blunt, with sensillae on dorsal surface. Middle valve (fig. 84e) with cuspis much shorter than digitus; digitus broad, very curved, broadest in middle, distal end long, blunt. Inner valve (fig. 84f), excluding anterior apodeme, 0.9 times as long as deep; anterior extension of anterior apodeme 0.4 times length of rest of segment; ventral lobe long, narrow, serrated distally; postero-dorsal margin rounded; posterior margin expanded ventrally to form a postero-ventral lobe lacking spines and serrations.

Karyotype: Unknown

Taxa included

(1) *crassinoda* colour form

(2) *pulchra*, *s.s.* colour form

(3) *fallax* colour form

(4) *murina* colour form

Nest structure

One colony of *pulchra* (*pulchra*, *s.s.* colour form) was observed at Rocky River (Kangaroo Island, S.A.). The nest entrance (d ≃ 2 cm) was located between two rocks with a single gallery below. Excavation of the entire nest was impracticable because of the rocky ground and only five very timid workers were collected. I suspect that there were probably less than a fifty in the whole nest.

Biological references (including unpublished theses)

Browning (1979)

Comments

M. pulchra is a species, or possibly a complex of sibling species, with variable colouration (as indicated above). Four other names (crassinoda, picticeps, fallax and murina) have been used for different colour forms but at present there is no strong evidence from worker morphology, chromosomes or male terminalia to support recognition of these. Consequently, I have accepted Brown's (1953b) synonymies, and propose a new synonymy of picticeps, which appears to be identical to crassinoda colour form. However, its Western Australian distribution suggests that its status as a separate species warrants further investigation because all other species of the esuriens group are from east of Kangaroo Island (S.A.).

3.4.2 Subgenus Promyrmecia Emery

Diagnosis

Moderately small to very small jumping Myrmecia (largest workers less than 15 mm long), which have all workers in a colony of similar size.

Composition

(1) nigrocincta group
(2) harderi group
(3) pilosula group
(4) mandibularis group
(5) picta group
(6) sp.15 group
(7) fucosa group

(8) *urens* group

[*Note* - Except for the *nigrocincta* group, these groups were all placed in genus *Promyrmecia* by Clark (1951).]

Distribution

All Australian states and mainland territories

New Caledonia

Comments

Subgenus *Promyrmecia* is well delimited from *Myrmecia*, *s.s.* by its worker locomotion, worker size and lack of division in worker size. Otherwise, its worker morphology and male terminalia do not appear to have any truly diagnostic features. Chromosome numbers range from n = 1-35 (N.F. = 4-70), but are of limited value for recognizing *Promyrmecia* because of the large overlap with *Myrmecia*, *s.s.* (n = 5-44, N.F. = 18-88).

3.4.2.1. The *Myrmecia nigrocincta* group

Diagnosis

Moderately small, jumping *Myrmecia* with proportionately longer petioles than other jumpers (PNI = 45-52, PNI2 = 46-56 for the *nigrocincta* group; PNI = 59-106, PNI2 = 60-107 for all other jumpers). The male terminalia are easily recognized by the inner valve which has a sclerotized ridge in middle, near posterior margin (fig. 85f).

Composition

(1) *apicalis* Emery
(2) *cardigaster* Brown, *nom.nov.* = *cordata* Clark
(3) *flammicollis* Brown
(4) *nigrocincta* Smith
(5) *petiolata* Emery

[*Note* - These species have previously been placed in the *nigrocincta* group by both Emery (1911) and Clark (1951).]

Distribution

N.S.W., Qld, Vic.

New Caledonia

Comments

The *nigrocincta* group is well delimited from all other species groups by its workers and male terminalia. Unfortunately, male terminalia are known for only one species (*nigrocincta*), so that the unity of the group is yet to be tested by characters from that source. One species (*nigrocincta*) karyotyped by Imai et al. (1977) had 2n = 22 (N.F. = 42).

35. *Myrmecia apicalis* Emery

(Fig. 51b)

Myrmecia apicalis Emery, 1883, p. 150 [♀]; 1911, p. 20; 1914, p. 394. Wheeler, 1927, p. 129. Clark, 1951, p. 111, fig. 85. Brown, 1953b, p. 25. Taylor, 1987, p. 46.

Types

apicalis: syntype workers, New Caledonia, in MNHP.

Worker diagnosis (see Clark, 1951, p. 111)

Material examined (fig. 51b)

New Caledonia: New Caledonia (HB).

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *apicalis*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. apicalis is known from a few specimens only, but appears to be a well-defined biological species, restricted to New Caledonia, which can be distinguished by its worker morphology. It is the only *Myrmecia* which is not endemic to Australia.

36. *Myrmecia cardigaster* Brown

(Fig. 51b)

Myrmecia cordata Clark, 1951, p. 116, fig. 90 [♀]. [*non Myrmecia cordata* Fabricius, 1805 = *Daceton armigerum* Latreille, 1802].

Myrmecia cardigaster Brown, 1953b, p. 28. Taylor and Brown, 1985, p. 7. Taylor, 1987, p. 42. [*nom. nov.* for *Myrmecia cordata* Clark, 1951].

Type

cordata: holotype worker, Malanda, Qld (G.F. Hill), in ANIC (examined).

Worker diagnosis (see Clark, 1951, pp 116-117)

Material examined (fig. 51b)

Queensland: Malanda (GFH) [*cordata* holotype].

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *cardigaster*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. cardigaster is known from a single specimen only, but appears to be a well-defined biological species, restricted to northern Queensland. It is easily distinguished by its peculiar gaster, which is unlike that of any other *Myrmecia*.

37. *Myrmecia flammicollis* Brown

(Fig. 51b)

Myrmecia flammicollis Brown, 1953b, p. 23 [♀]. Taylor and Brown, 1985, p. 9. Taylor, 1987, p. 43.

Type

flammicollis: holotype worker, 'The Rocky Scrub', McIlwraith Range, Queensland (P.J. Darlington), in MCZ.

Worker diagnosis (see Brown, 1953b, pp 23-25)

Material examined (fig. 51b)

Queensland: 'The Rocky Scrub', McIlwraith Range (PJD; in QM) [flammicollis paratype].

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical flammicollis

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. flammicollis is a well-defined biological species, restricted to northern Queensland, which can be distinguished by its worker morphology.

38. Myrmecia nigrocincta Smith

(Figs 32, 52a, 85a-f)

Myrmecia nigrocincta Smith, 1858, p. 147 [♀]. Mayr, 1862, pp 724, 728; 1876, p. 95 [♀♂]. Lowne, 1865, p. 336. Froggatt, 1905, pp 5, 10. Forel, 1910, p. 8; 1915, p. 5. Emery, 1911, p. 20. Viehmeyer, 1924, p. 222. Crawley, 1926, p. 381, fig. 7. Wheeler, 1933, p. 48, fig. 17. Clark, 1951, p. 113, figs 87-89. Wheeler and Wheeler, 1971, p. 251 [larva]. Imai, Crozier and Taylor, 1977, p. 345, figs 2, 12 [karyotype]. Taylor and Brown, 1985, p. 13. Taylor, 1987, p. 44.

Myrmecia (Halmamyrmecia) nigrocincta Smith. Wheeler, 1922, p. 194, fig. 2.

Types

nigrocincta: syntype workers, Australia, in BMNH.

Worker diagnosis

Measurements and proportions as given and illustrated (figs 32a-c).

Head, mesonotum, metanotum, postpetiole and gaster black; mandibles, antennae, pronotum, epinotum, tarsi and petiole yellow; femora and tibiae brown.

Material examined (fig. 52a)

New South Wales: Asquith (HPS); Brunswick Heads (DHa); Collaroy (KRN); Ellenborough Falls (KHLK); Galston Gorge (BBL); Leumeah (C&I) [K]; Lismore (CFD); 10 km S of Mangrove Mountain (BBL); Narrabeen (WWF); Pymble [67] [SEM, ♀; MT, ♂, 10.x.1956]; 10 km S of Swansea (BBL) [MT, ♂, 15.iv.1976]; Sydney (BBL); 6 km N of The Entrance (BBL). Queensland: Atherton (EM); Babinda (FXW); Beaudesert (SHP); Blackall Range (BBL); Brisbane (BBL); Burleigh Heads (CPL); Byfield (CBa); Cairns (cu); Cunningham's Gap (BBL); Daisy Hill S.F. (BBL); East Palmerston (RWT); Eungella N.P. [529]; Fletcher (ESu); Innisfail (TG); Lamington N.P. (RJKo); Landsborough (BBL); Mission Beach (RWT); Mossman (MG); Mount Bauple [534]; Mount Coot-tha [266]; Mount Tamborine (JFT; F71 in TM); Mount Windsor Tableland (RWT); Nebo (EW); 12 km W of Paluma [513]; Stanthorpe (BBL); Toowoomba (TG); 10 km N of Yarraman (BBL); Yeppoon (ANB); Warwick (ASm). Victoria: Cann River (JCl); Millgrove (FEW).

Male terminalia (fig. 85a-f)

No variation has been observed in the male terminalia of nigrocincta.

Ninth and tenth tergites (fig. 85a) 3.7 times wider than long; median lobe broadly rounded, extending almost to tips of pygostyles. Pygostyles slender; length 0.3 times width of segment. Eighth sternite (fig. 85b) trapezoidal; 1.5 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. A few short setae associated with serrate longitudinal sculpturing in posterior quarter. Ninth sternite (fig. 85c) 1.4 times longer than wide; moderately long anterior apodeme; antero-lateral lobes well developed; lateral lobes present; posterior margin narrow tapering to rounded tip. Short setae scattered over much of posterior two-thirds. Basal ring 1.6 times wider than long; 1.6 times wider posteriorly than anteriorly. Outer valve (fig. 85d) 2.0 times longer than deep; posterior end pointed; dorsal median projection long, roundly pointed. *Middle valve* (fig. 85e) with cuspis much shorter than digitus; digitus moderately narrow, very curved, similar breadth throughout, distal end bluntly pointed. *Inner valve* (fig. 85f), excluding anterior apodeme, 1.3 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe rounded, bearing 9-10 small spines ($\bar{x}$ = 9.3, N = 4); postero-dorsal margin rounded, bearing 16-18 small spines ($\bar{x}$ = 17.0, N = 4); *sclerotized ridge* (SR) in middle, towards posterior margin.

Karyotype

No variation has been observed in the karyotype of *nigrocincta*.

2n = 22 (Imai et al., 1977; 3 colonies from Leumeah, N.S.W.)

Taxa included: Typical *nigrocincta*

Nest structure

One colony of *nigrocincta* was observed at Mount Coot-tha (Qld). The nest was almost completely concealed by a stone, and could not be excavated because its galleries went between large stones. This agrees well with Wheeler (1933) who says that *nigrocincta* '... constructs among the stones low mound nests about a foot in diameter, with a central opening ... [and] ... sometimes the nest is partially or even entirely concealed beneath a stone'. Gray (1974a) says that the internal structure of the nest is complex and diffuse. Two nests he excavated at Banyabba S.F. and Lane Cove (both N.S.W.) contained 455 and 1,187 workers and were 93 and 108 cm deep respectively.

Biological references (including unpublished theses)

Turner (1897); Haskins and Haskins (1950); Gray (1974a, 1974b); Browning (1979)

Comments

M. nigrocincta is a well-defined biological species, restricted to the eastern coast of Australia, which can be distinguished by its worker morphology, male terminalia and karyotype.

39. *Myrmecia petiolata* Emery

(Fig. 51b)

Myrmecia petiolata Emery, 1895, p. 345 [♀]; 1911, p. 20. Clark, 1951, p. 112, fig. 86. Taylor and Brown, 1985, p. 14. Taylor, 1987, p. 45.

Type

petiolata: holotype worker, Mount Bellenden Ker, Qld (G. Podenzana), in MCSN.

Worker diagnosis (see Clark, 1951, pp 112-113)

Material examined (fig. 51b)

Queensland: 6 km W of Babinda (Ds).

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *petiolata*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. petiolata is known from a few specimens only, but appears to be a well-defined biological species, restricted to northern Queensland, which can be distinguished by its worker morphology.

3.4.2.2. The *Myrmecia harderi* group

Diagnosis

Small *Myrmecia* with no distinctive characters of the worker morphology. However, they can be characterized by the following combination: (1) coarse sculpturing on the postpetiole (fig. 33a,c); and (2) restricted to South Australia and the eastern states. The male terminalia can be easily recognized by the ninth sternite which has its posterior margin forming a small rounded posterior lobe, flanked by rounded postero-lateral lobes.

Composition

harderi Forel = *scabra* (Clark) = *celaena* (Clark) = *maloni* (Clark)

[*Note* - This species has previously been placed in the *pilosula* group by both Emery (1911) and Clark (1943, 1951).]

Distribution

N.S.W., Qld, S.A., Vic., W.A.

Comments

The *harderi* group is well delimited by its male terminalia, but if I had examined only workers I would have placed its only species (*harderi*) in the *pilosula* group, as did Emery (1911) and Clark (1943, 1951). I still suspect that *harderi* is closely related to the *pilosula* group, but its male terminalia are so distinct that I am unwilling to draw that conclusion based only upon worker morphology which appears to contradict other evidence from male terminalia.

40. *Myrmecia harderi* Forel

(Figs 33a-c, 52b, 86a-f)

Myrmecia harderi Forel, 1910, p. 8 [♀]. Emery, 1911, p. 21. Brown, 1953b, p. 16. Wheeler and Wheeler, 1971, p. 250 [larva]. Taylor and Brown, 1985, p. 11. Taylor, 1987, p. 43.

Promyrmecia harderi (Forel). Clark, 1943, p. 118, pl. 13, figs 28-29 [☿]; 1951, p. 215, figs 181-182.

Promyrmecia scabra Clark, 1943, p. 118, pl. 14, figs 40-41 [♀ ☿]; 1951, p. 217, figs 183-184.

Promyrmecia celaena Clark, 1943, p. 120, pl. 14, fig. 42, *syn*. *nov*. [♀]; 1951, p. 220, fig. 187.

Myrmecia celaena (Clark). Taylor and Brown, 1985, p. 7. Taylor, 1987, p. 42.

Promyrmecia maloni Clark, 1943, p. 121, pl. 14, fig. 43 [♀]; 1951, p. 221, fig. 188.

Types

harderi: syntype worker, Gunnedah, N.S.W. (16.xi.1902, W.W. Froggatt), in NMV (examined); syntype workers, Gunnedah, N.S.W. (W.W. Froggatt), in GMNH.

scabra: syntype workers (2) and female, Leigh Creek, S.A., in NMV (examined). [Synonymy by Brown, 1953b].

celaena: syntype worker, Pilliga, N.S.W. (W.W. Froggatt), in NMV (examined); syntype worker, Narrabri, N.S.W. (W.W. Froggatt), in NMV (examined); syntype worker, Milmerran, Qld (29.xii.1940, J. MacQueen), in NMV (examined). [NEW SYNONYMY].

maloni: syntype workers (6), Inglewood, Vic. (Sept. 1939, J. Clark), in NMV (examined). [Synonymy by Brown, 1953b].

Worker diagnosis

Measurements and proportions as given and illustrated (figs 33a-c).

Colour variable. Combinations intergrade from: (1) Head, most of postpetiole, and gaster black; mandibles, antennae and tarsi yellow; mesosoma, petiole and centre of postpetiole red; femora and tibiae brown [harderi, s.s. colour form]; to (2) Head, half of pronotum, mesonotum, metanotum, postpetiole and gaster black; mandibles, antennae and tarsi yellow; half of pronotum, epinotum and petiole red; femora and tibiae brown [scabra colour form; includes maloni]; to (3) Head, scapes, mesosoma, petiole, postpetiole and gaster black; mandibles, funiculi and tarsi yellow; femora and tibiae brown [celaena colour form].

Material examined (fig. 52b)

New South Wales: Apsley (BBL); 25 km N of Barooga (BBL); Berrigan S.F. (BBL); 15 km S of Berrigan S.F. (BBL); Bookong S.F. (BBL) [SEM, ♀; MT, ♂, 12.vi.1979]; Buckingbong S.F. (BBL); Bullawa Creek S.F. (BBL); 10 km N of Dubbo (BBL); Goolgowi (BBL); 30 km N of Grenfell (BBL); Gunnedah (WWF; in NMV) [harderi syntype]; Moruncah (BBL); 10 km E of

Morundah (BBL); Narrabri (WWF; in NMV) [celaena syntype]; Palmer S.F. (BBL); Pilliga (WWF; in NMV) [celaena syntype]; Urana (BBL). Queensland: Milmerran (JMacQ; in NMV) [celaena syntype]. South Australia: Bunyeroo Gorge (BBL); Leigh Creek (in NMV) [scabra syntypes]; Melrose (BBL); Sevenhill (BBL); Wilpena Pound (BBL); Yudnamutana [396]. Victoria: Inglewood (JCl; in NMV) [maloni syntypes]; Pyramid Hill (BBL).

Male terminalia (fig. 86a-f)

No variation has been observed in the male terminalia of harderi; celaena colour form has been examined but the others have not.

Ninth and tenth tergites (fig. 86a) 1.4 times wider than long; median lobe rounded, extending almost to tips of pygostyles. Pygostyles moderately narrow; length 0.4 times width of segment. Eighth sternite (fig. 86b) trapezoidal; 1.9 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Numerous short setae concentrated in two large areas flanking midline in middle half. Ninth sternite (fig. 86c) 1.3 times longer than wide; long anterior apodeme; antero-lateral lobes slightly developed; lateral lobes absent; posterior apex forming a small rounded lobe, flanked by rounded postero-lateral lobes. Moderately few short setae flanking midline in middle third; long sensory setae around posterior margin. Basal ring 1.6 times wider than long; 1.6 times wider posteriorly than anteriorly. Outer valve (fig. 86d) 1.8 times longer than deep; posterior end abrupt, ventral margin slightly turned dorsally; dorsal median projection moderately short, bluntly pointed. Middle valve (fig. 86e) with cuspis much shorter than digitus; digitus broad, slightly curved, broadest in middle, distal end roundly pointed. Inner valve (fig. 86f), excluding anterior apodeme, 1.4 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe very short, almost absent, bluntly pointed; postero-dorsal margin turned laterally; 28-31 small spines ($\bar{x}$ = 29.5, N = 2) along posterior margin from middle to postero-ventral lobe.

Karyotype: Unknown

Taxa included

(1) harderi, s.s. colour form

(2) scabra colour form

(3) celaena colour form

Nest structure

No nests of harderi were seen during this study. However, Brown (1953b) says that '... the entrance to the nest [is] a slender, tapered turret fashioned from fine vegetable detritus and projecting upwards through the thin leaf litter to a height of about 2 centimeters, with the circular opening at the apex.' Brown also notes that nests of this species were often found beneath 'native pines' (Callitris sp.) in sandy soils, which agrees with habitat data written on many of the ANIC specimen labels by B.B. Lowery.

Biological references (including unpublished theses): None

Comments

M. harderi has previously been placed in the pilosula group by Emery (1911) and Clark (1943, 1951), but examination of the male terminalia shows them to be quite dissimilar. The species is widely distributed, with variable colouration, and may represent a complex of siblings. The synonyms listed here are distinguished by colour only and this appears to intergrade between forms. Unfortunately, the male terminalia are known for one colour form only (celaena) and no karyotypes have been determined, so that evidence which might be expected to demonstrate interspecific differences is not yet available.

3.4.2.3. *Myrmecia pilosula* group

Diagnosis

Moderately small, jumping *Myrmecia* with worker mandibles which vary considerably between species but male terminalia which are more uniform. All species have worker mandibles with outer border slightly concave and inner border with no angulate broadening near base. The most distinctive species (*aberrans*) has mandibles with large, chunky teeth. The others all have slender mandibles but may differ by having basal teeth reduced (*clarki* Crawley, *swalei* Crawley and *tepperi*) or teeth backwardly directed (*varians* Mayr). The male terminalia are easily recognized by the ninth sternite which has posterior extension of posterior margin turned dorsally and expanded to form a barbed hook.

Composition

(1) *aberrans* Forel = *froggatti* Forel = *maura* Wheeler = *haematosticta* Wheeler = *formosa* Wheeler = *taylori* Wheeler = *sericata* Wheeler = *nobilis* (Clark) = *eupoecila* (Clark) = *greavesi* (Clark) = *excavata* (Clark)

(2) *cephalotes* (Clark) = *hilli* (Clark) = *callima* (Clark)

(3) *chasei* Forel = *mediorubra* Forel = *ludlowi* Crawley

(4) *chrysogaster* (Clark)

(5) *clarki* Crawley

(6) *dispar* (Clark)

(7) *michaelseni* Forel = *perthensis* Crawley

(8) *pilosula* Smith, *s.l.* = *ruginoda* (Smith)

(9) *queenslandica* Forel = *overbecki* Viehmeyer = *cydista* (Clark)

(10) *rugosa* Wheeler = *ruginodis* (Clark)

(11) *swalei* Crawley = *testaceipes* (Clark) = *dixoni* (Clark)

(12) *tepperi* Emery

(13) *varians* Mayr = *rufonigra* Crawley = *occidentalis* (Clark) = *elegans* (Clark) = *opaca* (Clark) = *wilsoni* (Clark) = *shepherdi* (Clark) = *goudiei* (Clark) = *marmorata* (Clark)

(14) *sp.8*, *sp. nov.* (ANIC)

(15) *sp.M1* (GPB), *sp. nov.* [known only from one male]

(16) *sp.M2* (GPB), *sp. nov.* [known only from one male]

[*Note* - These species have previously been placed in the *aberrans* and *pilosula* groups of Emery (1911), and the *aberrans*, *cephalotes*, *tepperi*, *varians* and *pilosula* groups of Clark (1943, 1951).]

Distribution

All Australian states and mainland territories

Comments

The *pilosula* group is well delimited by its male terminalia, but the workers are quite variable. There are several quite different worker mandible types represented in the group, which led Clark (1943, 1951) to place its species in five groups: *aberrans*, *cephalotes*, *pilosula*, *tepperi* and *varians* groups.

The most distinctive workers belong to *aberrans*, and have such aberrant heads and mandibles that if workers only were known I would undoubtedly have followed Clark and placed them in a separate group. Other species in the *pilosula* group have fairly similar heads but their mandibles vary in the number and shape of the teeth. Based on mandible type I recognise five subgroups of the *pilosula* group: (1) *aberrans*; (2) *varians*; (3) *clarki*, *swalei* and *tepperi*; (4) *chrysogaster*, *michaelseni*, *queenslandica*, *sp.8* and *rugosa*; and (5) *cephalotes*, *chasei*, *dispar* and *pilosula*. Despite the variation seen in worker morphology, male terminalia of the group are relatively uniform. The most distinctive are found in *sp.M1*, which is the only species in the group with spines on the inner valve. *M. sp.M2* also has a quite distinctive inner valve with a narrow postero-ventral lobe. *M. aberrans* is also fairly distinct but falls within the range of variation found in the group as a whole. The other species have more similar male terminalia, but each can be recognized by a few species specific features.

Five species of the *pilosula* group have been karyotyped and these have chromosome numbers of 2n = 2-70 (N.F. = 4-70). The large range is mainly due to *pilosula*, *s.l.* with 2n = 2-32 (N.F. = 4-c.32). The other species have 2n = 26-35 (N.F. = 50-70). To derive the two terminal karyotypes in the group (2n = 2 and 2n = 70) from one another requires at least 34 Robertsonian rearrangements and 33 pericentric inversions.

41. *Myrmecia aberrans* Forel

(Figs 34, 53a, 87a-e)

Myrmecia aberrans Forel, 1900, p. 54 [♀]; 1910, p. 9. Taylor and Brown, 1985, p. 6. Taylor, 1987, p. 41.

Myrmecia (*Promyrmecia*) *aberrans* Forel. Emery, 1911, p. 19, pl. 1, fig. 10. Clark, 1925, p. 136; 1927, p. 39; 1934a, p. 9. Wheeler, 1933, p. 50, fig. 18.

Promyrmecia aberrans (Forel). Clark, 1943, p. 93, pl. 12, fig. 1; 1951, p. 122, fig. 92.

Myrmecia froggatti Forel, 1910, p. 9, *emend.*, *syn. nov.* [♀] [introduced as *froggati*, incorrect spelling of collector]. Brown, 1953b, p. 17. Taylor and Brown, 1985, p. 10. Taylor, 1987, p. 43.

Myrmecia (*Promyrmecia*) *froggatti* Forel. Emery, 1911, p. 19.

Myrmecia (*Promyrmecia*) *aberrans* Forel subsp. *froggatti* Forel. Wheeler, 1933, p. 52.

Promyrmecia froggatti (Forel). Clark, 1943, p. 96, pl. 12, fig. 5; 1951, p. 128, figs 96-97 [♀].

Myrmecia (*Promyrmecia*) *aberrans* Forel subsp. *maura* Wheeler, 1933, p. 51, *syn. nov.* [♀].

Promyrmecia maura (Wheeler). Clark, 1943, p. 95, pl. 12, figs 6-7 [♀]; 1951, p. 132, figs 100-101.

Myrmecia maura maura Wheeler. Brown, 1953b, p. 18. Taylor and Brown, 1985, p. 12. Taylor, 1987, p. 44.

Myrmecia (*Promyrmecia*) *aberrans* Forel subsp. *haematosticta* Wheeler, 1933, p. 51, *syn. nov.* [♀].

Promyrmecia aberrans (Forel) subsp. *haematosticta* (Wheeler). Clark, 1943, p. 94.

Promyrmecia haematosticta (Wheeler). Clark, 1951, p. 130, fig. 98.

Myrmecia (*Promyrmecia*) *aberrans* Forel subsp. *formosa* Wheeler, 1933, p. 52, fig. 19, *syn. nov.* [♀].

Promyrmecia aberrans (Forel) subsp. *formosa* (Wheeler). Clark, 1943, p. 94.

Promyrmecia formosa (Wheeler). Clark, 1951, p. 131, fig. 99.

Myrmecia maura formosa Wheeler. Brown, 1953b, p. 19. Taylor and Brown, 1985, p. 12. Taylor, 1987, p. 44.

Myrmecia (*Promyrmecia*) *aberrans* Forel subsp. *taylori* Wheeler, 1933, p. 53 [♀].

Promyrmecia aberrans (Forel) subsp. *taylori* (Wheeler). Clark, 1943, p. 95.

Promyrmecia nobilis taylori (Wheeler). Clark, 1951, p. 127.

Myrmecia (*Promyrmecia*) *aberrans* Forel subsp. *sericata* Wheeler, 1933, p. 53 [♀].

Promyrmecia aberrans (Forel) subsp. *sericata* (Wheeler). Clark, 1943, p. 94.

Promyrmecia nobilis sericata (Wheeler). Clark, 1951, p. 127.

Promyrmecia nobilis Clark, 1943, p. 97, pl. 12, figs 2-4, *syn. nov.* [♀☿♂]; 1951, p. 124, figs 93-95.

Myrmecia nobilis (Clark). Brown, 1953b, p. 19. Taylor and Brown, 1985, p. 13. Taylor, 1987, p. 44.

Promyrmecia eupoecila Clark, 1943, p. 98, pl. 12, fig. 8, *syn. nov.* [☿]; 1951, p. 134, figs 102-103 [♀].

Myrmecia eupoecila (Clark). Taylor and Brown, 1985, p. 9. Taylor, 1987, p. 43.

Promyrmecia greavesi Clark, 1943, p. 99, pl. 12, fig. 9, *syn. nov.* [☿]; 1951, p. 136, fig. 104.

Myrmecia greavesi (Clark). Taylor and Brown, 1985, p. 11. Taylor, 1987, p. 43.

Promyrmecia excavata Clark, 1951, p. 137, figs 105-106, *syn. nov.* [♀☿].

Myrmecia excavata (Clark). Taylor and Brown, 1985, p. 9. Taylor, 1987, p. 43.

Types

aberrans: syntype workers, Gawler, S.A., in GMNH.

froggatti: holotype worker, Manilla, N.S.W. (W.W. Froggatt), in GMNH. [NEW SYNONYMY].

maura: syntype workers (4), Bathurst, N.S.W. (16.xii.1914, W.M. Wheeler; 17.xii.1914, W.M. Wheeler), in ANIC (examined); syntype worker, Bathurst, N.S.W. (16.xii.1914, W.M. Wheeler), in NMV (examined);

syntype workers, Bathurst, N.S.W. (W.M. Wheeler), in MCZ. [*Note* - Wheeler (1933) designated 15 syntype workers]. [NEW SYNONYMY].

haematosticta: syntype worker, Uralla, N.S.W. (27.xi.1914, W.M. Wheeler), in ANIC (examined); syntype workers, Uralla, N.S.W. (W.M. Wheeler), in MCZ. [*Note* - Wheeler (1933) designated 3 syntype workers] [NEW SYNONYMY; synonymy with *formosa* by Brown, 1953b].

formosa: syntype workers (3), Uralla, N.S.W. (26.xi.1914, W.M. Wheeler), in ANIC (examined); syntype worker, Uralla, N.S.W. (11.ii.1914, W.M. Wheeler), in NMV (examined); syntype workers, Uralla, N.S.W. (W.M. Wheeler), in MCZ. [*Note* - Wheeler (1933) designated 13 syntype workers] [NEW SYNONYMY].

taylori: holotype worker, Roma district, Qld (F.H. Taylor), in MCZ. [Synonymy by Brown, 1953b].

sericata: holotype worker, Wagga Wagga, N.S.W. (W.W. Froggatt), in MCZ. [Synonymy by Brown, 1953b].

nobilis: syntype worker, female and male, Altona, Vic. (29.iii.1930, T. Greaves), in NMV (examined) [labelled as *acrita* (unpublished name) types]; syntype worker, Coburg, Vic. (17.ix.1924, C. Oke), in NMV (examined); syntype worker and male, Patho, Vic. (1.iv.1934, H.A. Potter), in ANIC (examined); syntype worker, Altona, Vic. (29.iii.1930, T. Greaves), in ANIC (examined); syntypes, Bacchus Marsh, Broadmeadows and Geelong, Vic. have not been located. [*Note* - Clark (1943) mentions specimens from '*Victoria*: Altona (J.E. Dixon, ♀; T. Greaves, ♀♀♂; J. Clark, ♀♀♂); Bacchus Marsh and Coburg (C. Oke, ♀♀); Broadmeadows (F.P. Spry, ♀); Geelong (A.D. Butcher, ♀); Patho (H.A. Potter).'] [NEW SYNONYMY].

eupoecila: holotype female, Adelaide, S.A. (25.viii.1927, R. Blackwood), in NMV (examined). [NEW SYNONYMY].

greavesi: holotype female, Mareeba, Qld (1909, T. Greaves), in NMV (examined). [NEW SYNONYMY].

excavata: holotype worker, Bundarra, N.S.W. (Nov. 1946, T. Greaves), in ANIC (examined). [NEW SYNONYMY].

Worker diagnosis

Measurements and proportions as given and illustrated (figs 34a-c).

Colour very variable, though constant within nests and populations. Combinations intergrade from: (1) head, mesosoma and petiole red;

mandibles and antennae yellow; postpetiole, gaster and legs black (*greavesi* colour form); to (2) same as (1) except for small amount of black on head (*eupoecila* colour form; includes *excavata*); to (3) same as (1) except front half of head black (*froggatti* colour form; includes *taylori* and *sericata*); to (4) same as (3) except mesosoma with black on sides (*formosa* colour form; includes *haematosticta*); to (5) same as (4) except head entirely black (*aberrans*, *s.s.* colour form; includes *nobilis*); to (6) same as (5) except mesosoma and postpetiole black (*maura* colour form).

Material examined (fig. 53a)

Australian Capital Territory: Canberra (TG). *New South Wales*: Armidale (RWT); Bathurst (WMW) [*maura* syntypes]; Bundarra (TG) [*excavata* holotype]; 5 km N of Condobolin (BBL); Manilla (WWF); Monaro (MRF; in NMV); Moree (WWF; in NMV); Mungindi (BBL); Numeralla (EFR); Quirindi (CVM; in NMV); Trundle (BBL); Uralla (WMW) [*formosa* and *haematosticta* syntypes]. *Queensland*: Mareeba (TG; in NMV) [*greavesi* holotype]. *South Australia*: Adelaide (RBl; in NMV) [*eupoecila* holotype]; Brownhill Creek [406]; Findon (BBL); 13 km WNW of Florieton (KHLK); Maslins Beach [527]; Middleton (RDR; in SAM); 7 km NW of Morgan [526]; Strathalbyn (RDR; in SAM); Waitpinga [405]; Wilpena Pound (HMH; in NMV). *Victoria*: Altona (TG; in NMV) [*nobilis* syntypes]; Coburg (CO; in NMV) [*nobilis* syntype]; Ferntree Gully (cu); Lara (WLB); Patho (HAP) [*MT*, ♂, 1.iv.1934] [*nobilis* syntypes]; Redcliffs (CO; in NMV); Wallan (CO; in NMV); Werribee Gorge (BBL) [*SEM*, ♀; *MT*, ♂, 7.iv.1958].

[*Note* - Taylor and Brown (1985, pp 6, 9-13) did not record this species from A.C.T.]

Male terminalia (fig. 87a-e)

No variation has been observed in the male terminalia of *aberrans*; *aberrans*, *s.s.* colour form has been examined but the others have not.

Ninth and tenth tergites (fig. 87a) 1.6 times wider than long; median lobe rounded, extending almost to tips of pygostyles. Pygostyles moderately stout; length 0.3 times width of segment. *Eighth sternite* (fig. 87b) trapezoidal; 1.5 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Moderate number of short setae concentrated in two large areas flanking midline in middle half. *Ninth sternite* (fig. 87c) 1.1 times longer than wide; long anterior apodeme; antero-lateral lobes slightly developed; lateral lobes absent; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a barbed hook. Short setae scattered on and near posterior extension; a few short undulate setae flanking midline in middle third. *Basal ring* and *middle valve* similar to *pilosula*, *s.l.* *Outer valve* (fig. 87d) 1.7 times longer than deep; posterior end abrupt; dorsal median projection absent. *Inner valve* (fig. 87e), excluding anterior apodeme, 1.1 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe moderately narrow, moderately long, serrated distally; postero-dorsal margin rounded; posterior margin indented noticeably, with large ridge of 6-9 serrations ($\bar{x} = 7.5$, $N = 4$) at dorsal end.

Karyotype: Unknown

Taxa included

(1) *greavesi* colour form

(2) *eupoecila* colour form

(3) *froggatti* colour form

(4) *formosa* colour form

(5) *aberrans*, *s.s.* colour form

(6) *maura* colour form

Nest structure

No nests of *aberrans* were seen during this study. However, Wheeler (1933, pp 54-55) reports that the nest is moundless with a single entrance (d ≃ 6 mm), '... leading into a perpendicular gallery terminating at a depth of somewhat more than a foot in a small chamber.' Another nest, seen by Brown (1953b, p. 19), was '... surmounted by a slender earthern spout about one cm. high'. Gray (1973, 1974a) excavated one nest of froggatti colour form at Nyngan (N.S.W.) which contained only 17 workers and went to a depth of 56 cm. It seems that all nests of aberrans have very small populations (B.B. Lowery, pers. comm.).

Biological references (including unpublished theses)

Gray (1973, 1974a, 1974b)

Comments

M. aberrans is a species, or complex of sibling species, with highly variable colour patterning (as indicated above). Ten other names have been used for different colour forms but, at present there is no evidence from worker morphology, male terminalia or karyotypes to support their recognition. Several names were synonymized by Brown (1953b) but, because the colour patterns intergrade so completely from greavesi colour form through to maura colour form, I propose an additional six synonymies. All specimens have been collected in the south-eastern corner of Australia, except for a single queen from Mareeba (north Queensland).

It is notable that on at least three occasions aberrans workers (aberrans, s.s. and froggatti colour forms) have been seen amongst meat ants (Iridomyrmex purpureus (Smith)) in South Australia. This was true for workers collected by P. Christy (pers. comm.) at Waitpinga [405], by P.J.M. Greenslade (pers. comm) at Maslins Beach [527] and by me at Dry Creek (a worker which later escaped from captivity). The importance of these observations is unclear, but at Dry Creek I noted that the *aberrans* worker was broadly similar in colouration to the meat ants, although it was noticeably larger. I consider this to be another example of possible mimicry in *Myrmecia*, with the model belonging to another ant genus.

42. *Myrmecia cephalotes* (Clark)

(Figs 35, 53b, 88e-g)

Promyrmecia cephalotes Clark, 1943, p. 123, pl. 14, figs 32-24 [☿♀♂]; 1951, p. 145, figs 113-115.

Myrmecia cephalotes (Clark). Imai, Crozier and Taylor, 1977, p. 345, fig. 12 [karyotype]. Taylor and Brown, 1985, p. 7. Taylor, 1987, p. 42.

Promyrmecia hilli Clark, 1943, p. 125, pl. 14, fig. 35, *syn*. *nov*. [☿]; 1951, p. 147, fig. 116.

Myrmecia hilli (Clark). Taylor and Brown, 1985, p. 11. Taylor, 1987, p. 44.

Promyrmecia callima Clark, 1943, p. 125, pl. 14, fig. 36, *syn*. *nov*. [☿]; 1951, p. 148, fig. 117.

Myrmecia callima (Clark). Taylor and Brown, 1985, p. 7. Taylor, 1987, p. 42.

Types

cephalotes: syntype worker, Cooper's Creek, S.A. (J.G. Reuther), in NMV (examined); syntype(s), Killalpaninna, S.A. (H.J. Hillier) have not been located. [*Note* - Clark (1943) mentions specimens from '*South Australia*: Cooper's Creek (J.G. Reuther); Killalpaninna (H.J. Hillier).']

hilli: holotype worker (probable), 'Finke River', S.A. (2.vii.1911, G.F. Hill), in NMV (examined). [*Note* - Clark (1943) mentions specimens from '*Central Australia*: Finke River (G.F. Hill).' I have found no specimens with this data but a worker (in NMV) bearing a holotype label in Clark's handwriting is labelled '160 mi N Barclay Expdn Camp N-4, Cent. Aust., 2.7.11, G.F. Hill' and is presumed to be the holotype.] [NEW SYNONYMY].

callima: syntype workers (17), Kiata, Vic. (10.x.1940, I.H. Cole; 10.xi.1940, J. Clark), in NMV (examined) [labelled as *colei* (unpublished name) types]. [NEW SYNONYMY].

Worker diagnosis

Measurements and proportions as given and illustrated (figs 35a-c).

Colour variable, though constant within nests and populations. Combinations are: (1) head and gaster black; antennae, mesosoma, petiole, postpetiole and legs yellowish red; mandibles yellow (*cephalotes*, *s.s.* colour form); (2) same as (1) except first two segments of gaster yellowish red (*hilli* colour form); and (3) same as (1) except gaster yellowish red (*callima* colour form).

Material examined (fig. 53b)

New South Wales: Black Hill Creek [511] [*SEM*, ♀; *MT*, ♂, 20.iv.1969]; 12 km S of Coombah (C,I&W) [*K*]. *Northern Territory*: Finke River (GFH) [*hilli* holotype]. *South Australia*: Cooper's Creek (JGR) [*cephalotes* syntype]; Curdimurka (GFG; in SAM); Lake Eyre (MSU); Lake Frome (KP-J&p; in SAM); 20 km S of Lameroo (RDR; in SAM); 25 km W of Marree (JEF). *Victoria*: Kiata (IHC; JC) [*callima* syntypes]. *Western Australia*: 42 km NE of Cardawan H.S. (McI&D); 40 km S of Coolgardie (EFR); Lake Cronin [472]; Mount Ant (DDG; in WAM); 51 km W of Mount Samuel (McI&D); 24 km W of Southern Cross (EFR).

[*Note* - Taylor and Brown (1985, pp 7, 11) did not record this species from N.S.W. or W.A.].

Male terminalia (fig. 88e-g)

No variation has been observed in the male terminalia of *cephalotes*; *cephalotes*, *s.s.* colour form has been examined but the others have not.

Ninth and tenth tergites, *eighth sternite*, *basal ring* and *middle valve* similar to *pilosula*, *s.l.* *Ninth sternite* (fig. 88e) 1.2 times longer than wide; long anterior apodeme; antero-lateral lobes slightly developed; lateral lobes absent; posterior extension of posterior margin extremely narrow, turned dorsally and expanded posteriorly to form a barbed hook. Short setae scattered over much of posterior third. *Outer valve* (fig. 88f) 1.5 times longer than deep; posterior end abrupt;

dorsal median projection absent. *Inner valve* (fig. 88g), excluding anterior apodeme, 1.1 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe moderately short, moderately broad, serrated distally; postero-dorsal margin rounded; posterior margin slightly indented, with tooth-like ridge at dorsal end.

Karyotype

No variation has been observed in the karyotype of *cephalotes*; *cephalotes*, *s.s.* colour form has been examined but the others have not.

2n = 66 (Imai et al., 1977; colony from 12 km S of Coombah, N.S.W.)

Taxa included

(1) *cephalotes*, *s.s.* colour form

(2) *hilli* colour form

(3) *callima* colour form

Nest structure

No nests of *cephalotes* were seen during this study. However, Clark (1951, p. 150) says that nests of *callima* colour form are '... inconspicuous and indicated only by a few small holes scattered round the roots of small bushes; usually there is no mound'.

Biological references (including unpublished theses): None

Comments

M. cephalotes is a species, or complex of sibling species, with variable colour patterning. Two other names (*hilli* and *callima*) have been used for different colour forms but at present there is no other evidence (e.g. worker morphology, male terminalia, chromosomes) to support recognition of these. Therefore, I propose that they be treated as synonyms unless such evidence is found.

43. *Myrmecia chasei* Forel

(Figs 54a, 89d-g)

Myrmecia chasei Forel, 1894, p. 235 [♀]; 1907, p. 267. Emery, 1911, p. 21. Crawley, 1922a, p. 431. Wheeler and Wheeler, 1971, p. 247 [larva].

Promyrmecia chasei (Forel). Clark, 1943, p. 115, pl. 13, figs 25-27 [♀♂]; 1951, p. 212, fig. 180.

Myrmecia chasei chasei Forel. Taylor and Brown, 1985, p. 7. Taylor, 1987, p. 42.

Myrmecia pilosula Smith subsp. *mediorubra* Forel, 1910, p. 7 [♀]. Emery, 1911, p. 21.

Myrmecia chasei Forel var. *ludlowi* Crawley, 1922a, p. 431, *syn. nov.* [♀]; 1925, p. 578.

Promyrmecia chasei (Forel) var. *ludlowi* (Crawley). Clark, 1943, p. 117 [♀].

Promyrmecia chasei ludlowi (Crawley). Clark, 1951, p. 215.

Myrmecia chasei ludlowi Crawley. Taylor and Brown, 1985, p. 7. Taylor, 1987, p. 42.

Types

chasei: holotype worker, Perth, W.A. (Chase), in GMNH.

mediorubra: holotype worker, King George Sound, W.A. (A.Forel), in GMNH. [Synonymy by Clark, 1943].

ludlowi: syntype workers, Ludlow, W.A., in OUM. [NEW SYNONYMY].

Worker diagnosis (see Clark, 1951, pp 212-213, 215)

Material examined (fig. 54a)

Western Australia: Albany (JCl); Armadale (JCl); Bunbury (EFR); 18 km N of Cape le Grand [285]; Denmark (BBL); East Mount Barron [433]; Esperance (BBL); 112 km E of Esperance (BBL); 8 km N of Gibson [245]; Hill River (EFR); 105 km W of Israelite Bay [415]; Jacup (EFR); Jerramungup [228, 440]; Kukerin (AMD); Lort River (BBL); Ludlow (JCl); Morley (LMO'H) [*MT*, ♂, 12.i.1968]; 24 km N of Mount Arid (KHLK); Mount Barker (TG); 5 km SW of Mount Ragged (RWT); Mundaring (JCl); Newdegate (TG); Perth (JCl); 16 km S of Perth (EFR); Pingrup (TG); Point d'Entre Casteaux (CU); 64 km E of Ravensthorpe (EFR); Thomas River (EFR); Yallingup (EFR).

Male terminalia (fig. 89d-g)

No variation has been observed in the male terminalia of *chasei*.

Ninth and tenth tergites, *basal ring* and *middle valve* similar to *pilosula*, *s.l.* *Eighth sternite* (fig. 89d) trapezoidal; 1.4 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Numerous short setae concentrated in two large areas flanking midline in anterior two-thirds. *Ninth sternite* (fig. 89e) 1.0 times longer than wide; moderately short anterior apodeme; antero-lateral lobes barely developed; lateral lobes absent; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a barbed hook. Short setae scattered over much of posterior half; others concentrated in three more or less defined areas in anterior half. *Outer valve* (fig. 89f) 1.5 times longer than deep; posterior end abrupt; dorsal median projection absent. *Inner valve* (fig. 89g), excluding anterior apodeme, 1.1 times as long as deep; anterior extension of anterior apodeme 0.5 times length of rest of segment; postero-ventral lobe moderately narrow, moderately short, serrated distally; postero-dorsal margin rounded; posterior margin indented slightly with large ridge near dorsal end.

Karyotype: Unknown

Taxa included: Typical *chasei*

Nest structure

I observed colonies of *chasei* at four localities in south-west Western Australia. Each colony consisted of a single nest, with a single entrance (d ≃ 7 mm) in the middle of a shallow, circular depression (d_{max} ≃ 15 cm). The nests were located a metre or two away from any vegetation in very hard clays, and could not be excavated. However, the queen of one colony [228] was collected by keeping its nest filled with water and waiting about an hour while the ants inside slowly emerged. Partial excavation of this nest showed it to have a simple internal structure, with several chambers located just below the surface and only one main shaft beneath. The number of workers collected from this colony was 177, but I estimate that some of the other *chasei* colonies I observed would contain at least 300.

Biological references (including unpublished theses): None

Comments

M. chasei is a well-defined biological species confined to south-west Western Australia. Two other names (*mediorubra* and *ludlowi*) have been used for slight colour variants but, in the absence of supporting evidence from worker morphology, male terminalia or karyotypes, I prefer to treat these as synonyms.

The species is exceptional because its queens are much larger than the largest workers. In *chasei* the maximum length for queens is 1.5 times the maximum length for workers, while in all other *Myrmecia* this index has values of 1.0 - 1.3. Furthermore, as indicated by Clark (1951), *chasei* appears to have more size variation amongst its workers than other jumpers. It is possible that a morphometric analysis of workers in this species would reveal the presence of two subcastes.

44. *Myrmecia chrysogaster* (Clark)

(Fig. 54a)

Promyrmecia chrysogaster Clark, 1943, p. 114, pl. 13, fig. 23 [♀]; 1951, p. 209, fig. 178.

Myrmecia chrysogaster (Clark). Taylor and Brown, 1985, p. 7. Taylor, 1987, p. 42.

Types

chrysogaster: syntype worker (probable), Brisbane, Qld (8.ix.1918, H. Hacker), in NMV (examined). [*Note* - Clark (1943) mentions specimens from '*Queensland*: Brisbane (C. Barrett).' There are no specimens with this label known but a worker bearing a type label in Clark's handwriting (in NMV) is presumed to be a syntype or possibly the holotype.]

Worker diagnosis (see Clark, 1951, pp 209-210)

Material examined (fig. 54a)

Queensland: Brisbane (HH; in NMV) [*chrysogaster* syntype]; 24 km SE of Brisbane (BBL); Cedar Creek N.P. (RWT); Mount Coot-tha (BBL).

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *chrysogaster*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. chrysogaster appears to be a valid biological species, which is very similar to *queenslandica*. The two species are broadly sympatric in southern Queensland, and their workers can only be distinguished by leg colour which is brown in *queenslandica* but yellow in *chrysogaster*. This difference could be due to a colour polymorphism within a single species but, unless individuals with legs of an intergrading colour or nests containing individuals with both colours are observed, I prefer to treat *queenslandica* and *chrysogaster* as separate species. Future examination of the male terminalia and karyotypes of the two species will undoubtedly aid evaluation of this decision.

45. *Myrmecia clarki* Crawley

(Fig. 54b)

Myrmecia clarki Crawley, 1922a, p. 432 [♀]. Wheeler and Wheeler, 1971, p. 247 [larva]. Taylor and Brown, 1985, p. 7. Taylor, 1987, p. 42.

Myrmecia (Promyrmecia) clarki Crawley. Wheeler, 1933, p. 61, fig. 23 [♀].

Promyrmecia clarki (Crawley). Clark, 1943, p. 132, pl. 16, figs 74-76 [♂]; 1951, p. 174, figs 141-143.

Types

clarki: syntype workers, Mundaring Weir, W.A. (J.Clark), in OUM.

Worker diagnosis (see Clark, 1951, p. 174)

Material examined (fig. 54b)

Western Australia: Armadale (JCl); 8 km NW of Augusta (C&U); Blackwood River (EFR); Condingup [288]; Denmark (TG); Esperance (BBL); Margaret River (EFR); Mundaring (JCl); Thomas River (TG); Walpole (B&UB); William Bay (EBB); Yallingup (WHM).

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *clarki*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. clarki is a well-defined biological species, restricted to south-west Western Australia, which is distinguished by its worker morphology. Its mandible shape is similar to *tepperi* and *swalei* but it is unlikely to be confused with either species.

46. *Myrmecia dispar* (Clark)

(Figs 54b, 88d)

Promyrmecia dispar Clark, 1951, p. 226, fig. 193 [♀].
Myrmecia dispar (Clark). Taylor and Brown, 1985, p. 8. Taylor, 1987, p. 42.

Types

dispar: syntype workers (2), Cowra, N.S.W. (12.vi.1900, W.W. Froggatt), in ANIC (examined); syntype workers (4), Junee, N.S.W. (10.xi.1943, E.L. Smith), in ANIC (examined).

Worker diagnosis (see Clark, 1951, pp 226-227)

Material examined (fig. 54b)

New South Wales: Condobolin (BBL); Cowra (WWF) [dispar syntypes]; Glen Emu (BBL); Hillston (BG); Junee (ELS) [dispar syntypes]; Lake Cawndilla (BBL); 5 km W of Merriwagga (BBL); 15 km E of Weethalle (BBL). Queensland: 48 km N of Tambo (BBL). South Australia: Lake Hart (BBL); Melrose (BBL); Wilpena Pound (BBL).

[Note - Taylor and Brown (1985, p. 8) only recorded this species from Victoria.]

Male terminalia (fig. 88d)

No variation has been observed in the male terminalia of dispar.

Ninth and tenth tergites, eighth sternite, basal ring, outer valve, middle valve and inner valve unknown. Ninth sternite (fig. 88d) 1.3 times longer than wide; long anterior apodeme; antero-lateral lobes absent; lateral lobes absent; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a barbed hook. Details of setae unknown.

This description is based on Gray's (1966) figures of the male terminalia of dispar (which he called hillstonensis [unpublished name]) which are presumed to have been drawn from a male or males with the following data:- New South Wales: Matakana (1-5♂♂, April 1965, BG) [whereabouts of specimen(s) unknown]. Gray also figured the posterior end of the male gaster, the outer and middle valves, and the inner valve, but these were difficult to compare with my drawings and so have not been redrawn here. All were consistent with belonging to a species of the pilosula group.

Karyotype: Unknown

Taxa included: Typical dispar

Nest structure

No nests of dispar were seen during this study. Gray (1974a) excavated one nest at Matakana (N.S.W.) which contained 36 workers and went to a depth of 15 cm. In addition Gray (1966, 1971c) collected all workers from 28 colonies at Hillston (N.S.W.) and these contained 11, 15, 17, 19, 27, 40, 42, 55, 68, 79, 90, 91, 91, 127, 131, 146, 158, 161, 176, 182, 192, 196, 203, 206, 229, 291, 329 and 368 workers. The mean number of workers in the 29 colonies is 130 (S.D. = 96.8, C.V. = 74.4%). Gray (1966) estimates that the maximum worker population of a *dispar* nest is about 500. The nests examined by Gray (1966) were concealed by leaves, twigs and grasses (often a tufted grass - *Eragrostis setifolia* Nees). Larger nests had small mounds up to 3 cm high. All nests had one entrance (usually semi-circular; d = 1-4 cm) and ranged in depth from 15 to 77 cm. The internal nest structure was simple.

Biological references (including unpublished theses)

Gray (1966 [as *hillstonensis* (unpublished name)], 1971a, 1971b, 1971c, 1974a, 1974b); Gray and Lamb (1968)

Comments

M. dispar is a well-defined biological species which can be distinguished by its worker morphology.

47. *Myrmecia michaelseni* Forel

(Figs 55a, 90a-e)

Myrmecia michaelseni Forel, 1907, p. 267 [♀]. Emery, 1911, p. 21.
Viehmeyer, 1924, p. 221. Wheeler and Wheeler, 1971, p. 250 [larva].
Myrmecia (Promyrmecia) michaelseni Forel. Wheeler, 1933, p. 59, fig. 22.
Promyrmecia michaelseni (Forel). Clark, 1943, p. 111, pl. 13, figs 17-18
[♀]; 1951, p. 204, figs 173-174.
Myrmecia michaelseni michaelseni Forel. Taylor and Brown, 1985, p. 12.
Taylor, 1987, p. 44.
Myrmecia michaelseni Forel var. *perthensis* Crawley, 1922a, p. 431 [♀].

Types

michaelseni: syntype worker, Albany, W.A. (17.viii.1905, A. Forel), in ANIC (examined); syntype workers (2), Albany, W.A. (17.viii.1905, A. Forel), in NMV (examined); syntype worker(s), Albany, W.A., in GMNH.

perthensis: syntype workers (3), Perth, W.A. (J. Clark), in NMV (examined); syntype worker(s), Perth, W.A., in OUM. [Synonymy by Wheeler, 1933].

Worker diagnosis (see Clark, 1951, pp 204-205)

Material examined (fig. 55a)

Western Australia: Albany (AF) [michaelseni syntype]; 16 km SW of Borden (TG); Cape le Grand [287, 419] [MT, 2♂♂, collected as pupae, 6.x.1983; K, 3 ♀ prepupae]; 10 km N of Denmark (BBL) [MT, ♂, 19.xii.1969]; Esperance (BBL); Mundaring (JCl); 16 km E of Nornalup (EFR); Perth (JCl; in NMV) [perthensis syntypes]; Porongorup N.P. (AP; in WAM).

Male terminalia (fig. 90a-e)

No variation has been observed in the male terminalia of michaelseni.

Ninth and tenth tergites (fig. 90a) 2.0 times wider than long; median lobe rounded, extending just beyond tips of pygostyles. Pygostyles moderately slender; length 0.3 times width of segment. Eighth sternite (fig. 90b) trapezoidal; 1.5 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Very few short setae flanking midline in middle. Ninth sternite (fig. 90c) 1.0 times longer than wide; moderately long anterior apodeme; antero-lateral lobes barely developed; lateral lobes absent; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a barbed hook. Short setae scattered over much of posterior half. Basal ring and middle valve similar to pilosula, s.l. Outer valve (fig. 90d) 1.2 times longer than deep; posterior end abrupt; dorsal median projection absent. Inner valve (fig. 90e), excluding anterior apodeme, 0.8 times as long as deep; anterior extension of anterior apodeme 0.8 times length of rest of segment; postero-ventral lobe long, narrow, serrated distally; postero-dorsal margin rounded; posterior margin indented with large ridge of 4-6 serrations ($\bar{x}$ = 5.0, N = 5) near dorsal end.

Karyotype

No variation has been observed in the karyotype of michaelseni.

2n = c.64 (N.F. = c.70)

Four out of 40 cells had 2n = 64 while in the others I saw 2n = 49 (X1), 54 (X1), 55 (X3), 56 (X2), 57 (X2), 58 (X5), 59 (X3), 60 (X8), 61 (X2), 62 (X3), 63 (X5) and 65 (X1). The karyotype appears to consist of 6M and 58A chromosomes (i.e. N.F. = c.70).

Taxa included: Typical michaelseni

Nest structure

I observed two nests of michaelseni at Cape le Grand (W.A.) which were both located beneath rocks and could not be excavated from the rocky ground. The internal structure was simple with one main gallery (d ≃ 7 mm) descending from a chamber (containing pupae) beneath the covering rock. Only a few ants were seen in each nest, which is consistent with Gray's (1974a) report of 17 workers from one nest. However, I suspect from its locality (Bunyabba S.F., N.S.W.) that his nest was queenslandica.

Biological references (including unpublished theses): None

Comments

M. michaelseni is a well-defined biological species, restricted to south-west Western Australia, which can be distinguished from all other Myrmecia, except queenslandica, chrysogaster and sp.8, by its worker morphology. The four species can be easily distinguished by their colour patterns which do not intergrade.

48. *Myrmecia pilosula* Smith, *s.l.*

(Figs 36, 55b, 91a-f, 92a-b, 113b-c, 125a-d)

Myrmecia pilosula Smith, 1858, p. 146 [⚲♀].

Myrmecia pilosula Smith. Roger, 1861a, p. 35. Mayr, 1862, pp 726, 729. Forel, 1910, p. 7; 1913a, p. 173; 1914, p. 179; 1915, p. 4. Emery, 1911, p. 21. Crawley, 1926, p. 383, fig. 9. Santschi, 1928, p. 465. Brown, 1953b, p. 6. Wheeler and Wheeler, 1971, p. 252 [larva]. Imai, Crozier and Taylor, 1977, p. 345, figs 2, 5, 9, 12 [karyotype]. Taylor and Brown, 1985, p. 14. Crosland and Crozier, 1986, p. 231 [karyotype]. Taylor, 1987, p. 45.

Myrmecia (*Halmamyrmecia*) *pilosula* Smith. Wheeler, 1922, p. 195.

Myrmecia (*Promyrmecia*) *pilosula* Smith. Clark, 1925, p. 140; 1928, p. 39; 1929, p. 121; 1934 , p. 51. Wheeler, 1933, p. 56.

Promyrmecia pilosula (Smith). Clark, 1943, p. 109, pl. 14, figs 37-39; Clark, 1951, p. 202, figs 170-172.

Ponera ruginoda Smith, 1858, p. 93 [♂].

Ectatomma ruginodum (Smith). Roger, 1861b, p. 168.

Rhytidoponera ruginoda (Smith). Emery, 1911, p. 38.

Ponera ruginoda Smith. Clark, 1936, p. 14.

Formica forficata Fabricius, *auct.* (*non* Fabricius, 1775). Latreille, 1802, p. 216.

Types

pilosula: syntype male, Australia, in BMNH (examined); syntype worker(s) and female(s), Australia and Tasmania, in BMNH. [*Note* - The syntype male has been dissected and is not the same species as the other syntypes. Rather it is a species of the *mandibularis* group (probably *gilberti* Forel).]

ruginoda: holotype male, Australia, in BMNH (examined). [Synonymy by Brown, 1953b].

Worker diagnosis

Measurements and proportions as given and illustrated (figs 36a-c).

Head, mesosoma, femora, petiole, postpetiole and gaster black; mandibles, antennae, tibiae and tarsi yellow.

Material examined (fig. 55b)

Australia: Australia (cu; 44.14 in BMNH) [ruginoda holotype; MT, ♂ only, du]. Australian Capital Territory: Black Mountain (BBL); Brindabella Range (RWT) [MT, ♂, 16.ii.1969]; Gibraltar Creek (BBL); Mount Aggie (RWT); Mount Gingera (EFR); 3 km S of Orroral (BBL); Picadilly Circus (I,K&T) [K]; Smokers Gap (cu); Uriarra (TG). New South Wales: Alpine Creek (GFH); Armidale (BBL); Batemans Bay (BBL); Beecroft Peninsula (BBL); Blackheath (BBL); Bomaderry (BBL); 8 km N of Boorowra (BBL); 20 km NW Braidwood (BBL); 10 km S of Breadalbane (BBL); 10 km NW of Bungendore (BBL); Burrinjuck Dam (BBL); 12 km N of Coonabarabran (BBL); 38 km S of Eden (EFR); Eucumbene (EFR); Jenolan Caves (BBL); Kiandra (BBG; in MCZ) [MT, ♂, Feb. 1952]; Lawson (BBL); Leumeah (C&I) [K]; Morton N.P. (BBL); Mount Victoria (BBL); Mudgee (BBL); Nelligen (BBL); New South Wales (JJW; 1904.167 in BMNH) [MT, ♂ only, 1904]; Nimmitabel (BBL); 8 km E of Nimmitabel (BBL); Pipers Creek (EFR); Rosedale (BBL); Sawpit Creek (EFR); Sydney (BBL); 5 km N of Tathra (BBL); Tinderry Mountains (BBL); Wellington (BBL); Wyangala Dam (BBL). Queensland: Beaudesert (SHP); Milmerran (RMacQ); Stanthorpe [368]; Tamborine Village (BBL); Townsville (GFH). South Australia: Admirals Arch [315, 320]; Ashbourne (RDR; in SAM); Carpenter Rocks (BBL); Cherryville [54]; Hanson Bay [100, 114]; Little Desert (BBL); Myponga [389]; Penola (GFH); Rocky River [23, 48, 51, 53, 56, 321-322, 324, 336] [MT, ♂, 4.iv.1983; K, ♀ prepupa]; Uraidla [45-47; 531] [SEM, ♀; MT, ♂, 6.iv.1979]; Vivonne Bay [343]; West Bay [332]; Western River C.P. [503] [K, 3 ♀ prepupae]. Tasmania: Bagdad (SS; F74 in TM); Blackmans Bay (LR; F76 in TM); Blythe Siding (TG); Boat Harbour (TG); Cox Bight (CDK; F75 in TM); Derby (TG); Ellendale (TG); Flinders Island (JSW; F463 in TM); Grassy (KHLK); Great Lake (TG); Hermit Camp (HDB; in TM); Hobart (EFR); Hobart (JJW; 91.155 in BMNH) [MT, ♂ only, 1891]; Kingston (JCC); Lake Dove (TG); Lake Pedder (CDK; F72 in TM); Lower Gordon River (CHea; F1509 in TM); Maggs Mountain (RHG; in QVM); Maxwell River Valley (H,Hea; F1510 in TM); 4 km SSE of Mount Rufus (L&W); Mount Wellington (DCP; F73 in TM); Olga River (CHea; F1508 in TM); 11 km W of Rosebery (C&U); 10 km SE of Scottsdale (TG); Sloping Main (JFG; F134 in TM); Taroona (HDB; F236 in TM); The Lea (JCC); Upper Gordon River (LHea; F1507 in TM); 16 km N of Wilmot (TG). Victoria: Ben Cairn (TG); Buxton (EFR); 13 km SE of Camperdown (WLB; in MCZ) [MT, ♂, 17.ii.1951]; Ferntree Gully

(TG); Flinders (BBL); Macedon (TG); Romsey (EFR); Spring Vale (TG); Wallan (BBL); Werribee Gorge (TG). *Western Australia*: Albany (JCl); Denmark (TG); 12 km N of Denmark [221]; Esperance [425]; Kenton (RWT); 16 km E of Nornalup (EFR); Porongorup N.P. (BBL); Quinnup (RWT).

Male terminalia (figs 91a-f, 92a-b)

No variation has been observed in the male terminalia of *pilosula*, *s.l.*

Ninth and tenth tergites (fig. 91a) 1.7 times wider than long; median lobe broadly rounded, extending almost to tips of pygostyles. Pygostyles moderately stout; length 0.2 times width of segment. *Eighth sternite* (fig. 91b) trapezoidal; 1.5 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Numerous short setae concentrated in two large areas flanking midline in anterior two-thirds. *Ninth sternite* (fig. 91c) 1.4 times longer than wide; long anterior apodeme; antero-lateral lobes absent; lateral lobes slightly developed; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a *barbed hook* (BH). Moderately few short setae scattered in posterior half, except on posterior extension; few short undulate setae near lateral lobes. *Basal ring* 1.7 times wider than long; 1.5 times wider posteriorly than anteriorly. *Outer valve* (fig. 91d) 1.6 times longer than deep; posterior end bifurcate, with deep *ventral indentation* (VI); dorsal median projection absent. *Middle valve* (fig. 91e) with cuspis shorter than digitus; digitus moderately broad, slightly curved, broadest in middle, distal end rounded. *Inner valve* (fig. 91f), excluding anterior apodeme, 0.8 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe long, narrow, serrated distally; postero-dorsal margin rounded; posterior margin broadly indented.

The terminalia of the male holotype of *Ponera ruginoda* were dissected (figs 92a-b) and appeared to be very similar to *pilosula*, *s.l.* If *P. ruginoda* is not synonymous with *pilosula*, *s.s.* it is undoubtedly a synonym of one of its siblings.

Karyotype (figs 113b-c, 125a-d)

The variation in the karyotype of *pilosula*, *s.l.* is too great to be considered intraspecific and it is likely that some of the following cytotypes represent sibling species:

(1) n = 1, 2n = 2 (N.F. = 4; Crosland and Crozier, 1986; colony from Tidbinbilla Nature Reserve, A.C.T.)

(2) 2n = 10 [2SM + 6ST + 2A] (N.F. = 18; Imai et al., 1977; colony from Leumeah, N.S.W.)

(3) 2n = 9,10 [1M + 2SM + 5ST + 1A (+1A)] (N.F. = 17,18; Imai et al., 1977; colony from Leumeah, N.S.W.)

(4) 2n = 16 (N.F. = 19; see below)

(5) 2n = 24 (N.F. = 32; see below)

(6) n = 15 (Crozier, 1975; colony from Victoria), 2n = 30,31 (Imai et al., 1977; colony from Picadilly Circus, A.C.T.)

Western River C.P., S.A. (figs 113b, 125c): Sixty-two out of 69 cells had 2n = 16 while in the others I saw 2n = 15 (X4), 31 (X1) and 32 (X2). The karyotype consists of 1M, 2SM and 13A chromosomes (i.e. N.F. = 19).

Rocky River H.S., S.A. (figs 113c, 125d): Sixteen out of 21 cells had 2n = 24 while in the others I saw 2n = 20 (X2), 21 (X1), 22 (X1) and 23 (X1). The karyotype consists of 4M, 4SM and 16A chromosomes (i.e. N.F. = 32).

I karyotyped two populations of *pilosula*, *s.l.* and they differed in their chromosome numbers (2n = 16 and 24) and *nombres fondamentaux*

(N.F. = 19 and 32). The diploid karyotypes appear to be separated by at least eight Robertsonian rearrangements and 13 pericentric inversions. Similar large differences between karyotypes of pilosula, s.l. populations have been noted previously by Imai et al. (1977) and Crosland and Crozier (1986). This one broad species has 2n = 2-60 and N.F. = 4-60. To relate the terminal karyotypes of this series requires at least 29 Robertsonian rearrangements and 28 pericentric inversions in the haploid condition. Such immense variation is unlikely to be intraspecific. Three populations (with 2n = 10, N.F. = 18; 2n = 16, N.F. = 19; and 2n = 24, N.F. = 32) have a pericentric inversion polymorphism and the same three also have a complex translocation polymorphism involving six pairs of chromosomes. The arm length ratios of the chromosomes involved in these rearrangements are different in each of the karyotypes but nonetheless their presence appears to be due to homology.

Taxa included

(1) n = 1, 2n = 2 cytotype

(2) 2n = 10 [2SM + 6ST + 2A] cytotype

(3) 2n = 9,10 [1M + 2SM + 5ST + 1A (+1A)] cytotype

(4) 2n = 16 cytotype

(5) 2n = 24 cytotype

(6) n = 15, 2n = 30,31 cytotype

Nest structure

I observed colonies of pilosula, s.l. at numerous localities in South Australia, Western Australia and Queensland. These nests varied in structure from: (1) small nests marked only by a single entrance with some excavated soil scattered nearby (Queensland); to (2) small nests located beneath rocks (Kangaroo Island and Mount Lofty Range, S.A.); to

(3) medium-sized nests beneath fallen logs (near Denmark, W.A.); to (4) large nests with medium-sized mounds ($d_{max} \simeq 50$ cm; Mount Lofty Range, S.A. and Esperance, W.A.). The small and medium-sized nests had a simple internal structure but that of the large nests (with mounds) was of the less complex, diffuse type. Populations can be very large with Gray (1974a) collecting 33, 97, 104, 296 and 354 workers from 5 nests (15-41 cm deep) at Mudgee, Nowra, Bulgadie, Mount Canobolas and Kanangra Walls (all N.S.W.) respectively, and Haskins and Haskins (1950) obtaining 549 and 807 workers from 2 nests at Ferntree Gully (Vic.). Wheeler (1933) estimated that colonies usually contained 50-150 but this is inapplicable to the entire species range.

Biological references (including unpublished theses)

Haskins and Haskins (1950); Gray (1974a, 1974b); Muir (1975); Craig and Crozier (1979); Morrison (1983)

Comments

M. pilosula, s.l. is a complex of sibling species with indistinguishable workers. The existence of siblings is suggested by the variety of nest structures observed and the wide distribution of the 'species', and is confirmed by the available genetic evidence (Imai et al., 1977; Crosland and Crozier, 1986; present study).

Many mature nests of *pilosula, s.l.* contain more than one dealate queen. Multiple queens have otherwise only been reported in recently established colonies of a few *Myrmecia* species. Gray (1974a) found 38 dealate queens in a nest of 296 workers, and Haskins and Haskins (1950) found 4 dealate queens in a nest of 549 workers. I have observed more than one queen in most nests excavated in South Australia and Wheeler (1933) reported that as many as four dealate queens could be found in some nests.

49. *Myrmecia* *queenslandica* Forel

(Fig. 55a)

Myrmecia *michaelseni* Forel race *queenslandica* Forel, 1915, p. 4 [☿].

Promyrmecia *michaelseni* (Forel) subsp. *queenslandica* (Forel). Clark, 1943, p. 112, pl. 13, fig. 19 [☿].

Promyrmecia *michaelseni* *queenslandica* (Forel). Clark, 1951, p. 206.

Myrmecia *michaelseni* *queenslandica* Forel. Taylor and Brown, 1985, p. 12. Taylor, 1987, p. 44.

Myrmecia *michaelseni* Forel subsp. *overbecki* Viehmeyer, 1924, p. 222 [☿♀].

Promyrmecia *cydista* Clark, 1943, p. 115, pl. 13, fig. 24, *syn*. *nov*. [☿]; 1951, p. 210, fig. 179.

Myrmecia *cydista* (Clark). Taylor and Brown, 1985, p. 8. Taylor, 1987, p. 42.

Types

queenslandica: holotype worker, Lamington Plateau, Qld , in NHRM.

overbecki: syntype worker(s) and female(s), Trial Bay, N.S.W., in ZMB. [Synonymy by Clark, 1943].

cydista: syntype workers (3), Lismore, N.S.W. (C.F. Deuquet), in NMV (examined); syntype (probable) worker, Wahroonga, N.S.W. (13.i.1944, Nicholson), in NMV (examined); syntype workers, Dorrigo (W. Heron) and Sydney (W.W. Froggatt), N.S.W. have not been located. [*Note* - Clark (1943) mentions specimens from '*New South Wales*: Lismore (C.F. Denquet [sic]); Dorrigo (W. Heron); Sydney (W.W. Froggatt); Wahroonga (H.J. Carter).'] [NEW SYNONYMY].

Worker diagnosis (see Clark, 1951, pp 206, 210-211)

Material examined (fig. 55a)

New South Wales: 6 km E of Berry (BBL); Gilgai (BBL); Glenugie S.F. (BBL); Lismore (CFD) [*cydista* syntypes]; Rosedale (BBL); Sydney (BBL); Wahroonga (Nicholson) [*cydista* syntype]. *Queensland*: Archerfield (GBM); Blackall Ranges (CHB). *South Australia*: Cortina (AWF; in SAM); Malinong (RDR; in SAM); Sandy Creek C.P. [55]; 32 km S of Tailem Bend (BBL); 3 km NW of Woods Well (H,G&G; in SAM).

[*Note* - Taylor and Brown (1985, pp 8, 13) did not record this species from S.A. but believed it to be present in Vic.].

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *queenslandica*

Nest structure

I observed one nest of *queenslandica* at Sandy Creek C.P. (S.A.). The nest was moundless, with a single entrance (d ≃ 7 mm), and located in loose sand. Unfortunately, the galleries collapsed as I began excavation and could not be traced. Only three workers were collected.

Gray (1974a) collected 17 workers from a nest at Bunyabba S.F. (N.S.W.) which was 18 cm deep. Gray identified the species as *michaelseni* but based on distribution data I conclude that it was *queenslandica*.

Biological references (including unpublished theses)

Gray (1974a) [as *michaelseni*]

Comments

M. queenslandica appears to be a valid biological species which is very similar to *michaelseni*. The main feature used to separate the two is colour of gastric pubescence, which in *michaelseni* is reddish-gold but in *queenslandica* is greenish-gold (as it also is in *chrysogaster* and *sp.8*). The species with greenish-gold gastric pubescence are found only to the east of the Nullarbor Plain while *michaelseni* is found only to the west.

50. *Myrmecia rugosa* Wheeler

(Fig. 56a)

Myrmecia michaelseni Forel subsp. *rugosa* Wheeler, 1933, p. 60 [♀].
Myrmecia mandibularis Smith subsp. *rugosa* Wheeler, 1933, p. 72, *lapsus*.
    [Decision by Brown, 1953b].
Myrmecia rugosa Wheeler. Brown, 1953b, p. 5. Taylor and Brown, 1985,
    p. 15. Taylor, 1987, p. 45.

Promyrmecia ruginodis Clark, 1943, p. 113, pl. 13, figs 20-22 [☿♀♂]; 1951, p. 207, figs 175-177. [non Ponera ruginoda Smith, 1858 = Myrmecia pilosula Smith, 1858].

Types

rugosa: syntype workers (2), Ludlow, W.A. (J. Clark), in ANIC (examined); syntype workers, Ludlow, W.A. (J. Clark), in MCZ.

ruginodis: syntype worker, female and male, Perth, W.A. (J. Clark), in NMV (examined); syntype workers (2), Ludlow, W.A. (J. Clark), in NMV (examined); syntype(s), Armadale, W.A. (J. Clark) have not been located. [Note - Clark (1943) mentions specimens from 'Western Australia: Perth; Armadale; Ludlow (J. Clark).'] [Synonymy by Brown, 1953b].

Worker diagnosis (see Clark, 1951, pp 207-208)

Material examined (fig. 56a)

Western Australia: Ludlow (JCl) [rugosa syntypes]; Ludlow (JCl; in NMV) [ruginodis syntypes]; Margaret River (GWK; in WAM); Mundaring (JCl; in NMV); Nedlands (KRN); Perth (JCl; in NMV) [ruginodis syntypes].

Male terminalia

Ninth and tenth tergites, eighth sternite, basal ring, outer valve, middle valve and inner valve unknown. Ninth sternite with posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a barbed hook. Other details unknown.

This description is based on an external examination (without dissecting the terminalia) of the male syntype using a dissecting microscope.

Karyotype: Unknown

Taxa included: Typical rugosa

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. rugosa is a well defined biological species with workers which are very similar to harderi (celaena colour form). However, its male terminalia indicate that it belongs to the *pilosula* group. It can be distinguished from all other *Myrmecia* by its worker morphology.

51. *Myrmecia swalei* Crawley

(Figs 37, 56b, 88a-c, 114a, 124b)

Myrmecia harderi Forel race *swalei* Crawley, 1922a, p. 429 [⚲].

Promyrmecia swalei (Crawley). Clark, 1943, p. 133, pl. 16, figs 72-73 [♀]; 1951, p. 176, figs 144-145.

Myrmecia swalei Crawley. Wheeler and Wheeler, 1971, p. 253 [larva]. Taylor and Brown, 1985, p. 16. Taylor, 1987, p. 46.

Promyrmecia testaceipes Clark, 1943, p. 134, pl. 15, fig. 69, *syn. nov.* [⚲]; 1951, p. 178, fig. 146.

Myrmecia testaceipes (Clark). Taylor and Brown, 1985, p. 17. Taylor, 1987, p. 46.

Promyrmecia dixoni Clark, 1943, p. 135, pl. 16, figs 77-78, *syn. nov.* [⚲♀]; 1951, p. 179, figs 147-148.

Myrmecia dixoni (Clark). Wheeler and Wheeler, 1971, p. 247 [larva]. Taylor and Brown, 1985, p. 8. Taylor, 1987, p. 42.

Myrmecia (*Promyrmecia*) *mediorubra* Forel, *auct.* (*non* Forel, 1910). Wheeler, 1933, p. 58.

Types

swalei: holotype worker, Albany, W.A. (H. Swale), in OUM.

testaceipes: syntype workers (3), Albany, W.A. (J. Clark), in NMV (examined); syntype worker, Albany, W.A. (J. Clark), in SAM (examined). [NEW SYNONYMY].

dixoni: syntype workers (6) and females (2), Eltham, Vic. (19.viii.1923, J.E. Dixon; 28.vii.1927, J.E. Dixon; J.E. Dixon; 13.ix.1919, F.E. Wilson; 16.x.1928), in NMV (examined); syntype workers (7), Albury, N.S.W. (3.vii.1927, F.E. Wilson), in NMV (examined); syntype(s), Canberra, A.C.T. (T. Greaves), have not been located. [*Note* - Clark (1943) mentions specimens from '*Victoria*: Eltham (J.E. Dixon, F.E. Wilson). *New South Wales*: Albury (F.E. Wilson). *Federal Capital Territory*: Canberra (T. Greaves).'] [NEW SYNONYMY].

Worker diagnosis

Measurements and proportions as given and illustrated (fig. 37a-c). Colour variable. Combinations are: (1) head and gaster black;

mandibles and antennae yellow; mesosoma, legs, petiole and postpetiole red (dixoni colour form; includes testaceipes); and (2) same as (1) except postpetiole black (swalei, s.s. colour form).

Material examined (fig. 56b)

New South Wales: Albury (FEW; in NMV) [dixoni syntypes]; Cowan (BBL); Wallerawang (BBL). South Australia: Calca (BBL); Cortina (AWF; in SAM); 5 km N of Fishery Bay [297] [K, ♀ prepupa]; Stenhouse Bay (BBL). Victoria: Eltham (JED; FEW; in NMV) [dixoni syntypes]; Heathcote (BBL). Western Australia: Albany (JCl; in NMV and SAM) [testaceipes syntypes]; Bunbury (EFR); 10 km N of Denmark (BBL) [SEM, ♀; MT, ♂, 19.xii.1969]; Dwellingup (JCl); Esperance (BBL); Foul Bay (EBB); Ludlow (JCl); Margaret River (EFR); Mundaring (JCl; in SAM).

[Note - Clark (1951) also records dixoni from 'Australian Capital Territory: Canberra' and, although I have not seen any specimens from the A.C.T. referable to swalei, it almost certainly occurs there. Taylor and Brown (1985, pp 8, 16-17) also recorded this species from A.C.T. but did not mention its occurrence in S.A.]

Male terminalia (fig. 88a-c)

No variation has been observed in the male terminalia of swalei; dixoni colour form has been examined but swalei, s.s. has not.

Ninth and tenth tergites, eighth sternite, basal ring and middle valve similar to pilosula, s.l. Ninth sternite (fig. 88a) 1.1 times longer than wide; long anterior apodeme; antero-lateral lobes slightly developed; lateral lobes absent; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a barbed hook. A few short setae on and near posterior extension. Outer valve (fig. 88b) 1.3 times longer than deep; posterior end bifurcate, with deep ventral indentation; dorsal median projection absent. Inner valve (fig. 88c), excluding anterior apodeme, 0.8 times as long as deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe moderately broad, moderately long, serrated distally; postero-dorsal margin rounded; posterior margin indented noticeably.

Karyotype (figs 114a, 124b)

No variation has been observed in the karyotype of swalei; dixoni colour form has been examined but swalei, s.s. has not.

2n = 52 (N.F. = 60)

5 km N of Fishery Bay, S.A.: Six out of 13 cells had 2n = 52 while in the others I saw 2n = 42 (X1), 44 (X1), 45 (X1), 46 (X1), 49 (X1), 53 (X1) and 54 (X1). The karyotype consists of 4M, 4SM and 42A chromosomes (i.e. N.F. = 60).

Taxa included

(1) dixoni colour form

(2) swalei, s.s. colour form

Nest structure

I observed one nest of swalei near Fishery Bay (S.A.). The nest was located beneath a small stone in limestone soil. The internal structure was very simple, with a single gallery extending between other rocks to a depth of about 15 cm. Five workers, six pupae and six larvae were collected but no queen was found, so I am not sure that I secured the entire nest. Gray (1974a) excavated one nest of swalei (identified as dixoni) at Wallerawang (N.S.W.) which contained only 14 workers and was 31 cm deep.

Biological references (including unpublished theses)

Haskins and Haskins (1950); Gray (1974a)

Comments

M. swalei is a species, or possibly a complex of sibling species, with slightly variable colour patterning, which can be distinguished from all other *Myrmecia* (except *tepperi* and *clarki*) by its worker mandibles. It can be easily distinguished from *tepperi* and *clarki* by its colour. Clark (1943, 1951) recognized three species (*swalei*, *testaceipes* and *dixoni*) but, in the absence of other evidence (e.g. differences in male terminalia or karyotype), I prefer to treat them as synonyms.

52. *Myrmecia tepperi* Emery

(Figs 38, 57a, 92c-f, 114b, 124c)

Myrmecia tepperi Emery, 1898, p. 231 [♀♂]; 1911, p. 21. Wheeler and Wheeler, 1971, p. 253 [larva]. Taylor and Brown, 1985, p. 17. Taylor, 1987, p. 46.

Promyrmecia tepperi (Emery). Clark, 1943, p. 130, pl. 16, figs 70-71 [♀]; 1951, p. 172, figs 139-140.

Types

tepperi: syntype female and male, S.A. (J.G.O. Tepper), have not been located.

Worker diagnosis

Measurements and proportions as given and illustrated (figs 38a-c).

Entirely black. Apex of gaster (from halfway along second segment) densely clothed with gold pubescence.

Material examined (fig. 57a)

New South Wales: Bungonia (BBL); 15 km S of Dubbo (BBL); 30 km N of Grenfell (BBL); Mudgee (BBL); Queanbeyan (BBL); Tinderry Mountains (BBL); White Munghorns (BBL); Wellington (BBL); Wyangala Dam (BBL). *South Australia*: 10 km NE of d'Estrees Bay [346]; Inneston [271] [*SEM*, ♀; *MT*, ♂, 13.i.1983; *K*, 4 ♀ prepupae]; 5 km NW of Kingscote [311, 313]; Lincoln N.P. [301] [*K*, ♀ prepupa; Marble Range (GFG; in SAM); 13 km E of Marion Bay (M,H&H; in SAM); Nepean Bay (BBL); Ravine de Casoars [329]; Wilpena Pound (BBL); Yudnamutana [390]. *Victoria*: Heathcote (BBL). *Western Australia*: Hovea (JCl; in SAM); 4 km W of Wagin [454].

[*Note* - Taylor and Brown (1985, p. 17) also record this species from A.C.T. and I am sure that it would occur there.].

Male terminalia (fig. 92c-f)

No variation has been observed in the male terminalia of *tepperi*.

Ninth and tenth tergites, basal ring and middle valve similar to *pilosula*, *s.l*. Eighth sternite (fig. 92c) trapezoidal; 1.8 times wider than long; 1.3 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Numerous short setae concentrated in two large areas flanking midline in middle half. Ninth sternite (fig. 92d) 1.2 times longer than wide; long anterior apodeme; antero-lateral lobes absent; lateral lobes absent; posterior extension of posterior margin narrow, turned dorsally and expanded posteriorly to form a barbed hook. Moderately few short setae scattered in posterior third. Outer valve (fig. 92e) 1.6 times longer than deep; posterior end bifurcate, with deep ventral indentation; dorsal median projection absent. Inner valve (fig. 92f), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe long, moderately broad, serrated distally; postero-dorsal margin rounded; posterior margin broadly indented with large ridge near dorsal end.

Karyotype (figs 114b, 124c)

No variation has been observed in the karyotype of *tepperi*.

2n = 70 (N.F. = 70)

Inneston, S.A. (figs 114b, 124c): Six out of 39 cells had 2n = 70 while in the others I saw 2n = 57 (X1), 58 (X1), 59 (X1), 60 (X3), 61 (X1), 62 (X1), 63 (X1), 64 (X1), 65 (X3), 66 (X3), 67 (X3), 68 (X7) and 69 (X7). The karyotype consists of 70A chromosomes (i.e. N.F. = 70).

Lincoln N.P., S.A.: The worker prepupa may have had a chromosome number of 2n = 70 because in one cell I saw 2n = 66. The karyotype appears to consist of 70A chromosomes.

Taxa included: Typical *tepperi*

Nest structure

I observed nests of *tepperi* at five localities in South Australia and one in Western Australia. The nests were all located beneath stones and did not appear to contain very many workers. The only nest excavated completely (colony 271) contained 17 workers, had a simple internal structure and was 20 cm deep. Gray (1974a) collected 12 and 220 workers from two nests at Bulgadie and Nyngan (both N.S.W.) which were 20 and 93 cm deep respectively.

Biological references (including unpublished theses)

Gray (1974a)

Comments

M. tepperi is a well-defined, widely distributed biological species, which is distinguished by its worker morphology, male terminalia and karyotype. It is superficially similar to *michaelseni*, but differs in mandible shape and the extent of the gastric pubescence. Its mandible shape is similar to that of *swalei* and *clarki* which caused Clark (1943, 1951) to group these species together in his *tepperi* group.

53. *Myrmecia varians* Mayr

(Figs 57b, 89d-g)

Myrmecia varians Mayr, 1876, p. 94 [♀].

Myrmecia varians Mayr. Emery, 1911, p. 21. Forel, 1915, p. 5. Brown, 1953b, p. 14. Wheeler and Wheeler, 1971, p. 254 [larva]. Taylor and Brown, 1985, p. 17. Taylor, 1987, p. 46.

Promyrmecia varians (Mayr). Clark, 1943, p. 126, pl. 15, figs 67-68 [♀]; 1951, p. 181, figs 149-150.

Myrmecia rufonigra Crawley, 1921, p. 87 [♀].

Promyrmecia occidentalis Clark, 1943, p. 119, pl. 13, figs 30-31, *syn. nov.* [♀♀]; 1951, p. 218, figs 185-186.

Myrmecia occidentalis (Clark). Taylor and Brown, 1985, p. 13. Taylor, 1987, p. 45.

Promyrmecia elegans Clark, 1943, p. 122, pl. 14, figs 44-45, *syn. nov.* [☿♀]; 1951, p. 222, figs 189-190.

Myrmecia elegans (Clark). Wheeler and Wheeler, 1971, p. 248 [larva]. Taylor and Brown, 1985, p. 8. Taylor, 1987, p. 42.

Promyrmecia opaca Clark, 1943, p. 123, pl. 14, figs 46-47, *syn. nov.* [☿♀]; 1951, p. 224, figs 191-192.

Myrmecia opaca (Clark). Taylor and Brown, 1985, p. 13. Taylor, 1987, p. 45.

Promyrmecia wilsoni Clark, 1943, p. 127, pl. 15, fig. 66 [☿]; 1951, p. 183, fig. 151.

Myrmecia wilsoni (Clark). Wheeler and Wheeler, 1971, p. 254 [larva].

Promyrmecia shepherdi Clark, 1943, p. 128, pl. 15, figs 50-52 [☿♀♂]; 1951, p. 184, figs 152-154.

Promyrmecia goudiei Clark, 1943, p. 129, pl. 15, figs 48-49 [☿♀]; 1951, p. 186, figs 155-156.

Promyrmecia marmorata Clark, 1951, p. 188, fig. 157 [☿].

Types

varians: syntype worker, Rockhampton, Qld, in NMV (examined); syntype workers, Peak Downs and Rockhampton, Qld, in NHMW.

rufonigra: syntype workers, Townsville, Qld (July 1902, F.P. Dodd), in OUM. [Synonymy by Clark, 1943].

occidentalis: syntype workers (4), Tammin, W.A. (J. Clark), in NMV (examined); syntype workers (3) and female, Eradu, W.A. (J. Clark), in NMV (examined); syntype workers (4), Merredin, W.A. (L.J. Newman), in NMV (examined); syntype workers (2), Beverley, W.A. (E.F. DuBoulay), in NMV (examined). [NEW SYNONYMY].

elegans: syntype worker, Hovea, W.A. (J. Clark), in NMV (examined); syntype worker, Mount Dale, W.A. (1.viii.1921, J. Clark), in NMV (examined); syntype workers (3) and female, Mundaring, W.A. (J. Clark), in NMV (examined); syntype worker, Mount Dale, W.A. (1.viii.1921, J. Clark), in ANIC (examined). [NEW SYNONYMY].

opaca: syntype worker and female, Tammin, W.A. (J. Clark), in NMV (examined); syntype workers (4), Dowerin, W.A. (L.J. Newman), in NMV (examined); syntype(s), Eradu, W.A. (J. Clark), have not been located. [*Note* - Clark (1943) mentions specimens from '*Western Australia*: Tammin; Eradu (J Clark); Dowerin (L.J. Newman).'] [NEW SYNONYMY].

wilsoni: syntype workers (3), Mutchilba, Qld (Nov. 1933, A.D. Selby), in NMV (examined). [Synonymy by Brown, 1953b].

shepherdi: syntype workers (3), Broken Hill, N.S.W. (F.W. Shepherd), in NMV (examined); syntype workers (2), 'Finke River', S.A. (2.iii.1911, G.F. Hill), in NMV (examined); syntypes, Dubbo, N.S.W. (W.W. Froggatt), Murray Bridge, S.A. (A.H. Elston), and Nhill, Vic. (J. Clark), have not been located. [*Note* - Clark (1943) mentions specimens from '*New South Wales*: Broken Hill (F.W. Shepherd); Dubbo (W.W. Froggatt). *South Australia*: Finke River (G.F. Hill); Murray Bridge (A.H. Elston). *Victoria*: Nhill (J. Clark).'] [Synonymy by Brown, 1953b].

goudiei: syntype workers (2), Sea Lake, Vic. (J.C. Goudie), in NMV (examined); syntype workers (4), Redcliffs, Vic. (W.S. Creek; Sept. 1939, J. Clark), in NMV (examined); syntype workers (2), Hattah, Vic. (Sept. 1939, J. Clark), in NMV (examined); syntype workers (3) (probable), Lake Hattah, Vic. (J.E. Dixon), in ANIC (examined). [*Note* - Clark (1951) lists the type data of *marmorata* as '*Victoria*: Patho (H.A. Potter)' but specimens in the ANIC bearing the *marmorata* type labels are from Sea Lake, Vic. (J.E. Dixon). These specimens appear to be syntypes of *goudiei* (which could not be located in the NMV otherwise) while a worker in the ANIC (Patho, Vic., 6.xii.1943, H.A. Potter) is probably the holotype of *marmorata*.] [Synonymy by Brown, 1953b].

marmorata: holotype worker (probable), Patho, Vic. (6.xii.1943, H.A. Potter), in ANIC (examined). [*Note* - See note regarding *goudiei* types above] [Synonymy by Brown, 1953b].

Worker diagnosis

For measurements and proportions see Clark (1951, pp 181-189, 218-219, 222-225).

Colour variable, though constant within nests. Combinations include: (1) head and gaster black; mandibles yellow; antennae, mesosoma, petiole, postpetiole and legs yellowish red (*wilsoni* colour form); (2) same as (1) except apex of pronotum brown (*shepherdi* colour form); (3) same as (1) except pronotum, mesonotum and metanotum black (*occidentalis* colour form; includes *marmorata* and *opaca*); (4) same as

(1) except postpetiole and coxae black (*elegans* colour form); (5) same as (1) except mesosoma black (*varians*, *s.s.* colour form; includes *rufonigra*); and (6) head, mesosoma, postpetiole and gaster black; mandibles yellow; antennae and legs brown; petiole red (*goudiei* colour form).

Material examined (fig. 57b)

Australian Capital Territory: Canberra (EFR). *New South Wales*: Apsley (BBL); Broken Hill (FWS; in NMV) [*shepherdi* syntypes]; Condobolin (BBL); Glen Emu (BBL); Lake Cawndilla (BBL); Matakana (BBL); Mootwingee (BBL); Wee Waa (WWF). *Queensland*: Beaudesert (SHP); 4 km S of Cloncurry (DHi); Cunnamulla (BBL); Mareeba (HEH); 19 km E of Morven (EFR); Mutchilba (ADS; in NMV) [*wilsoni* syntypes]; Rockhampton (in NMV) [*varians* syntype]. *South Australia*: 56 km E of Ceduna (EFR); 5 km W of Copper Hills (HF; in SAM); Cortina (AWF; in SAM); 'Finke River' (GFH; in NMV) [*shepherdi* syntypes]; 54 km NNW of Fraser Range H.S. (RWT); 59 km S of Hawker (G&M; in SAM); Kirton Point (RPa; in SAM); Lake Gilles C.P. [282]; Langhorne Creek (RDR; in SAM); Little Dip C.P. [492] [*MT*, ♂ only, 28.i.1984]; 50 km NE of Marree (JEF); 8 km S of Morgan (HMin; in SAM); Sevenhill (BBL; in SAM); Sleaford Bay [164]; Tea Tree Gully (RVS; in SAM); Vivonne Bay (RDR; in SAM); Waikerie [533]; Waitpinga [142]; Wilpena Pound (WLB); 5 km NW of Woods Well (H,G&G; in SAM). *Victoria*: Bright (TG); Hattah (JCl; in NMV) [*goudiei* syntypes]; Lake Hattah (JED) [*goudiei* syntypes]; Patho (HAP) [*marmorata* holotype]; Redcliffs (W.S. Creek; JCl; in NMV) [*goudiei* syntypes]; Sea Lake (JCG; in NMV) [*goudiei* syntypes]. *Western Australia*: 10 km W of Coonana (RWT); Dowerin (LJN; in NMV) [*opaca* syntypes]; Eradu (JCl; in NMV) [*occidentalis* syntypes]; Eucla (cu; in SAM); Hovea (JCl; in NMV) [*elegans* syntype]; Lake Cronin [473]; 53 km SE of Karonie (RWT); Madura (C&U); Merredin (LJN; in NMV) [*occidentalis* syntypes]; Mount Dale (JCl; in NMV) [*elegans* syntype]; Mundaring (JCl; in NMV) [*elegans* syntypes]; Murchison River (TG); 19 km N of Norseman (EFR); Pingrup (EFR); 6 km S of Ravensthorpe (BBL); Tammin (JCl; in NMV) [*occidentalis* and *opaca* syntypes]; Warbla Cave (CW; in SAM); 11 km SSE of Widgiemooltha (RWT).

[*Note* - Taylor and Brown (1985, pp 8, 13, 17) did not record this species from A.C.T. but believed it to occur in N.T.]

Male terminalia (fig. 89d-g)

No variation has been observed in the male terminalia of *varians*; *wilsoni* colour form has been examined but the others have not.

Ninth and tenth tergites, *eighth sternite*, *basal ring* and *middle valve* similar to *pilosula*, *s.l.* *Ninth sternite* (fig. 89a) 1.2 times longer than wide; long anterior apodeme; antero-lateral lobes slightly developed; lateral lobes absent; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a barbed hook. Short setae scattered over much of posterior two-thirds; others concentrated on two small *mounds* (Mo) flanking midline in anterior third. *Outer valve* (fig. 89b) 1.5 times longer than deep; posterior end abrupt; dorsal median projection absent. *Inner valve* (fig. 89c), excluding anterior apodeme, 0.9 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe long, narrow, serrated distally; postero-dorsal margin rounded; posterior margin broadly indented with large ridge near dorsal end.

Karyotype: Unknown

Taxa included

(1) *wilsoni* colour form

(2) *shepherdi* colour form

(3) *occidentalis* colour form

(4) *elegans* colour form

(5) *varians*, *s.s.* colour form

(6) *goudiei* colour form

Nest structure

I observed colonies of *varians* at three localities in South Australia. The nests were moundless and had a single entrance (d ≃ 7 mm). Colony 164 was amongst limestone and located next to a rock, but the other two (colonies 142 and 282) were in hard clay away from rocks and vegetation. Colonies 142 and 164 were excavated completely and contained 79 and 30 workers respectively. The internal structure of the nests was simple and went to depths of 45 cm and 30 cm respectively. Gray (1974a) excavated 7 nests of *varians*, *s.s.* colour form at Hillston, Box Tank and Goorawin Siding (all N.S.W.) and collected 11, 11, 67, 68, 111, 150 and 225 workers. He also excavated 9 nests of *goudiei* colour form at Nyngan, Jemalong, Matakana and Goorawin Siding (all N.S.W.) and collected 5, 13, 13, 14, 25, 94, 99, 211, and 219 workers. The 16 nests were 10-77 cm deep. The mean size of the 18 colonies is 80 workers (S.D. = 76.0, C.V. = 94.7%).

Biological references (including unpublished theses)

Gray (1973, 1974a, 1974b)

Comments

M. varians is a widely distributed species, or complex of sibling species, with variable colour patterning, which can be distinguished from all other *Myrmecia* by their worker mandibles. These have a full complement of teeth which are directed posteriorly. Eight other names have been used for different colour forms, but at present there is no evidence from worker morphology, male terminalia or karyotypes to support their recognition. Clark (1951) and Brown (1953b) synonymized most of these but, because the colour patterns intergrade so completely from *wilsoni* through to *goudiei* colour forms, I propose the new synonymy of *occidentalis*, *elegans* and *opaca*.

54. Myrmecia sp.8 (ANIC), sp. nov.

(Fig. 56a)

Worker diagnosis

Head, mandibles, antennae, mesosoma, postpetiole, gaster and legs dark brown to black; petiole red. Greenish-gold pubescence on dorsum of gaster.

Material examined (fig. 56a)

South Australia: 10 km NE of d'Estrees Bay [347]; Emu Bay (CU; in SAM); 3 km SW of Kingscote (BBL); Marble Range (NBT; in SAM).

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical sp.8

Nest structure

I observed one nest of sp.8 at 10 km NE of d'Estrees Bay. The nest was located beneath a small rock and had its entrance (d ≃ 7 mm) at the side of the rock. Complete excavation of the nest was impracticable because its galleries went between two very large rocks but it was at least 15 cm deep and had a simple internal structure.

Biological references (including unpublished theses): None

Comments

This species is close to michaelseni but can be easily distinguished by the red petiole and gastric pubescence which is greenish gold instead of reddish gold. Workers of this description have not been mentioned by any previous authors. The possibility that sp.8 is merely a colour form of queenslandica should be investigated but I treat them as separate species because no specimens with intermediate colouration or nests containing workers with both colour patterns have been located.

55. *Myrmecia sp.M1* (GPB), *sp. nov.*

(Figs 56a, 93a-e)

Worker diagnosis: Workers unknown

Material examined (fig. 56a)

New South Wales: Terrey Hills (BBL) [*MT*, ♂ only, 13.ii.1977].

Male terminalia (fig. 93a-e)

No variation has been observed in the male terminalia of *sp.M1*.

Ninth and tenth tergites (fig. 93a) 1.4 times wider than long; median lobe rounded, extending almost to tips of pygostyles. Pygostyles slender; length 0.4 times width of segment. *Eighth sternite* (fig. 93b) trapezoidal; 1.9 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Very few short setae flanking midline in middle. *Ninth sternite* (fig. 93c) 1.1 times longer than wide; long anterior apodeme; antero-lateral lobes barely developed; lateral lobes absent; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a barbed hook. Short setae scattered over much of posterior half. *Basal ring* and *middle valve* similar to *pilosula*, *s.l.* *Outer valve* (fig. 93d) 1.8 times longer than deep; posterior end abrupt; dorsal median projection sharply pointed. *Inner valve* (fig. 93e), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe very long, narrow, serrated distally; postero-dorsal margin angulate; posterior margin broadly indented, with 19-22 small spines and serrations ($\bar{x}$ = 20.5, N = 2) near dorsal end.

Karyotype: Unknown

Taxa included: Typical *sp.M1*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. sp.M1 is known from one male only. The male terminalia are broadly similar to other species in the *pilosula* group, but I am unable to include it with any of them because it has spines on the inner valve. The male is black with greenish-gold pubescence on the dorsum of its gaster which suggests that its workers will resemble *queenslandica*.

56. *Myrmecia sp.M2* (GPB), *sp. nov.*

(Figs 56b, 94a-f)

Worker diagnosis: Workers unknown

Material examined (fig. 56b)

South Australia: Mount Lofty (JGOT; in MCZ) [*MT*, ♂ only, cu].

Male terminalia (fig. 94a-f)

No variation has been observed in the male terminalia of *sp.M2*.

Ninth and tenth tergites (fig. 94a) 1.6 times wider than long; median lobe rounded, extending just beyond tips of pygostyles. Pygostyles stout; length 0.3 times width of segment. *Eighth sternite* (fig. 94b) trapezoidal; 1.5 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Numerous short setae concentrated in two moderately large areas flanking midline in middle third. A few small sensillae in antero-lateral corners. Serrate longitudinal sculpturing in posterior quarter. *Ninth sternite* (fig. 94c) 1.2 times longer than wide; long anterior apodeme; antero-lateral lobes barely developed; lateral lobes absent; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly to form a barbed hook. Short setae scattered over much of posterior three-quarters. *Basal ring* 1.9 times wider than long; 1.5 times wider posteriorly than anteriorly. *Outer* valve (fig. 94d) 1.6 times longer than deep; posterior end divided into two small lobes; dorsal median projection absent. Middle valve (fig. 94e) with cuspis shorter than digitus; digitus very broad, curved, broadest in middle, distal end rounded. Inner valve (fig. 94f), excluding anterior apodeme, 1.1 times as long as deep; anterior extension of anterior apodeme 0.5 times length of rest of segment; postero-ventral lobe long, narrow, serrated distally; postero-dorsal margin rounded; posterior margin broadly indented, with large ridge of about 10 serrations (N = 1) at dorsal end.

Karyotype: Unknown

Taxa included: Typical *sp*.*M2*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. *sp*.*M2* is known from one male only. The male terminalia are broadly similar to other species in the *pilosula* group but I am unable to include it with any of them because of the shape of the inner valve. The male is black with gold pubescence on the dorsum of its gaster, which suggests that its workers will resemble *tepperi*. However the male is noticeably larger than *tepperi*.

3.5.2.4. The *Myrmecia mandibularis* group

Diagnosis

Moderately small, jumping *Myrmecia* with very distinctive worker mandibles. These have the outer border more or less convex and a reduced number of teeth on the inner border. The male terminalia can be easily recognized by the ninth sternite which has lateral inclusions.

Composition

(1) *fulviculis* Forel

(2) *fulvipes* Roger, *s.l.* = *femorata* Santschi = *barbata* Wheeler = *coelatinoda* Wheeler

(3) *luteiforceps* Wheeler

(4) *mandibularis* Smith = *aureorufa* Forel = *postpetiolaris* Wheeler = *laevinodis* (Clark)

(5) *piliventris* Smith, *s.l.* = *rectidens* Forel = *gilberti* Forel = *regina* Santschi = *potteri* (Clark) [includes *piliventris*, *s.s.* and *gilberti*]

[*Note* - These species have previously been placed in the *mandibularis* group by both Emery (1911) and Clark (1943, 1951).]

Comments

The *mandibularis* group is well delimited from all other species groups by its workers and male terminalia. The worker mandibles are broadly similar to *forceps* mandibles so it is likely that they perform a similar function. Although no direct evidence is yet available, I suspect that species of the *mandibularis* group are probably predators of insects which are larger than those taken by other jumpers. All workers from the *mandibularis* group have four long setae (about half as long as mandibles) arising from the frontal area of the head and extending into the gape of the mandibles (e.g. fig. 39b). Any setae in similar positions on workers of other groups are less than a quarter the length of the mandibles. I suspect that these setae could function as trigger hairs to close the mandibles.

All segments of the male terminalia are broadly similar for all species. Two putative species (*fulvipes*, *s.l.* and *piliventris*, *s.l.*) karyotyped by Imai et al. (1977) and Imai and Taylor (1986) each contained sibling species. Chromosome numbers ranged from 2n = 4-68 and *nombres fondamentaux* from N.F. = 8-68.

Distribution

A.C.T., N.S.W., Qld, S.A., Tas., Vic., W.A.

57. Myrmecia fulviculis Forel

(Fig. 58b)

Myrmecia (Pristomyrmecia) fulvipes Roger race fulviculis Forel, 1913a, p. 174 [♀].

Myrmecia (Promyrmecia) fulvipes Roger subsp. fulviculis Forel. Wheeler, 1933,p. 70.

Promyrmecia fulviculis (Forel). Clark, 1943, p. 144, pl. 17, fig. 97; 1951, p. 162, figs 130-132 [♀♂].

Myrmecia fulviculis Forel. Taylor and Brown, 1985, p. 10. Taylor, 1987, p. 43.

Types

fulviculis: syntype workers, Sydney, N.S.W. (A.M. Lea), in GMNH (see Clark, 1943).

Worker diagnosis (see Clark, 1951, pp 162-163)

Material examined (fig. 58b)

New South Wales: 70 km S of Dubbo (BBL); Fassifern (BBL); Iluka (BBL); Martinsville (BBL); Mudgee (BBL); Sydney (BBL); 10 km W of West Wyalong (BBL); 37 km W of West Wyalong (BBL); White Munghorns (BBL). Queensland: Bribie Island (cu); Fletcher (ESu); Mount Coot-tha (BBL); Nanango (BBL); Stanthorpe (BBL); Tabbimoble S.F. (TG).

[Note - Taylor and Brown (1985, p. 10) only recorded this species from Tas.]

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical fulviculis

Nest structure

No nests of fulviculis were observed during this study. However, Wheeler (1933, p. 71) reported that he found one colony nesting under a stone at Como (N.S.W.) which contained about 50 workers. Another colony he observed at Brisbane (Qld) '... was nesting in a low, pebble-covered mound about 10 inches in diameter.'

Collecting months for males: Unknown

Biological references (including unpublished theses): None

Comments

M. fulviculis is a well-defined biological species which can be distinguished by its worker morphology. The workers are similar to other species of the *mandibularis* group, but they can be recognised by their terminal gastral segments which are yellow. The species is sympatric with *fulvipes*, *s.l.* in parts of New South Wales and southern Queensland, but no individuals with intergrading colour pattern or nests with workers of both colour patterns are known.

58. *Myrmecia fulvipes* Roger, *s.l.*

(Figs 58a, 97c-d)

Myrmecia fulvipes Roger, 1861a, p. 36 [♀]. Mayr, 1862, p. 726; 1876, p. 93. Brown, 1953b, p. 21. Wheeler and Wheeler, 1971, p. 249 [larva]. Imai, Crozier and Taylor, 1977, p. 345, figs 2, 12. Taylor and Brown, 1985, p. 10. Taylor, 1987, p. 43.

Myrmecia (*Pristomyrmecia*) *fulvipes* Roger. Emery, 1911, p. 21. Forel, 1913b, p. 173.

Myrmecia (*Promyrmecia*) *fulvipes* Roger. Wheeler, 1933, p. 69. Clark, 1934b, p. 52.

Promyrmecia fulvipes (Roger). Clark, 1943, p. 145, pl. 16, figs 81-83 [♀♂]; 1951, p. 165, figs 133-135.

Myrmecia (*Pristomyrmecia*) *piliventris* Smith var. *femorata* Santschi, 1928, p. 466 [♀].

Myrmecia (*Promyrmecia*) *fulvipes* Roger var. *femorata* Santschi. Wheeler, 1933, p. 70.

Promyrmecia piliventris (Smith) var. *femorata* (Santschi). Clark, 1943, p. 142, pl. 17, figs 88-90 [♀♂].

Promyrmecia piliventris femorata (Santschi). Clark, 1951, p. 158.

Myrmecia piliventris femorata Santschi. Wheeler and Wheeler, 1971, p. 252 [larva].

Myrmecia (*Promyrmecia*) *fulvipes* Roger subsp. *barbata* Wheeler, 1933,
p. 71 [♀♀].

Promyrmecia *fulvipes* (Roger) subsp. *barbata* (Wheeler). Clark, 1943,
p. 146.

Myrmecia (*Promyrmecia*) *fulvipes* Roger subsp. *coelatinoda* Wheeler, 1933,
p. 72, *syn*. *nov*. [♀].

Promyrmecia *fulvipes* (Roger) subsp. *coelatinoda* (Wheeler). Clark, 1943,
p. 147.

Promyrmecia *fulvipes* *coelatinoda* (Wheeler). Clark, 1951, p. 167.

Myrmecia *mandibularis* Smith, *auct*. (*non* Smith, 1858). Brown, 1953b,
p. 4, *partim*.

Types

fulvipes: holotype worker, Australia, in MNHP.

femorata: syntype workers, Franktown (= Frankston), Vic. (C. Barrett), in NHMB. [Synonymy by Brown, 1953b].

barbata: syntype workers, Dorrigo, N.S.W. (W. Heron), in MCZ; syntype worker and female, Belgrade (= Belgrave), Vic., in MCZ. [*Note* - Wheeler (1933) designated 10 syntype workers from Dorrigo.] [Synonymy by Clark, 1951].

coelatinoda: holotype worker (probable), Belair, S.A. (J.W. Haacke), in ANIC (examined). [NEW SYNONYMY].

Worker diagnosis (see Clark, 1951, pp 158, 165-168)

Material examined (fig. 58a)

Australian Capital Territory: Bendora (EFR); Black Mountain (BBL); Brindabella Range (TG); Cotter River (TG); Gibraltar Creek (BBL); 5 km SW of Orroral (BBL); Smokers Gap (BBL) [*MT*, ♂, 7.ii.1978]. *New South Wales*: Armidale (BBL); 8 km E of Braidwood (EFR); Brown Mountain (RWT) [*MT*, ♂, 29.xii.1973]; Ebor (BBL); Fassifern (BBL); Fitzroy Falls (EFR); Guyra (EFR); Heaton S.F. (BBL); Kanangra Walls N.P. (BBL); Kangaroo Valley (EFR); Mogo S.F. (BBL) [*MT*, ♂, 30.xii.1973]; Monga (EFR); Mount Cambewarra (BBL); Mount Canobolas (EFR); Mount Warning (BBL); Mudgee (BBL); 12 km E of Nimmitabel (BBL); Pine Creek S.F. (TG); Queanbeyan (BBL); Rosedale (BBL); Sydney (BBL); Tallaganda S.F. (BBL); 5 km N of Tathra (BBL); Tumbulgum (BBL); Tumut (BBL); Yarramundi (BBL). *South Australia*: Belair (JWH) [*coelatinoda* holotype]. *Tasmania*: Domain (LW; F77 in TM); Steppes (TG); Vinegar Hill (JHC). *Victoria*: Belgrave (JCl);

Fern Tree Gully (BBL); Harrietville (BBL); Kilmore (BBL); Lakes Entrance (BBL); Mount Disappointment (BBL); Romsey (EFR).

Male terminalia (fig. 97c-d)

No variation has been observed in the male terminalia of fulvipes, s.l.

Ninth and tenth tergites, eighth sternite, basal ring, outer valve and middle valve similar to gilberti. Ninth sternite (fig. 97c) 1.2 times longer than wide; moderately long anterior apodeme; antero-lateral lobes barely developed; lateral lobes absent; posterior extension of posterior margin narrow, expanded posteriorly. Lateral inclusions present in anterior half. Short setae scattered on and near posterior extension. Inner valve (fig. 97d), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.5 times length of rest of segment; postero-ventral lobe moderately broad, moderately long; postero-dorsal margin rounded; 8-25 small spines ($\overline{x}$ = 18.6, N = 5) along posterior and postero-ventral margins.

Karyotype

The variation in the karyotype of fulvipes, s.l. is too great to be considered intraspecific and it is likely that the following karyotypes are from sibling species:

(1) 2n = 12 (Imai et al., 1977; 2 colonies from Leumeah, N.S.W.)

(2) 2n = 60 (Imai et al., 1977; colony from Picadilly Circus, A.C.T.)

Taxa included

(1) n = 6 cytotype

(2) n = 30 cytotype

Nest structure

No nests of fulvipes, s.l. were seen during this study. However, Wheeler (1933, p. 70) reported that he found this species '... nesting under stones in colonies of about 50 individuals.' Gray (1974a) excavated two nests at Nowra and Mudgee (both N.S.W.) which contained 216 and 122 workers, and were 62 and 28 cm deep respectively.

Biological references (including unpublished theses)

Gray (1974a, 1974b)

Comments

M. fulvipes, *s.l.* is a species, or complex of siblings, which can be distinguished by its worker morphology and male terminalia. Within the *mandibularis* group, it is easily distinguished from *mandibularis*, *piliventris*, *s.l.* and *luteiforceps* by its yellow legs, and from *fulviculis* by its gaster colour which is entirely black (though largely concealed by brassy pubescence). I have accepted the synonymy of *barbata* and *femorata* by Clark (1951) and Brown (1953b) respectively and have also synonymized *coelatinoda*. Brown (1953b), believing the holotype to be lost, synonymized *coelatinoda* with *mandibularis*, but I have examined a specimen which I am satisfied is the holotype and conclude that it belongs to *fulvipes*, *s.l.* However, it should be noted that this is the only specimen of *fulvipes*, *s.l.* I have seen from South Australia, although Clark (1951) recorded the species from Murray Bridge.

59. *Myrmecia luteiforceps* Wheeler

(Fig. 58b)

Myrmecia (*Promyrmecia*) *gilberti* Forel var. *luteiforceps* Wheeler, 1933, p. 74 [♀]. [Introduced as a quadranomen by Forel, 1915].

Myrmecia (*Pristomyrmecia*) *fulvipes* Roger race *gilberti* Forel var. *luteiforceps* Forel, 1915, p. 9. [Invalid quadranomen; see Taylor, 1986].

Promyrmecia luteiforceps (Forel) [sic]. Clark, 1943, p. 143, pl. 17, fig. 96; 1951, p. 161, fig. 129.

Myrmecia luteiforceps (Clark) [sic]. Taylor and Brown, 1985, p. 12.

Myrmecia luteiforceps Wheeler. Taylor, 1986, p.36; 1987, p. 44.

Types

luteiforceps: syntype worker, Herberton, Qld (E. Mjöberg), in NMV (examined); syntype worker, Herberton, Qld (E. Mjöberg), in ANIC (examined); syntype worker(s), Herberton, Qld, in GMNH.

Worker diagnosis (see Clark, 1951, pp 161-162)

Material examined (fig. 58b)

Queensland: Herberton (EM) [*luteiforceps* syntypes].

Male terminalia: Unknown

Karyotype: Unknown

Taxa included: Typical *luteiforceps*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. luteiforceps is known from just one nest and is only distinguished from *piliventris*, *s.l.* by its yellow mandibles. The mandibles of all other species of the *mandibularis* group are brown or black and I suspect that *luteiforceps* may merely represent a colour polymorphism. However, in the absence of further evidence I prefer to recognize it as a separate species.

60. *Myrmecia mandibularis* Smith

(Figs 58b, 97a-b)

Myrmecia mandibularis Smith, 1858, p. 145 [♀]. Mayr, 1862, p. 727. Crawley, 1926, p. 385, fig. 10. Brown, 1953b, p. 4, *partim*. Taylor and Brown, 1985, p. 12. Taylor, 1987, p. 44.

Myrmecia (*Pristomyrmecia*) *mandibularis* Smith. Emery, 1911, p. 21, pl. 1, fig. 11. Santschi, 1928, p. 465.

Myrmecia (*Promyrmecia*) *mandibularis* Smith. Wheeler, 1933, p. 64, figs 22, 24.

Promyrmecia mandibularis (Smith). Clark, 1943, p. 137, pl. 17, figs 91-93 [♀♂]; 1951, p. 151, figs 118-120.

Myrmecia mandibularis Smith subsp. *aureorufa* Forel, 1910, p. 6 [♀].

Myrmecia (*Pristomyrmecia*) *mandibularis* Smith subsp. *aureorufa* Forel.
Emery, 1911, p. 21.

Myrmecia (*Promyrmecia*) *mandibularis* Smith subsp. *postpetiolaris* Wheeler,
1933, p. 65 [♀♀].

Promyrmecia laevinodis Clark, 1943, p. 139, pl. 17, figs 94-95 [♀♀];
1951, p. 154, figs 121-122.

Myrmecia piliventris Smith, *auct*. (*non* Smith, 1858). Brown, 1953b,
p. 20, *partim*.

Types

mandibularis: syntype workers, Adelaide, S.A., in BMNH.

aureorufa: holotype worker, Australia (A. Forel), in GMNH. [Synonymy by Clark, 1943].

postpetiolaris: syntype worker and male, Mount Lofty, S.A. (J.G.O. Tepper), in MCZ. [Synonymy by Clark, 1943].

laevinodis: syntype workers (2), Armadale, W.A. (J. Clark), in NMV (examined); syntype worker, Albany, W.A. (J. Clark), in NMV (examined); syntype workers (3), Lucindale, S.A., in NMV (examined); syntype workers (2), Melrose, S.A. (A.M. Lea), in NMV (examined); syntype worker, Kangaroo Island, S.A. (A. Campbell), in NMV (examined); syntype worker, Mallee, Vic. (J.E. Dixon), in NMV (examined); syntype(s), Bunbury, W.A. (J. Clark) have not been located. [*Note* - Clark (1943) mentions specimens from '*Western Australia*: Armadale; Albany; Bunbury (J. Clark). *South Australia*: Lucindale; Melrose (A.M. Lea); Kangaroo Island (A. Campbell). *Victoria*: Mallee (J.E. Dixon).'] [Synonymy by Brown, 1953b].

Worker diagnosis (see Clark, 1951, pp 151-152, 154-155)

Material examined (fig. 58b)

South Australia: Admirals Arch [316, 318-319, 325]; Bay of Shoals [249]; Clare (BBL); 4 km NE of d'Estrees Bay [345]; Fishery Bay [298]; Gemmells (RDR; in SAM); Hanson Bay [398]; Kangaroo Island (AC; in NMV) [*laevinodis* syntype]; 3 km W of Kingscote (BBL); 16 km N of Kingston, S.E. (BBL); Lucindale (cu; in NMV) [*laevinodis* syntypes]; Melrose (AML; in NMV) [*laevinodis* syntypes]; Mount Lofty (AHE), (JGOT; in MCZ) [*MT*, ♂ only, du]; Mount Remarkable (FEW); Nepean Bay (BBL); 5 km E of Norwood (BBL); Point Reynolds (K,W&p); Ravine de Casoars [330]; Rocky River [333, 337]; Sevenhill (BBL); Stenhouse Bay (BBL). *Victoria*: Mallee

(JED; in NMV) [laevinodis syntype]. Western Australia: Albany (TG); Armadale (JCl; in NMV) [laevinodis syntypes]; 16 km N of Bunbury (BBL); Denmark (TG); Kalamunda (TG); Madura (C&U); Manjimup (JCl); 16 km E of Nornalup (EFR); 5 km E of Norseman [397]; 16 km E of Northcliffe (RWT); Pemberton (KRN); 16 km W of Pemberton (RWT); Quinnup (RWT); 4 km W of Wagin [455]; 24 km NW of Walpole (EFR).

Male terminalia (fig. 97a-b)

No variation has been observed in the male terminalia of mandibularis.

Ninth and tenth tergites, eighth sternite, basal ring, outer valve and middle valve similar to gilberti. Ninth sternite (fig. 97a) 1.3 times longer than wide; long anterior apodeme; antero-lateral lobes absent; lateral lobes absent; posterior extension of posterior margin very narrow, turned dorsally and expanded posteriorly. Lateral inclusions present in middle. Short setae scattered over much of posterior half; others in three more or less defined areas in anterior half. Inner valve (fig. 97b), excluding anterior apodeme, 1.0 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe broad, moderately short; postero-dorsal margin rounded; about 28 small spines (N = 1) along posterior and postero-ventral margins.

Karyotype: Unknown

Taxa included: Typical mandibularis

Nest structure

I observed nests of mandibularis at one locality in Western Australia and several on Kangaroo Island (S.A.). Each nest was located beneath a rock and was indicated by a single entrance (d ≃ 8 mm) at the rock's edge. Pupae and larvae were found in a large chamber beneath the covering rock and a single gallery led below. No nests were completely excavated, because of the rocky ground in which they were located, but the internal structure was simple. Mature colonies appeared to contain 100-200 workers.

Biological references (including unpublished theses)

Haskins and Haskins (1950)

Comments

M. mandibularis is a well-defined biological species which can be distinguished by its worker morphology and male terminalia. The workers are very similar to other species of the *mandibularis* group, but can be readily distinguished by the colour of the gastric pubescence. In *mandibularis* this is reddish-gold but in the others is brassy.

61. *Myrmecia piliventris* Smith, *s.l.*

(Figs 39a-c, 59a, 45a-f, 96a-d)

Myrmecia piliventris Smith, 1858, p. 146 [♀]. Roger, 1861a, p. 36. Mayr, 1862, p. 727; 1876, p. 93 [♀]. Crawley, 1926, p. 385, fig. 11. Brown, 1953b, p. 20, *partim*. Wheeler and Wheeler, 1971, p. 251 [larva]. Taylor and Brown, 1985, p. 14. Imai and Taylor, 1986, p.59 [karyotype]. Taylor, 1987, p. 45.

Myrmecia (*Pristomyrmecia*) *piliventris* Smith. Emery, 1911, p. 21.

Myrmecia (*Promyrmecia*) *piliventris* Smith. Wheeler, 1933, p. 67.

Promyrmecia piliventris (Smith). Clark, 1943, p. 140, pl. 17, figs 84-86 [♂]; 1951, p. 156, figs 123-125.

Myrmecia piliventris Smith var. *rectidens* Forel, 1910, p. 5 [♀].

Myrmecia (*Pristomyrmecia*) *piliventris* Smith var. *rectidens* Forel. Emery, 1911, p. 21.

Myrmecia (*Promyrmecia*) *piliventris* Smith subsp. *rectidens* Forel. Wheeler, 1933, p. 68.

Promyrmecia piliventris (Smith) subsp. *rectidens* Forel. Clark, 1943, p. 141, pl. 17, fig. 87.

Promyrmecia rectidens (Forel). Clark, 1951, p. 159, figs 126-128 [♀].

Myrmecia fulvipes Roger var. *gilberti* Forel, 1910, p. 6, *syn. nov.* [♀].

Myrmecia (*Pristomyrmecia*) *fulvipes* Roger var. *gilberti* Forel. Emery, 1911, p. 21.

Myrmecia (*Pristomyrmecia*) *fulvipes* Roger race *gilberti* Forel. Forel, 1913a, p. 173.

Myrmecia (*Promyrmecia*) *gilberti* Forel. Wheeler, 1933, p. 72 [♂].
Promyrmecia gilberti (Forel). Clark, 1943, p. 136, pl. 16, figs 79-80
[♀]; 1951, p. 169, figs 137-138.
Myrmecia gilberti Forel. Taylor and Brown, 1985, p. 10. Taylor, 1987,
p. 43.
Myrmecia (*Pristomyrmecia*) *regina* Santschi, 1928, p. 465 [♀].
Promyrmecia potteri Clark, 1951, p. 168, fig. 136, *syn. nov.* [♀].
Myrmecia potteri (Clark). Taylor and Brown, 1985, p. 14. Taylor, 1987,
p. 45.
Myrmecia mandibularis Smith, *auct.* (*non* Smith, 1858). Brown, 1953b,
p. 4, *partim*.

Types

piliventris: syntype workers, Australia, in BMNH.

rectidens: syntype workers, Kingstown (= Kingston), N.S.W. (W.W. Froggatt), in GMNH. [Synonymy by Brown, 1953b].

gilberti: syntype workers (2), Mackay, Qld (G. Turner), in ANIC (examined); syntype worker(s), Mackay, Qld (G. Turner), in GMNH. [NEW SYNONYMY].

regina: syntype workers, Townsville, Qld (19.iv.1902, F.P. Dodd; 23.v.1902, F.P. Dodd; 18.vi.1902, F.P. Dodd), in NHMB. [Synonymy by Wheeler, 1933].

potteri: holotype worker, Patho, Vic. (H.A. Potter), in ANIC (examined). [NEW SYNONYMY].

Worker diagnosis

Measurements and proportions as given and illustrated (figs 39a-c).

Head, mesosoma, petiole and postpetiole dark brown to black; mandibles, antennae and legs dark brown; gaster black. Gaster densely clothed with greenish gold pubescence.

Material examined (fig. 59a)

Australia: Australia (cu; 50.7 in BMNH) [*pilosula* paratype; *MT*, ♂ only, du]. *Australian Capital Territory*: Black Mountain (BBL) [*MT*, ♂, 6.i.1978]; Mount Pleasant (BBL); Tidbinbilla N.R. (BBL). *New South Wales*: Apsley (BBL); Armidale (BBL); Berrigan S.F. (BBL); Bomaderry (BBL); Bowenfels (BBL); 20 km NW of Braidwood (BBL); Brown Mountain (RWT); Central Mangrove (BBL); Colo Vale (WJMV); Condobolin (BBL) [*SEM*,

♀; MT, ♂, 16.i.1967]; Durras (GFH); Gerroa (BBL); Gilgai (BBL); Goodradigbee Valley (BBL); Gwandalan (BBL); Hampton (BBL); Kiandra (EFR); Lake Durras (BBL); Meadow Flat (BBL); Milton (GFH); 4 km N of Moruya (BBL); Mount Victoria (BBL); Mudgee (BBL); Nerriga (TG); Rosedale (BBL); Sydney (BBL); Tamworth (BBL); Trundle (BBL); Woy Woy (BBL). Queensland: Atherton (RWT); Blackhall Ranges (CHB); Captain Billy Creek (GBM); Gin Gin (WWF); 12 km N of Gin Gin (TG); Mackay (GT) [gilberti syntypes]; 20 km E of Mount Garnet (cu; in MCZ) [MT, ♂, 13.ii.1958]; Mount Mort (SHP); Stanthorpe (BBL); Townsville (FPD). South Australia: Taratap (RDR; in SAM). Victoria: Heathcote (BBL); Patho (HAP) [potteri holotype].

[Note - Clark (1951) also records piliventris from 'Tasmania: Burnie.' Taylor and Brown (1985, pp 11, 14) also recorded this species from Tas. but did not record it from A.C.T. I have not seen any specimens from Tas. referable to piliventris, s.l. and consider its presence there unlikely.]

Male terminalia (figs 95a-f, 96a-d)

The male terminalia examined for piliventris, s.l. suggest that the following are distinct biological species:

(1) Myrmecia piliventris Smith, s.s.

(Fig. 96c-d)

Ninth and tenth tergites, eighth sternite, basal ring, outer valve and middle valve similar to gilberti. Ninth sternite (fig. 96c) 1.3 times longer than wide; long anterior apodeme; antero-lateral lobes slightly developed; lateral lobes absent; posterior extension of posterior margin narrow, blunt. Lateral inclusions present in anterior half. Short setae scattered on and near posterior extension. Inner valve (fig. 96d), excluding anterior apodeme, 0.9 times as long as deep; anterior extension of anterior apodeme 0.7 times length of rest of segment; postero-ventral lobe broad, moderately short; postero-dorsal margin rounded; 21-31 small spines ($\bar{x}$ = 25.8, N = 4) along posterior and postero-ventral margins.

(2) Myrmecia gilberti Forel

(Figs 95a-f, 96a-b)

Ninth and tenth tergites (fig. 95a) 1.1 times wider than long; median lobe rounded, extending just beyond tips of pygostyles. Pygostyles stout; length 0.3 times width of segment. Eighth sternite (fig. 95b) trapezoidal; 1.2 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Numerous short setae concentrated in two moderately large areas flanking midline in anterior two-thirds. A few small sensillae in antero-lateral corners. Ninth sternite (fig. 95c) 1.4 times longer than wide; long anterior apodeme; antero-lateral lobes absent; lateral lobes absent; posterior extension of posterior margin narrow, expanded posteriorly. Lateral inclusions (LI) present in anterior half. Short setae scattered over much of posterior half; others concentrated in two moderately large areas flanking midline in anterior half. Basal ring 1.5 times wider than long; 1.5 times wider posteriorly than anteriorly. Outer valve (fig. 95d) 1.9 times longer than deep; posterior end abrupt; dorsal median projection absent; postero-dorsal ridge present. Middle valve (fig. 95e) with cuspis shorter than digitus; digitus moderately broad, curved, broadest in middle, distal end rounded. Inner valve (fig. 95f), excluding anterior apodeme, 1.1 times as long as deep; anterior extension of anterior apodeme 0.5 times length of rest of segment; postero-ventral lobe moderately broad, moderately long; about 27 small spines (N = 1) along posterior and postero-ventral margins.

Terminalia of the male syntype of pilosula were dissected (fig. 96a-b) and appeared to be very similar to gilberti.

Karyotype

The variation in the karyotype of *piliventris*, *s.l.* is too great to be considered intraspecific and it is likely that the following karyotypes are from sibling species:

(1) n = 2, 2n = 4 (Imai and Taylor, 1986; four colonies from Black Mountain, A.C.T. (1), Jerrabomberra Hill, N.S.W. (1) and Nelligen Creek Bridge, N.S.W.(2))

(2) n = 34 (Imai and Taylor, 1986; colony from Black Mountain, A.C.T.)

Both are presumed to be associated with *piliventris*, *s.s.* because their localities are in the southern part of the known distribution for *piliventris*, *s.s.* *M. gilberti* has not been karyotyped.

Taxa included

(1) *piliventris*, *s.s.*

(a) n = 2 cytotype

(b) n = 34 cytotype

(2) *gilberti*

Nest structure

No nests of *piliventris*, *s.l.* were observed during this study. However, Wheeler (1933, p. 68) observed several colonies and reported that each '... was nesting under a stone and comprised about 50 to 60 workers.' Gray (1974a) slightly contradicted this when he excavated two nests at Nyngan (N.S.W.) which contained 216 and 113 workers and were 77 and 51 cm deep respectively. He also reported that the internal nest structure was simple.

Biological references (including unpublished theses)

Turner (1897) [as *gilberti*]; Haskins and Haskins (1950); Gray

(1974a, 1974b); Muir (1975)

Comments

M. piliventris, s.l. consists of at least three closely related species which can be distinguished from other Myrmecia by their worker morphology. M. gilberti appears to be a valid biological species (based on male terminalia) and piliventris, s.s. contains two cytotypes which differ greatly in chromosome number but, because I am unable to distinguish workers of the three species I have dealt with them as one broad species. The known distribution of piliventris, s.l. (fig. 59a) can be roughly divided into northern (gilberti) and southern (piliventris, s.s.) parts by latitude 24°S.

3.4.2.5. The Myrmecia picta group

Diagnosis

Small, jumping Myrmecia with distinctive workers and male terminalia. Worker mandibles have noticeable angulate broadening near base of inner border. Outer valve of male terminalia has its dorsal median projection longer than the posterior end.

Composition

picta Smith

[Note - M. picta has previously been placed in the pilosula group of Emery (1911) and the picta group of Clark (1943, 1951).]

Distribution

N.S.W., Qld, S.A., W.A., [? Vic.]

Comments

The picta group is well delimited from all other species groups by its workers and male terminalia. Clark (1951) placed picta and fucosa Clark in the picta group on the basis of their mandibles being similar, but in the same work he stated that they were '... distinguished by the form of the mandibles' (p. 144). Even if males were unknown, I would not have placed them in the same group because *picta* mandibles are so different to *fucosa*.

Male terminalia of the *picta* group have eighth and ninth sternites, and middle valves similar to the *sp.15* group but the outer and inner valves are very different.

62. *Myrmecia picta* Smith

(Figs 59b, 98a-e)

Myrmecia picta Smith, 1858, p. 146 [♀♀]. Mayr, 1862, p. 727. Lowne, 1865, p. 336. Crawley, 1926, p. 382, fig. 8. Wheeler and Wheeler, 1971, p. 251 [larva]. Taylor and Brown, 1985, p. 14. Taylor, 1987, p. 45.

Myrmecia (*Promyrmecia*) *picta* Smith. Clark, 1927, p. 39 [♂]; 1934a, p. 11.

Promyrmecia picta (Smith). Clark, 1943, p. 100, pl. 12, figs 10-13; 1951, p. 139, figs 107-109.

Types

picta: syntype worker(s) and female(s), Adelaide, S.A., in BMNH.

Worker diagnosis (see Clark, 1951, pp 139-140)

Material examined (fig. 59b)

New South Wales: Lismore (CFD); 5 km W of Merriwagga (BBL); 3 km W of Mudgee (BBL); 6 km W of Mudgee(BBL); Nyngan (BBL). *Queensland*: Alpha Creek (BBL); Cunnamulla (BBL); St George (BBL); 48 km N of Tambo (BBL). *South Australia*: Ardrossan (cu); Lake Hart (BBL); Langhorne Creek (RDR; in SAM); Mambray Creek (EFR); Melrose (BBL); 13 km W of Morgan (BBL); Ngarkat C.P. (RDR; in SAM); 32 km S of Port Augusta (EFR). *Western Australia*: Balladonia Station (TG); 112 km N of Esperance (BBL); Mundaring (JCl) [*MT*, ♂, du]; Norseman (BBL); 6 km S of Ravensthorpe (BBL); 13 km NW of Wiggiemooltha (RWT).

[*Note* - Clark (1951) also records specimens from '*Victoria*: Maldon, Hattah, Wyperfield' and although I have not seen any specimens from

Victoria I think it likely that this species occurs there. Taylor and Brown (1985, p. 14) did not record this species from N.S.W., Qld or W.A.]

Male terminalia (fig. 98a-e)

No variation has been observed in the male terminalia of picta.

Ninth and tenth tergites damaged during dissection. Pygostyles moderately slender. Eighth sternite (fig. 98a) trapezoidal; 1.4 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Moderate number of short setae concentrated in two large contiguous areas in middle half. Ninth sternite (fig. 98b) 1.1 times longer than wide; short anterior apodeme; antero-lateral lobes developed; lateral lobes present; posterior margin moderately narrow, indented posteriorly. Short setae scattered over much of posterior half; a few flanking midline in anterior half. Basal ring 1.7 times wider than long; 1.5 times wider posteriorly than anteriorly. Outer valve (fig. 98c) 1.5 times longer than deep; posterior end bluntly pointed; dorsal median projection long, shouldered, roundly pointed. Middle valve (fig. 98d) with cuspis much shorter than digitus; digitus broad, curved, broadest in middle, distal end rounded. Inner valve (fig. 98e), excluding anterior apodeme, 1.5 times as long as deep; anterior extension of anterior apodeme 0.5 times length of rest of segment; postero-ventral lobe moderately short, moderately broad; postero-dorsal margin rounded; 15-16 small spines ($\overline{x}$ = 15.5, N = 2) near postero-dorsal margin; about 14 small spines and serrations ($\overline{x}$ = 14.0, N = 2) on postero-ventral lobe.

Karyotype: Unknown

Taxa included: Typical picta

Nest structure

No nests of picta were seen during this study. However, Gray

(1974a) reports that it has a simple nest structure with one main shaft and a single entrance. He completely excavated two nests at Bulgadie (N.S.W.) which contained 20 and 32 workers and were 36 and 50 cm deep respectively.

Biological references (including unpublished theses)

Gray (1974a)

Comments

M. picta has usually been grouped with fucosa (Clark, 1943, 1951; B.B. Lowery, pers. comm.) but examination of the male terminalia shows them to be quite dissimilar. The species is widely distributed and may represent a complex of siblings. Examination of karyotypes and more male terminalia will be important for assessing its species status.

3.4.2.6. The Myrmecia sp.15 group

Diagnosis

Workers superficially similar to the pilosula group but noticeably smaller. They can be easily recognized by their long pilosity which hides the petiolar sculpture. The male terminalia are quite distinct although they do have some segments similar to the picta group. However, the outer valve does not have a dorsal median projection and the inner valve has spines only on the ventral lobe.

Composition

sp.15 (ANIC), sp. nov.

Distribution

A.C.T.

Comments

The sp.15 group is well delimited from all other species groups by its male terminalia. These have some similarities to the picta group but have markedly different inner and outer valves. Workers of the *sp.15* group are similar to the *urens* group in size and mandible shape, and may have been placed there if male terminalia were not examined. However, its petiole differs by having less pronounced sculpture which is hidden by white pubescence. All segments of the male terminalia in the *sp.15* and *urens* groups are easily distinguished. No karyotypes are known.

63. *Myrmecia sp. 15* (ANIC), *sp. nov.*

(Figs 40a-c, 59b, 99a-f)

Worker diagnosis

Measurements and proportions as given and illustrated (figs 40a-c).

Head, mesosoma, femora, petiole, postpetiole and gaster black; mandibles, antennae, tibiae and tarsi yellow.

Material examined (fig. 59b)

Australian Capital Territory: 4 km W of Smokers Gap (BBL) [*SEM*, ♀; *MT*, ♂, 15.ii.1979].

Male terminalia (fig. 99a-f)

No variation has been observed in the male terminalia of *sp.15*.

Ninth and tenth tergites (fig. 99a) 1.3 times wider than long; median lobe rounded, extending just beyond tips of pygostyles. Pygostyles moderately stout; length 0.3 times width of segment. *Eighth sternite* (fig. 99b) trapezoidal; 1.4 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Numerous short setae concentrated in two large areas flanking midline in anterior two-thirds. *Ninth sternite* (fig. 99c) 1.0 times longer than wide; very short anterior apodeme; antero-lateral lobes developed; lateral lobes present; posterior margin moderately narrow, indented posteriorly. Short setae scattered over much of posterior third. *Basal ring* 1.6 times wider than long; 1.6 times wider posteriorly than anteriorly. *Outer valve* (fig. 99d) 1.7 times longer than deep; posterior end abrupt; dorsal median projection absent. *Middle valve* (fig. 99e) with cuspis much shorter than digitus; digitus moderately broad, curved, broadest in middle, distal end rounded. *Inner valve* (fig. 99f), excluding anterior apodeme, 1.1 times as long as deep; anterior extension of anterior apodeme 0.5 times length of rest of segment; postero-ventral lobe roundly pointed; postero-dorsal margin rounded; 30-33 small spines ($\overline{x} = 31.5$, $N = 2$) on postero-ventral lobe.

Karyotype: Unknown

Taxa included: Typical *sp.15*

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. sp.15 is a well-defined species, restricted to the Canberra area, which is superficially similar to *urens* Lowne, but can be easily distinguished by its male terminalia.

3.4.2.7. The *Myrmecia fucosa* group

Diagnosis

Workers superficially similar to the *pilosula* group but slightly smaller. They can be easily separated from other jumpers by viewing their mesosoma in lateral view. In *fucosa* the postero-dorsal surface slopes sharply to its junction with the petiole, but in all other jumpers the slope is much gentler. The male terminalia are very distinct and are easily recognized by the inner valve, which has the postero-dorsal lobe folded laterally and numerous spines along the posterior margin of the postero-ventral lobe.

Composition

fucosa Clark

[*Note* - This species has previously been placed in the *picta* group of Clark (1951). It is not clear whether Clark (1943) placed it in the *picta* or *pilosula* group, but the former seems more likely.]

Distribution

S.A., Vic., W.A.

Comments

The *fucosa* group is well delimited from all other species groups by its male terminalia. Its workers are similar to some species in the *pilosula* group, but they are noticeably smaller. Clark's (1951) placement of *fucosa* in the *picta* group cannot be supported on the basis of workers or male terminalia.

64. *Myrmecia fucosa* Clark

(Figs 41a-c, 59b, 100a-f)

Myrmecia (*Promyrmecia*) *fucosa* Clark, 1934a, p. 15 [♀♀].
Promyrmecia fucosa (Clark). Clark, 1943, p. 102, pl. 12, figs 14-16 [♂]; 1951, p. 142, figs 110-112.
Myrmecia fucosa Clark. Wheeler and Wheeler, 1971, p. 249 [larva]. Taylor and Brown, 1985, p. 10. Taylor, 1987, p. 43.

Types

fucosa: syntype workers (2), Lake Hattah, Vic. (J.E. Dixon), in NMV (examined); syntype workers (2), Sea Lake, Vic. (J.C. Goudie), in NMV (examined); syntype workers (3), Wyperfield, Vic. (3.x.1931, J. Clark), in NMV (examined); syntype worker, Murray Bridge, S.A. (A.M. Lea), in ANIC (examined); syntype female, Wyperfield, Vic. (J. Clark) and syntype worker(s), Ouyen, Vic. (J.E. Dixon) have not been located. [*Note* - Clark (1934a) mentions specimens from 'Victoria: Lake Hattah, Ouyen ♀ (J.E. Dixon), Sea Lake ♀ (J.C. Goudie), Wyperfield ♀ ♀ (J. Clark). South Australia: Murray Bridge (A.M. Lea, ♀).']

[*Note* - Taylor and Brown (1985, p. 10) did not record this species from W.A.]

Worker diagnosis

Measurements and proportions as given and illustrated (figs 41a-c).

Head black; mandibles, antennae, mesosoma, legs, petiole, first segment and most of second segment of gaster yellow; posterior margin of second segment and rest of gaster brown.

Material examined (fig. 59b)

South Australia: 24 km E of Kimba (BBL); Mount Lofty Ranges (cu; in NMV); Murray Bridge (AML) [*fucosa* syntype]; 19 km SW of Waikerie (BBL) [*SEM*, ♀; *MT*, ♂, 23.ii.1969]. *Victoria*: Lake Hattah (JED; in NMV) [*fucosa* syntypes]; Sea Lake (JCG; in NMV) [*fucosa* syntypes]; Wyperfield (JC1; in NMV) [*fucosa* syntypes]. *Western Australia*: 120 km W of Balladonia [525] [*MT*, ♂, 31.viii.1984].

Male terminalia (fig. 100a-f)

No variation has been observed in the male terminalia of *fucosa*.

Ninth and tenth tergites (fig. 100a) 1.2 times wider than long; median lobe rounded, extending noticeably beyond tips of pygostyles. Pygostyles slender; length 0.4 times width of segment. *Eighth sternite* (fig. 100b) trapezoidal; 1.4 times wider than long; 1.2 times wider posteriorly than anteriorly; anterior margin indented 0.3 times length of segment. Moderately few short setae flanking midline in posterior quarter. *Ninth sternite* (fig. 100c) 1.1 times longer than wide; moderately short anterior apodeme; antero-lateral lobes developed; lateral lobes absent; posterior margin moderately narrow, rounded. Short setae scattered over much of posterior third. *Basal ring* 1.6 times wider than long; 1.5 times wider posteriorly than anteriorly. *Outer valve* (fig. 100d) 1.8 times longer than deep; posterior end dorso-ventrally flattened; dorsal median projection bluntly pointed, shouldered on dorsal side. *Middle valve* (fig. 100e) with cuspis much shorter than digitus; digitus moderately broad, very curved, broadest in middle, distal end blunt. Inner valve (fig. 100f), excluding anterior apodeme, 1.1 times as long as deep; anterior extension of anterior apodeme 0.6 times length of rest of segment; postero-ventral lobe moderately broad, moderately long, rounded; postero-dorsal margin folded laterally; 44-83 small spines ($\bar{x}$ = 67.7, N = 3) along and near posterior and postero-ventral margins.

Karyotype: Unknown

Taxa included: Typical fucosa

Nest structure: Unknown

Biological references (including unpublished theses): None

Comments

M. fucosa is a widely distributed, well-defined biological species which can be distinguished by its worker morphology and male terminalia. It has previously been grouped with picta by Clark (1943, 1951), but this resemblance appears to be superficial.

3.4.2.8. The Myrmecia urens group

Diagnosis

Workers superficially similar to the pilosula group but much smaller. The most distinctive features are found in the male terminalia, although some segments are similar to the picta and sp.15 groups. However, they can be easily recognized by the outer valve which has a short and digitate dorsal median projection.

Composition

urens Lowne = pumilio Mayr = infima Forel = nigra Forel = dichospila Clark = rubicunda (Clark) = exigua (Clark)

[Note - This species has previously been placed in the pilosula group of Emery (1911) and the urens group of Clark (1951). It is not clear whether Clark (1943) placed it in the *picta* or *pilosula* group, but the latter seems more likely.]

Distribution

A.C.T., N.S.W., S.A., Vic., W.A., [? Qld, ? Tas.]

Comments

The *urens* group is well delimited from all other species groups by its male terminalia. Its workers are quite similar to the *pilosula*, *fucosa* and *sp.15* groups, except they are noticeably smaller than the first two. If male terminalia were unknown, I may have placed *sp.15* in the *urens* group based on superficial resemblance of their workers.

65. *Myrmecia urens* Lowne

(Figs 42, 60, 101a-f)

Myrmecia urens Lowne, 1865, p. 336 [♀]. Santschi, 1928, p. 465. Wheeler and Wheeler, 1971, p. 254 [larva]. Taylor and Brown, 1985, p. 17. Taylor, 1987, p. 46.

Myrmecia (*Promyrmecia*) *urens* Lowne. Clark, 1927, p. 40; 1929, p. 121; 1934a, p. 14. Wheeler, 1933, p. 62.

Promyrmecia urens (Lowne). Clark, 1943, p. 103, pl. 15, figs 56-58 [♀]; 1951, p. 190, figs 158-159.

Myrmecia pumilio Mayr, 1866, p. 896 [♀].

Myrmecia (*Promyrmecia*) *pumilio* Mayr. Clark, 1934a, p. 14.

Myrmecia picta Smith var. *infima* Forel, 1900, p. 54, *syn. nov.* [♀]; 1907, p. 267. Emery, 1911, p. 21.

Myrmecia (*Promyrmecia*) *infima* Forel. Wheeler, 1933, p. 62. Clark, 1934a, p. 14.

Promyrmecia infima (Forel). Clark, 1943, p. 105, pl. 15, figs 59-61 [♀♂]; 1951, p. 192, figs 160-162.

Myrmecia infima Forel. Taylor and Brown, 1985, p. 11. Taylor, 1987, p. 44.

Myrmecia picta Smith var. *nigra* Forel, 1907, p. 267, *syn. nov.* [♀]. Emery, 1911, p. 21.

Myrmecia (*Promyrmecia*) *nigra* Forel. Wheeler, 1933, p. 63.

Promyrmecia nigra (Forel). Clark, 1943, p. 106, pl. 15, figs 62-63 [♀]; 1951, p. 195, figs 164-165.

Myrmecia nigra Forel. Taylor and Brown, 1985, p. 13. Taylor, 1987, p. 44.

Myrmecia (*Promyrmecia*) *dichospila* Clark, 1938, p. 359, *syn*. *nov*. [⚲♀♂].

Promyrmecia dichospila (Clark). Clark, 1943, p. 108, pl. 15, figs 53-55; 1951, p. 198, figs 167-169.

Myrmecia dichospila Clark. Taylor and Brown, 1985, p. 8. Taylor, 1987, p. 42.

Promyrmecia exigua Clark, 1943, p. 107, pl. 15, fig. 64, *syn*. *nov*. [⚲]; 1951, p. 197, fig. 166.

Myrmecia exigua Clark. Taylor and Brown, 1985, p. 9. Taylor, 1987, p. 43.

Promyrmecia rubicunda Clark, 1943, p. 107, pl. 15, fig. 65 [⚲]; 1951, p. 194, fig. 163.

Myrmecia rubicunda Clark. Taylor and Brown, 1985, p. 15. Taylor, 1987, p. 45.

Myrmecia picta Smith, *auct*. (*non* Smith, 1858). Mayr, 1876, p. 94. Forel, 1900, p. 54; 1907, p. 267; 1915, p. 4. Emery, 1911, p. 21. Viehmeyer, 1924, p. 222.

Types

urens: syntype workers, Sydney, N.S.W., in BMNH.

pumilio: syntype workers, Sydney, N.S.W., in NHMW. [Synonymy by Clark, 1951].

infima: holotype worker, Perth, W.A. (Chase), in GMNH. [NEW SYNONYMY].

nigra: holotype worker, East Fremantle, W.A., probably destroyed in ZMH during World War II. [NEW SYNONYMY].

dichospila: syntype workers (9), female and male, Reevesby Island, S.A. (Dec. 1936, J. Clark), in NMV (examined). [NEW SYNONYMY].

rubicunda: holotype worker, Ooldea, S.A. (J.A. Kershaw), in NMV (examined). [NEW SYNONYMY].

exigua: syntype workers (3), Lake Hattah, Vic. (J.E. Dixon), in NMV (examined). [NEW SYNONYMY].

Worker diagnosis

Measurements and proportions as given and illustrated (figs 42a-c).

Colour variable, even within nests. Head and gaster always black;

mandibles yellow or brownish yellow; mesosoma red through to black with various combinations of red and black in between; petiole usually red but may be black or black with red dorsum; postpetiole usually black though occasionally red; antennae and legs yellow through shades of red to brown.

Material examined (fig. 60)

Australian Capital Territory: Canberra (BBL); Cotter (EFR); Cotter River (TGC). *New South Wales*: Berowra (RWT); 6 km S of Bungendore (BBL); Gerroa (BBL); 30 km N of Grenfell (BBL); Ingalba N.R. (BBL); Kangaroo Valley (EFR); Sydney (BBL); 15 km E of Weethalle (BBL) [*SEM*, ♀; *MT*, ♂, 16.iv.1978]. *South Australia* ; Aldgate (BBL) [*MT*, ♂, 4.v.1969]; Belair NP (GFG; in SAM); Blyth (BBL); 32 km W of Bordertown (EFR); Breakneck Creek (PJMG; in SAM); Cowell (BBL); Greenly Island (cu; in SAM); Inneston [273]; 64 km NW of Keith (EFR); Kuitpo (RBa) [*MT*, ♂ only, 8.iv.1985]; Langhorne Creek (RDR; in SAM); 13 km SW of Meningie (BBL); 8 km S of Morgan (HMin; in SAM); Mount Compass (RH; in SAM); Mount Magnificent (GFG; in SAM); Mount Monster (GFG; in SAM); Naracoorte Cave Reserve (GFG; in SAM); Ooldea (JAK) [*rubicunda* holotype]; 14 km NW of Padthaway (GFG; in SAM); Port Lincoln (TG); Reevesby Island (JCl) [*dichospila* syntypes]; Robe (GFG; in SAM); Sevenhill (BBL); Tea Tree Gully (RVS; in SAM); Two Hummock Point (RVS; in SAM); Upper Sturt (GFG; in SAM); Victor Harbor (HW; in SAM); Waitpinga (BBL). *Victoria*: Bendigo (JED); Lake Hattah (JED) [*exigua* syntypes]; Wedderburn (EFR); Wyperfield N.P. (RWT). *Western Australia*: Albany (TG); Augusta (DHC); 8 km NW of Augusta (C&U); Bickley (RPe) [*MT*, ♂ only, 2.v.1985]; Canningmills (RPe) [*MT*, ♂ only, 3.v.1984]; Denmark (TG); 18 km NNE of Denmark (EBB); Esperance (BBL); Gibson (BBL); Kalamunda (MH) [*MT*, ♂ only, 30.v.1985]; Kenton (RWT); Lake Muir (RPe) [*MT*, ♂ only, 22.v.1984]; Ludlow (JCl); Mundaring (JCl); Nornalup (JCl); 42 km ENE of Norseman (KHLK); 16 km S of Perth (EFR); Pinjar (RPe) [*MT*, ♂ only, 12.v.1985]; Porongorup (EFR); Stirling Range (EFR); Thomas River (TG); Walpole (EBB); 30 km NNW of Widgiemooltha (RWT).

[*Note* - Clark (1951) also records *urens* from '*Queensland*: Fletcher, Milmerran, Peak Downs. ... *Tasmania*: Launceston' and, although I have not seen specimens from either state referable to *urens*, the species probably occurs in both states. Taylor and Brown (1985, pp 8, 11, 13, 15, 17) did not record this species from A.C.T.]

Male terminalia (fig. 101a-f)

The variation in the male terminalia of urens is consistent with intraspecific variation.

Ninth and tenth tergites (fig. 101a) 2.3 times wider than long; median lobe rounded, extending just beyond tips of pygostyles. Pygostyles moderately stout; length 0.3 times width of segment. Eighth sternite (fig. 101b) trapezoidal; 1.4 times wider than long; 1.1 times wider posteriorly than anteriorly; anterior margin indented 0.2 times length of segment. Numerous short setae concentrated in two large areas flanking midline in anterior half. Ninth sternite (fig. 101c) 1.1 times longer than wide; moderately long anterior apodeme; antero-lateral lobes developed; lateral lobes absent; posterior margin moderately narrow, indented posteriorly. Basal ring 1.6 times wider than long; 1.4 times wider posteriorly than anteriorly. Outer valve (fig. 101d) 1.7 times longer than deep; posterior end blunt; dorsal median projection digitate, short. Middle valve (fig. 101e) with cuspis much shorter than digitus; digitus moderately broad, curved, broadest in middle, distal end rounded. Inner valve (fig. 101f), excluding anterior apodeme, 1.1 times as long as deep; anterior extension of anterior apodeme 0.5 times length of rest of segment; postero-ventral lobe moderately broad, moderately long, serrated distally; postero-dorsal margin rounded; 3-43 small spines ($\overline{x}$ = 18.7, N = 11) near posterior and postero-ventral margins.

Karyotype: Unknown

Taxa included: Typical urens

Nest structure: Unknown

Biological references (including unpublished theses)

Peakall (1984a, 1984b)

Comments

M. urens is a species, or possibly a complex of sibling species, with variable colour patterning (as indicated above), which can be distinguished by its worker morphology and male terminalia. Six other names have been used for different colour forms but at present there is no evidence to support recognition of these. However, because of the wide distribution of the species and the variable colour patterns, I expect that when karyotypes are examined it is possible that interspecific differences will be found.

3.5 Miscellaneous observations

This section records a number of observations of Myrmecia which do not fit readily into the species descriptions because they are of a less taxonomic nature. Despite the obvious heterogeneity of the information, due to it being collected somewhat incidentally to the main aims of the study, I consider it desirable that such useful data be recorded rather than risk its loss.

3.5.1 Size variation in workers

To investigate distribution and size variation of workers in a colony, an entire polydomous colony of fuscipes was excavated at 46 km N of Renmark, S.A. [146]. The colony was collected on a cool day, 26 May 1981, when the maximum temperature was c.20°C and the overnight minimum c.5°C.

From the surface, the colony appeared to consist of eight nests (A-H) placed within 2.5 m of a large sheoak (Casuarina sp.). Before excavation, paraffin wax was poured into nests A, B and C because these appeared to be the only ones containing workers. This was done at 9 a.m., 10 a.m. and 11 a.m. (Central Standard Time) respectively. Nest A required 5.6 l of molten wax to fill while nest B needed 6.0 l. Nest C was only partially filled but seemed to be similar in size to A and B. The depth of A was 87 cm, B, 76 cm and C, 51 cm. Excavation of all eight nests was completed at 2.00 p.m. the next day. All workers returning to the nests while I was pouring the wax and during excavation were collected. The appearances of the casts are illustrated in fig. 126a-b.

In the following weeks all workers trapped in the casts were recovered by melting the wax and their locations were recorded. The contents of the nests are listed in Table 6. I found that the colony consisted of: (i) a main nest (B; many workers, colony queen, pupae, larvae); (ii) four large satellite nests (A,C,D,F; few or no workers, no brood, possibly former main nests of the colony); and (iii) two small satellite nests (G,H; no workers or brood; newly excavated). Nest H was occupied by Rhytidoponera mayri (Emery) but may have originally belonged to the colony because it was very similar in appearance to the large satellite nests. The 452 workers collected from this colony were used for the morphometric analysis below.

Initially 14 measurements, which are defined in Chapter 2, were taken for each of 100 specimens. These were mandible length (ML), head length (HL), head width (HW), scape length (SL), eye length (EL), mesosoma length (MeL), pronotum width (PW), front femora length (FFL), middle femora length (MFL), hind femora length (HFL), petiolar node length (PNL), petiolar node height (PNH), postpetiole length (PPL) and postpetiole width (PPW). These measurements are summarized in Table 7. Pearson product moment correlation coefficients (r) were determined for

Table 6. Contents of nests in polydomous colony 146 (M. fuscipes).

Nest	Workers	Queens	Pupae	Larvae	Comments
A	2	0	0	0	Satellite nest, extensive system of galleries and chambers. *
B	407	2 **	14	144	Main nest, extensive system of galleries and chambers. *
C	3	0	0	0	Satellite nest, extensive system of galleries and chambers. ***
D	0	0	0	0	Abandoned nest, extensive system of galleries and chambers.
E	0	0	0	0	Nest inhabited by Rhytidoponera mayri, extensive system of galleries and chambers, possibly an abandoned nest of M. fuscipes.
F	0	0	0	0	Abandoned nest, extensive system of galleries and chambers.
G	0	0	0	0	Incipient nest, few small chambers.
H	0	0	0	0	Incipient nest, few small chambers.
On surface	40	0	0	0	Ants collected from outside the nests
TOTAL	452	2	14	144	

* Cast in paraffin wax.
** One dealate queen, one alate queen.
*** Partially cast in paraffin wax.

each pair of variables using SPSS (Statistical Package for the Social Sciences) on a CYBER computer (Table 8). In each case r was greater than 0.900 (indicating a strong linear relationship) and the significance (derived by using Student's t-test with N-2 degrees of freedom) was at the 0.001 level. I decided that fewer variables needed

TABLE 7 Worker measurements for colony 146

Measurement	No. of workers measured (N)	Mean (x)	Standard Deviation (S.D.)	Coefficient of Variability (C.V.)
ML	100,451	3.546,3.456	0.521,0.576	14.7,16.7
HL	100,452	3.331,3.241	0.422,0.449	12.7,13.8
HW	100,450	3.577,3.465	0.475,0.506	13.3,14.6
PW	100,449	1.974,1.978	0.294,0.315	14.9,15.9
SL	100	4.161	0.528	12.7
EL	100	1.299	0.172	13.2
MeL	100	6.450	0.782	12.1
FFL	100	3.888	0.498	12.8
MFL	99	4.374	0.561	12.8
HFL	100	5.783	0.692	12.0
PNL	99	2.252	0.305	13.6
PNH	98	1.117	0.168	15.0
PPL	99	1.517	0.221	14.6
PPW	99	1.520	0.231	15.2

to be measured and chose to continue measuring only ML, HL, PW and HW for the remaining 352 workers. I argued that if a species is polymorphic (i.e. has more than one caste) the polymorphism would show up as a sharp change in slope when a log-log plot of two variables is drawn (see Wilson, 1971; Oster and Wilson, 1979). Unfortunately, there are no rules as to which linear measurements could be involved in such polymorphism. Therefore scattergrams were drawn for each pair of variables (both unlogged and logged; figs 127-129) and straight lines with no apparent change in slope resulted. This indicated that <u>fuscipes</u>

TABLE 8. Pearson product moment correlation coefficients for each pair of variables

	ML	HL	HW	SL	EL	MeL	PW	FFL	MFL	HFL	PNL	PNH	PPL	PPW
ML	*	*	*	*	*	*	*	*	*	*	*	*	*	*
HL	.984	*	*	*	*	*	*	*	*	*	*	*	*	*
HW	.987	.984	*	*	*	*	*	*	*	*	*	*	*	*
SL	.969	.964	.972	*	*	*	*	*	*	*	*	*	*	*
EL	.970	.978	.967	.948	*	*	*	*	*	*	*	*	*	*
MeL	.980	.981	.987	.964	.967	*	*	*	*	*	*	*	*	*
PW	.943	.948	.960	.934	.946	.952	*	*	*	*	*	*	*	*
FFL	.977	.973	.981	.969	.959	.973	.948	*	*	*	*	*	*	*
MFL	.963	.959	.972	.952	.943	.959	.934	.974	*	*	*	*	*	*
HFL	.958	.953	.964	.953	.928	.958	.923	.976	.966	*	*	*	*	*
PNL	.977	.978	.983	.963	.964	.979	.945	.968	.951	.946	*	*	*	*
PNH	.966	.965	.979	.942	.956	.969	.957	.958	.947	.938	.973	*	*	*
PPL	.935	.935	.948	.915	.916	.942	.933	.942	.936	.931	.938	.948	*	*
PPW	.959	.963	.976	.935	.952	.965	.957	.955	.952	.935	.967	.983	.955	*

was not polymorphic with respect to any of the pairs of variables measured.

The next step was to see if the apparent division between nanitics and larger workers is borne out by size frequency distributions. Size frequency distributions at intervals of 0.125 mm were drawn for each of the four variables (fig. 130). For ML and HL these appeared to be bimodal but for HW and PW they were weakly trimodal. Replotting PW at intervals of 0.100 mm enhanced the trimodal appearance (fig. 131a) indicating that the third mode was not an artefact of the interval chosen. The existence of this weak third mode was more obvious when I examined a second colony [59] from the same locality (fig. 131b). Other nests of fuscipes from Port Parham, Port Germein and Laura Bay and nests of a closely related species, nigriceps, s.s., from Blewitt Springs did not have any suggestion of the third mode (figs 131c-d, 132-133).

In order to determine what functions workers of different sizes might perform in the nest I examined the distribution of various size classes in the different parts of colony 146. The locations of adult ants and brood within nests A and B are indicated in fig. 126.

In nest B (the main nest) pupae were located in the three lowest chambers, the nest queen in the fourth lowest chamber and the larvae were in the fifth to seventh lowest chambers.

The mean sizes (as judged by pronotal width) of workers in the 16 inhabited chambers of nest B and also those collected from nests A and C and outside the nests, are presented in Table 9. From Table 9 it appears that the largest workers are located in some of the upper chambers of nest B (B15, B19 and B20), in nests A and C, and on the surface. Smaller workers were mainly in the lower chambers of nest B. To investigate this further I have treated the colony as being composed of seven portions (1) B1-B3 (chambers with pupae), (2) B4 (chamber with colony queen), (3) B5-B7 (chambers with larvae), (4) B8, B9, B11, B12 (lower chambers - other than those above), (5) B10, B13, B15, B19, B20 (upper chambers), (6) A,C (other nests), and (7) surface. Similarly, workers are divided into five size classes on the basis of pronotum width (I: 1.300-1.599 mm, II: 1.600-1.899 mm, III: 1.900-2.199 mm, IV: 2.200-2.499 mm and V: 2.500-2.799 mm).

The number of each size class found in each portion of the colony is presented in Table 10. Similar tables present the same information as percentages of each size class (Table 11) and percentages of workers in each colony portion (Table 12). From the three tables it is clear

TABLE 9. Worker pronotum width in different parts of colony 146

Nest [& Chamber]	No. of workers measured (N)	Mean (x)	Standard Deviation (S.D.)	Coefficient of Variability (C.V.)
A	2	2.406	1.454	60.4
B1	17	1.669	1.207	72.3
B2	21	1.889	1.045	55.3
B3	15	2.030	1.079	53.2
B4	37	1.920	1.041	54.2
B5	94	1.845	1.038	56.2
B6	11	2.084	1.082	51.9
B7	44	1.894	1.056	55.8
B8	40	1.829	1.037	56.7
B9	46	2.058	1.062	51.6
B10	6	2.093	1.118	53.4
B11	33	2.094	1.059	50.6
B12	29	2.131	1.065	50.0
B13	3	1.796	1.294	72.0
B15	2	2.542	1.414	55.6
B19	3	2.390	1.244	52.1
B20	3	2.481	1.230	49.6
C	3	2.507	1.233	49.2
On surface	40	2.255	1.055	46.8

that although more workers are found in the lower chambers than the upper, the upper chambers contain mainly large workers (size classes IV and V) while the lower chambers contain mainly small workers (size

TABLE 10. Numbers of workers in each size class from each section of colony 146.

Section of polydomous colony	Number of workers in size class:					TOTAL
	I (1.300-1.599)	II (1.600-1.899)	III (1.900-2.199)	IV (2.200-2.499)	V (2.500-2.799)	
B1-B3 (with pupae)	4	28	16	3	2	53
B4 (with colony queen)	4	14	16	2	1	37
B5-B7 (with larvae)	23	65	44	14	3	149
B8,B9,B11,B12 (lower chambers)	15	37	57	25	14	149
B10,B13,B15,B19,B20 (upper chambers)	2	2	2	7	4	17
A,C (other nests)	0	0	1	1	3	5
On surface	2	2	12	14	10	40
TOTAL	50	148	148	66	37	449

TABLE 11. Percentage of workers in each size class occupying each section of colony 146.

Section of polydomous colony	Percentage of workers in each size class				
	I (1.300-1.599)	II (1.600-1.899)	III (1.900-2.199)	IV (2.200-2.499)	V (2.500-2.799)
B1-B3 (with pupae)	8	19	11	5	5
B4 (with colony queen)	8	9	11	3	3
B5-B7 (with larvae)	46	44	30	21	8
B8,B9,B11,B12 (lower chambers)	30	25	39	38	39
B10,B13,B15,B19,B20 (upper chambers)	4	1	1	11	11
A,C (other nests)	0	0	1	2	8
On surface	4	1	8	21	27

TABLE 12. Percentage of workers in each colony section occupied by each size class of colony 146.

Section of polydomous colony	Percentage of workers in each colony section I (1.300-1.599)	II (1.600-1.899)	III (1.900-2.199)	IV (2.200-2.499)	V (2.500-2.799)
B1-B3 (with pupae)	8	53	30	6	4
B4 (with colony queen)	11	38	43	5	3
B5-B7 (with larvae)	15	44	30	9	2
B8,B9,B11,B12 (lower chambers)	10	25	38	17	9
B10,B13,B15,B19,B20 (upper chambers)	12	12	12	41	26
A,C (other nests)	0	0	20	20	60
On surface	5	5	30	35	25

classes II and III).

3.5.2 Eucharitine parasites

Several unsupported statements to the effect that eucharitine parasites (Hymenoptera: Pteromalidae: Eucharitinae) are common in Myrmecia nests have been made by Wheeler (1933, p. 23), Haskins and Haskins (1950, p. 489) and Riek (1970, p. 921). I first found such parasites in a nest of sp.11 at Elliston (S.A.) [173]. The nest contained cocoons which had been spun by Myrmecia larvae but from which adult eucharitine wasps emerged. These were later identified by I.D. Naumann (pers.comm.) as 'Gen. et sp. nov. (near "Epimetagea" rufiventris (Ashmead))'. Conspecific wasps were also found in nests of nigriceps, s.s. at Cataby Brook (W.A.) [461] and Inneston (S.A.) [270], and in nests of atrata in Stirling Ranges N.P. (W.A.) [446]. These specimens are now lodged in the ANIC with voucher specimens from the host nests. Similar eucharitines have been reported as parasites of forficata, s.l. (Forel, 1890; Wheeler, 1910), vindex (Douglas and

McKenna, 1970; I.D. Naumann, pers. comm., from specimens in ANIC collected by J. Clark) and other unspecified *Myrmecia* (Wheeler, 1933; Haskins and Haskins, 1950). I estimate that about 5% of *Myrmecia* nests are parasitized by eucharitines.

The features of the life cycle of these wasps which enable them to penetrate the colony defences of *Myrmecia* have not been fully investigated but what is known is summarized below. The first instar larva, called a planidium, is a free-living creature which may enter the nest by attaching itself to a returning worker. Inside the nest the planidium finds a host *Myrmecia* larva and becomes an endoparasite. Some time after the host larva has spun its cocoon it dies and the wasp larva, by now stout and grub-like, pupates inside the *Myrmecia* cocoon. Eventually the adult wasp emerges by cutting a neat circular hole around one end of the cocoon. It is not certain how the adult wasps are then able to leave the nest without being killed by the *Myrmecia* workers. However, a chance observation of the emergence of the adult wasps from pupae of one colony enables me to speculate about how this may be achieved. Colony 446 (*atrata*) was collected on a fairly cool day and the captured pupae were placed near the heater of my car. Within about 10 minutes all the parasitized cocoons had eclosed suggesting that the rise in temperature had triggered this behaviour. Such an adaptation would be advantageous to the chances of the adult wasps eluding capture by *Myrmecia* workers because it would mean that their emergence would occur near the top of the nest (where cocoons are stored on warm days and quite high temperatures can be experienced) rather than near the bottom where the temperature is fairly constant year round. Depending on how close to the entrance a parasitized cocoon is placed, the number of *Myrmecia* workers an adult wasp must pass to reach safety may be greatly reduced.

3.5.3 Light-coloured individuals

Browning (1979) discussed the occurrence of a light-coloured worker in a fuscipes colony at Port Parham (S.A.) and speculated upon its identity. It is now clear that this specimen did not belong to a separate (socially parasitic) species as was suggested.

No such workers have since been found in any fuscipes nests but a colony of rufinodis at Marion Bay (S.A.) [269] was found to contain large numbers of similarly light-coloured workers. These workers had a mandible structure identical to that of rufinodis and quite distinct from that of the light-coloured worker from the fuscipes nest at Port Parham, which had mandibles identical to fuscipes. In addition, large numbers of light-coloured workers collected from pilosula, s.l. nests are present in museum collections and these are only distinguishable from pilosula, s.l. by their colour. It is therefore probable that such specimens are merely light-coloured intranidal variants of the species concerned. The reason for their lack of melanization was unknown until M.W.J. Crosland (pers. comm.) found that light-coloured pilosula, s.l. workers contained large numbers of spores of a species of gregarine protozoan. Workers from colony 269 sent to Crosland were also found to contain large numbers of these spores.

I also saw a light coloured worker in colony of sp.17 at Bellbird (N.S.W.) [365] but unfortunately it escaped beneath the surface before it could be collected.

3.5.4 Multiple queens

M. pilosula, s.l. is the only species of Myrmecia known to have polygynous mature colonies (i.e. containing more than one dealate, and presumably fertile, queen) as a common condition. The only other species reported to have supernumerary dealate queens are *varians* and *desertorum* (Gray, 1974a), but in each case only one nest was observed and they also contained large numbers of alate queens and males. This suggests that the dealate queens may have been virgins which had lost their wings prematurely, or possibly queens fertilized by a sibling. In neither nest was there evidence to suggest that excess dealate queens would have remained in the nest beyond the end of mating season.

However, there is some evidence to suggest that a few species may often start their nests with more than one queen. This was first reported by Brown (1953b) after he found six dealate queens and two large workers of *simillima* forming a colony at Burwood (Vic.) in September, 1952. This species probably has mating flights in about March or April so the colony apparently persisted for at least five or six months with more than one dealate queen.

I found seven dealate queens and one worker in one nest of *sp.11* at Elliston (S.A.) [129] and two queens and two larvae in another of the same species at the same locality [171] (collected on 20.i.1981 and 12.xii.1981 respectively). *M. sp.11* has mating flights in about January to February so these colonies may have included more than one dealate queen for almost twelve months.

The only other time I found more than one dealate queen together was in a nest of *vindex* containing three dealate queens at Cape Le Grand (W.A.) [420] - collected on 6.x.1983. This species has mating flights from about December through to April so the colony was probably formed at least six months before.

3.5.5 Carabid nest co-inhabitant

One nest of *atrata* at Ravensthorpe (W.A.) [241] was found to contain a 35 mm long carabid beetle, which I later identified as

Epilectus fortis Blackburn (Carabidae: Scaritinae). This species had previously been collected very few times (no specimens in WAM; holotype only in SAM; three specimens in NMV) and never from Western Australia. The beetle is heavily armoured and has grooves to receive the antennae and legs which were quickly used when I placed the specimen with live *Myrmecia*. The specimen thus appeared to be safe from the *Myrmecia* and was not killed. When offered *Myrmecia* larvae the beetle responded by quickly consuming them, so possibly it is a predator of *Myrmecia* (or ant) larvae. Unfortunately, there is no other evidence to suggest how frequently *E. fortis* is found in *Myrmecia* nests, and even this example may have been coincidental because colony 241 contained only four workers and had many disused chambers and galleries.

Figure 8a-c. Scanning electron micrographs of <u>Myrmecia forceps</u> Roger worker, from Rocky River H.S., S.A. [31], standard views. TL c.22, ML 4.02, HL 3.54, HW 3.63, SL 4.23, MeL 6.13, PW 2.11, PNH 1.08, PNL 2.13, PNW 1.11, CI 103, MI 114, MI2 111, SI 119, PNI 52, PNI2 51, MeI 34.

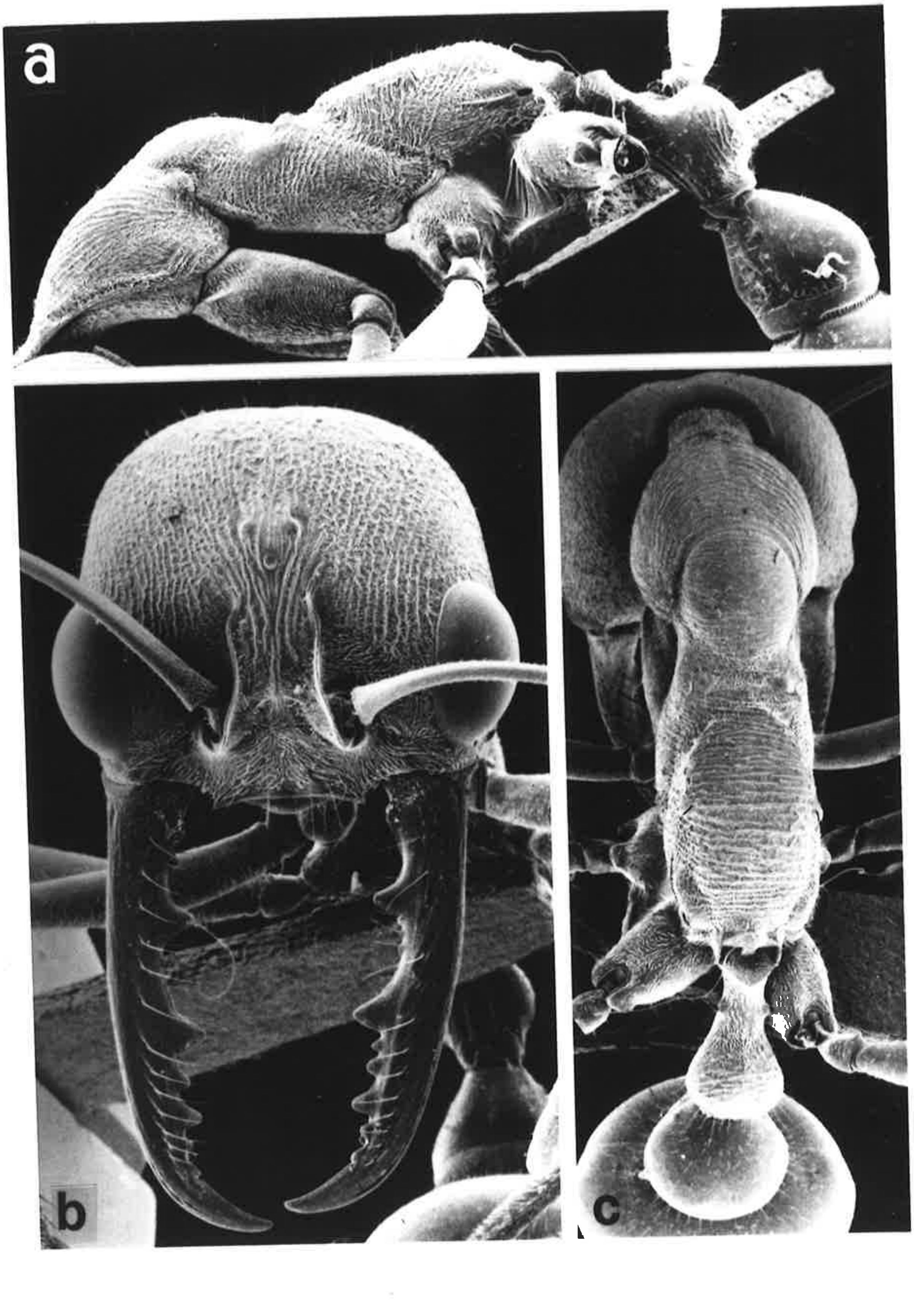
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Figure 9a-c. Scanning electron micrographs of Myrmecia pyriformis Smith worker, from Upper Hermitage, S.A. [36], standard views. TL c.21, ML 3.35, HL 3.21, HW 3.21, SL 3.28, MeL 6.03, PW 2.09, PNH 1.18, PNL 1.98, PNW 1.13, CI 100, MI 104, MI2 104, SI 102, PNI 57, PNI2 60, MeI 35.

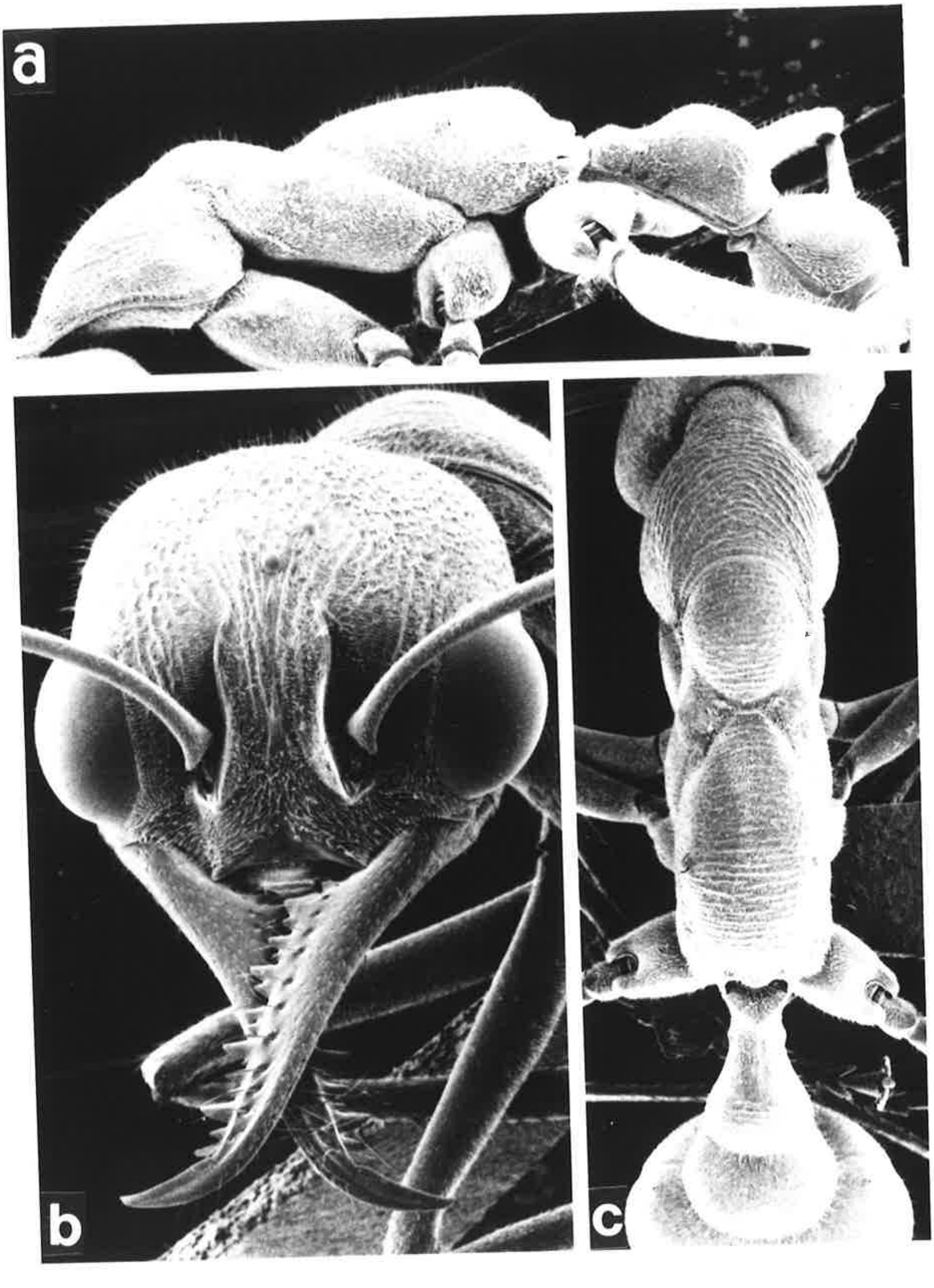
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Figure 10a-c. Scanning electron micrographs of Myrmecia sp.9 (ANIC) worker, from Rocky River H.S. [17], S.A., standard views. TL c.23, ML 3.97, HL 3.59, HW 3.49, SL 3.88, MeL 6.60, PW 2.42, PNH 1.28, PNL 2.11, PNW 1.28, CI 97, MI 111, MI2 114, SI 108, PNI 61, PNI2 61, MeI 37.

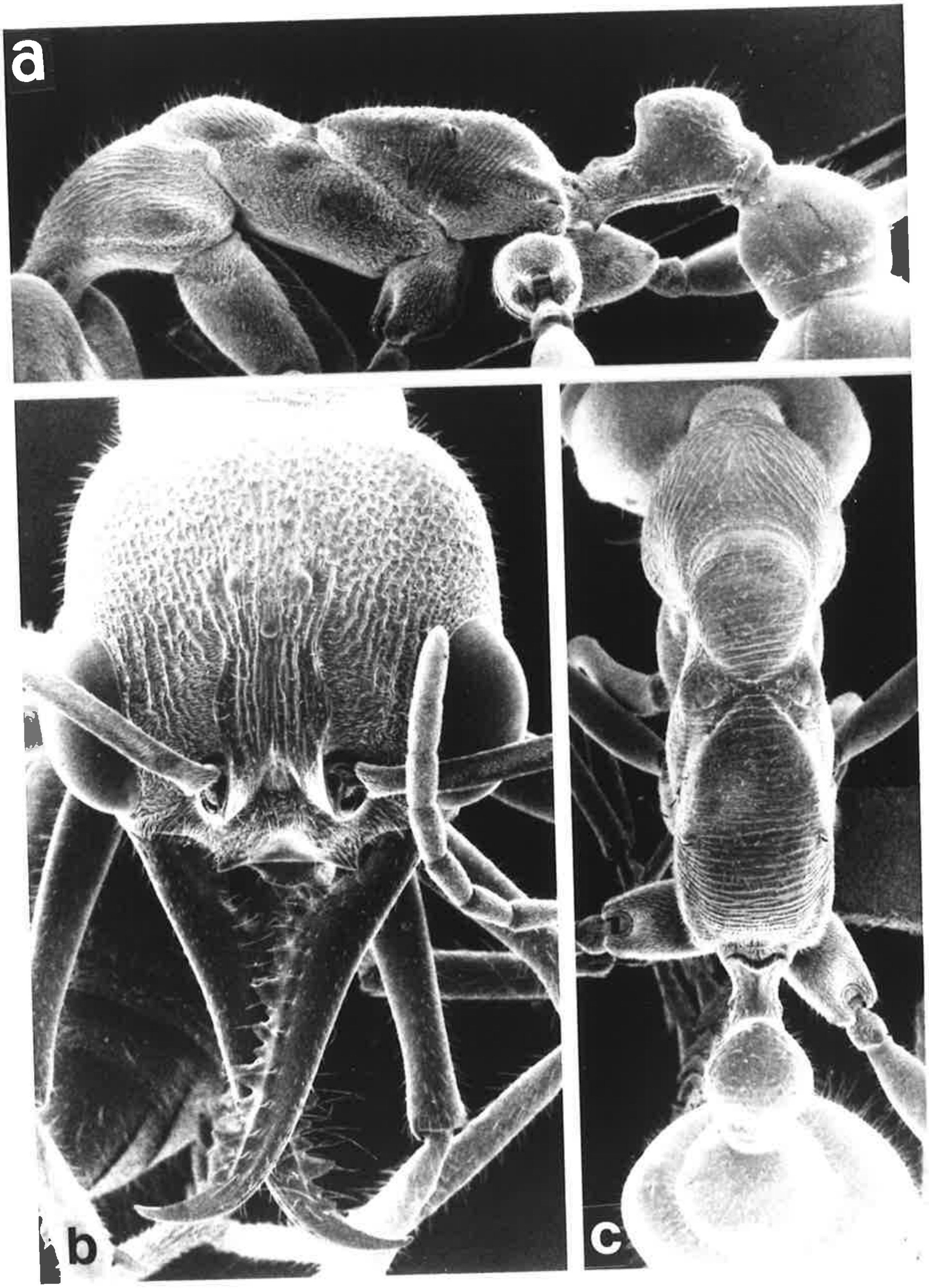
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Figure 11a-c. Scanning electron micrographs of *Myrmecia* *mjobergi* Forel worker, from Lake Barrine, Qld (RWT; in ANIC), standard views. TL c.29, ML 5.68, HL 4.69, HW 4.01, SL 5.54, MeL 8.23, PW 2.67, PNH 1.56, PNL 2.96, PNW 1.44, CI 86, MI 121, MI2 142, SI 118, PNI 49, PNI2 53, MeI 32.

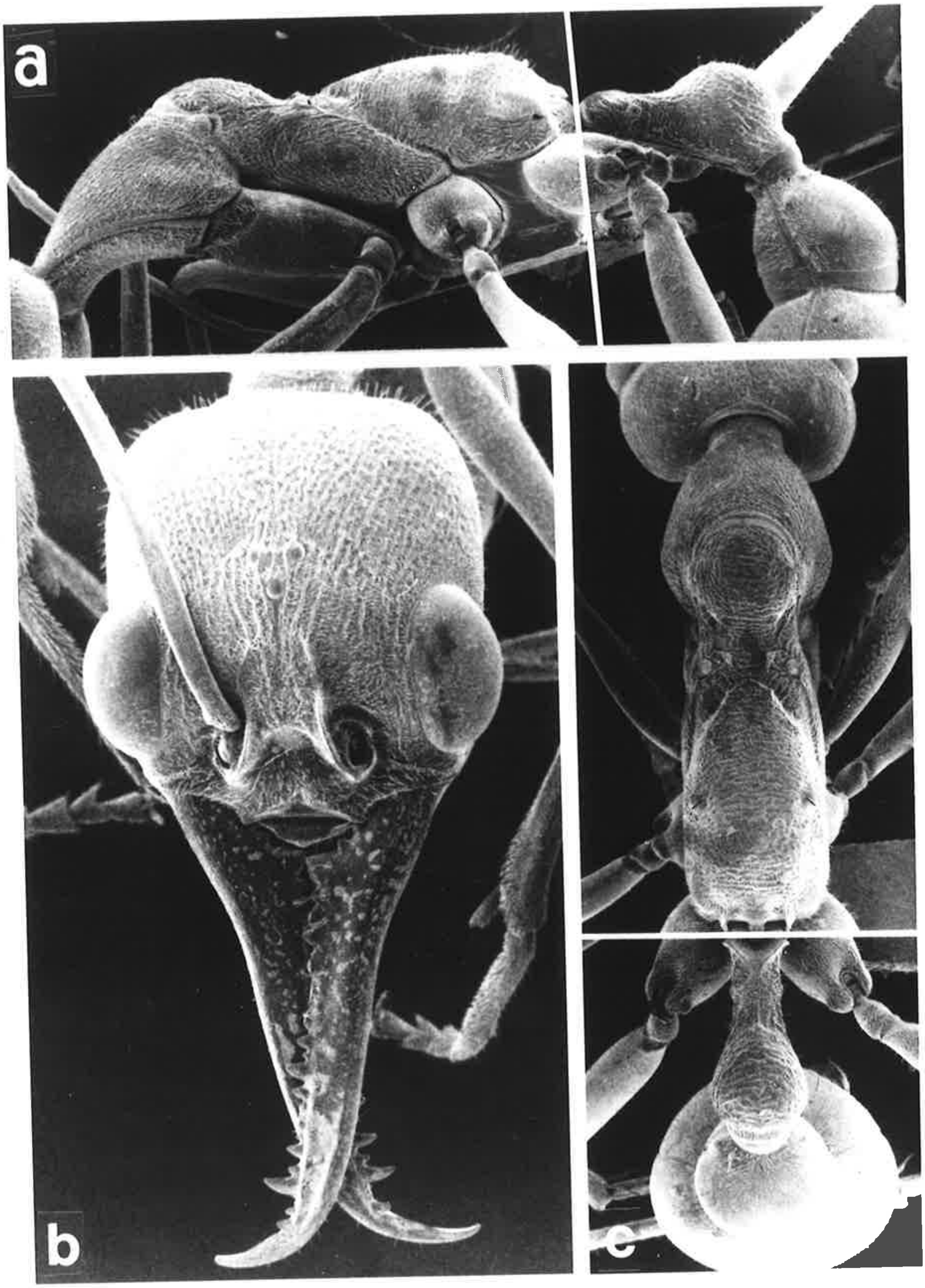
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Figure 12a-c. Scanning electron micrographs of <u>Myrmecia</u> <u>nigriscapa</u> Roger worker, from Point Avoid, S.A. [305], standard views. TL c.20, ML 3.58, HL 3.28, HW 3.23, SL 3.85, MeL 5.91, PW 2.13, PNH 1.26, PNL 1.90, PNW 1.17, CI 98, MI 109, MI2 111, SI 117, PNI 62, PNI2 66, MeI 36.

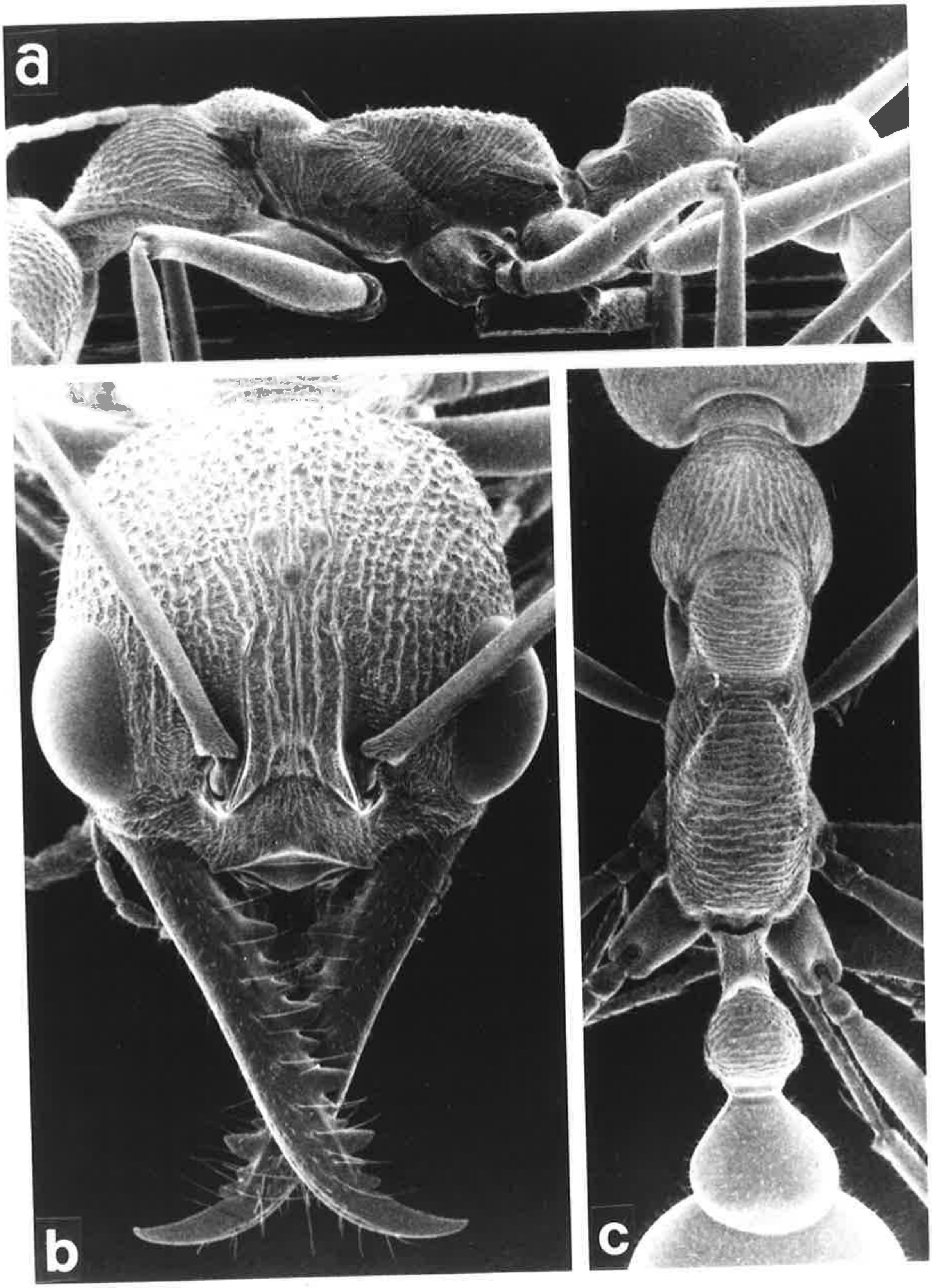
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Figure 13a-c. Scanning electron micrographs of Myrmecia tarsata Smith worker, from 20 km NW of Braidwood, N.S.W. [78], standard views. TL c.22, ML 3.51, HL 3.41, HW 3.43, SL 3.63, MeL 6.40, PW 2.37, PNH 1.39, PNL 1.83, PNW 1.30, CI 101, MI 103, MI2 102, SI 106, PNI 71, PNI2 76, MeI 37.

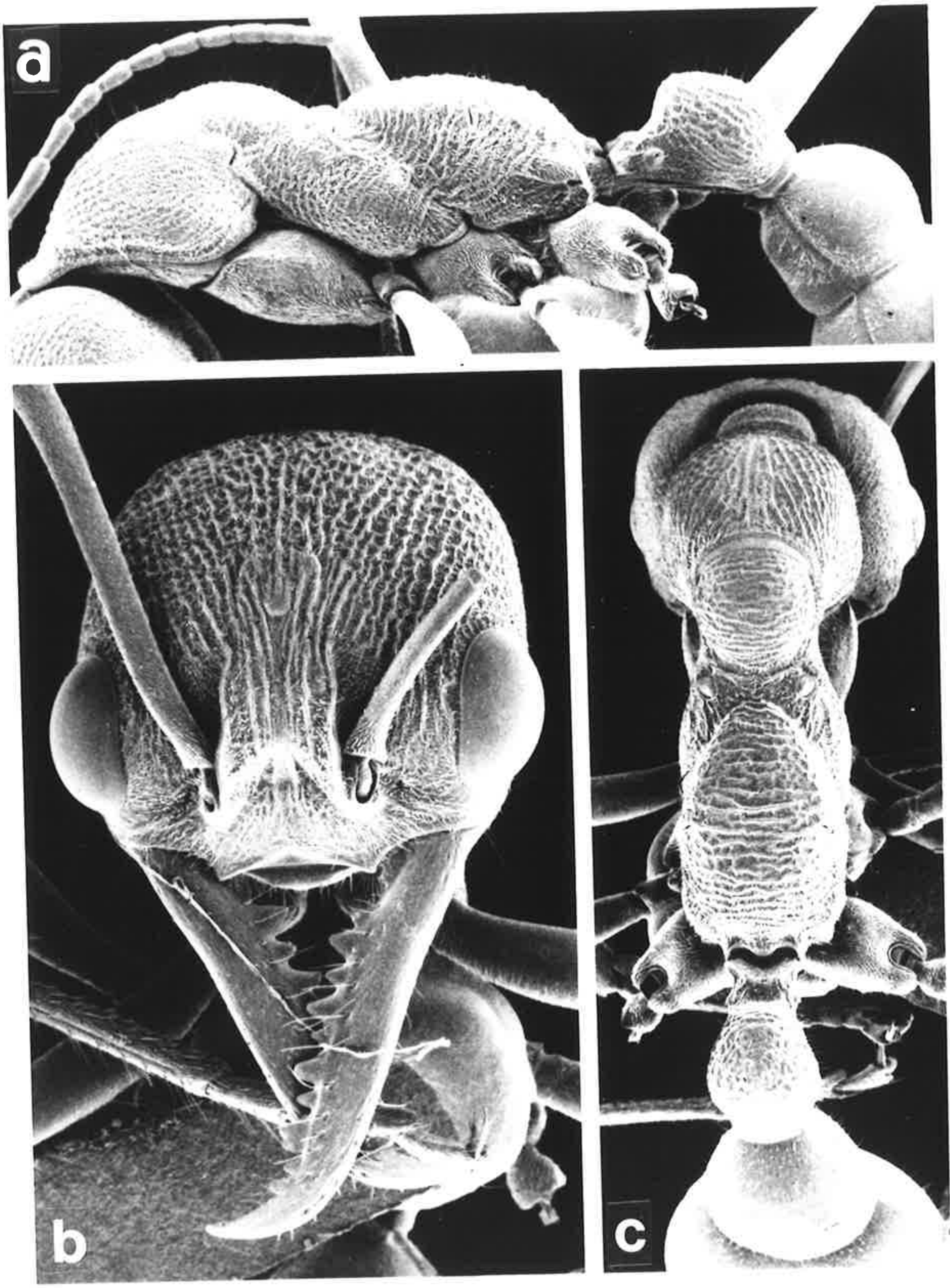
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Figure 14a-c. Scanning electron micrographs of _Myrmecia auriventris_ Mayr worker, from 12 km W of Paluma, Qld [510], standard views. TL c.19, ML 3.16, HL 3.18, HW 3.21, SL 2.99, MeL 5.48, PW 2.14, PNH 1.10, PNL 1.75, PNW 1.09, CI 101, MI 99, MI2 98, SI 94, PNI 62, PNI2 63, MeI 39.

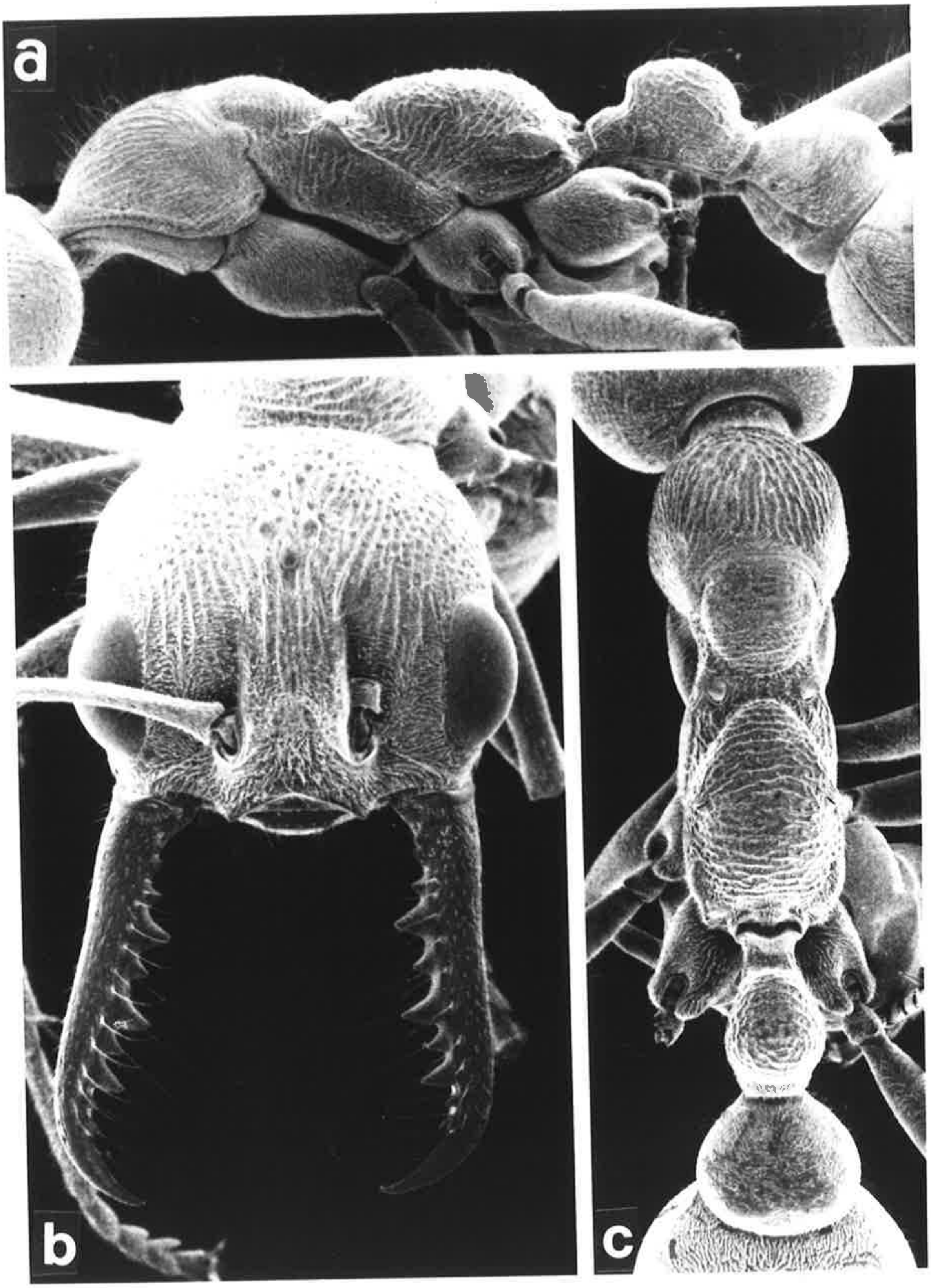
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Figure 15a-c. Scanning electron micrographs of *Myrmecia flavicoma* Roger worker, from 6 km N of Cooyar, Qld (BBL; in ANIC), standard views. TL c.20, ML 3.16, HL 3.10, HW 3.12, SL 3.48, MeL 5.93, PW 1.99, PNH 1.14, PNL 1.83, PNW 1.12, CI 101, MI 102, MI2 101, SI 112, PNI 61, PNI2 62, MeI 34.

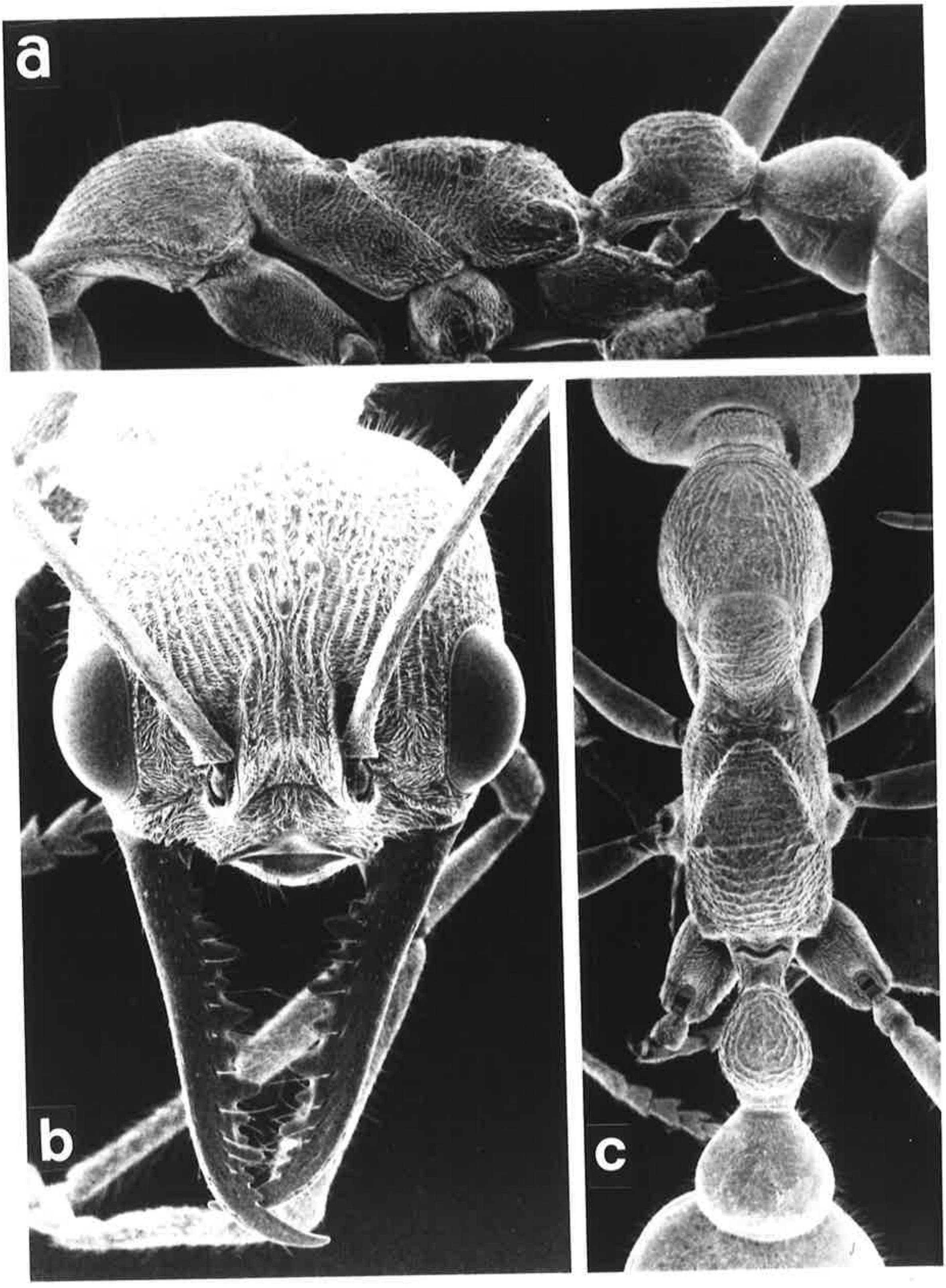
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Figure 16a-c. Scanning electron micrographs of Myrmecia gulosa (Fabricius) worker, from Bellbird, N.S.W. [364], standard views. TL c.23, ML 3.93, HL 3.68, HW 3.49, SL 4.41, MeL 6.80, PW 2.14, PNH 1.25, PNL 2.40, PNW 1.13, CI 95, MI 107, MI2 113, SI 120, PNI 47, PNI2 52, MeI 31.

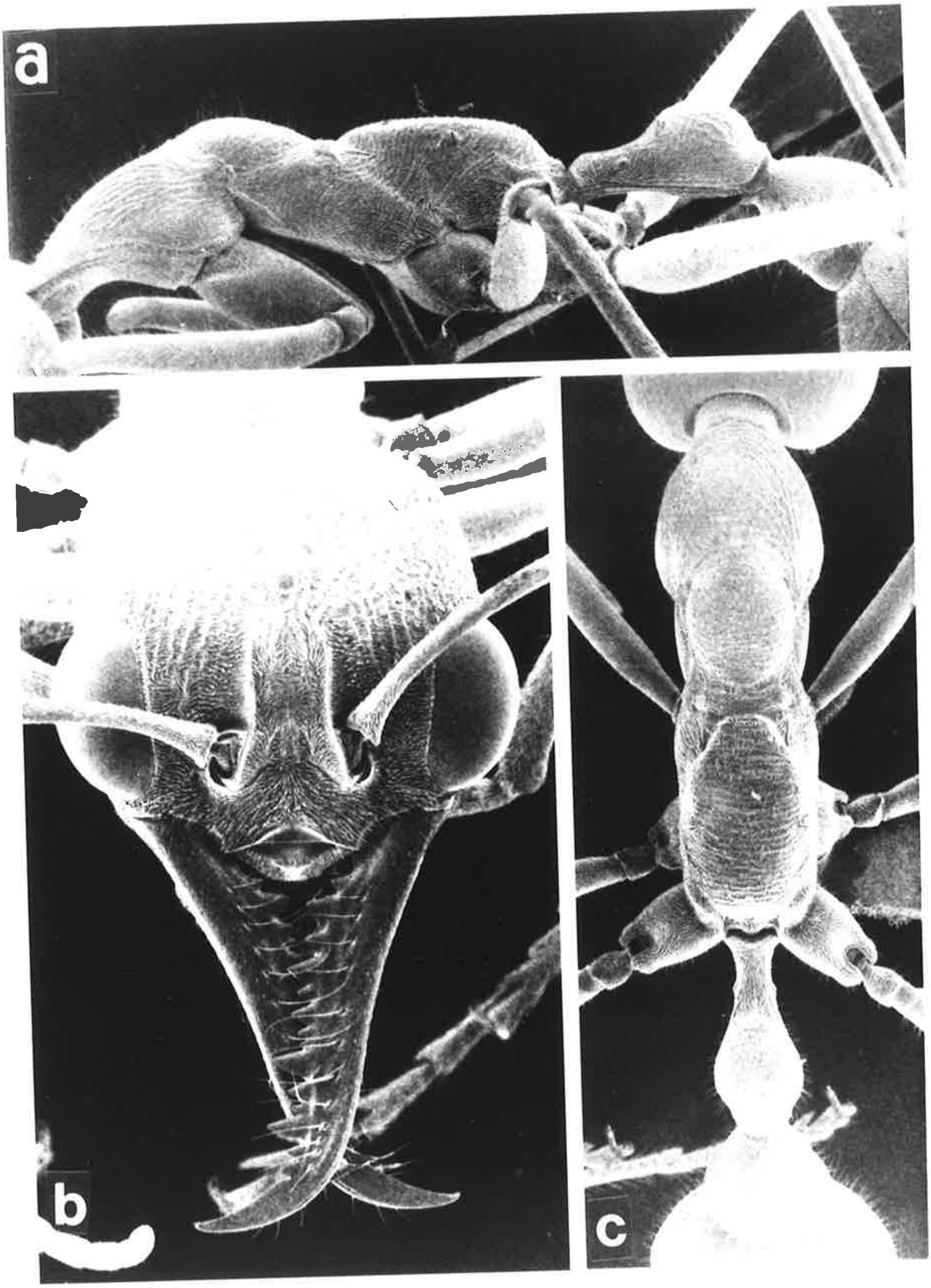
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Figure 17a-c. Scanning electron micrographs of Myrmecia arnoldi Clark worker, from Jerramungup, W.A. [437], standard views. TL c.23, ML 4.07, HL 3.78, HW 3.59, SL 4.71, MeL 6.70, PW 2.23, PNH 1.23, PNL 2.44, PNW 1.06, CI 95, MI 108, MI2 113, SI 125, PNI 43, PNI2 50, MeI 33.

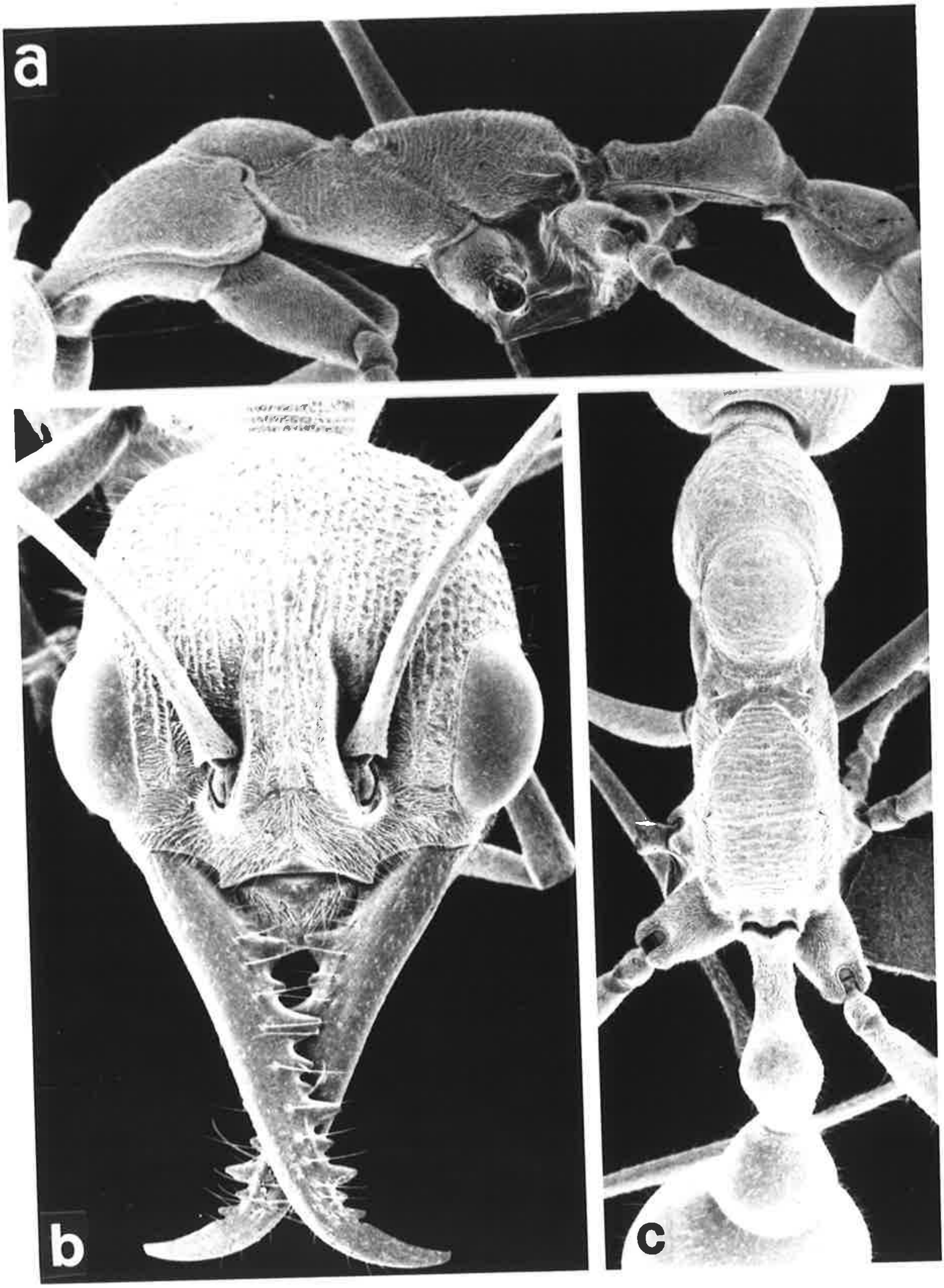
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Figure 18a-c. Scanning electron micrographs of *Myrmecia simillima* Smith worker, from Fitzgerald's Mountain, N.S.W. [509], standard views. TL c.22, ML 3.92, HL 3.65, HW 3.75, SL 3.96, MeL 6.20, PW 2.40, PNH 1.28, PNL 2.03, PNW 1.27, CI 103, MI 107, MI2 105, SI 108, PNI 63, PNI2 63, MeI 39.

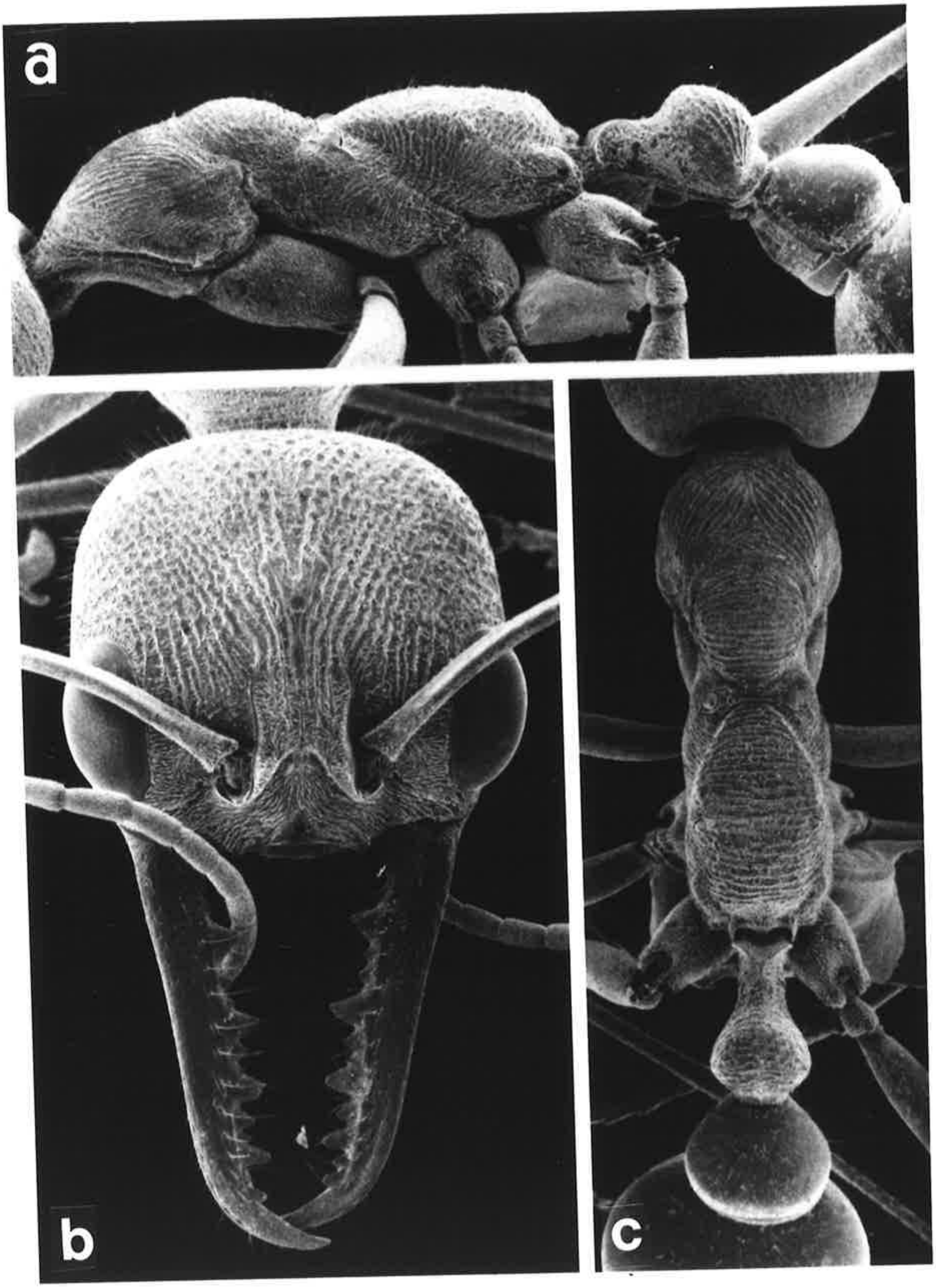
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Figure 19a-c. Scanning electron micrographs of Myrmecia atrata Clark worker, from Jerramungup, W.A. [226], standard views. TL c.23, ML 4.43, HL 3.98, HW 3.92, SL 4.42, MeL 7.32, PW 2.46, PNH 1.31, PNL 2.79, PNW 1.14, CI 98, MI 111, MI2 113, SI 111, PNI 41, PNI2 47, MeI 34.

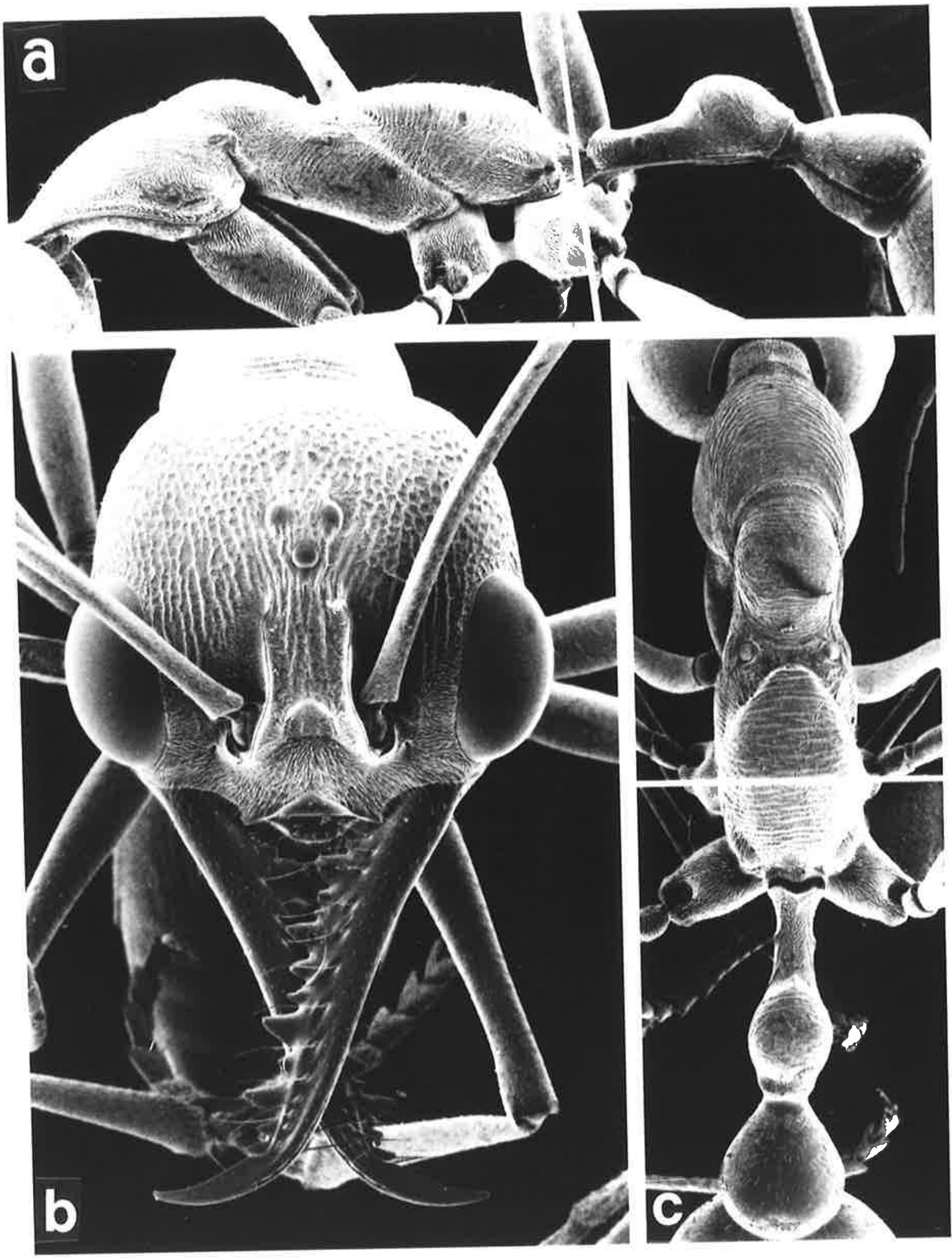
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Figure 20a-c. Scanning electron micrographs of Myrmecia atrata Clark worker, from Ravensthorpe, W.A. [240], standard views. TL c.23, ML 3.80, HL 3.57, HW 3.39, SL 4.46, MeL 6.68, PW 2.16, PNH 1.22, PNL 2.37, PNW 1.11, CI 95, MI 106, MI2 112, SI 125, PNI 47, PNI2 51, MeI 32.

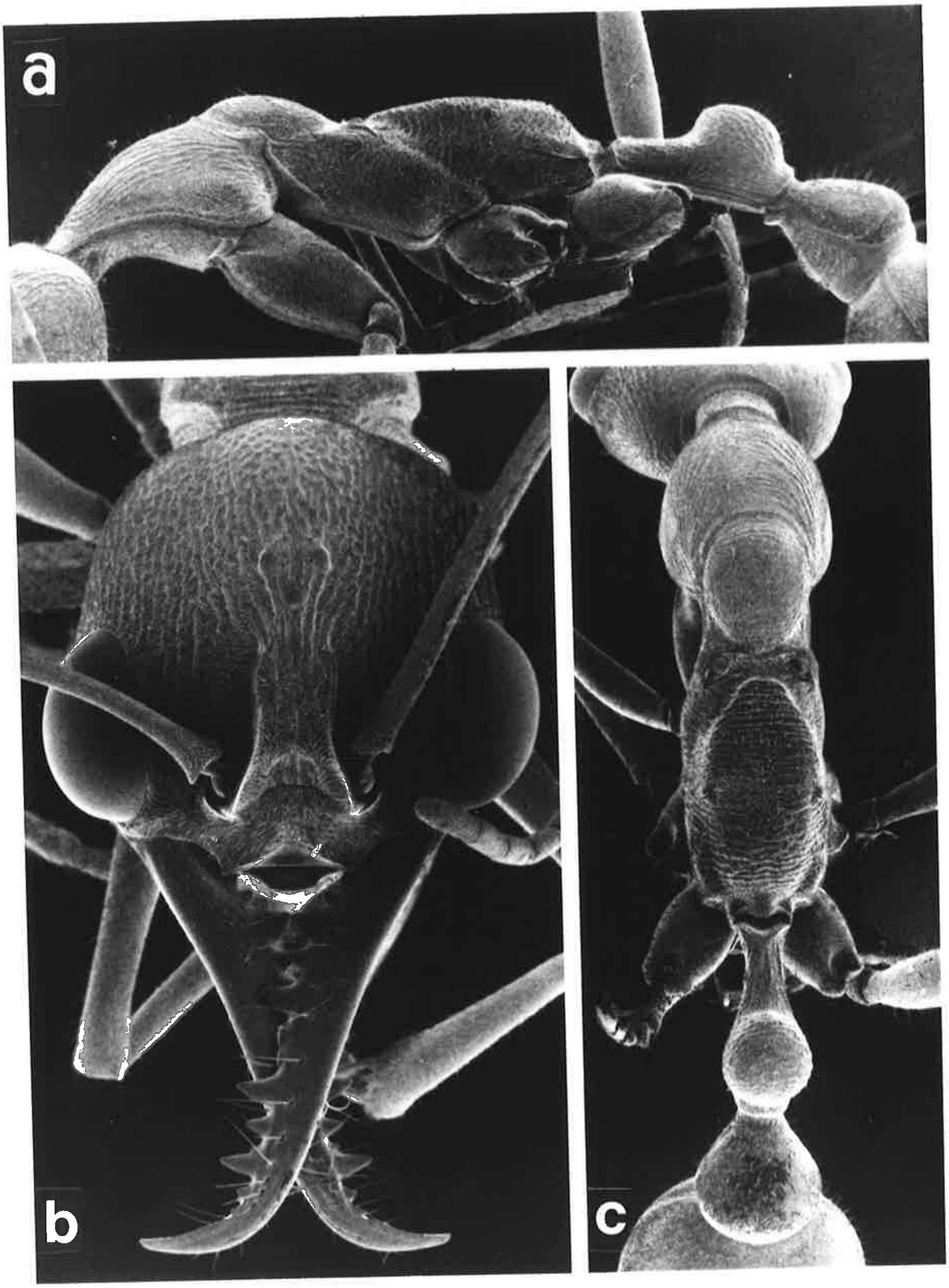
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Figure 21a-c. Scanning electron micrographs of Myrmecia fulgida Clark worker, from South Ironcap, W.A. [431], standard views. TL c.25, ML 4.25, HL 4.23, HW 4.08, SL 4.97, MeL 7.68, PW 2.71, PNH 1.42, PNL 2.60, PNW 1.44, CI 96, MI 100, MI2 104, SI 117, PNI 55, PNI2 55, MeI 35.

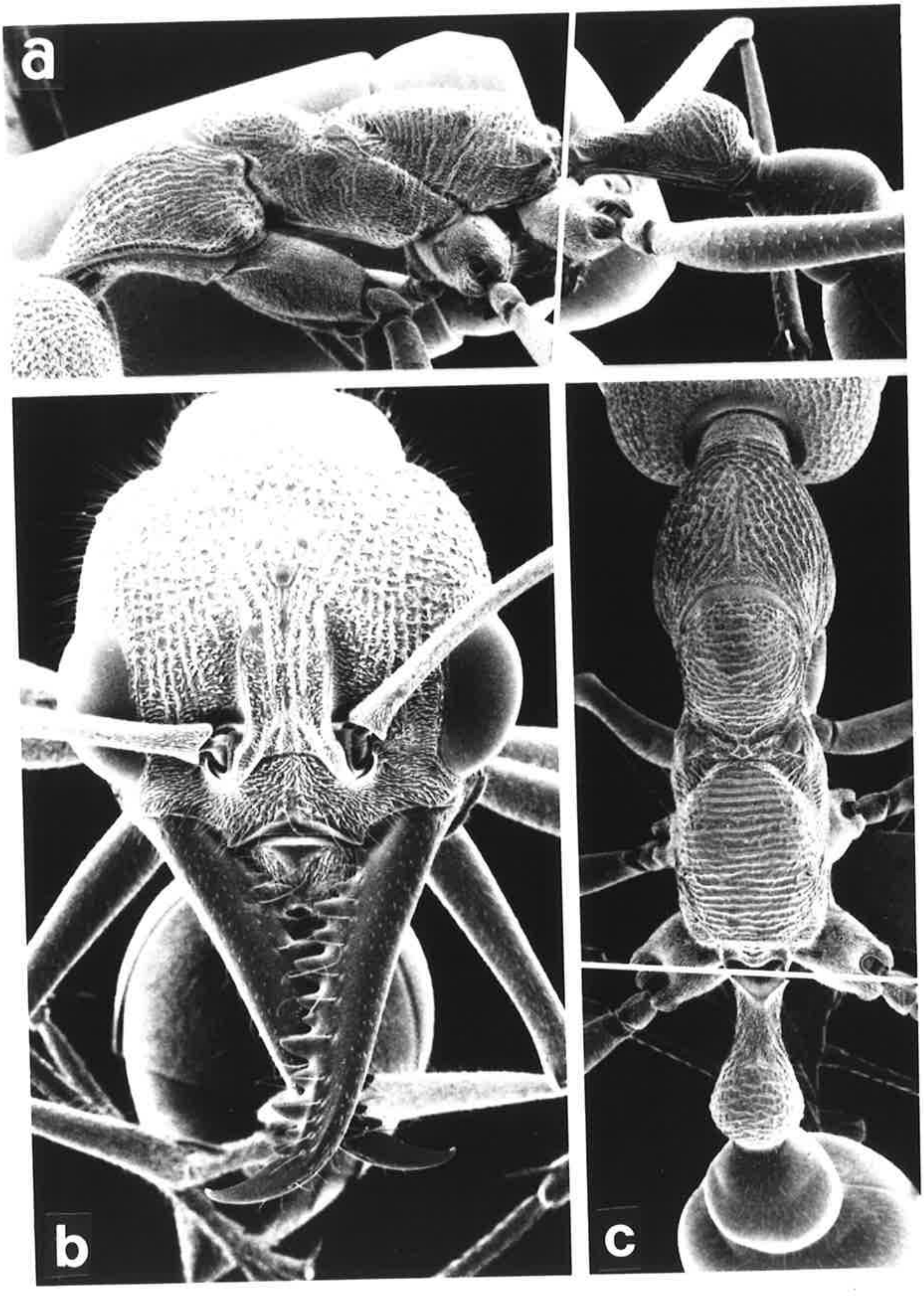
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Figure 22a-c. Scanning electron micrographs of *Myrmecia fuscipes* Clark worker, from 2 km S of Peak Charles, W.A. [430], standard views. TL c.23, ML 3.66, HL 3.59, HW 3.43, SL 4.30, MeL 6.68, PW 2.21, PNH 1.17, PNL 2.43, PNW 1.06, CI 96, MI 102, MI2 107, SI 120, PNI 44, PNI2 48, MeI 33.

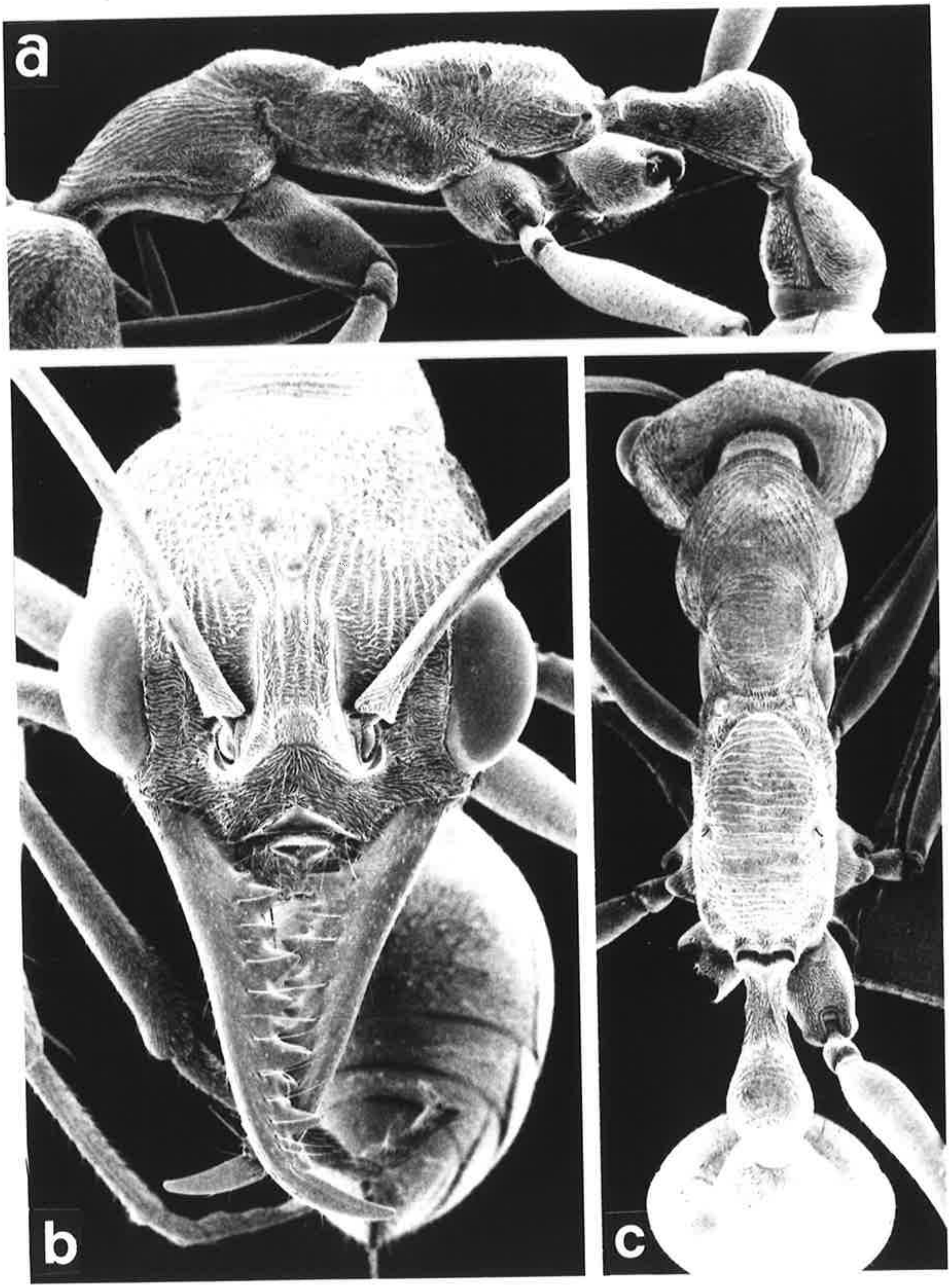
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Figure 23a-c. Scanning electron micrographs of Myrmecia fuscipes Clark worker, from 4 km W of Nullarbor, S.A. [471], standard views. TL c.20, ML 3.26, HL 3.12, HW 2.93, SL 3.84, MeL 5.60, PW 1.88, PNH 1.00, PNL 1.99, PNW 0.96, CI 94, MI 104, MI2 111, SI 123, PNI 48, PNI2 50, MeI 34.

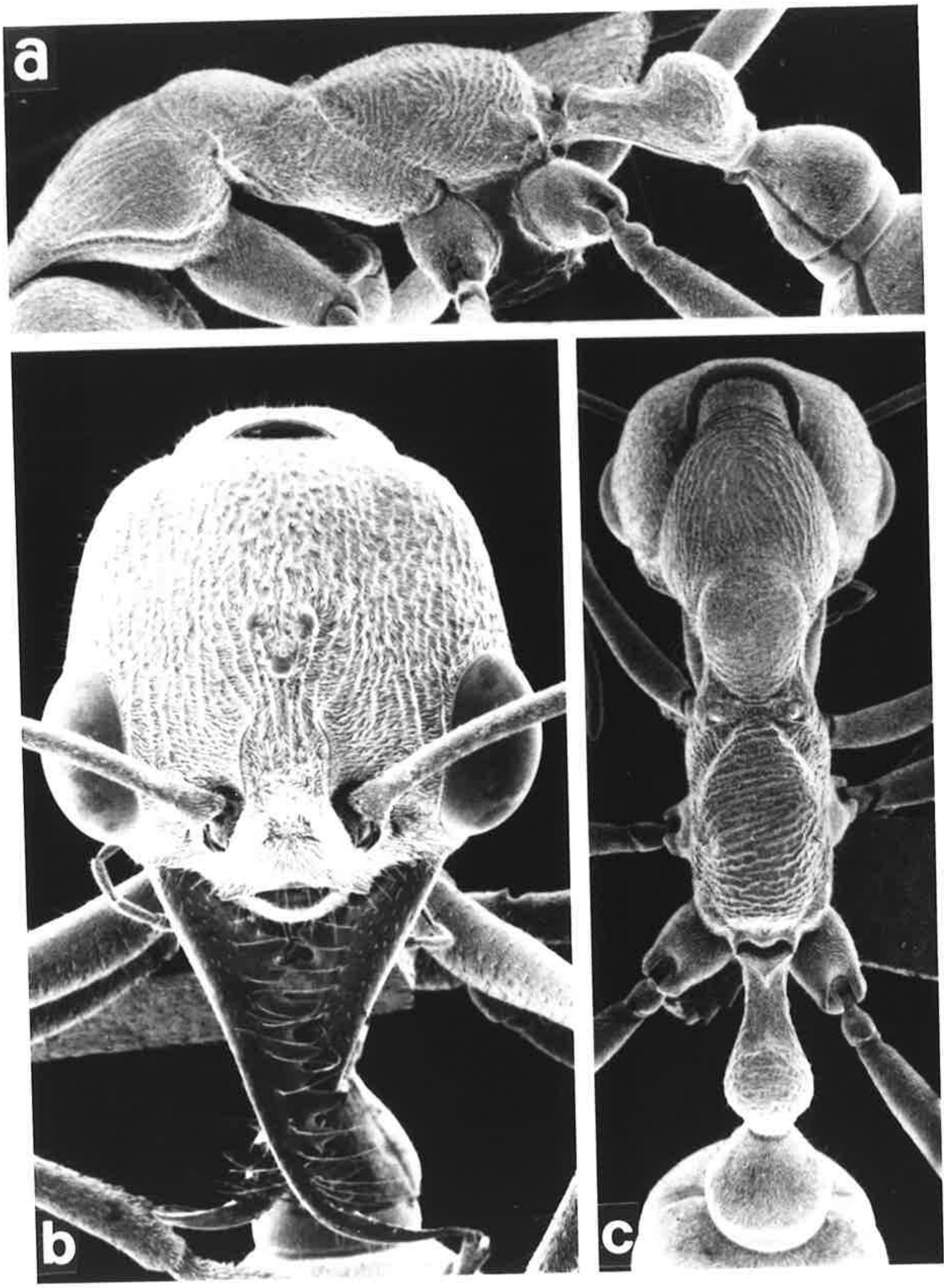
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Figure 24a-c. Scanning electron micrographs of Myrmecia fuscipes Clark worker, from Port Parham, S.A. [3], standard views. TL c.14, ML 2.05, HL 2.24, HW 2.07, SL 2.69, MeL 4.23, PW 1.37, PNH 0.78, PNL 1.50, PNW 0.68, CI 92, MI 92, MI2 99, SI 120, PNI 45, PNI2 52, MeI 32.

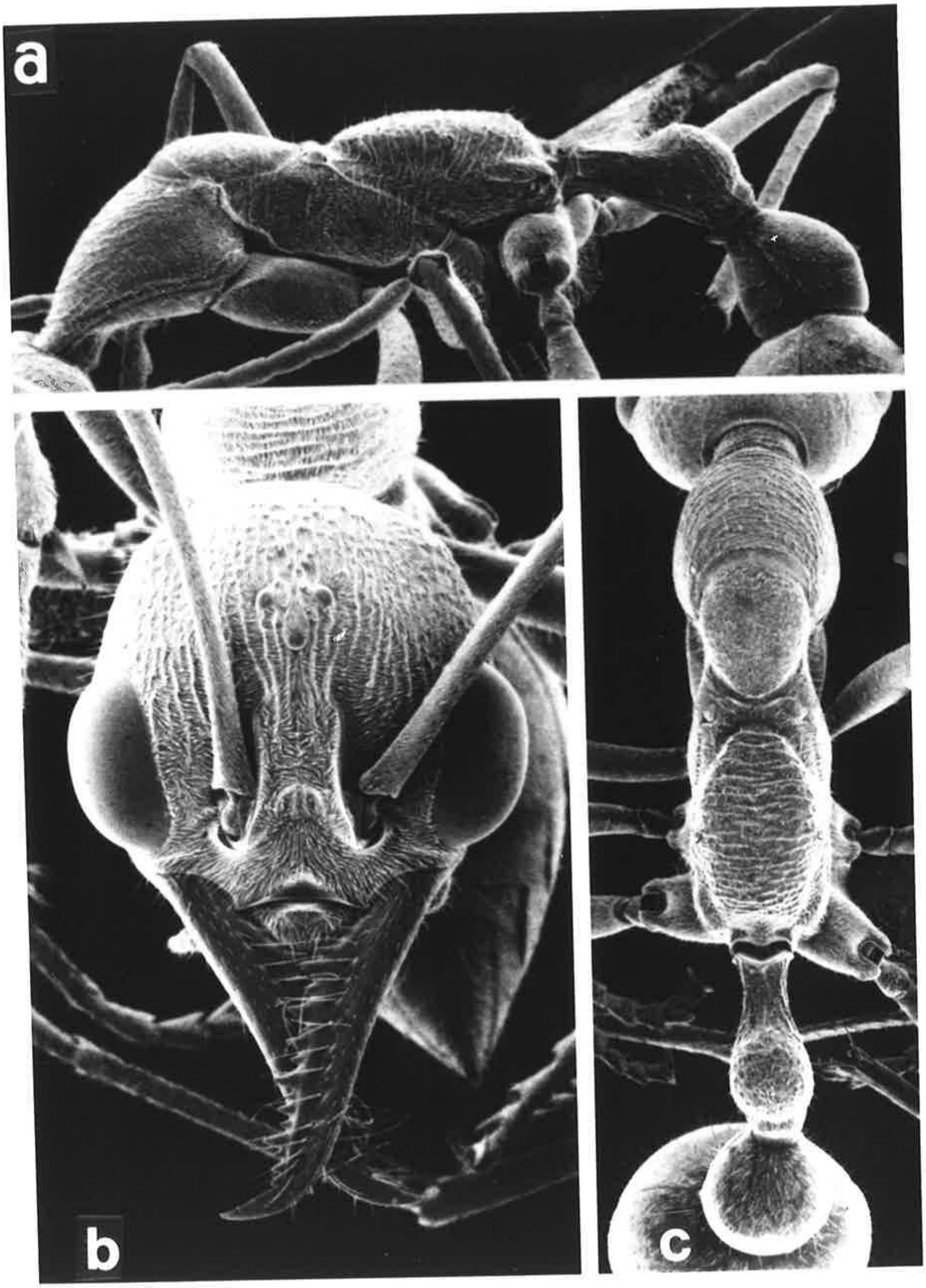
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Figure 25a-c. Scanning electron micrographs of *Myrmecia fuscipes* Clark worker, from Port Parham, S.A. [3], standard views. TL c.21, ML 3.31, HL 3.23, HW 3.01, SL 4.01, MeL 5.93, PW 2.01, PNH 1.10, PNL 2.15, PNW 1.05, CI 93, MI 102, MI2 110, SI 124, PNI 49, PNI2 51, MeI 34.

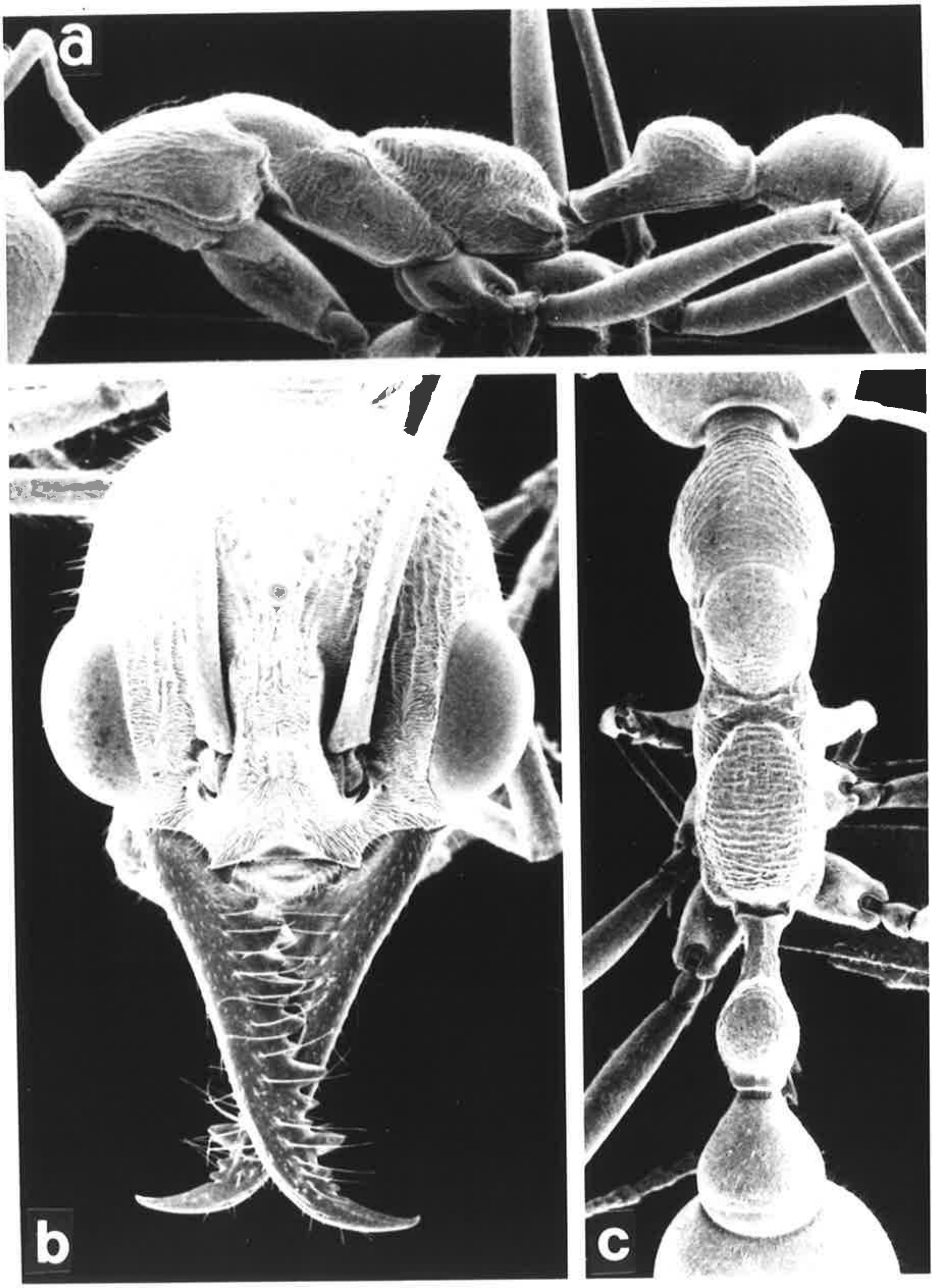
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Figure 26a-c. Scanning electron micrographs of Myrmecia sp.11 (ANIC) worker from Elliston, S.A. [170], standard views. TL c.21, ML 3.77, HL 3.40, HW 3.33, SL 4.03, MeL 6.10, PW 2.00, PNH 1.17, PNL 2.22, PNW 1.05, CI 98, MI 111, MI2 113, SI 119, PNI 47, PNI2 53, MeI 33.

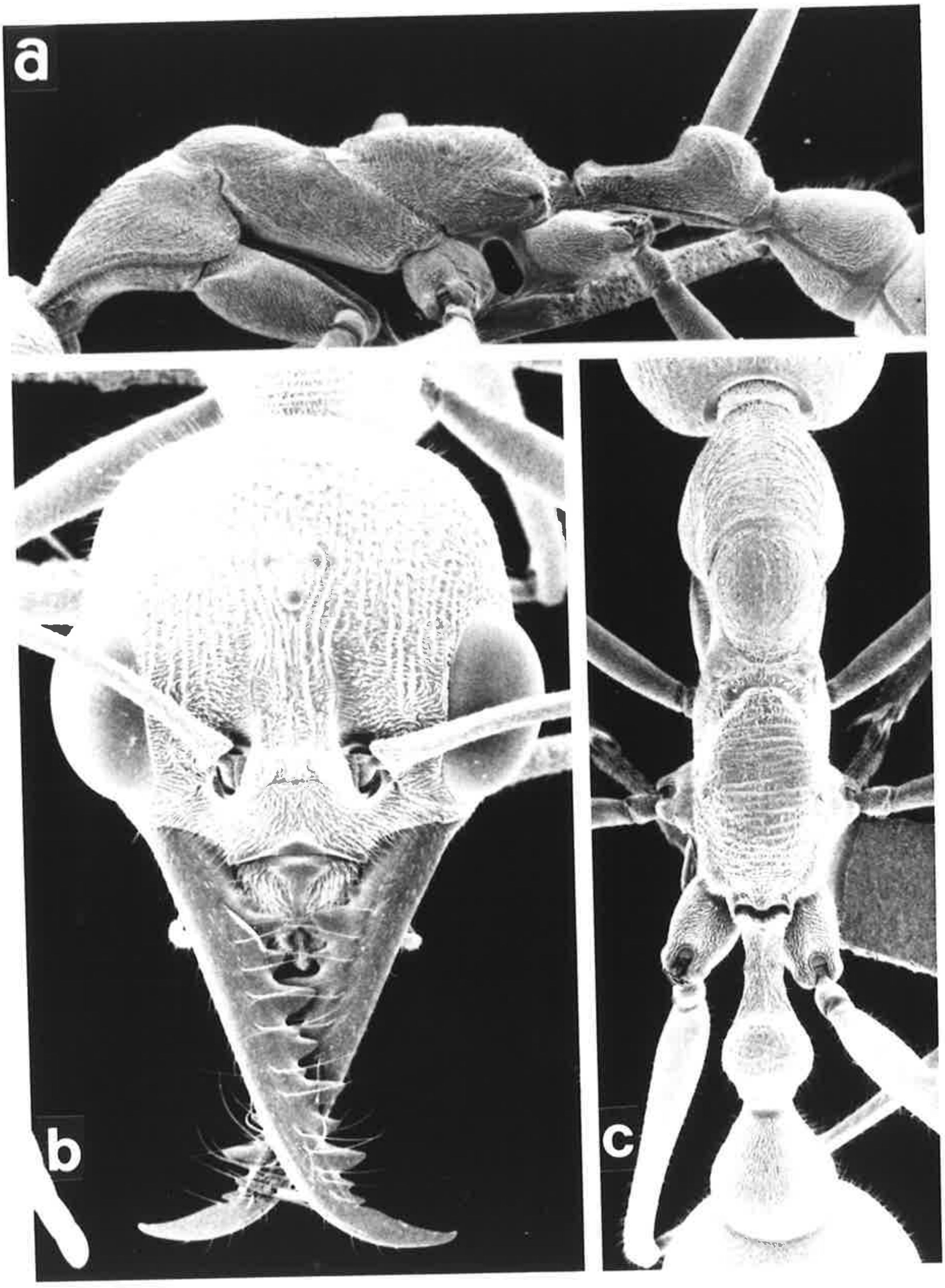
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Figure 27a-c. Scanning electron micrographs of <u>Myrmecia</u> <u>desertorum</u> Wheeler worker, from Todmorden, S.A. [147], standard views. TL c.24, ML 3.97, HL 3.68, HW 3.49, SL 4.53, MeL 6.70, PW 2.22, PNH 1.22, PNL 2.49, PNW 1.33, CI 95, MI 108, MI2 114, SI 123, PNI 53, PNI2 49, MeI 33.

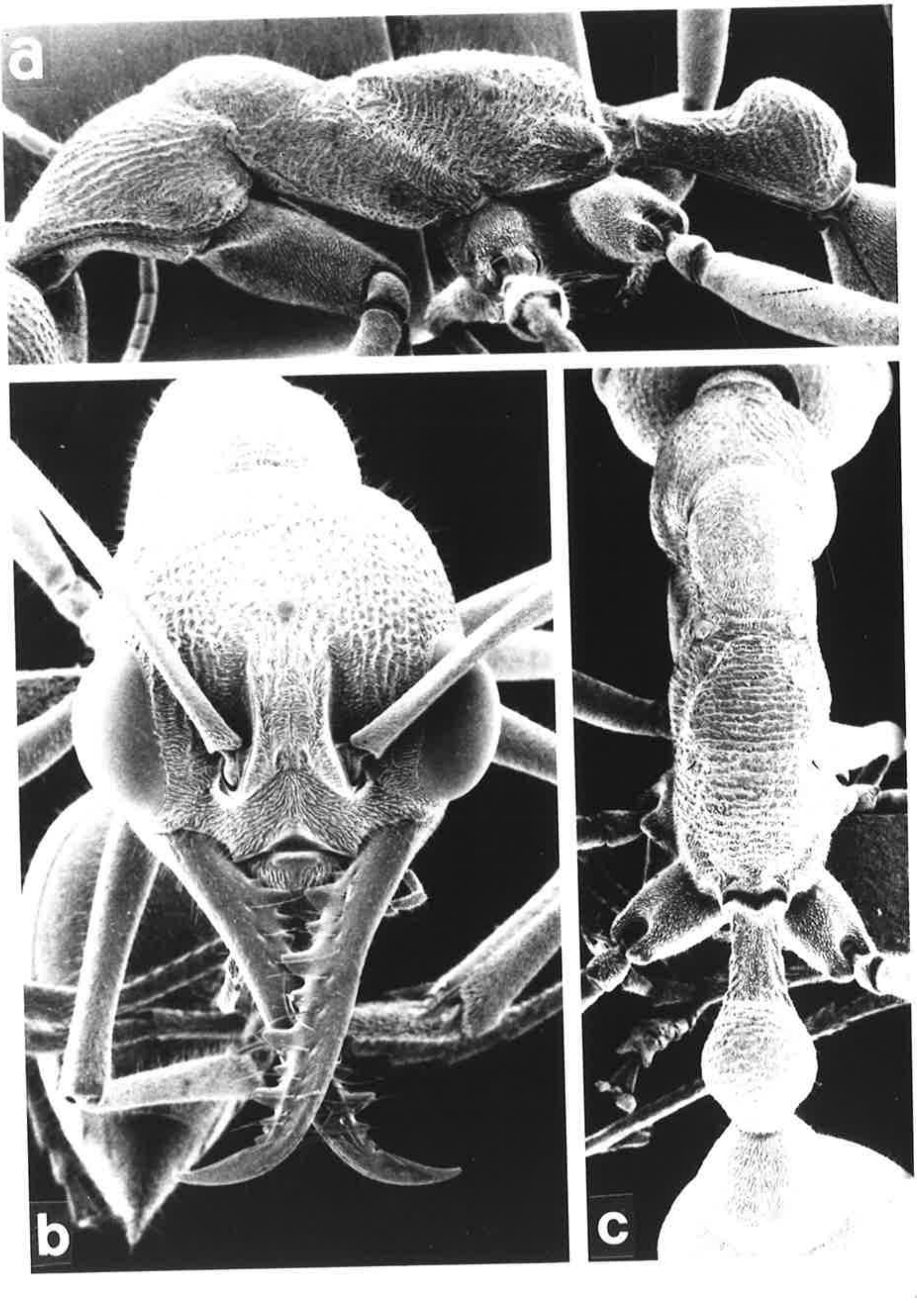
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Figure 28a-c. Scanning electron micrographs of Myrmecia princeps Clark worker, from Calperum, S.A. [161], standard views. TL c.27, ML 4.68, HL 4.20, HW 3.99, SL 5.15, MeL 7.65, PW 2.49, PNH 1.38, PNL 2.92, PNW 1.41, CI 95, MI 111, MI2 117, SI 123, PNI 48, PNI2 47, MeI 33.

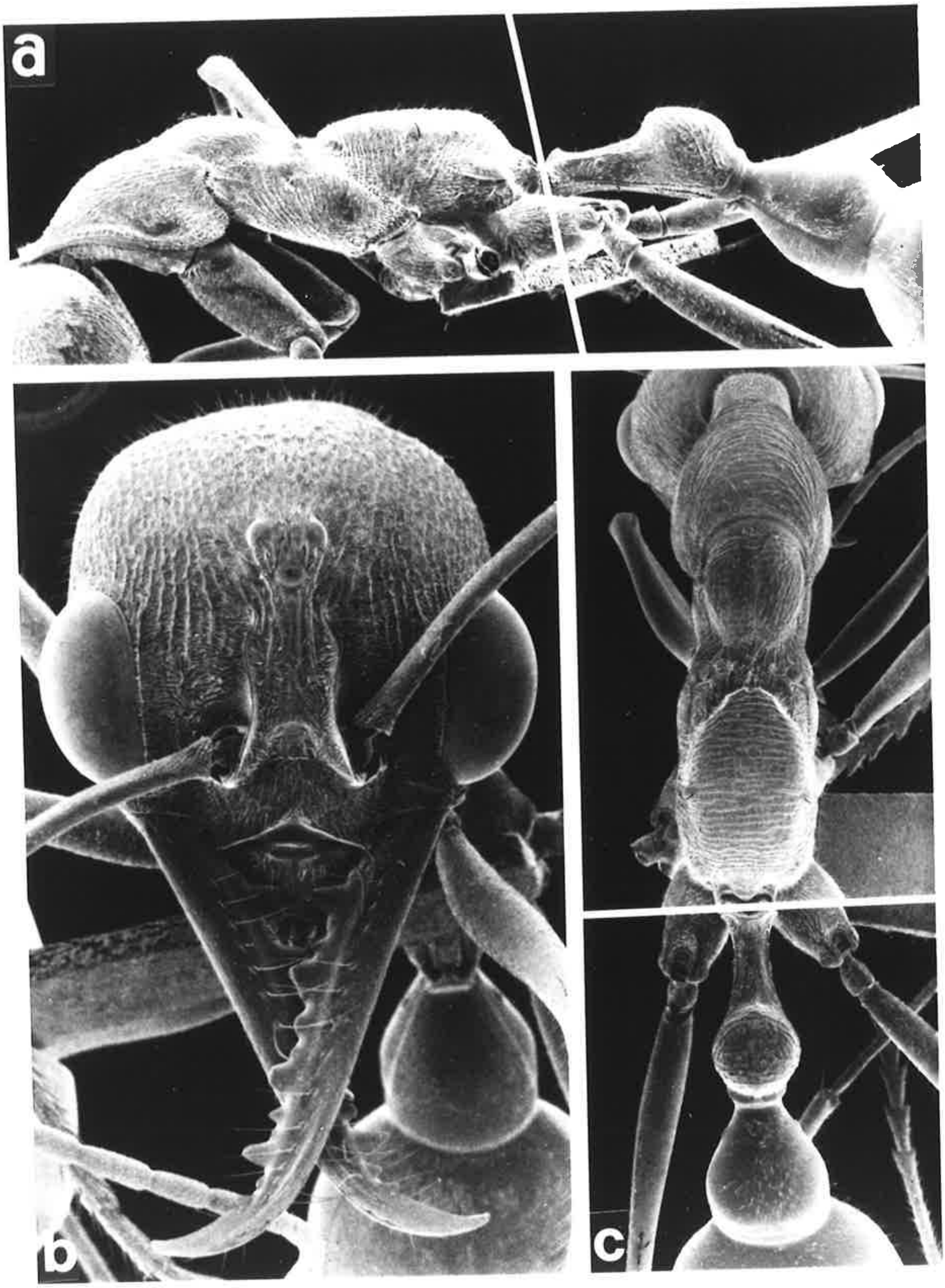
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Figure 29a-c. Scanning electron micrographs of *Myrmecia vindex* Smith worker, from Thistle Bay, W.A. [286], standard views. TL c.23, ML 3.84, HL 3.65, HW 3.51, SL 4.37, MeL 6.65, PW 2.24, PNH 1.41, PNL 2.53, PNW 1.28, CI 96, MI 105, MI2 109, SI 120, PNI 51, PNI2 56, MeI 34.

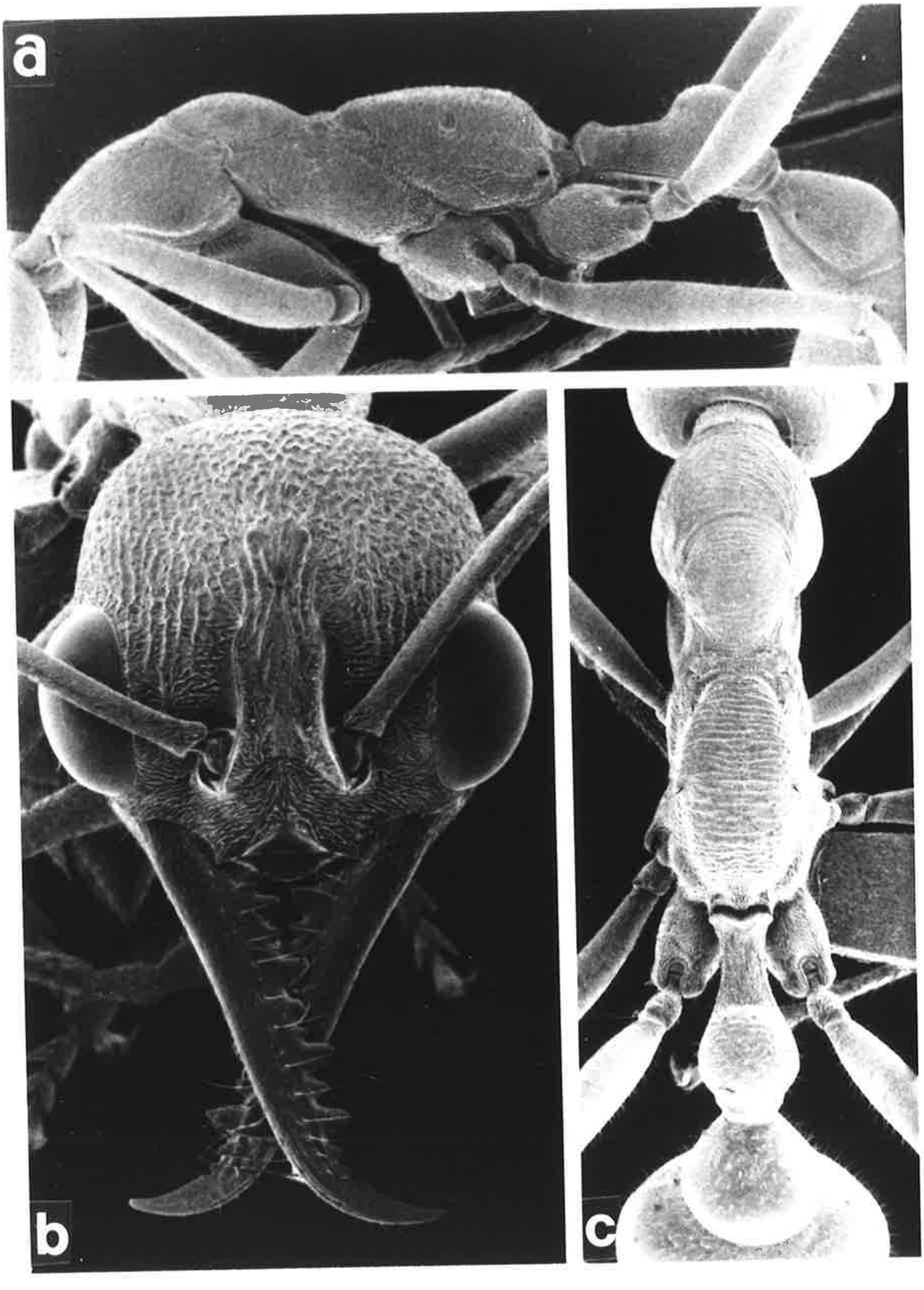
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Figure 30a-c. Scanning electron micrographs of *Myrmecia* *sp.17* (ANIC) worker, from 5 km NE of Bacchus Marsh, Vic. [493], standard views. TL c.19, ML 3.07, HL 2.95, HW 2.81, SL 3.63, MeL 5.50, PW 1.95, PNH 1.10, PNL 1.93, PNW 1.02, CI 95, MI 104, MI2 109, SI 123, PNI 53, PNI2 57, MeI 35.

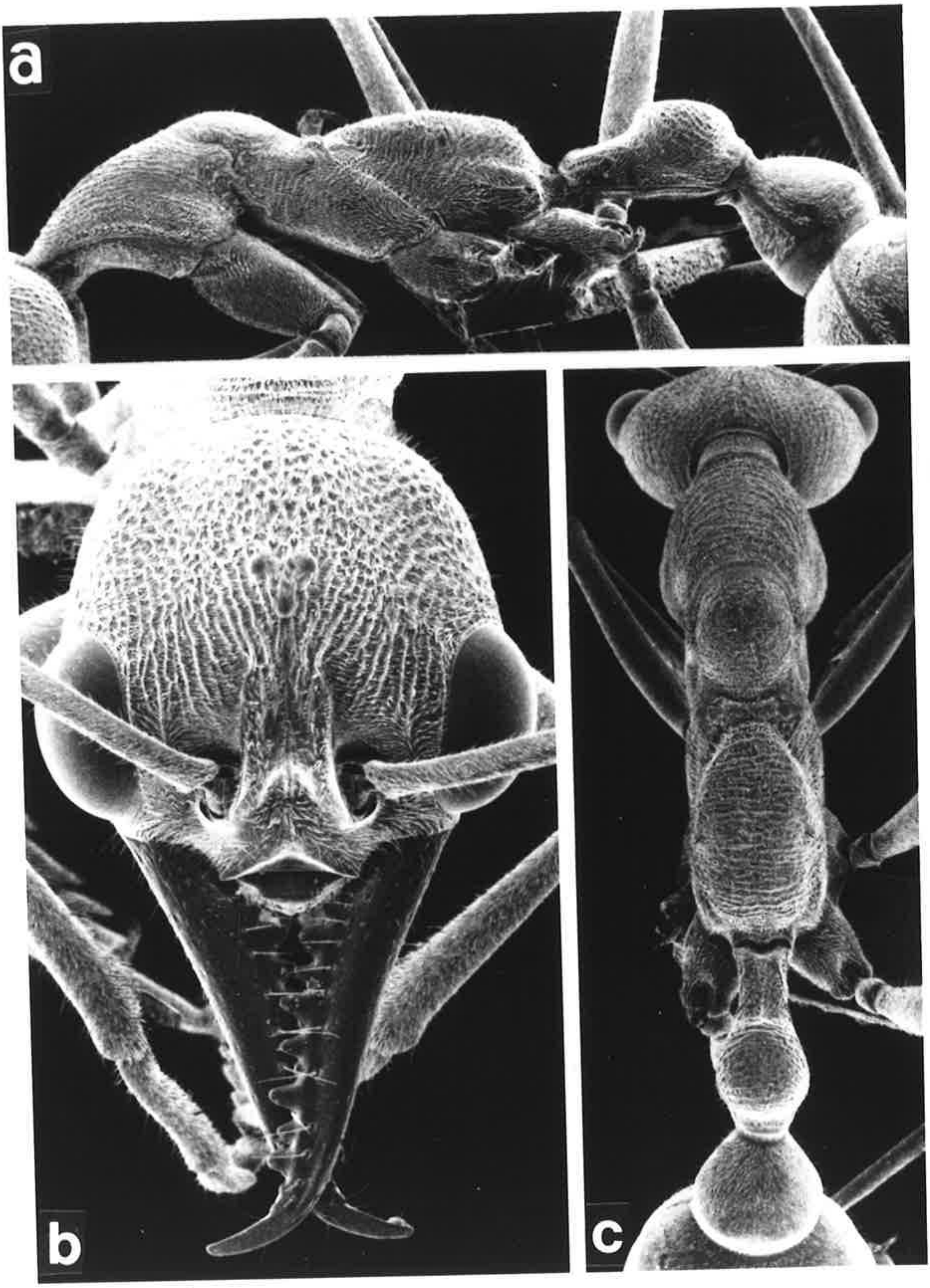
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Figure 31a-c. Scanning electron micrographs of Myrmecia pulchra Clark worker, from Mount Lofty, S.A. [73], standard views. TL c.18, ML 2.84, HL 3.04, HW 3.25, SL 3.08, MeL 5.40, PW 2.16, PNH 1.20, PNL 1.63, PNW 1.18, CI 107, MI 93, MI2 87, SI 101, PNI 72, PNI2 74, MeI 40.

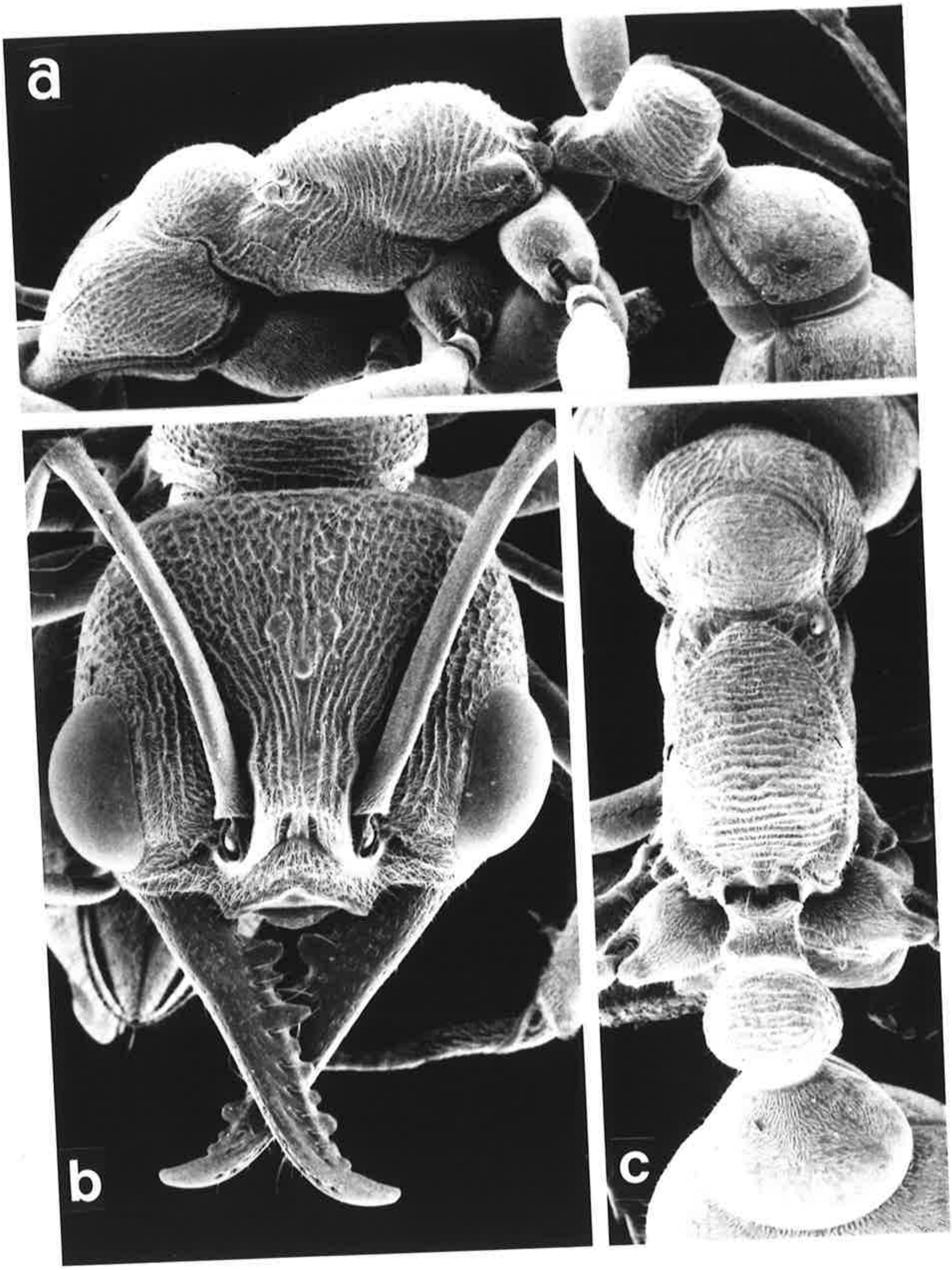
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Figure 32a-c. Scanning electron micrographs of Myrmecia nigrocincta Smith worker, from Pymble, N.S.W. [67], standard views. TL c.17, ML 2.79, HL 2.59, HW 2.52, SL 2.71, MeL 4.84, PW 1.77, PNH 0.94, PNL 1.68, PNW 0.85, CI 97, MI 108, MI2 111, SI 105, PNI 51, PNI2 56, MeI 37.

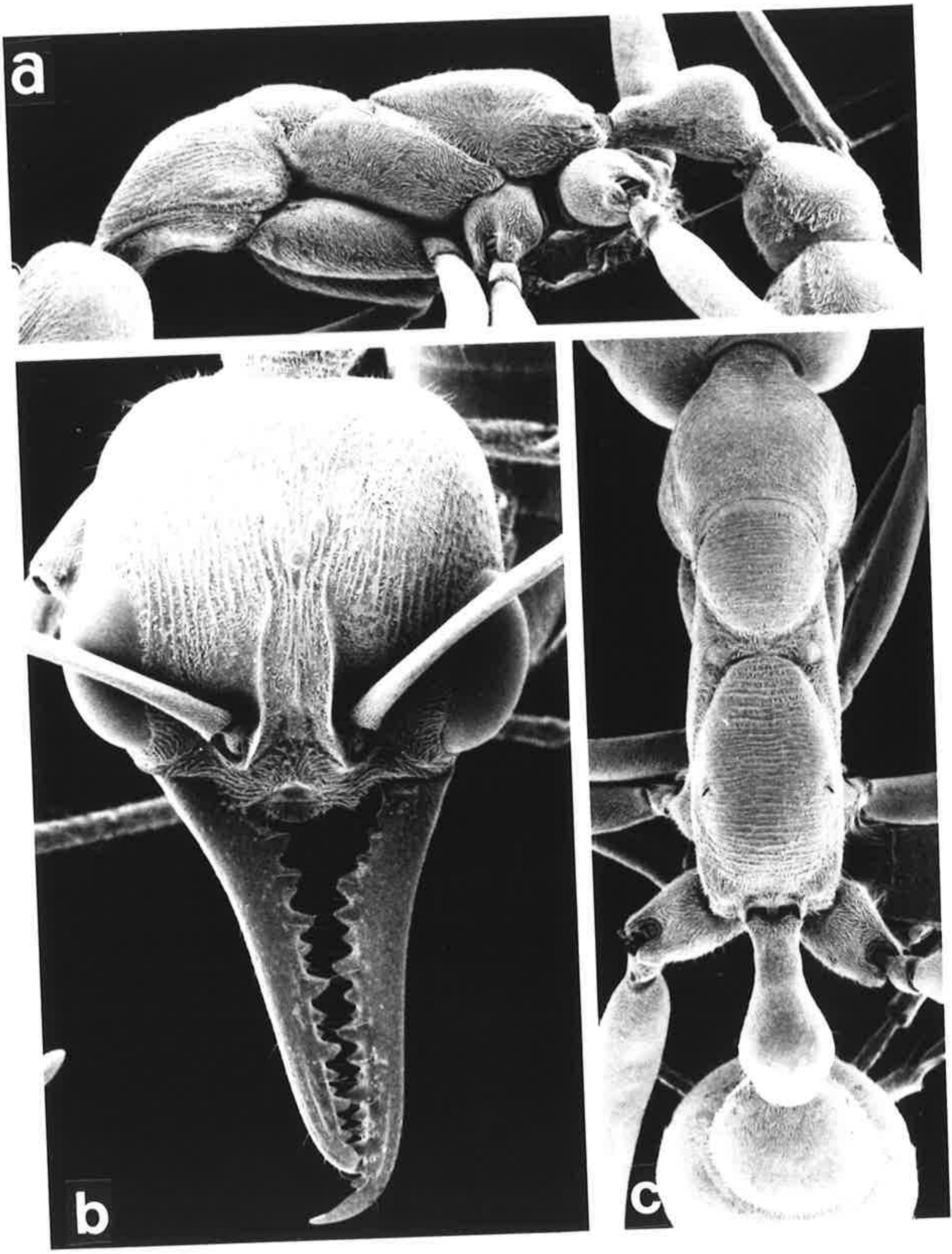
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Figure 33a-c. Scanning electron micrographs of Myrmecia harderi Forel worker, from Bookong S.F., N.S.W. (BBL; in ANIC), standard views. TL c.13, ML 2.00, HL 2.08, HW 2.14, SL 1.83, MeL 3.62, PW 1.57, PNH 0.91, PNL 1.20, PNW 0.86, CI 103, MI 96, MI2 97, SI 88, PNI 72, PNI2 76, MeI 43.

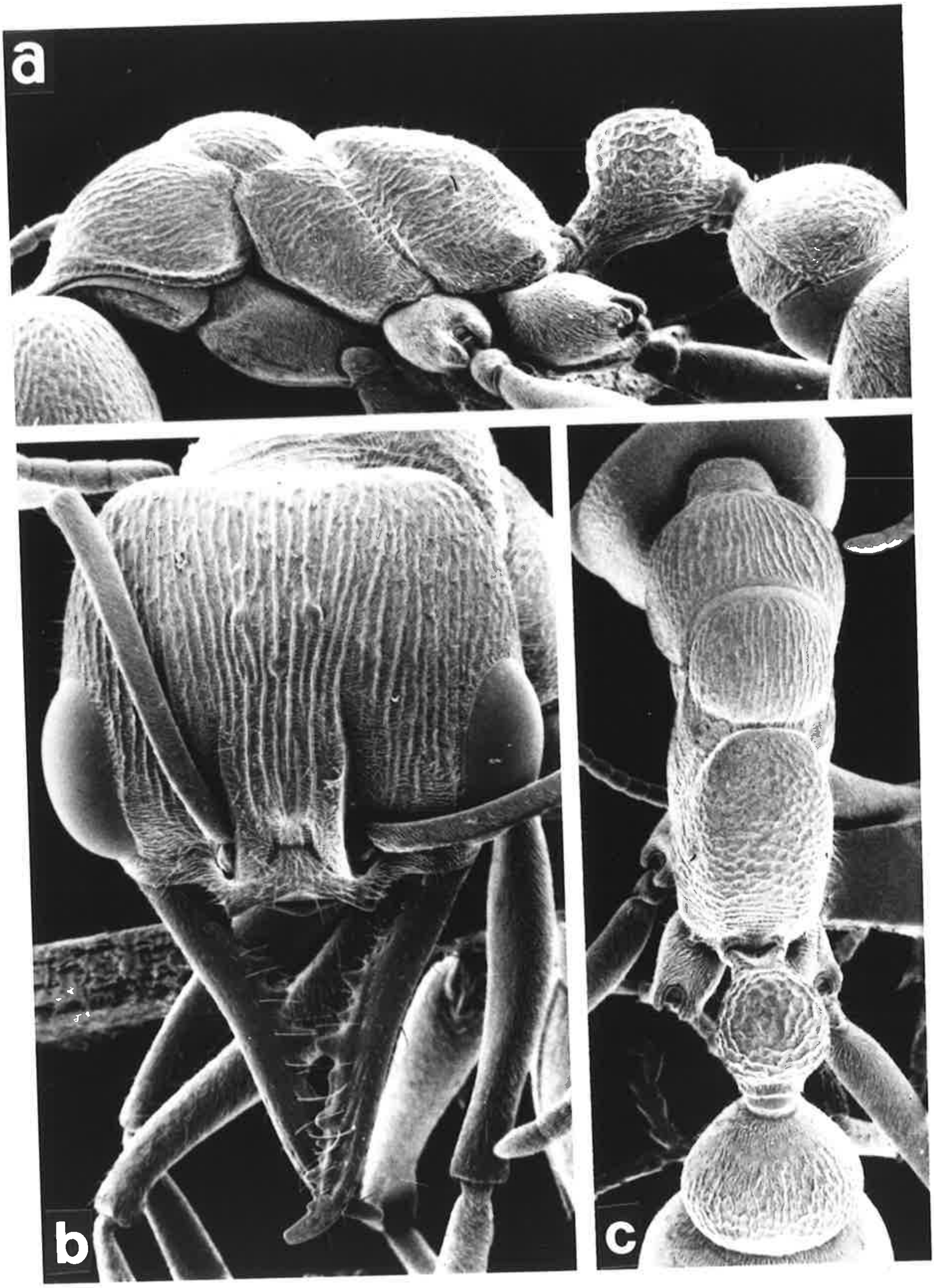
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Figure 34a-c. Scanning electron micrographs of <u>Myrmecia</u> <u>aberrans</u> Forel worker, from Werribee Gorge, Vic. (BBL; in ANIC), standard views. TL c.14, ML 2.00, HL 2.62, HW 2.76, SL 1.81, MeL 4.04, PW 1.80, PNH 1.06, PNL 1.17, PNW 0.89, CI 105, MI 76, MI2 72, SI 69, PNI 76, PNI2 91, MeI 45.

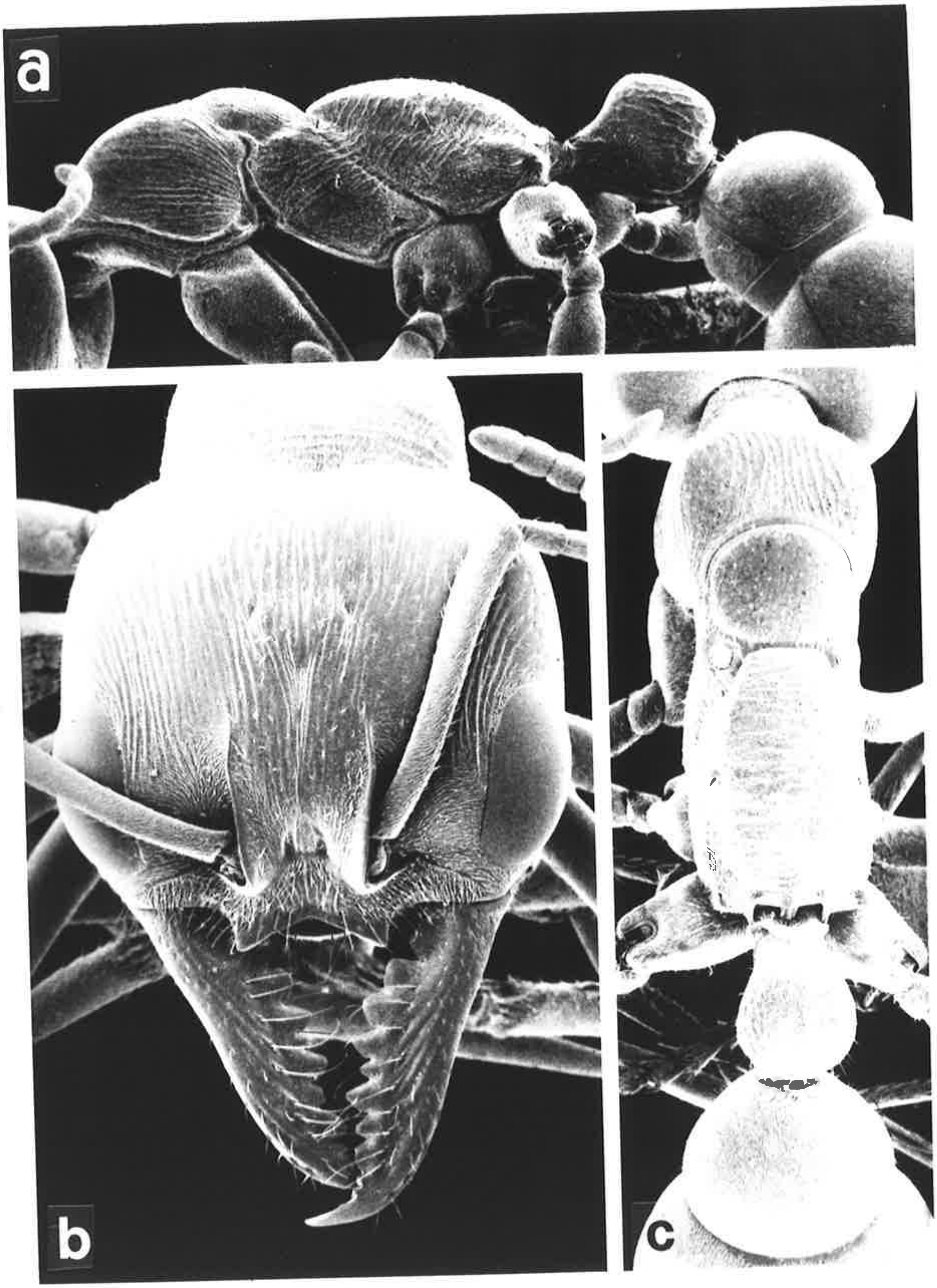
a
b
c

Figure 35a-c. Scanning electron micrographs of Myrmecia cephalotes (Clark) worker, from Black Hill Creek, N.S.W. [511], standard views. TL c.15, ML 2.28, HL 2.13, HW 2.45, SL 2.17, MeL 4.01, PW 1.72, PNH 0.94, PNL 1.28, PNW 0.93, CI 115, MI 107, MI2 93, SI 102, PNI 73, PNI2 73, MeI 43.

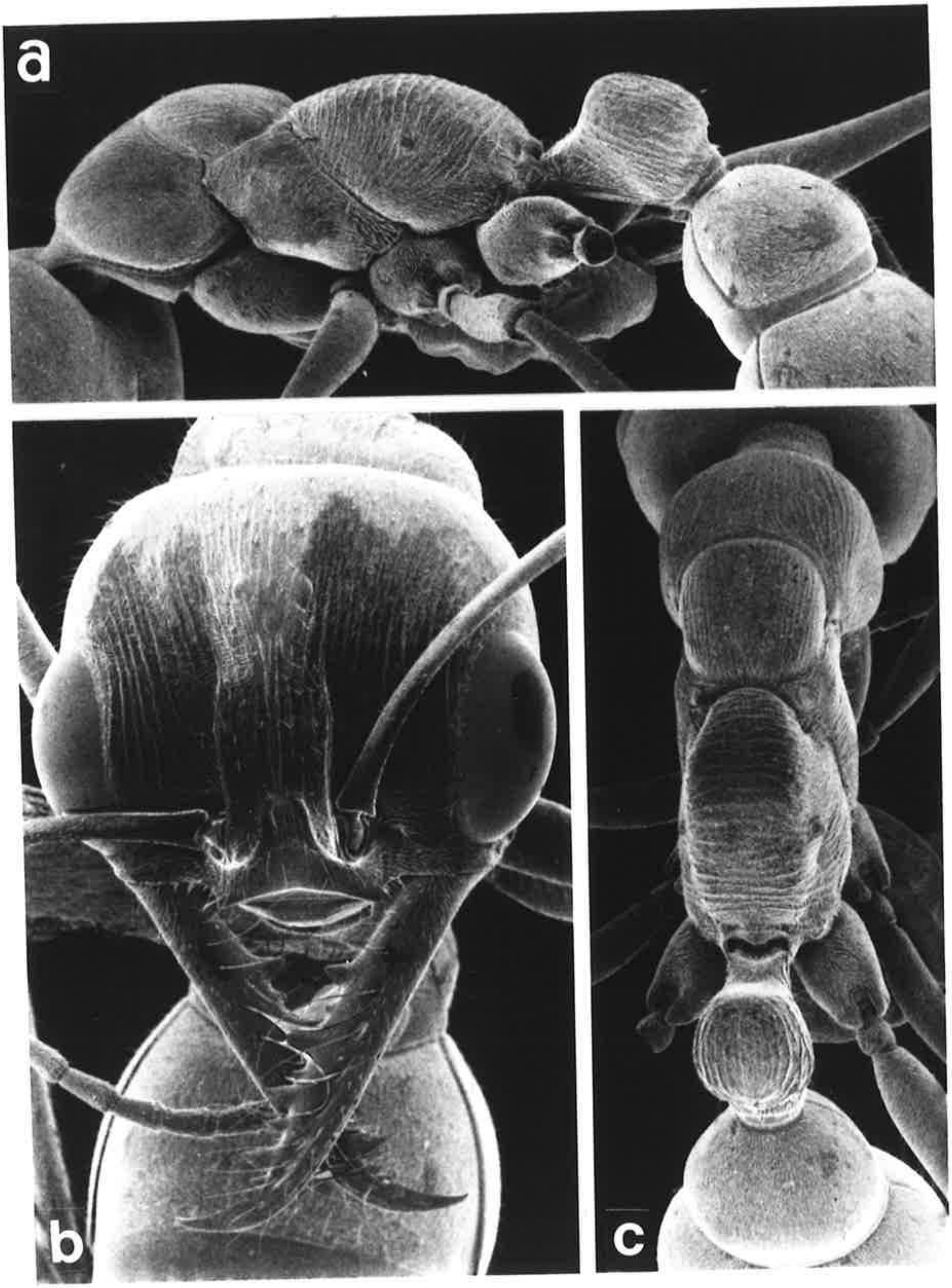
a
b
c

Figure 36a-c. Scanning electron micrographs of Myrmecia pilosula Smith, s.l. worker, from Uraidla, S.A. [46], standard views. TL c.13, ML 2.25, HL 2.14, HW 2.27, SL 1.95, MeL 3.73, PW 1.62, PNH 0.96, PNL 1.16, PNW 0.91, CI 106, MI 105, MI2 99, SI 91, PNI 78, PNI2 83, MeI 43.

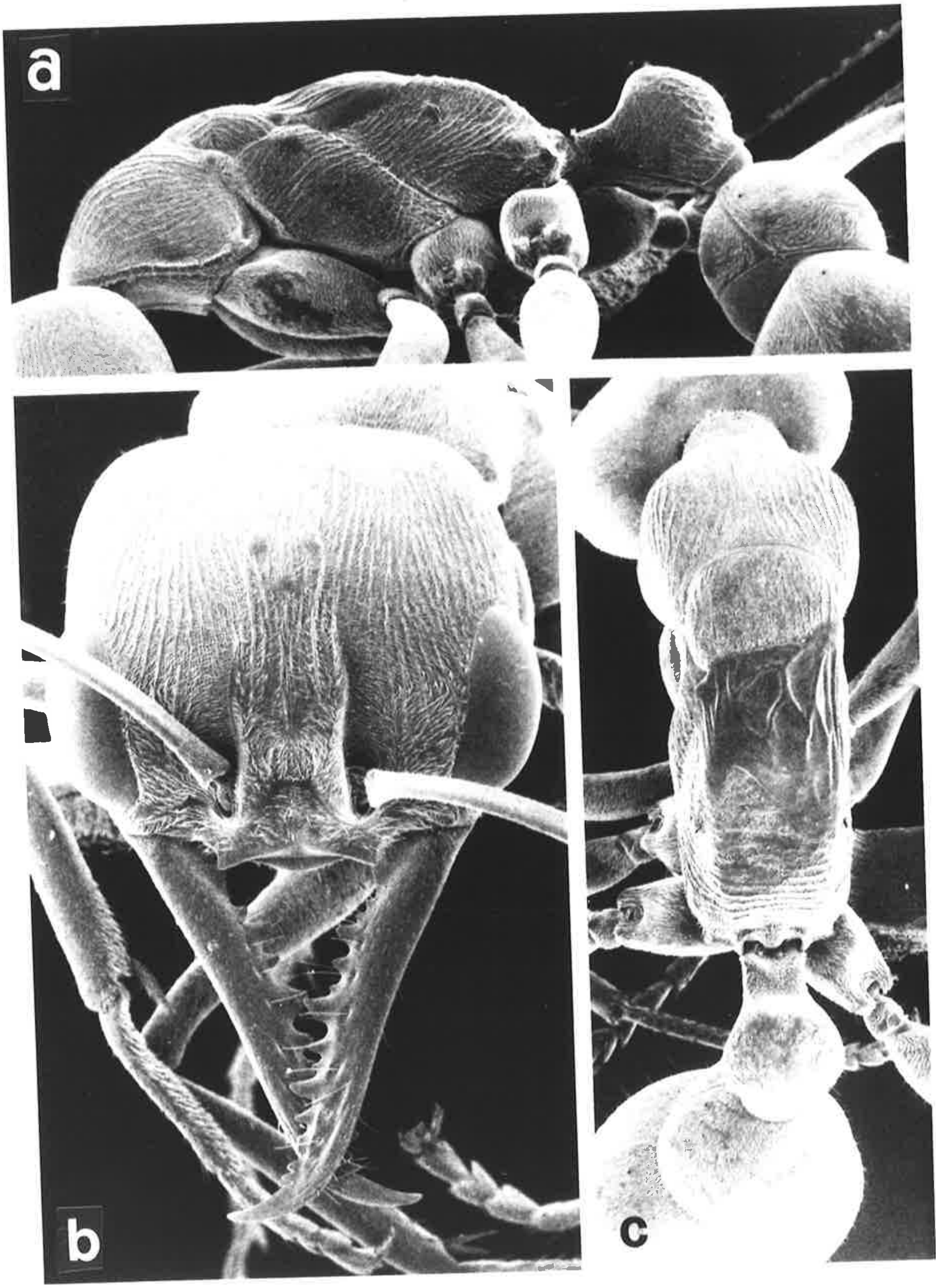
a
b
c

Figure 37a-c. Scanning electron micrographs of Myrmecia swalei Crawley worker, from 10 km N of Denmark, W.A. (BBL; in ANIC), standard views. TL c.13, ML 2.16, HL 2.10, HW 2.16, SL 1.67, MeL 3.57, PW 1.71, PNH 1.05, PNL 1.05, PNW 0.94, CI 103, MI 103, MI2 100, SI 80, PNI 90, PNI2 100, MeI 48.

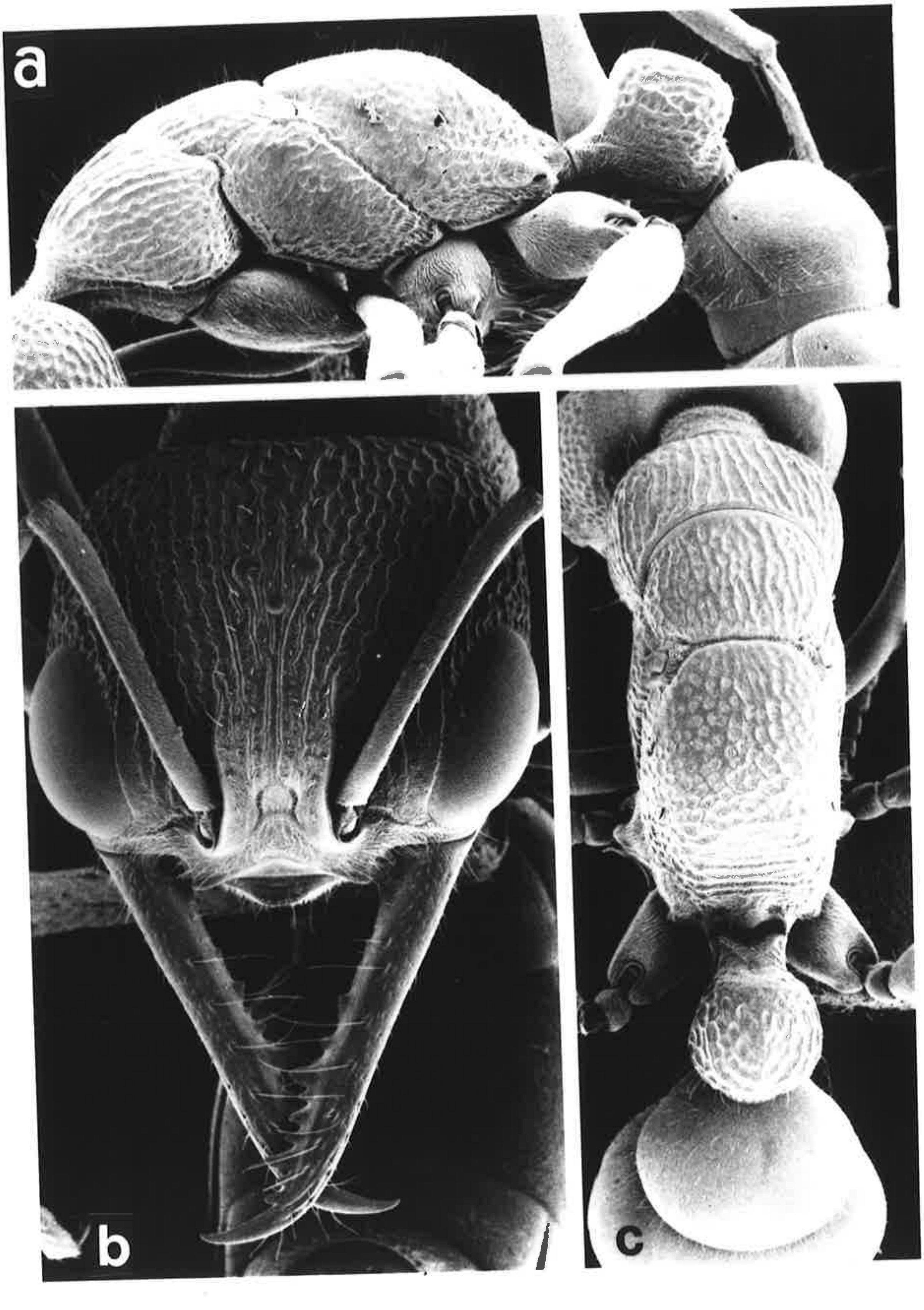
a
b
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Figure 38a-c. Scanning electron micrographs of *Myrmecia* *tepperi* Emery worker, from Inneston, S.A. [271], standard views. TL c.12, ML 2.17, HL 1.97, HW 2.05, SL 1.82, MeL 3.48, PW 1.53, PNH 0.94, PNL 1.07, PNW 0.91, CI 104, MI 110, MI2 106, SI 92, PNI 85, PNI2 88, MeI 44.

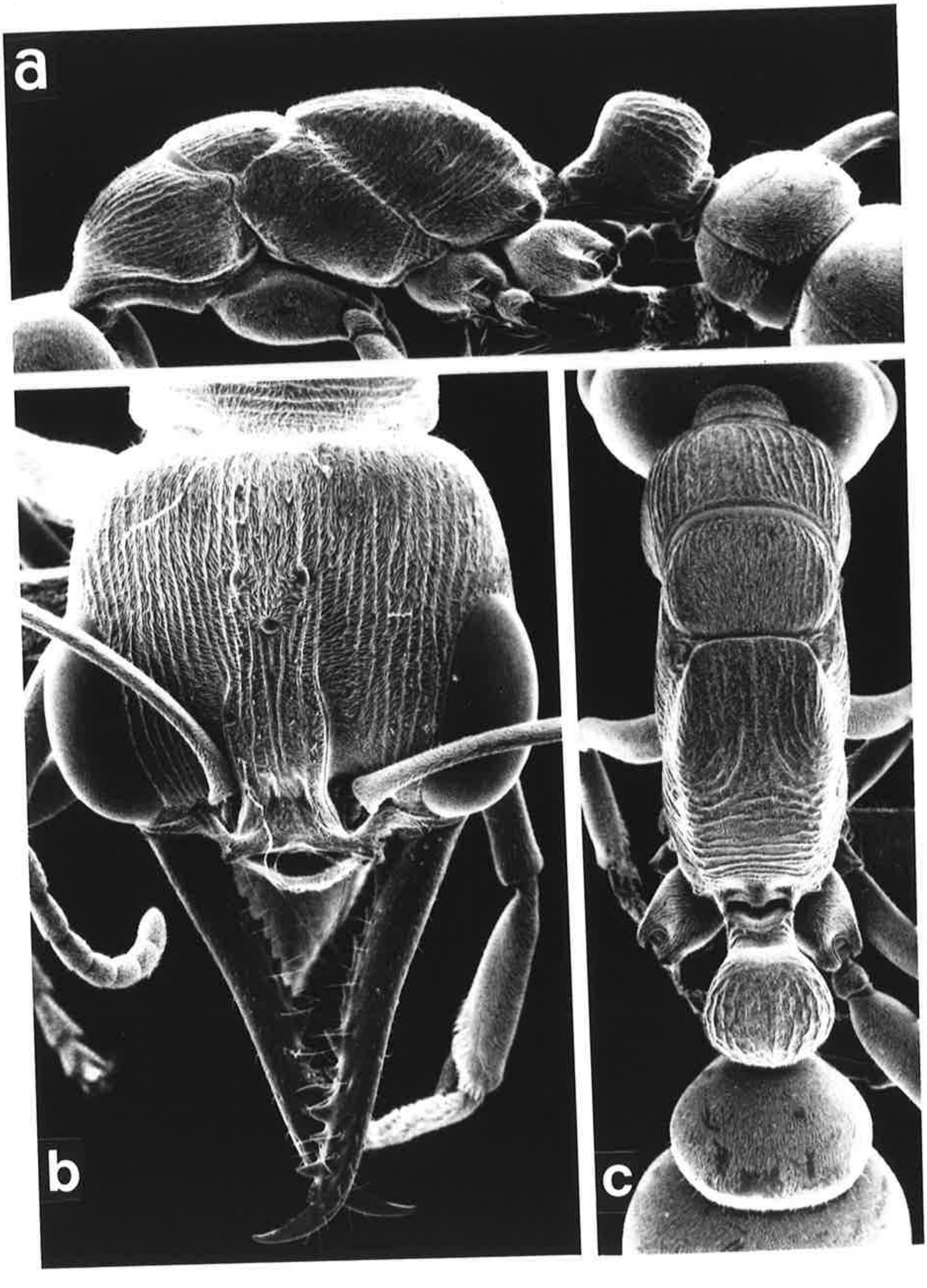

a
b
c

Figure 39a-c. Scanning electron micrographs of *Myrmecia piliventris* Smith, *s.s.* worker, from Condobolin, N.S.W. (BBL; in ANIC), standard views. TL c.15, ML 2.22, HL 2.37, HW 2.59, SL 1.97, MeL 4.26, PW 1.94, PNH 1.08, PNL 1.36, PNW 1.17, CI 109, MI 94, MI2 86, SI 83, PNI 86, PNI2 79, MeI 46.

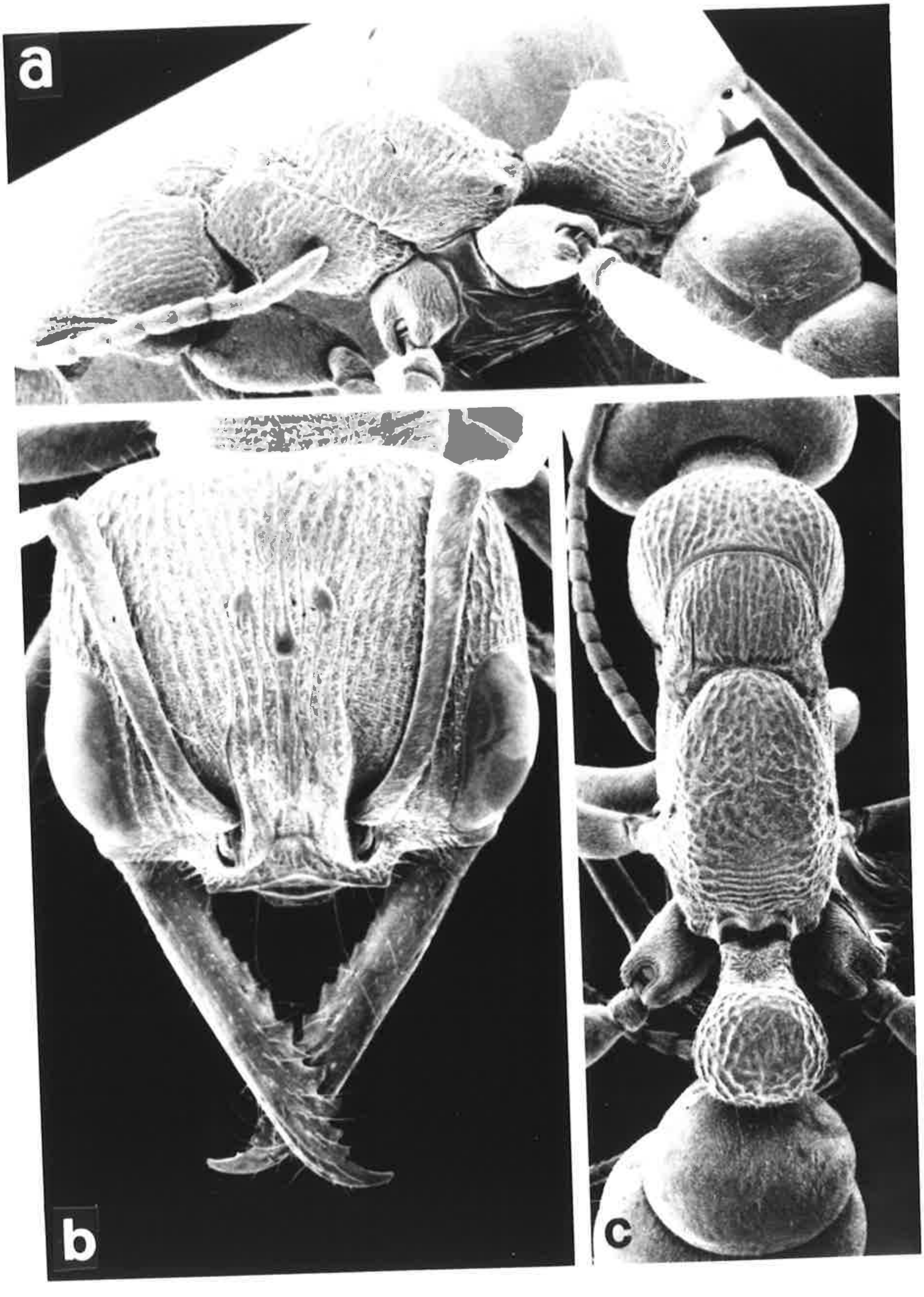

a
b
c

Figure 40a-c. Scanning electron micrographs of Myrmecia sp.15 (ANIC) worker, from Smokers Gap, A.C.T. (BBL; in ANIC), standard views. TL c.9, ML 1.22, HL 1.39, HW 1.43, SL 1.11, MeL 2.60, PW 0.96, PNH 0.63, PNL 0.81, PNW 0.53, CI 103, MI 88, MI2 85, SI 80, PNI 65, PNI2 78, MeI 37.

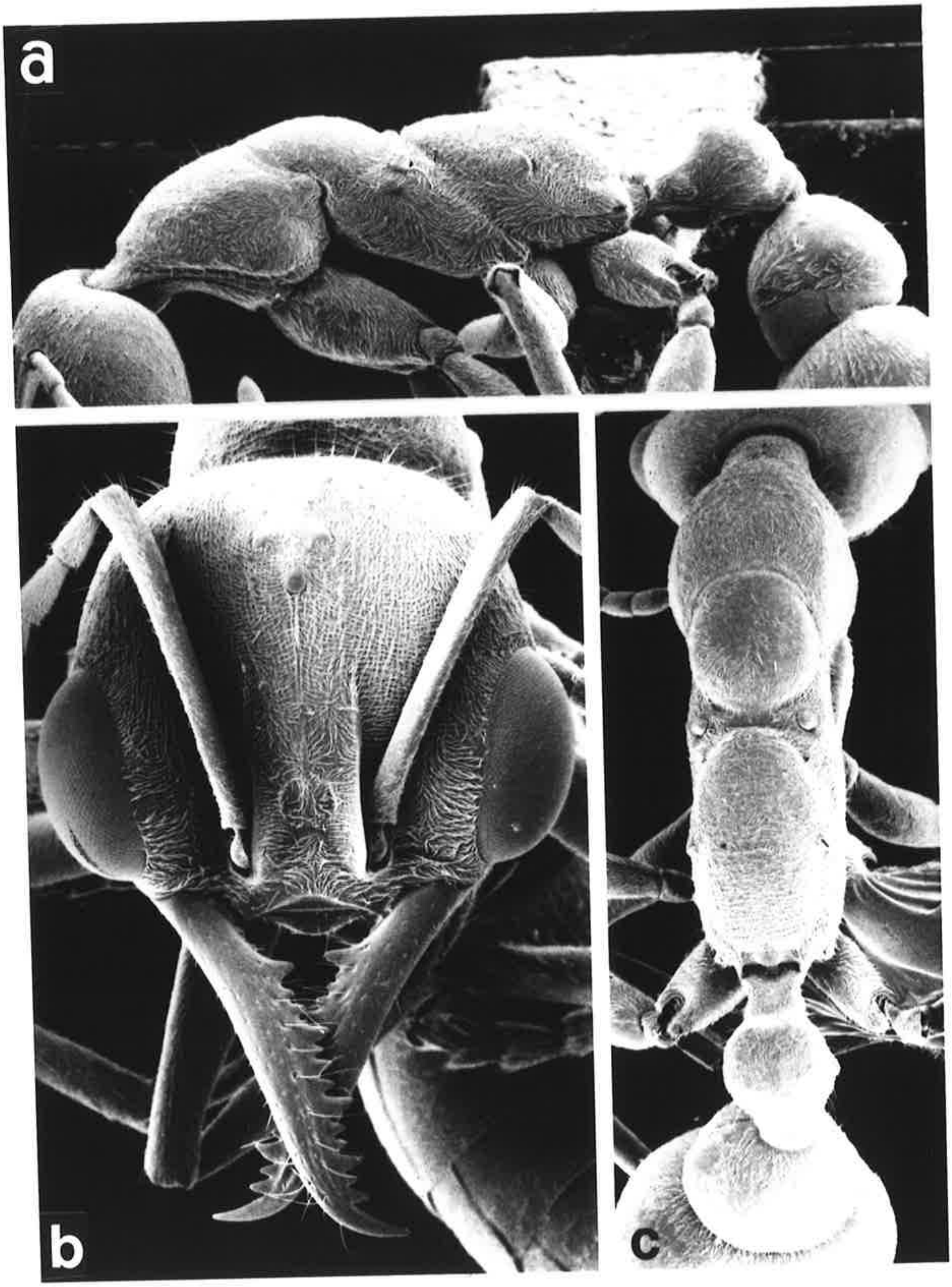

a
b
c

Figure 41a-c. Scanning electron micrographs of Myrmecia fucosa Clark worker, from 19 km SW of Waikerie, S.A. (BBL; in ANIC), standard views. TL c.12, ML 1.89, HL 1.98, HW 1.93, SL 1.55, MeL 3.31, PW 1.30, PNH 0.90, PNL 1.26, PNW 0.84, CI 97, MI 95, MI2 98, SI 78, PNI 67, PNI2 71, MeI 39.

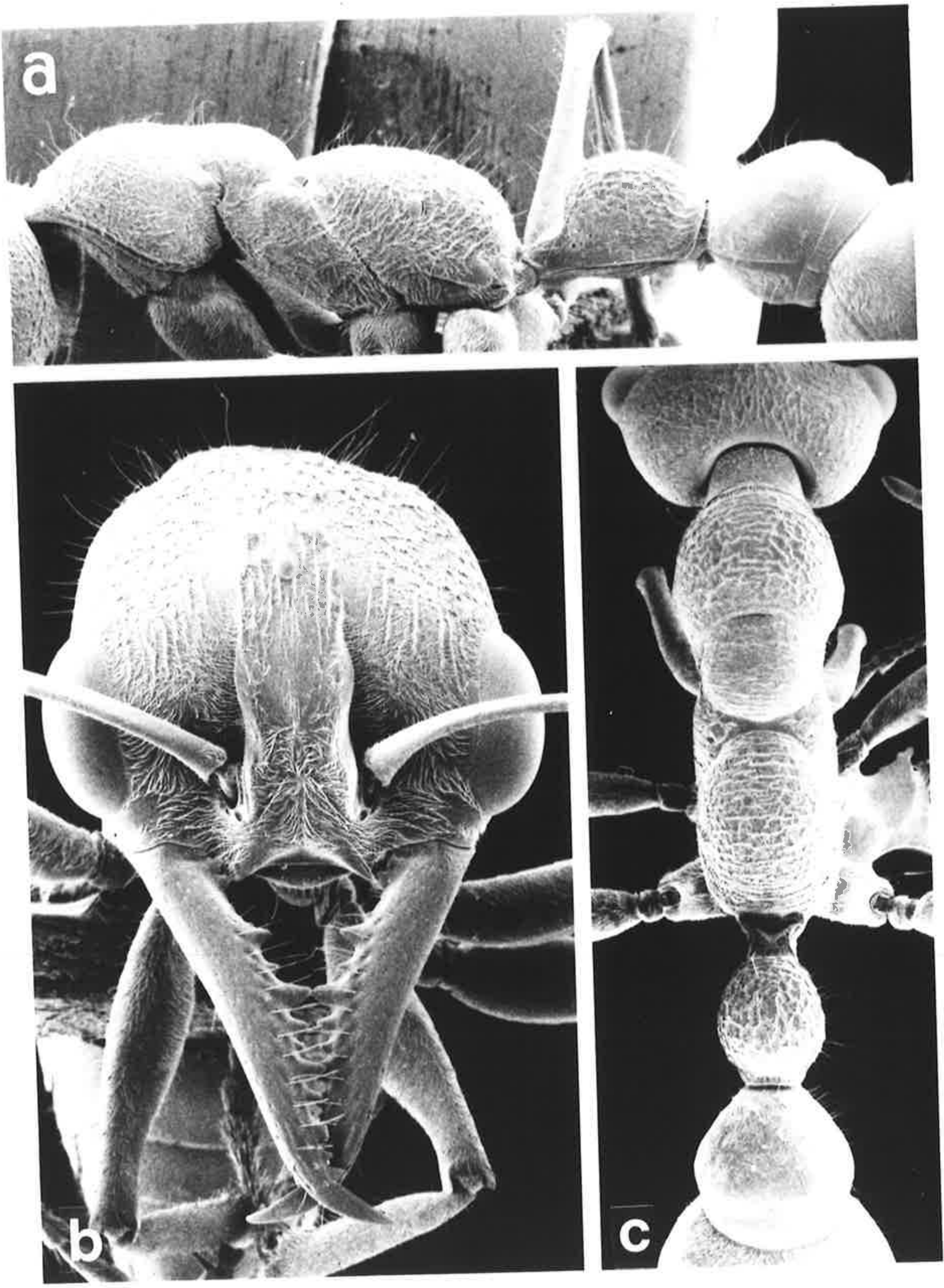

a
b
c

Figure 42a-c. Scanning electron micrographs of <u>Myrmecia</u> <u>urens</u> Lowne worker, from 15 km E of Weethalle, N.S.W. (BBL; in ANIC), standard views. TL c.8, ML 1.22, HL 1.37, HW 1.37, SL 1.12, MeL 2.42, PW 0.92, PNH 0.56, PNL 0.83, PNW 0.55, CI 100, MI 89, MI2 89, SI 82, PNI 66, PNI2 67, MeI 38.

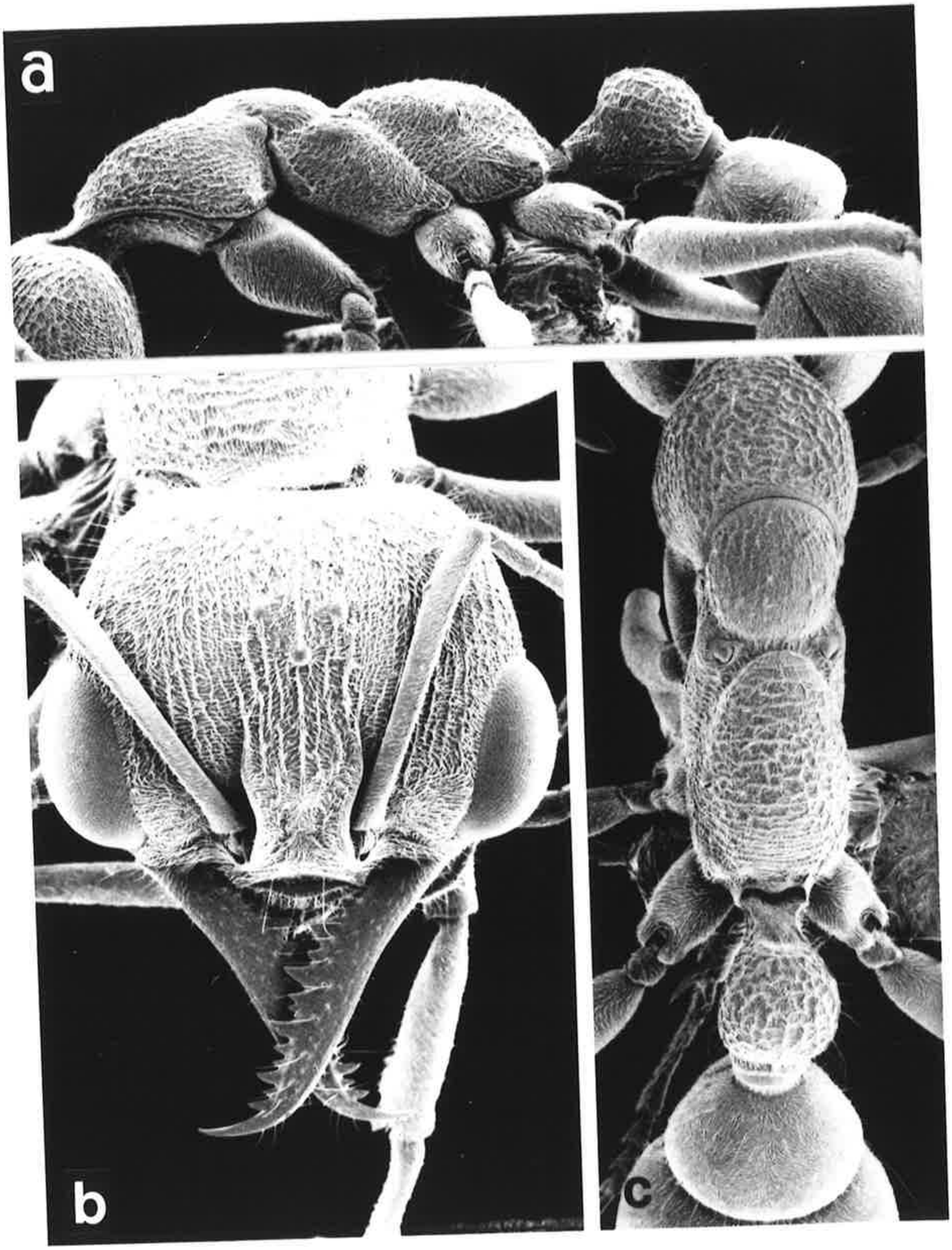
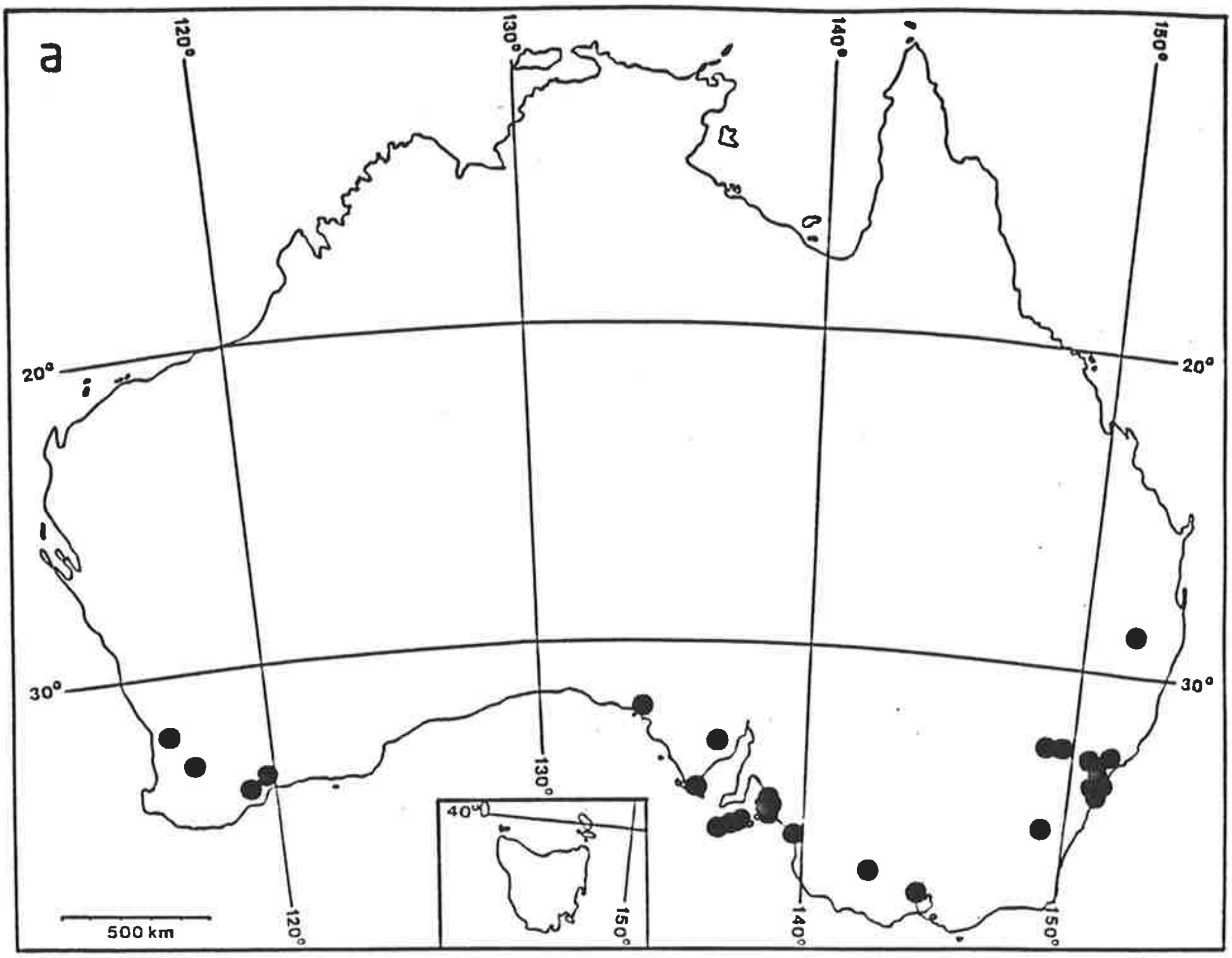

a
b
c

Figure 43a-b. Known distribution of:

(a) *Myrmecia forceps* Roger; and

(b) *Myrmecia brevinoda* Forel, *s.l.* (excluding introduced New Zealand population).


a
120°
130°
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30°
30°
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40°
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140°
150°
500 km

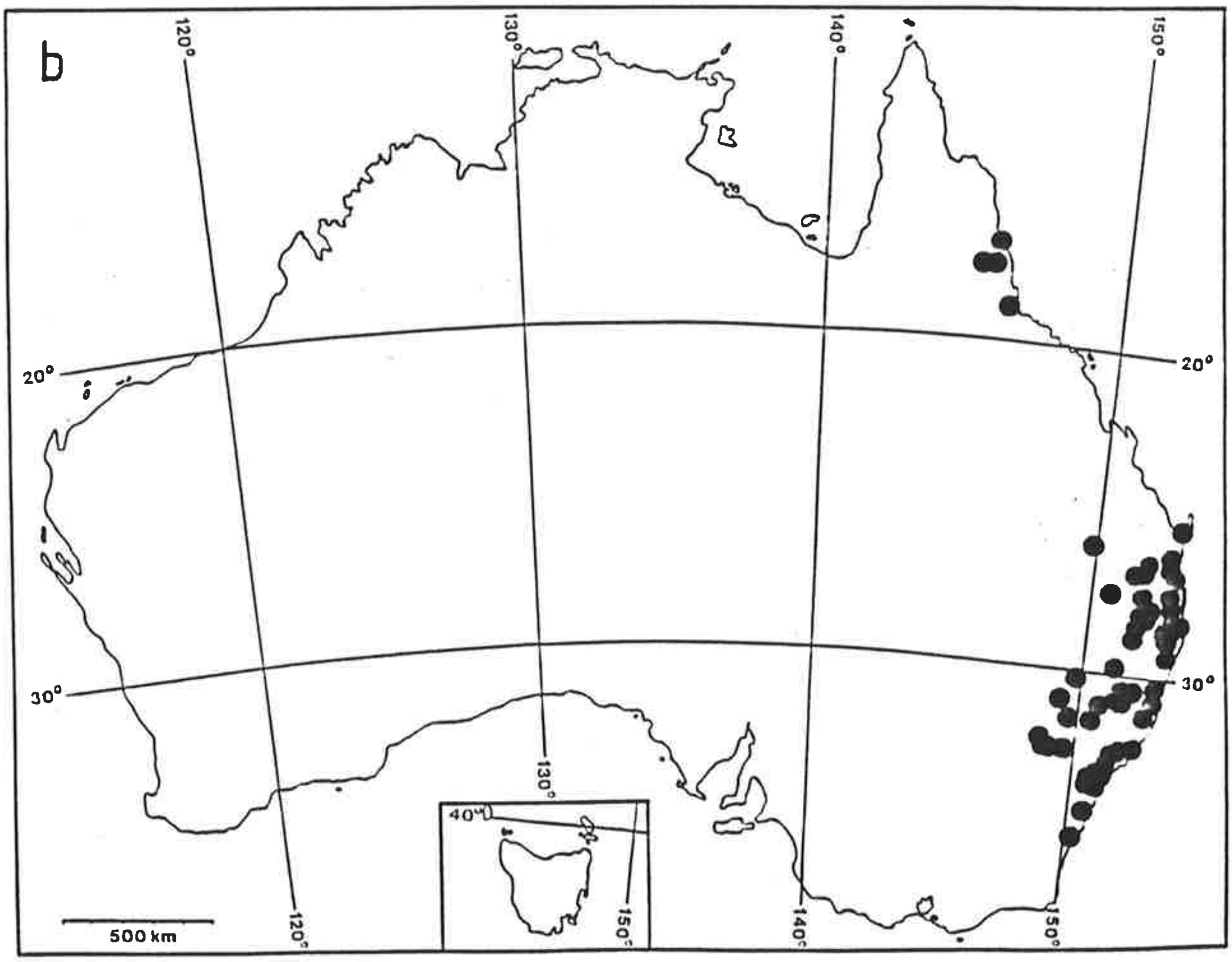
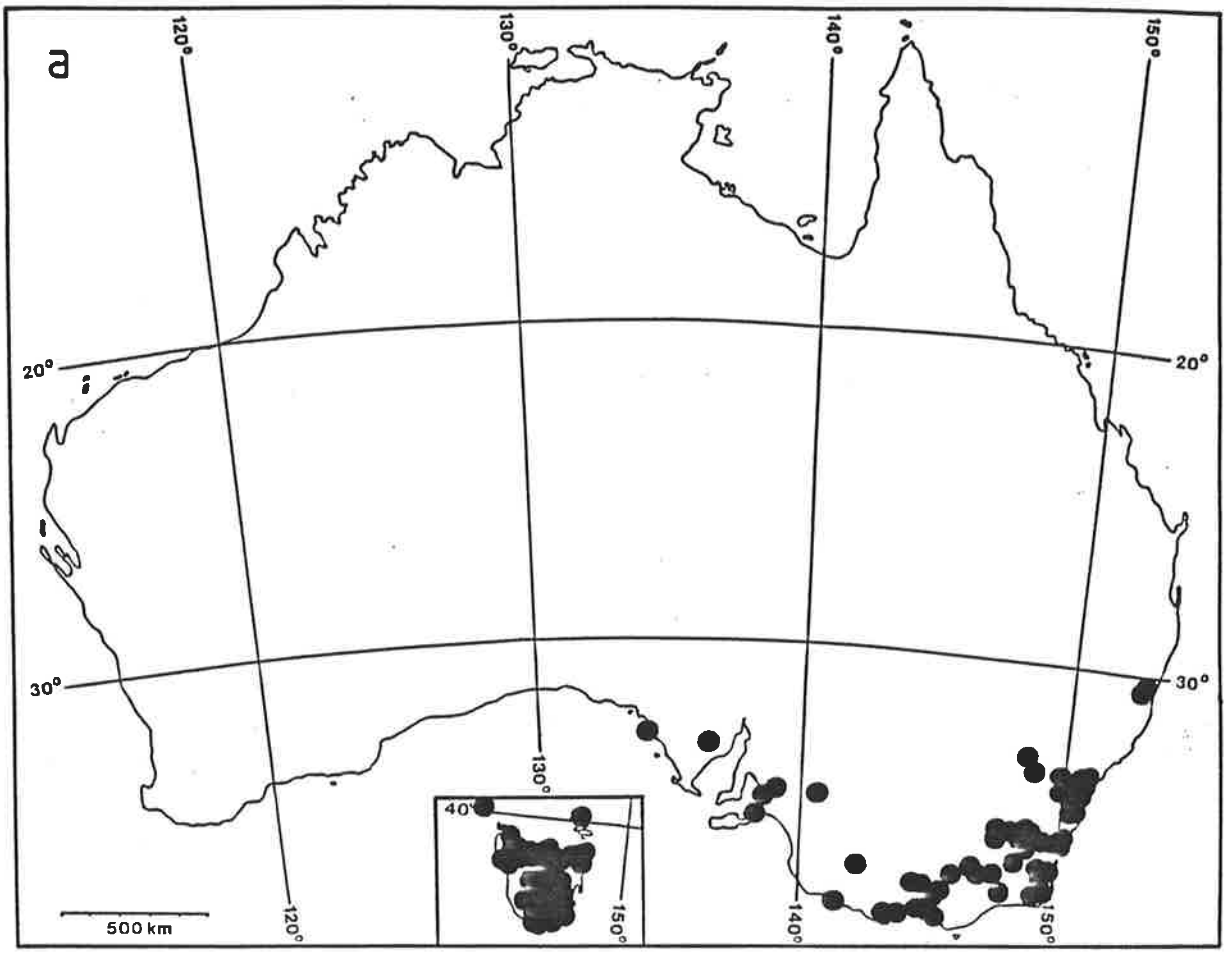

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
40°
150°
120°
140°
150°
500 km

Figure 44a-b. Known distribution of:

(a) Myrmecia forficata (Fabricius), s.l.; and

(b) Myrmecia pyriformis Smith.


a
120°
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120°
140°
150°
500 km

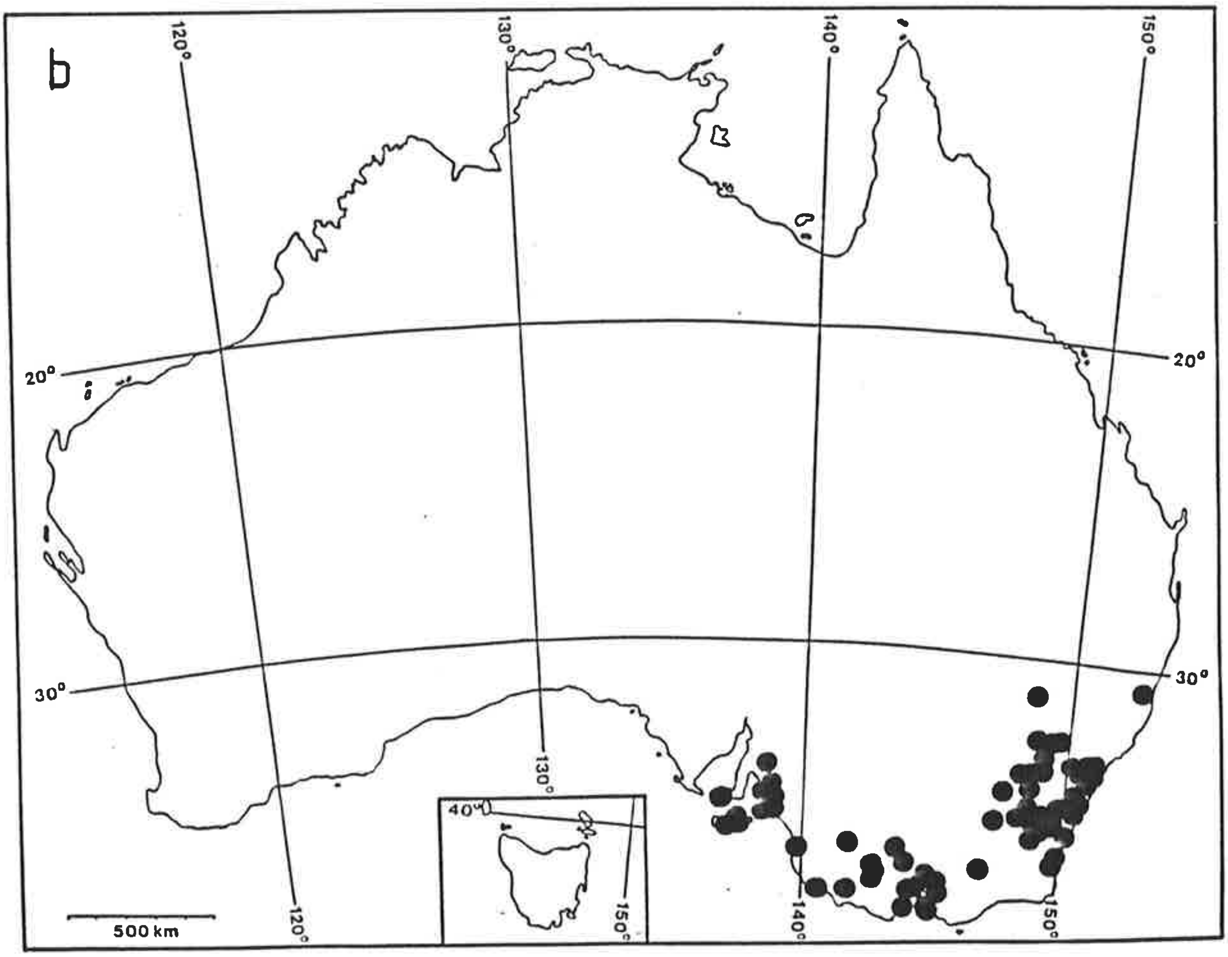
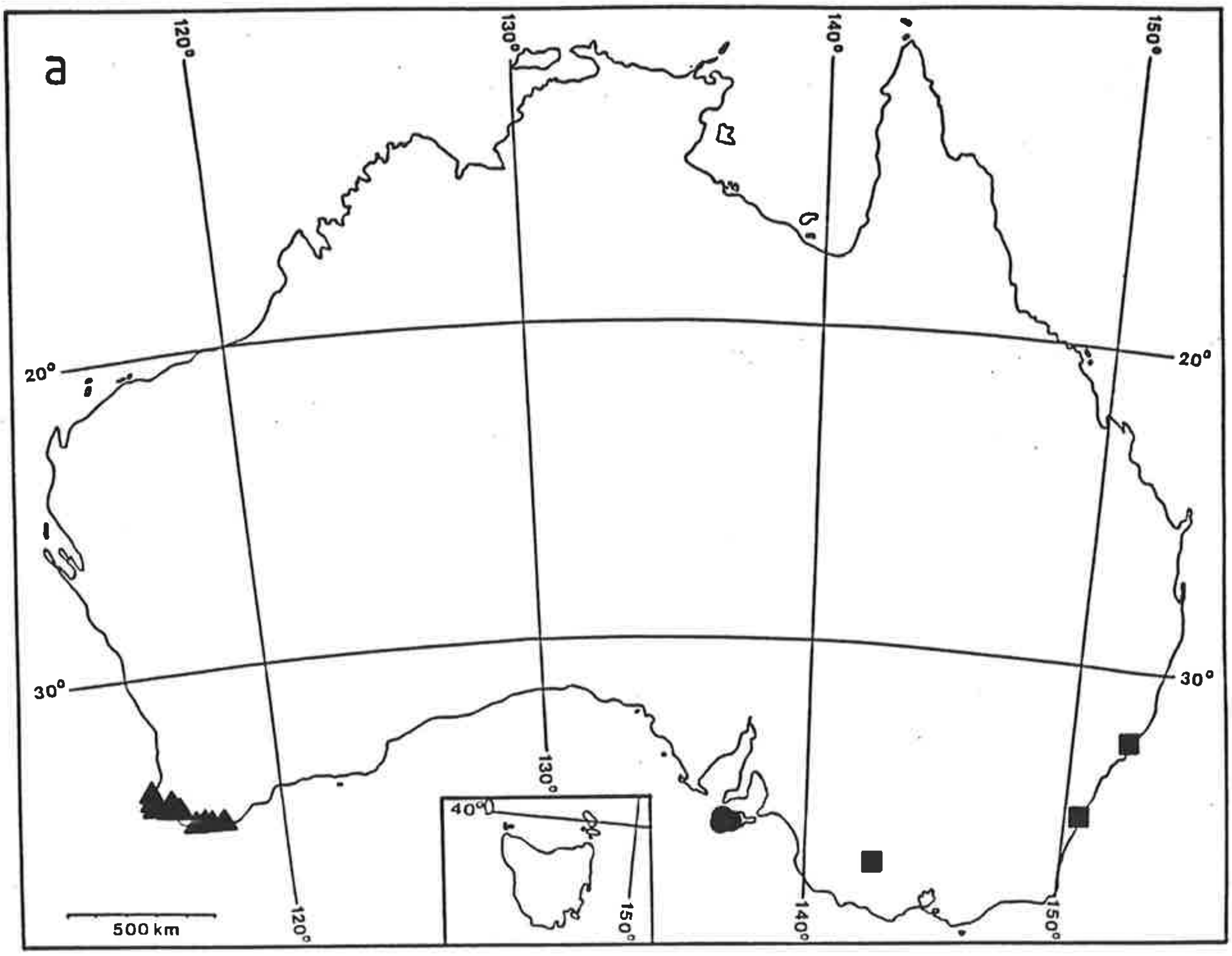

b
120°
130°
140°
150°
20°
20°
30°
30°
40°
130°
150°
120°
140°
150°
500 km

Figure 45a-b. Known distribution of:

(a) *Myrmecia hirsuta* Clark [■], *Myrmecia regularis* Crawley [▲] and *Myrmecia sp.9* (ANIC) [●]; and

(b) *Myrmecia mjobergi* Forel [▲] and *Myrmecia nigriscapa* Roger [●].


a
120°
130°
140°
150°
20°
30°
40°
500 km

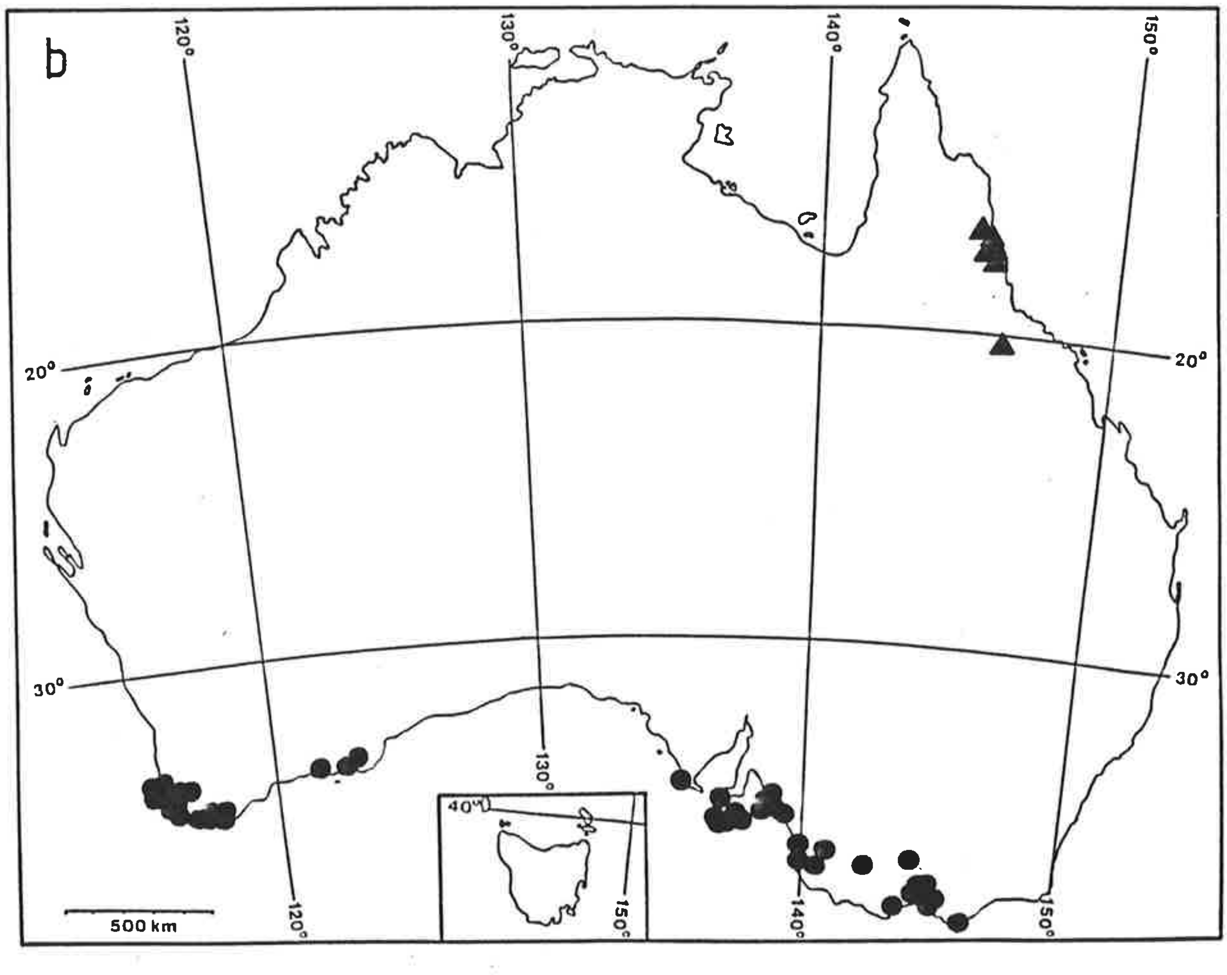
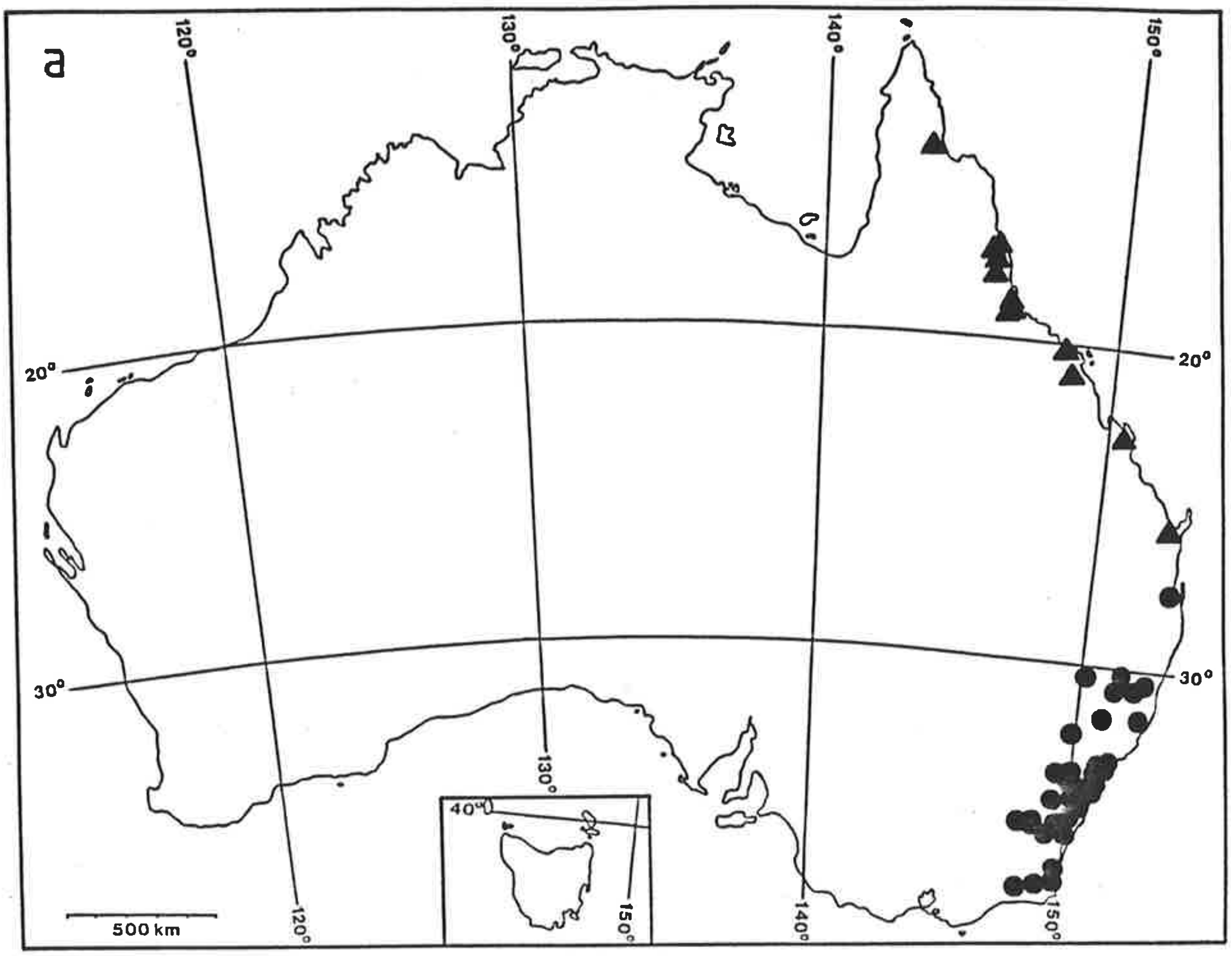

b
120°
130°
140°
150°
20°
30°
40°
500 km

Figure 46a-b. Known distribution of:

(a) *Myrmecia tarsata* Smith [●] and *Myrmecia auriventris* Mayr [▲]; and

(b) *Myrmecia flavicoma* Roger [■], *Myrmecia arnoldi* Clark [▲] and *Myrmecia rufinodis* Smith [●].


a
120°
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30°
30°
40°
500 km

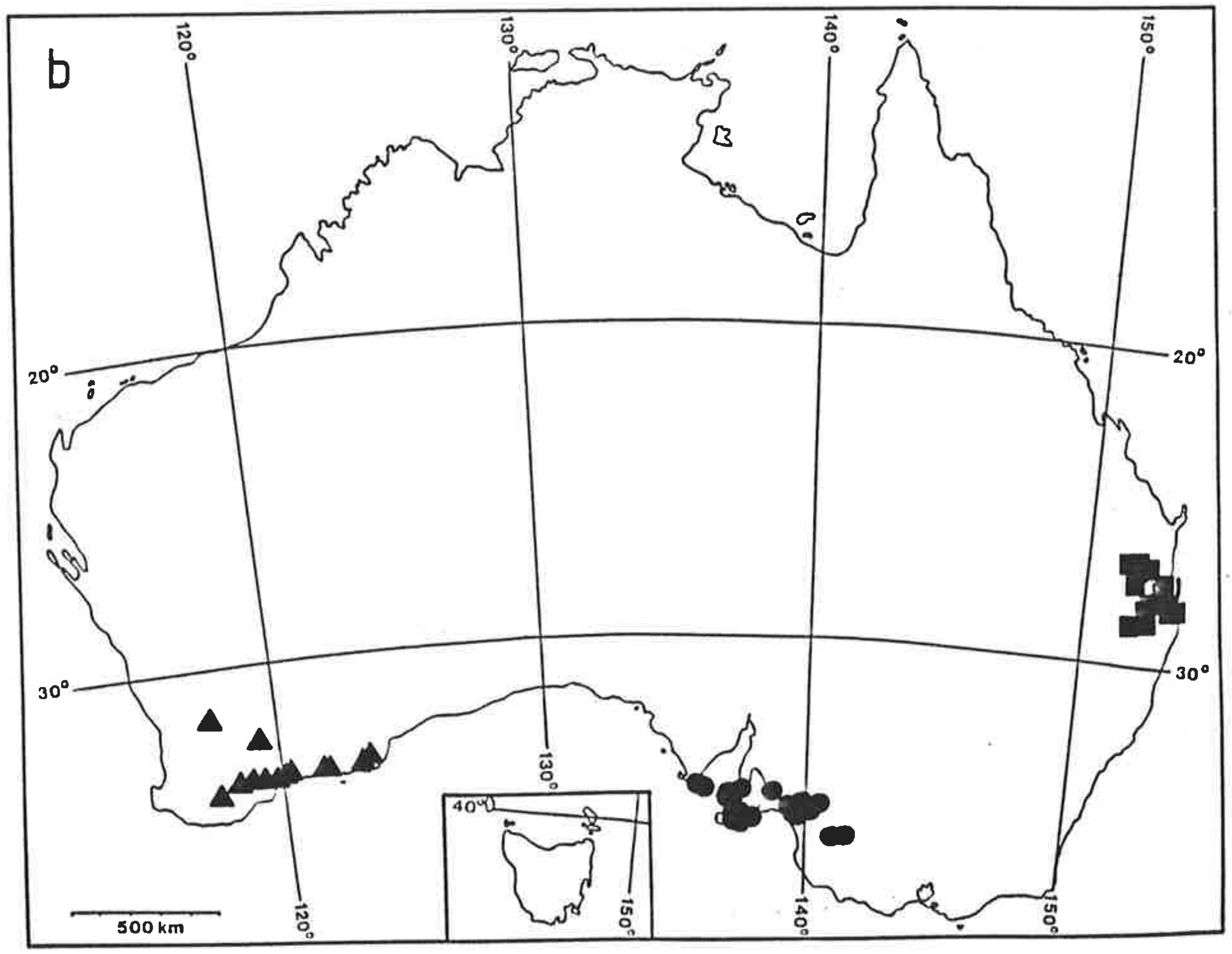
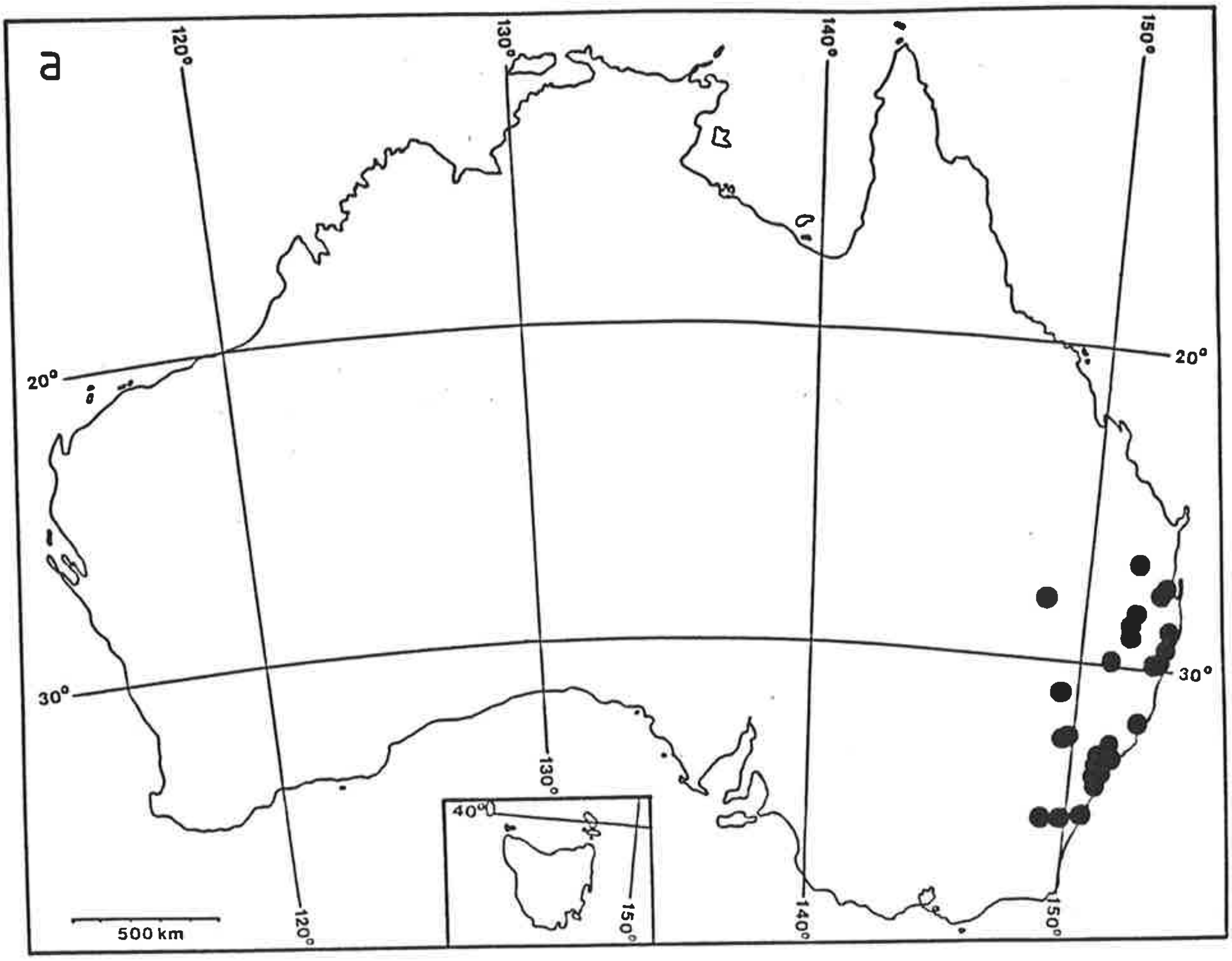

b
120°
130°
140°
150°
20°
20°
30°
30°
40°
500 km

Figure 47a-b. Known distribution of:
(a) *Myrmecia gulosa* (Fabricius); and
(b) *Myrmecia simillima* Smith.


a
120°
130°
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20°
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30°
30°
130°
40°
150°
120°
140°
150°
500 km

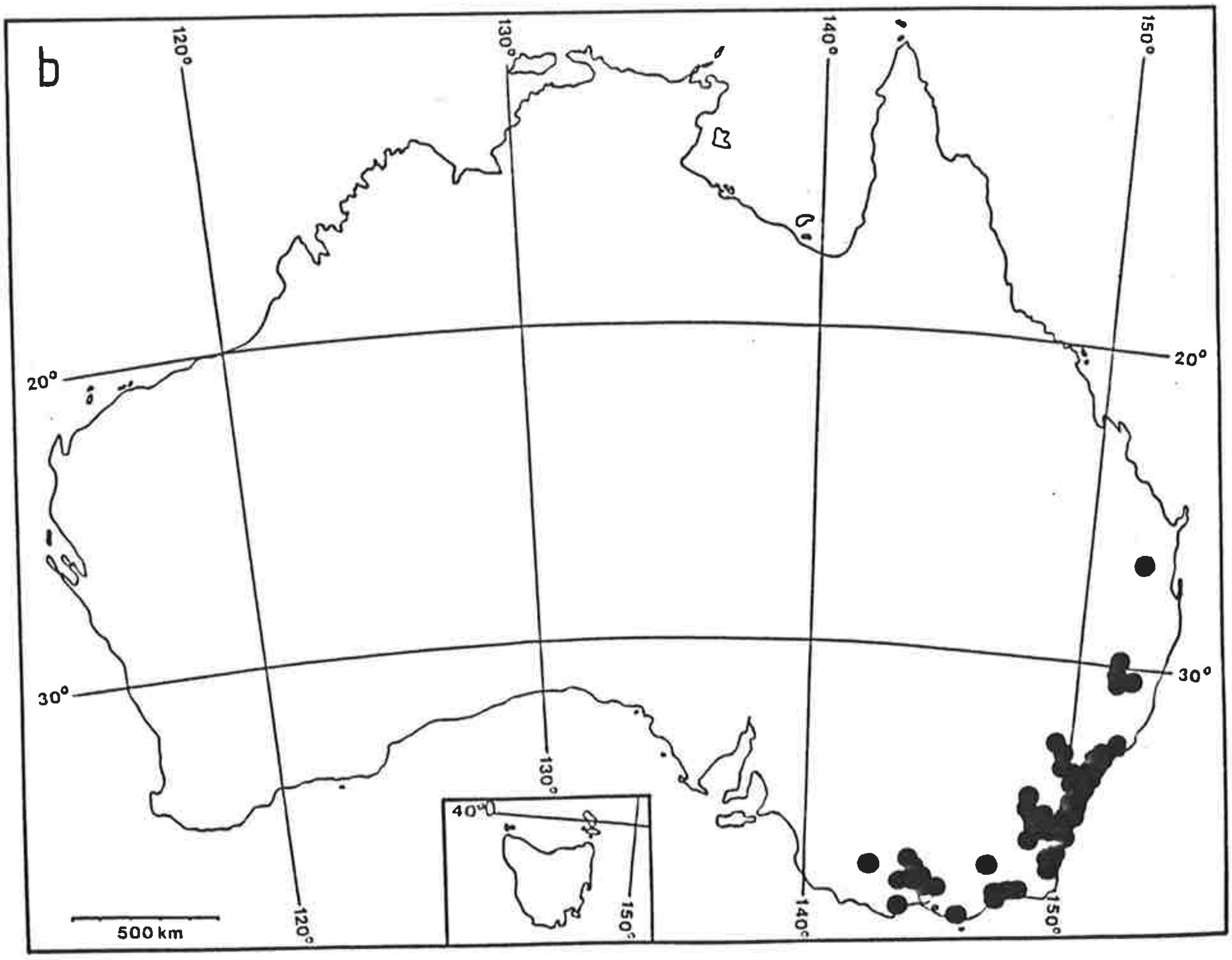
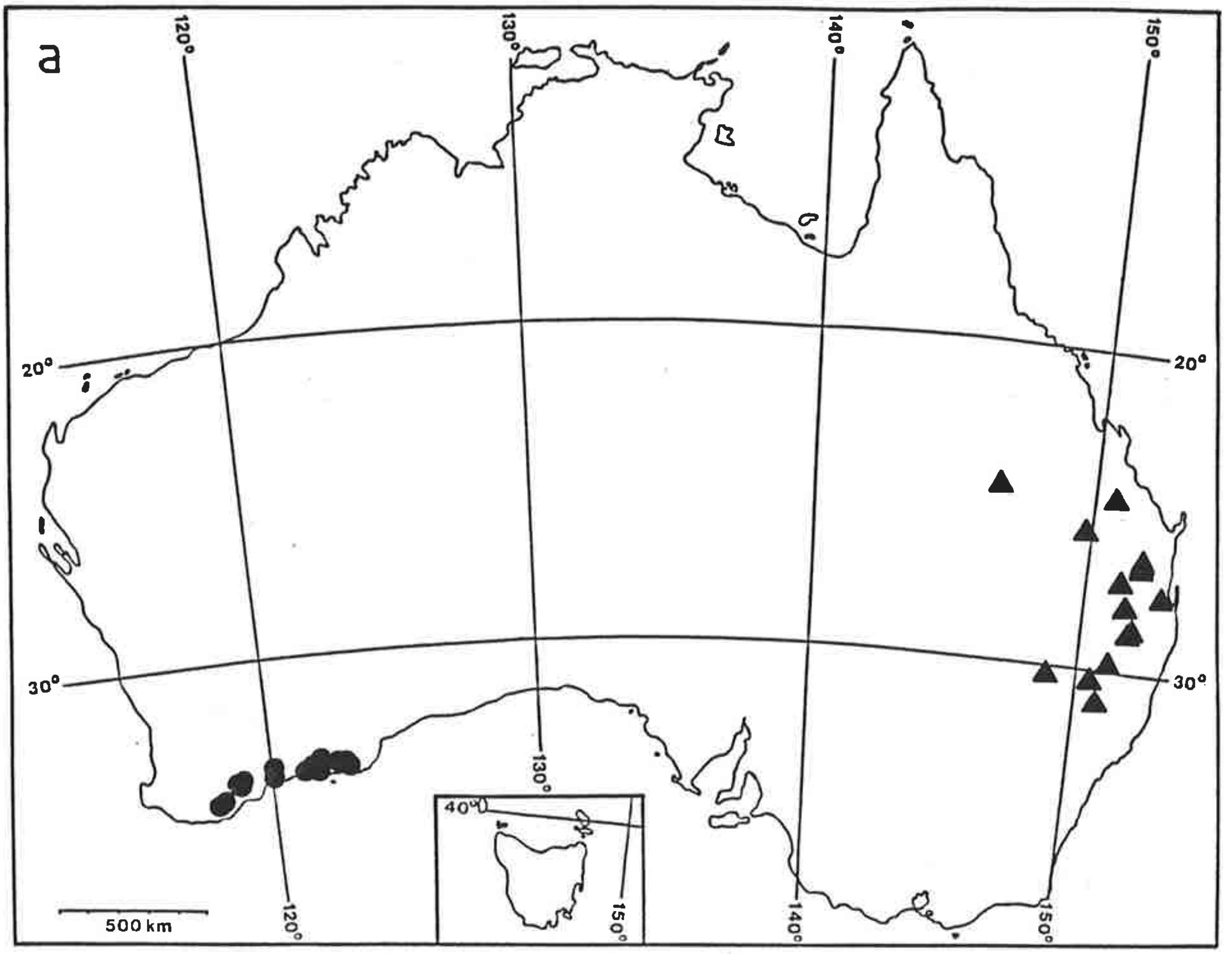

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
40°
150°
120°
140°
150°
500 km

Figure 48a-b. Known distribution of:

(a) *Myrmecia atrata* Clark [●] and *Myrmecia ferruginea* Mayr [▲]; and

(b) *Myrmecia fulgida* Clark [▲] and *Myrmecia fuscipes* Clark [●].


a
120°
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30°
30°
130°
40°
150°
120°
140°
150°
500 km

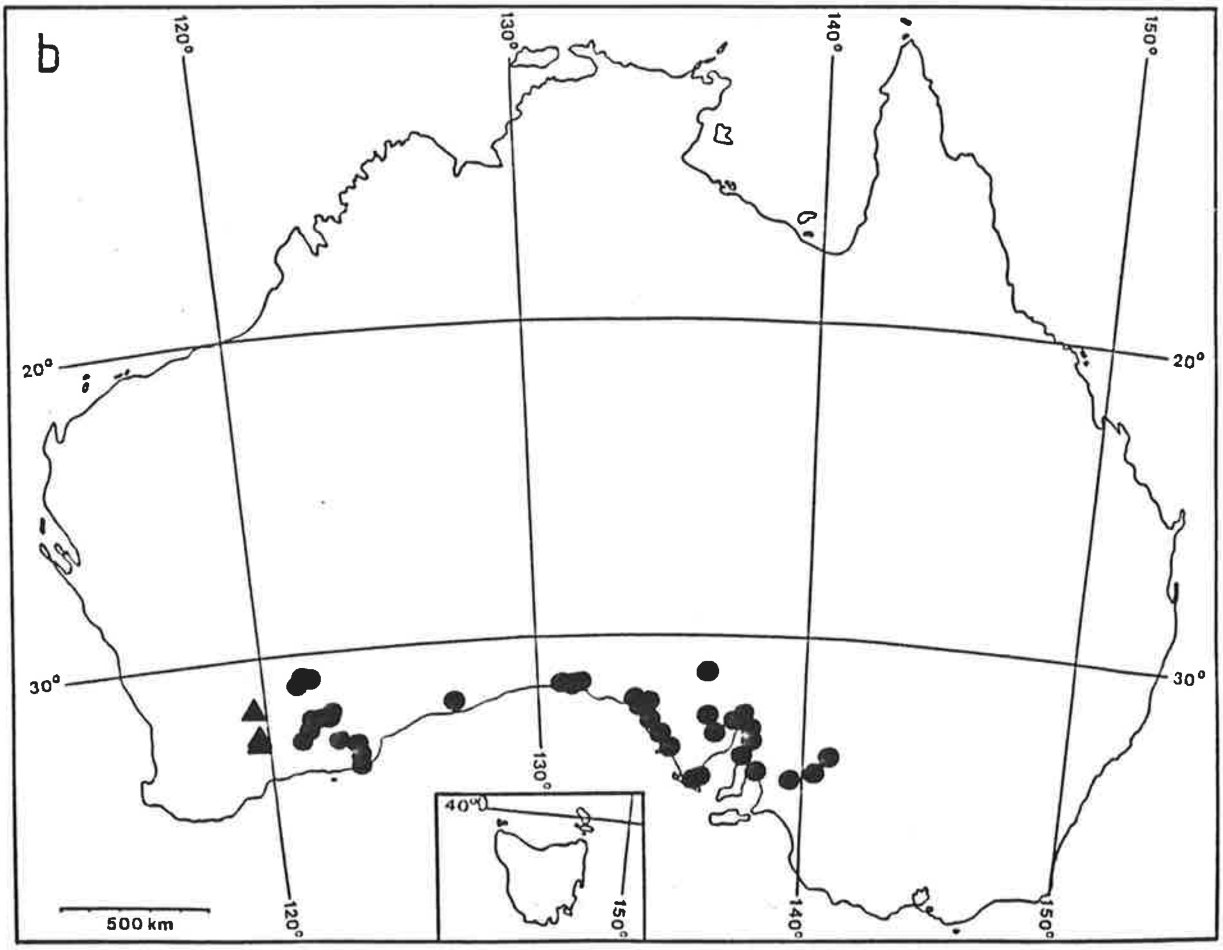
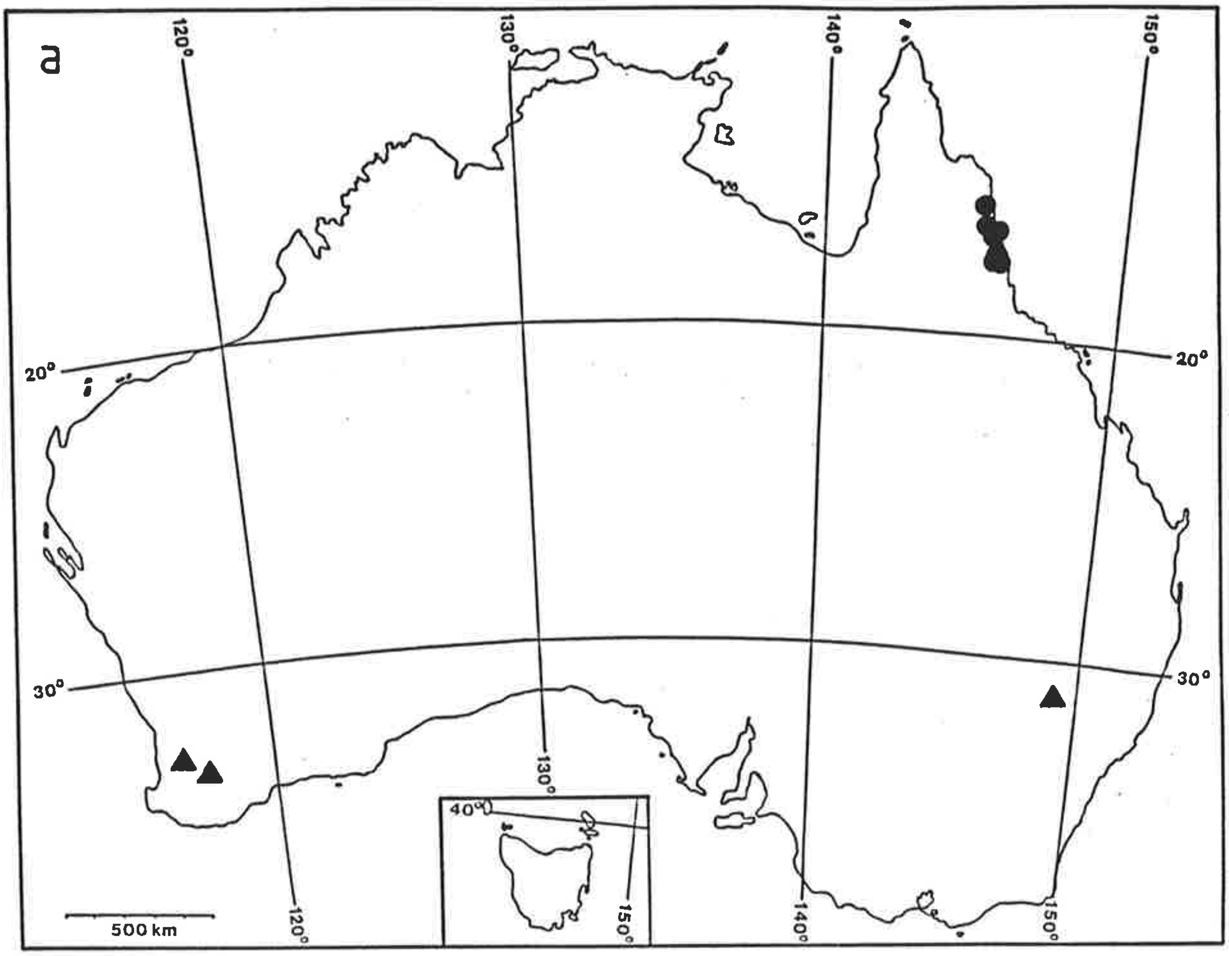

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
40°
150°
120°
140°
150°
500 km

Figure 49a-b. Known distribution of:

(a) *Myrmecia inquilina* Douglas and Brown [▲] and *Myrmecia rowlandi* Forel [●]; and

(b) *Myrmecia nigriceps* Mayr, *s.l.*


a
120°
130°
140°
150°
20°
20°
30°
30°
130°
40°
150°
500 km
120°
140°
150°

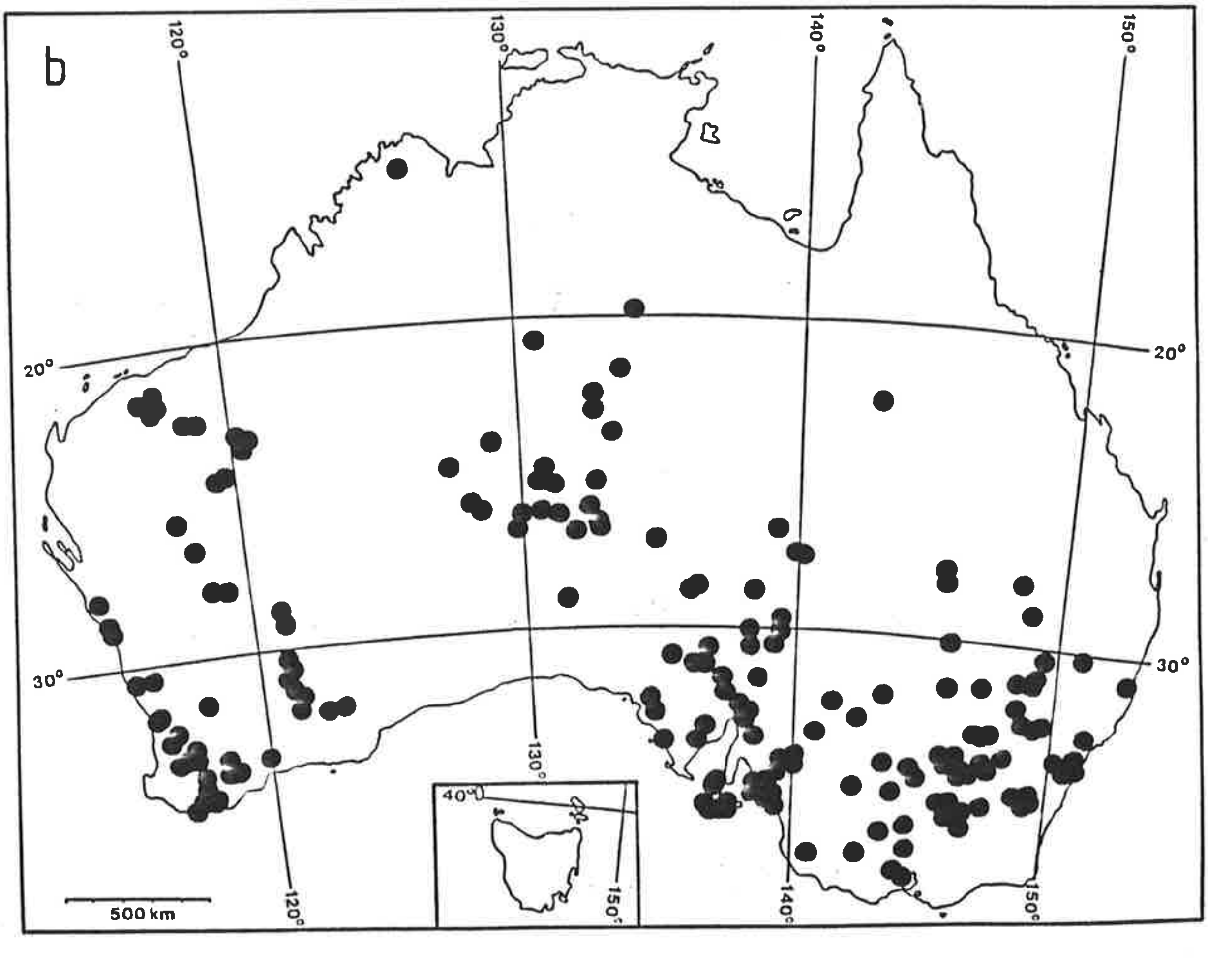
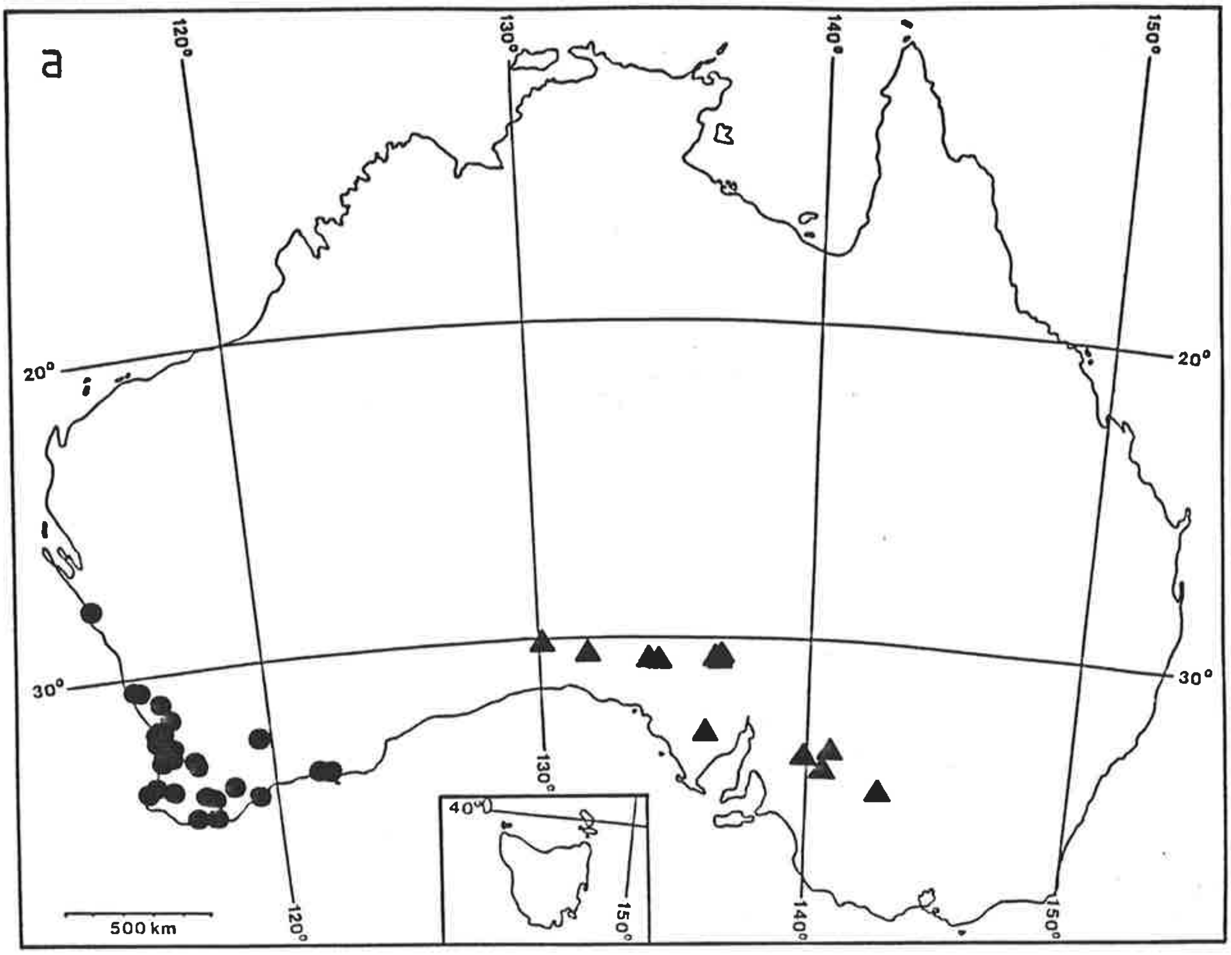

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
40°
150°
500 km
120°
140°
150°

Figure 50a-b. Known distribution of:

(a) *Myrmecia princeps* Clark [▲] and *Myrmecia vindex* Smith [●]; and

(b) *Myrmecia sp.12* (ANIC) [●], *Myrmecia sp.14* (ANIC) [⬢], *Myrmecia sp.16* (ANIC) [■] and *Myrmecia sp.17* (ANIC) [▲].


a
120°
130°
140°
150°
20°
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30°
30°
130°
120°
140°
150°
40°
500 km

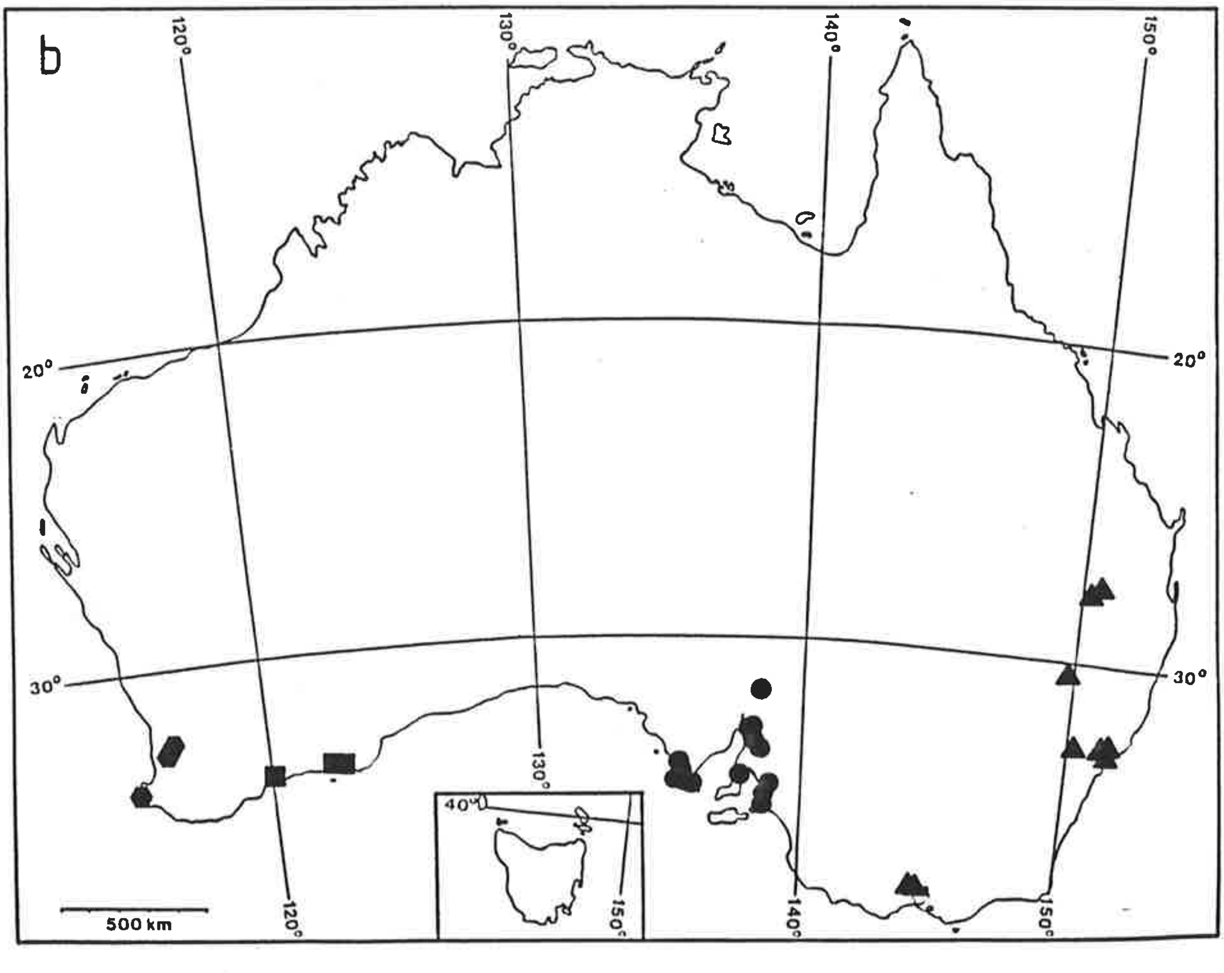
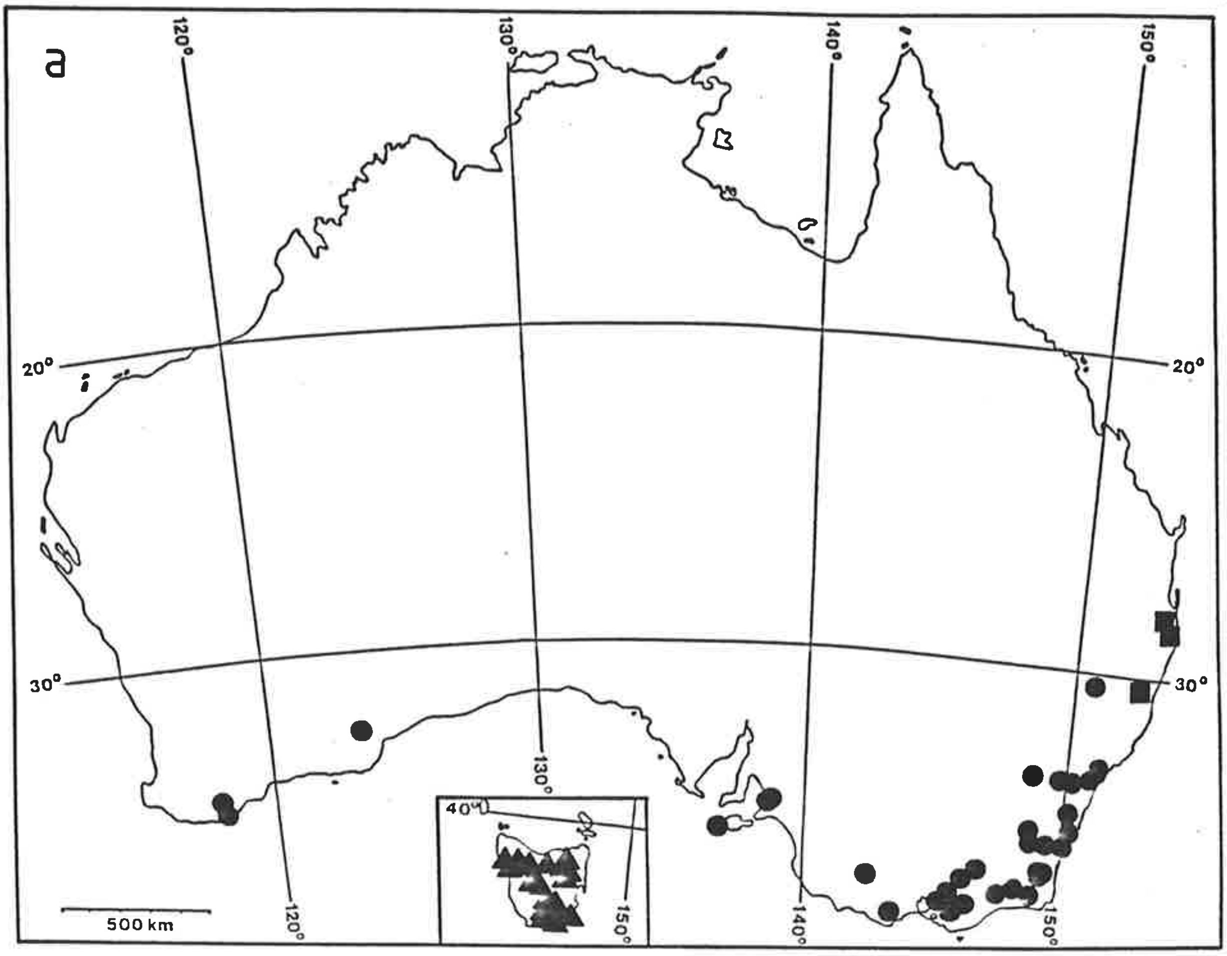

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
120°
140°
150°
40°
500 km

Figure 51a-b. Known distribution of:

(a) *Myrmecia esuriens* Fabricius [▲], *Myrmecia midas* Clark [■] and *Myrmecia pulchra* Clark [●]; and

(b) *Myrmecia apicalis* Emery [■], *Myrmecia cardigaster* Brown [▲], *Myrmecia flammicollis* Brown [⬢] and *Myrmecia petiolata* Emery [●].


a
120°
130°
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20°
20°
30°
30°
130°
120°
140°
150°
40°
150°
500 km

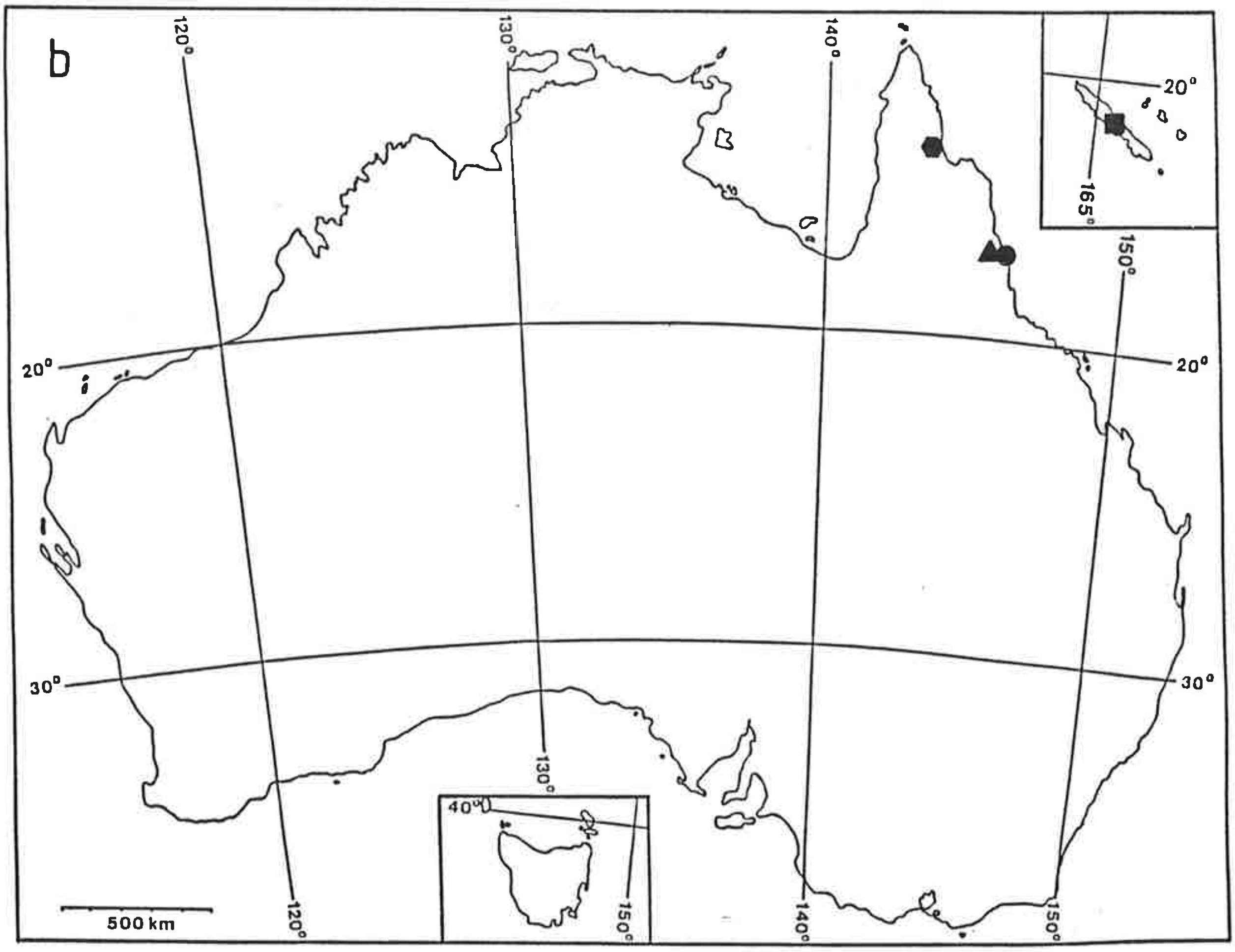
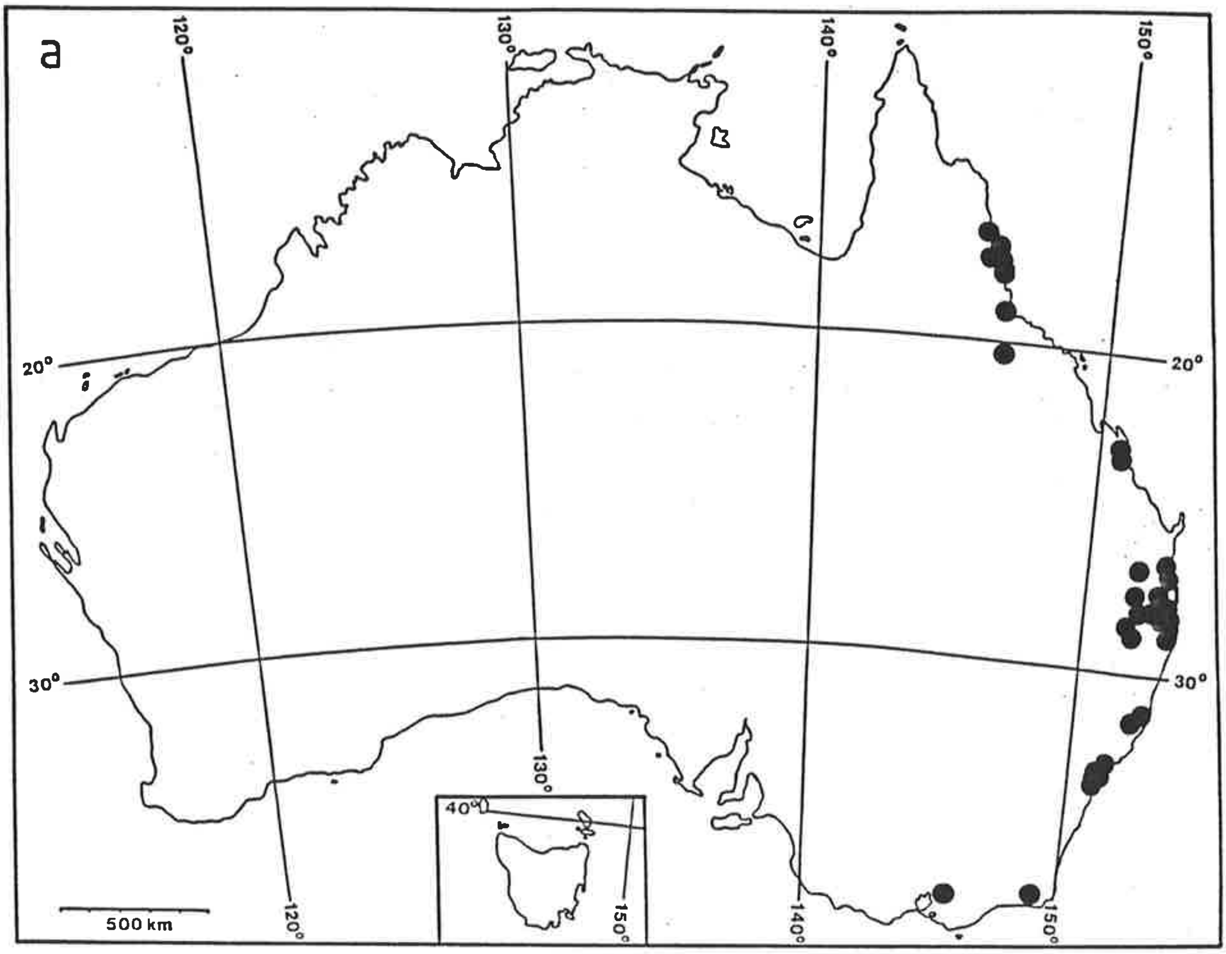

b
120°
130°
140°
20°
165°
150°
20°
20°
30°
30°
130°
40°
150°
120°
140°
150°
500 km

Figure 52a-b. Known distribution of:

(a) *Myrmecia nigrocincta* Smith; and

(b) *Myrmecia harderi* Forel.


a
120°
130°
140°
150°
20°
20°
30°
30°
130°
40°
150°
120°
140°
150°
500 km

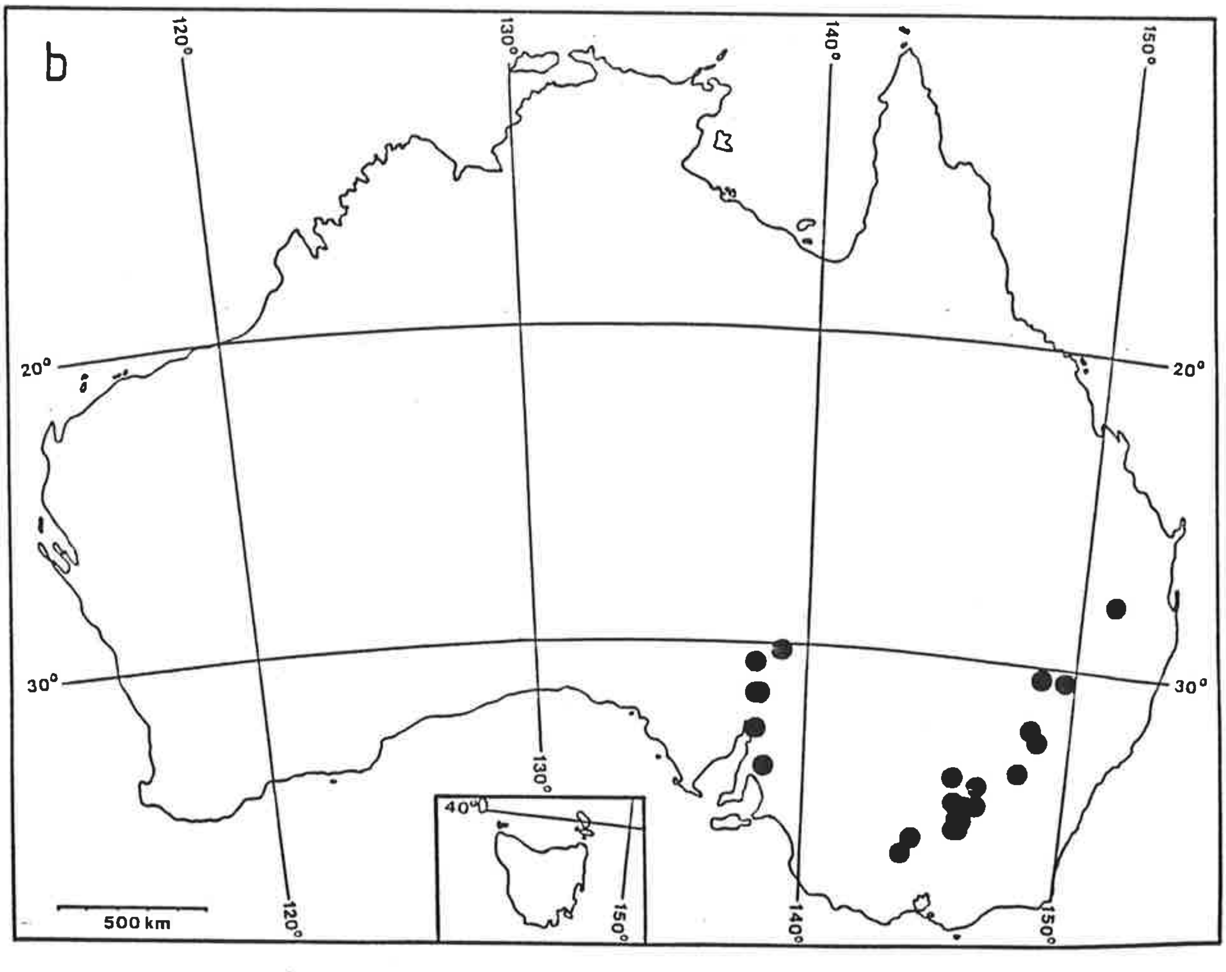
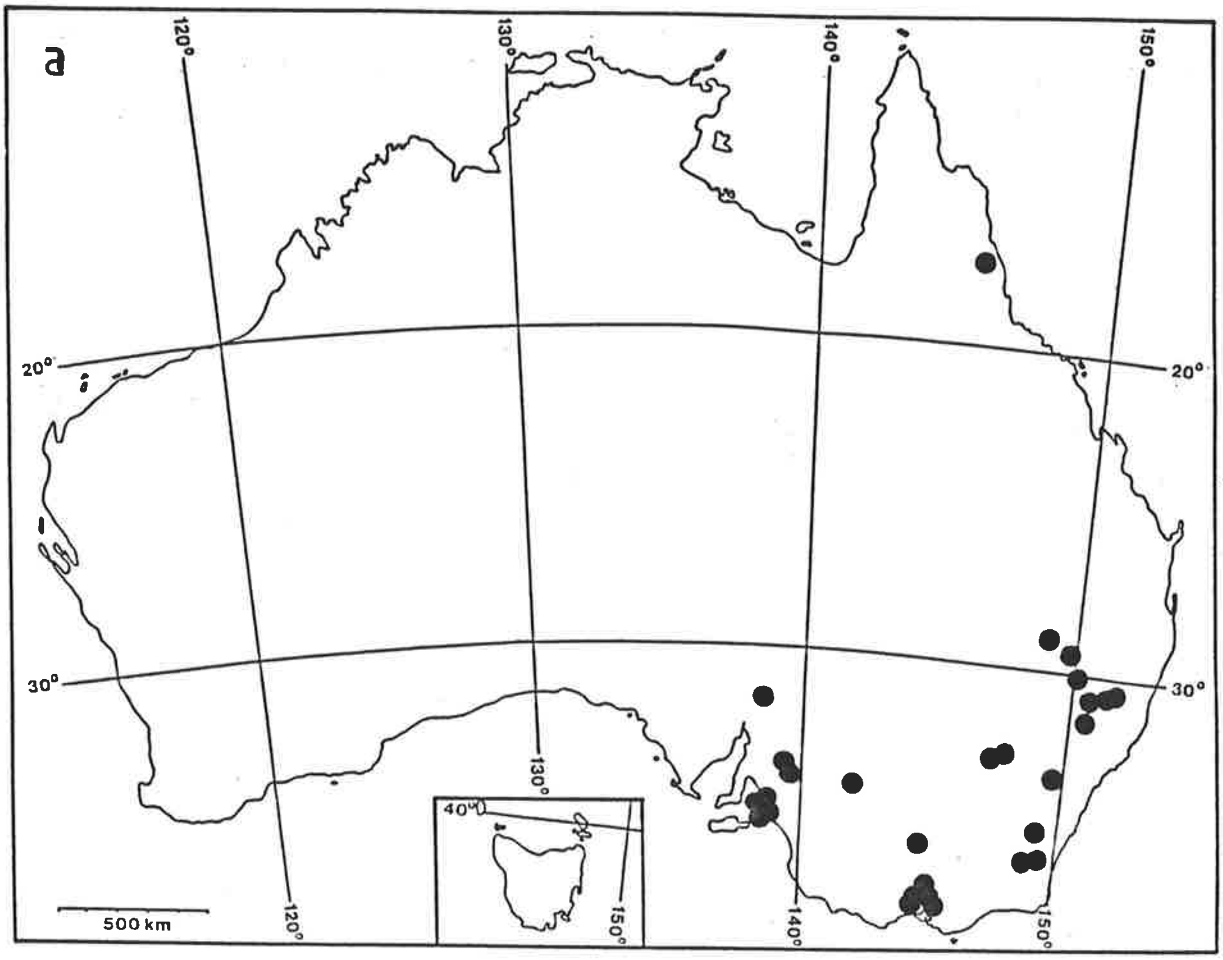

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
40°
150°
120°
140°
150°
500 km

Figure 53a-b. Known distribution of:

(a) Myrmecia aberrans Forel; and

(b) Myrmecia cephalotes (Clark).


a
120°
130°
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30°
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120°
140°
150°
40°
150°
500 km

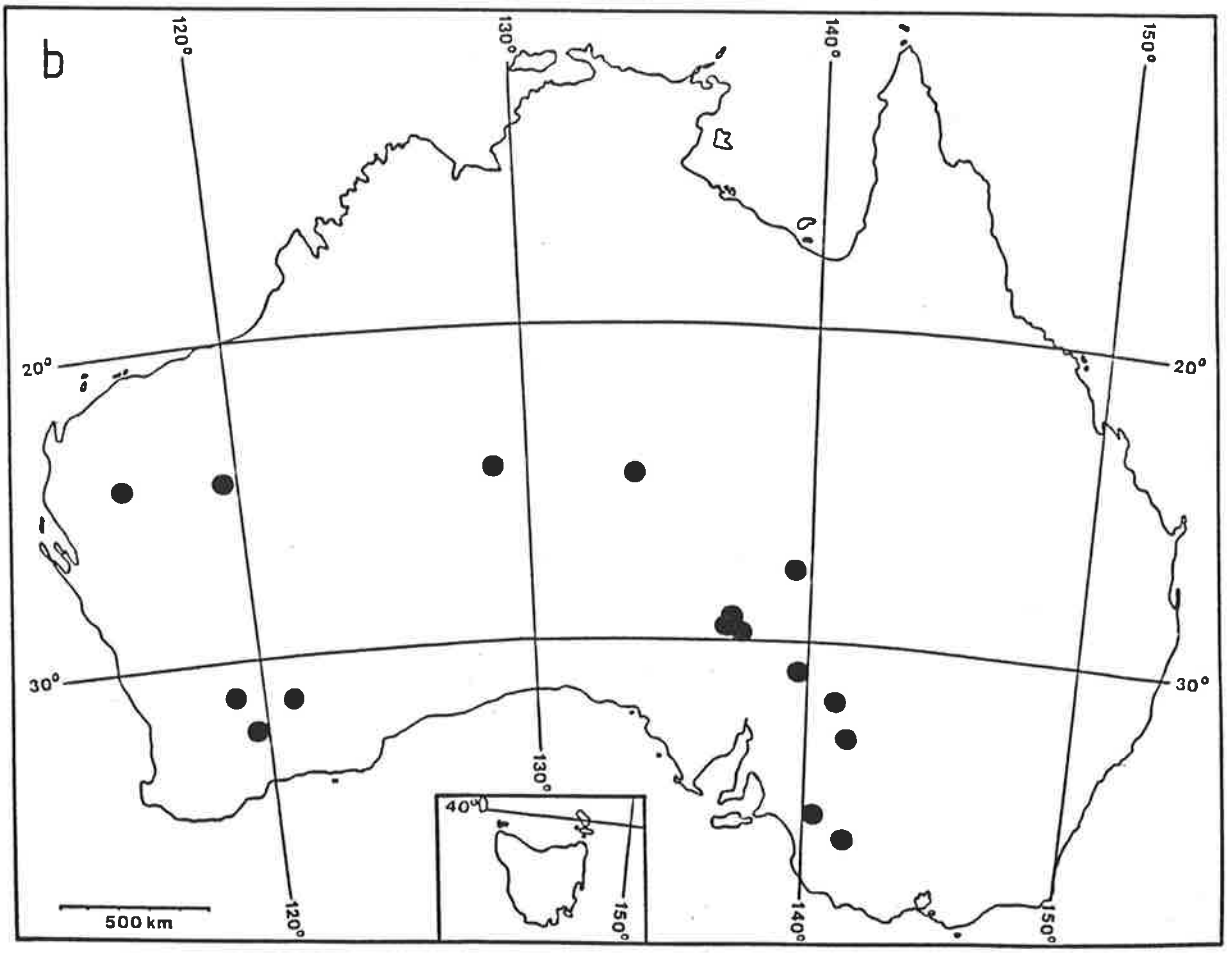
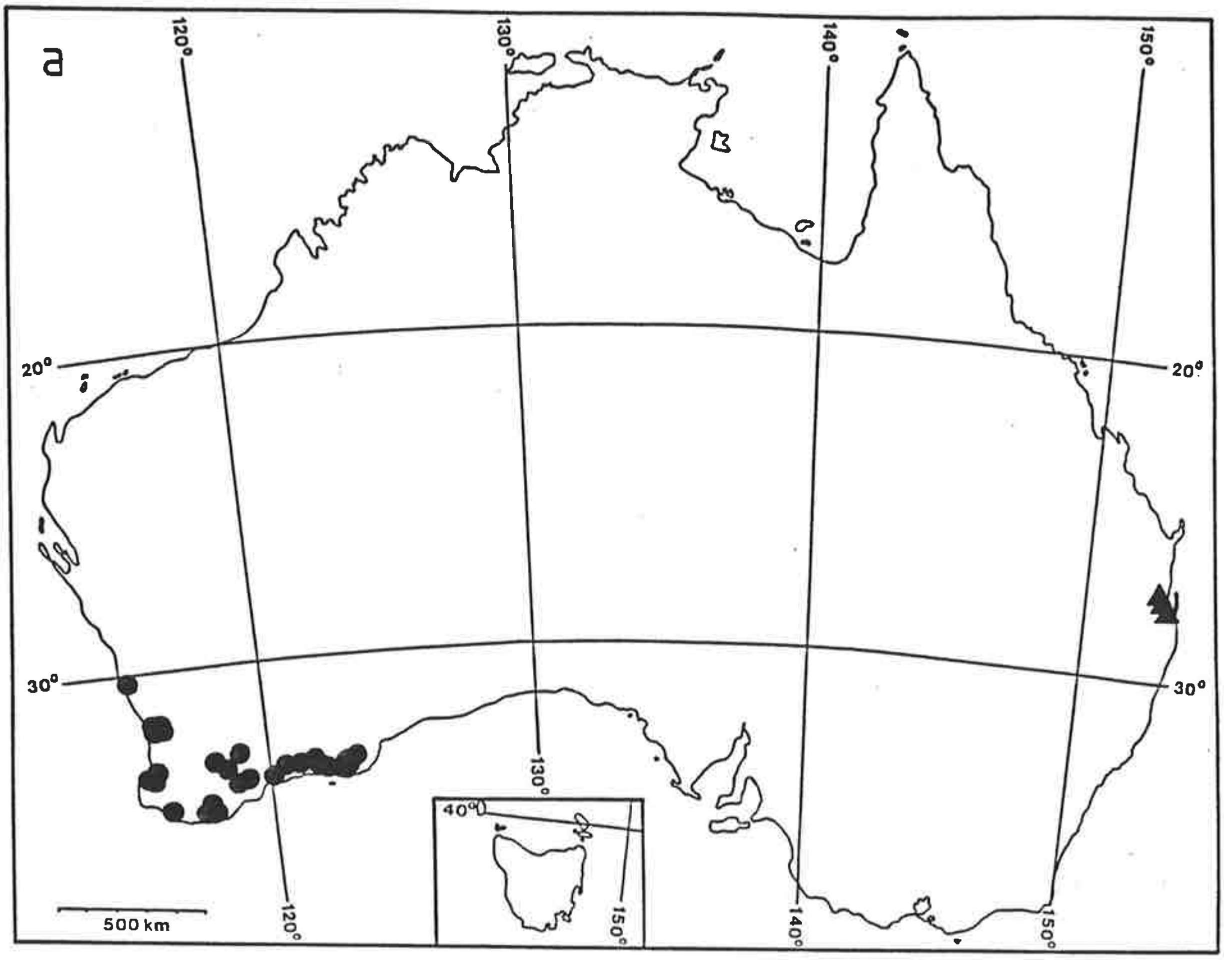

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
120°
140°
150°
40°
150°
500 km

Figure 54a-b. Known distribution of:

(a) *Myrmecia chasei* Forel [●] and *Myrmecia chrysogaster* (Clark) [▲]; and

(b) *Myrmecia clarki* Crawley [●] and *Myrmecia dispar* (Clark) [▲].


a
120°
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30°
30°
130°
120°
140°
150°
40°
150°
500 km

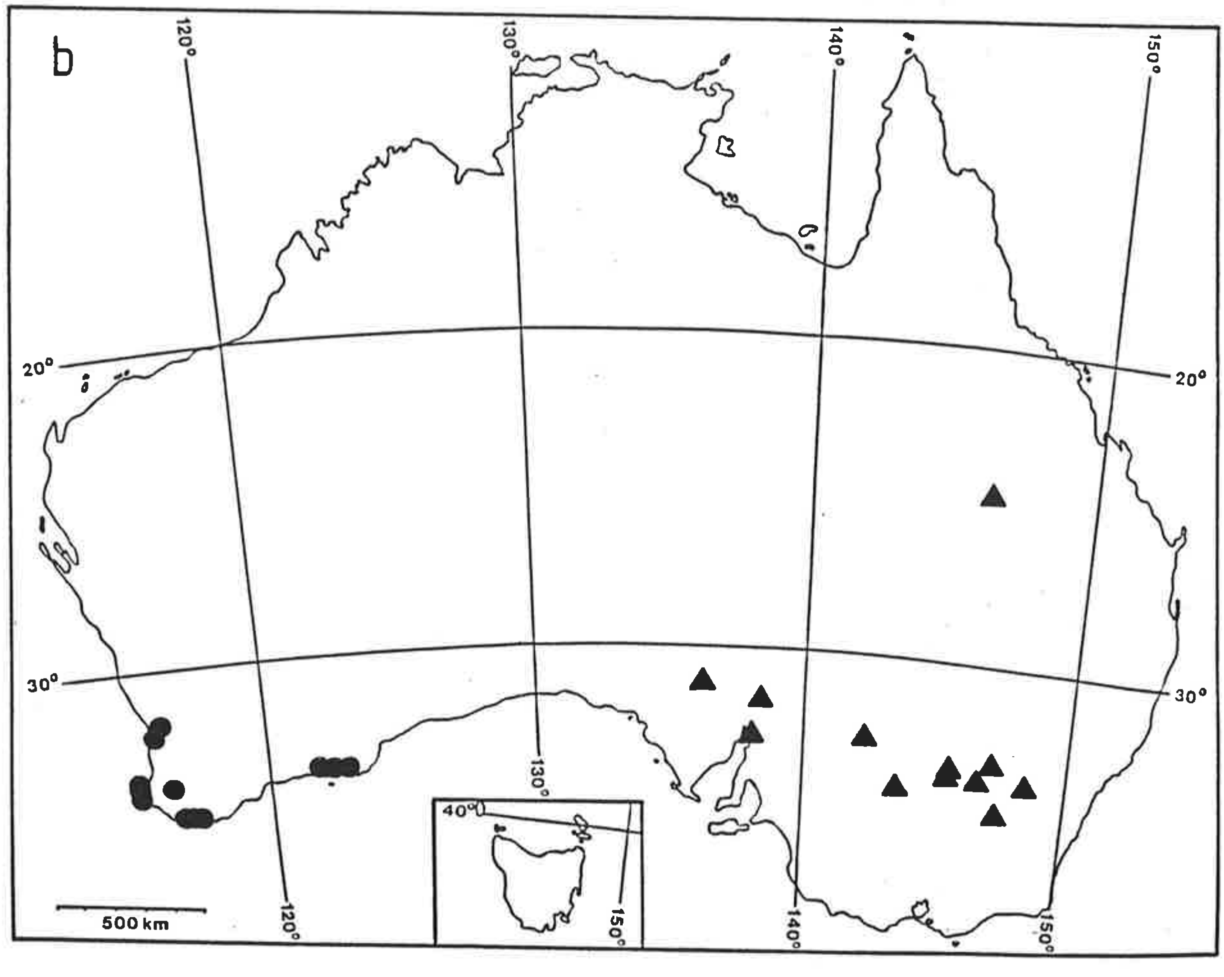
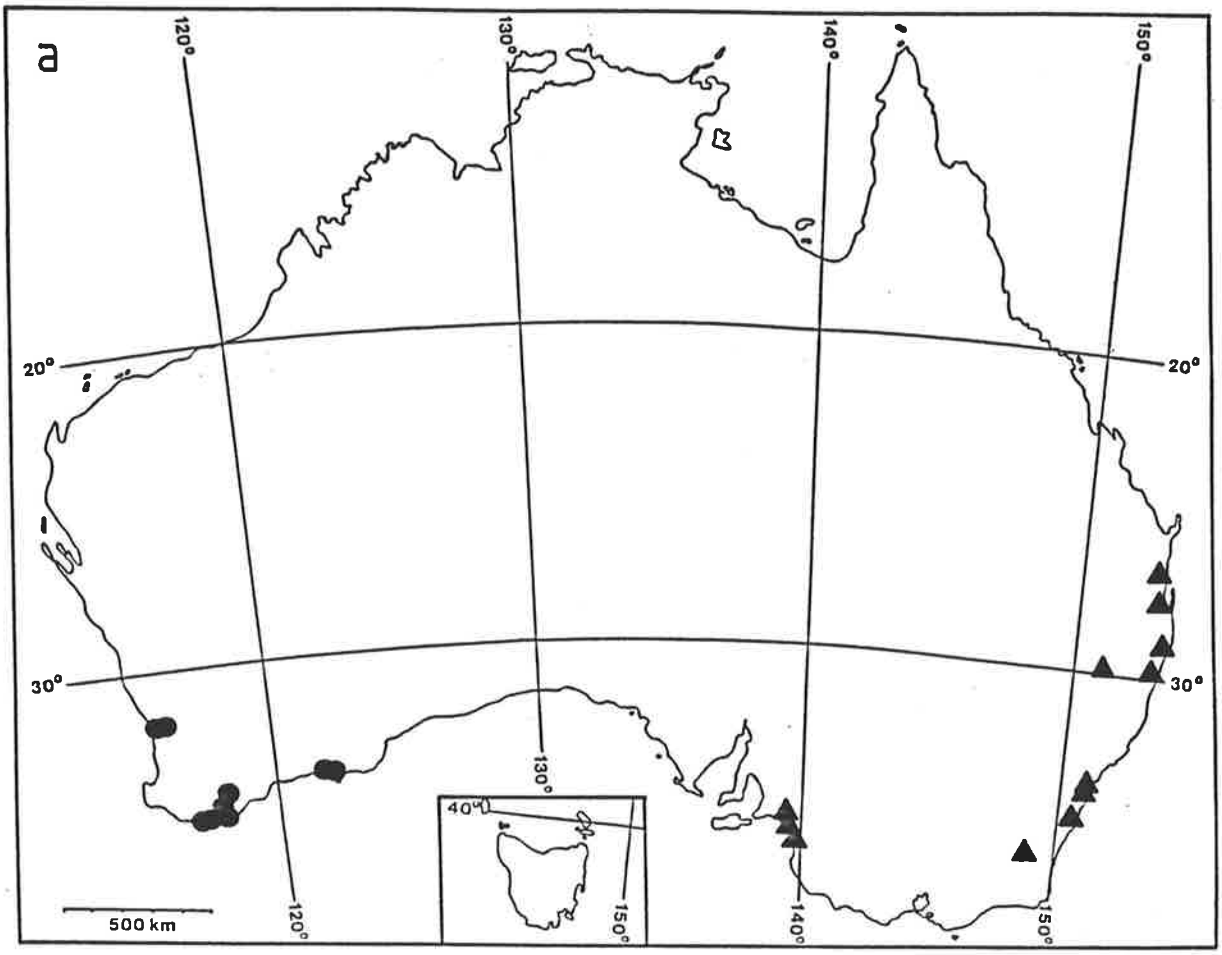

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
120°
140°
150°
40°
150°
500 km

Figure 55a-b. Known distribution of:

(a) Myrmecia michaelseni Forel [●] and Myrmecia queenslandica Forel [▲]; and

(b) Myrmecia pilosula Smith, s.l.


a
120°
130°
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150°
20°
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30°
30°
130°
40°
150°
120°
140°
150°
500 km

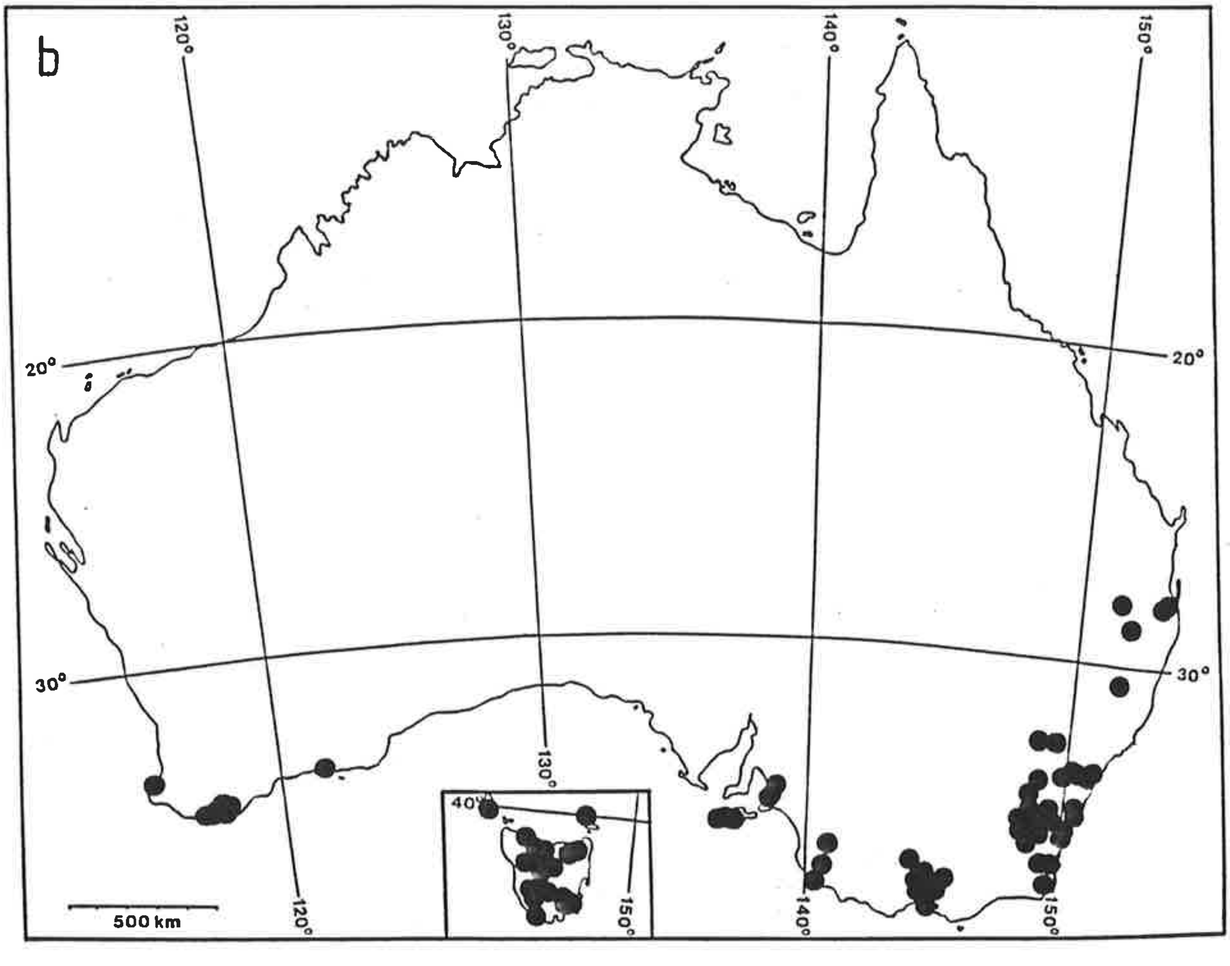
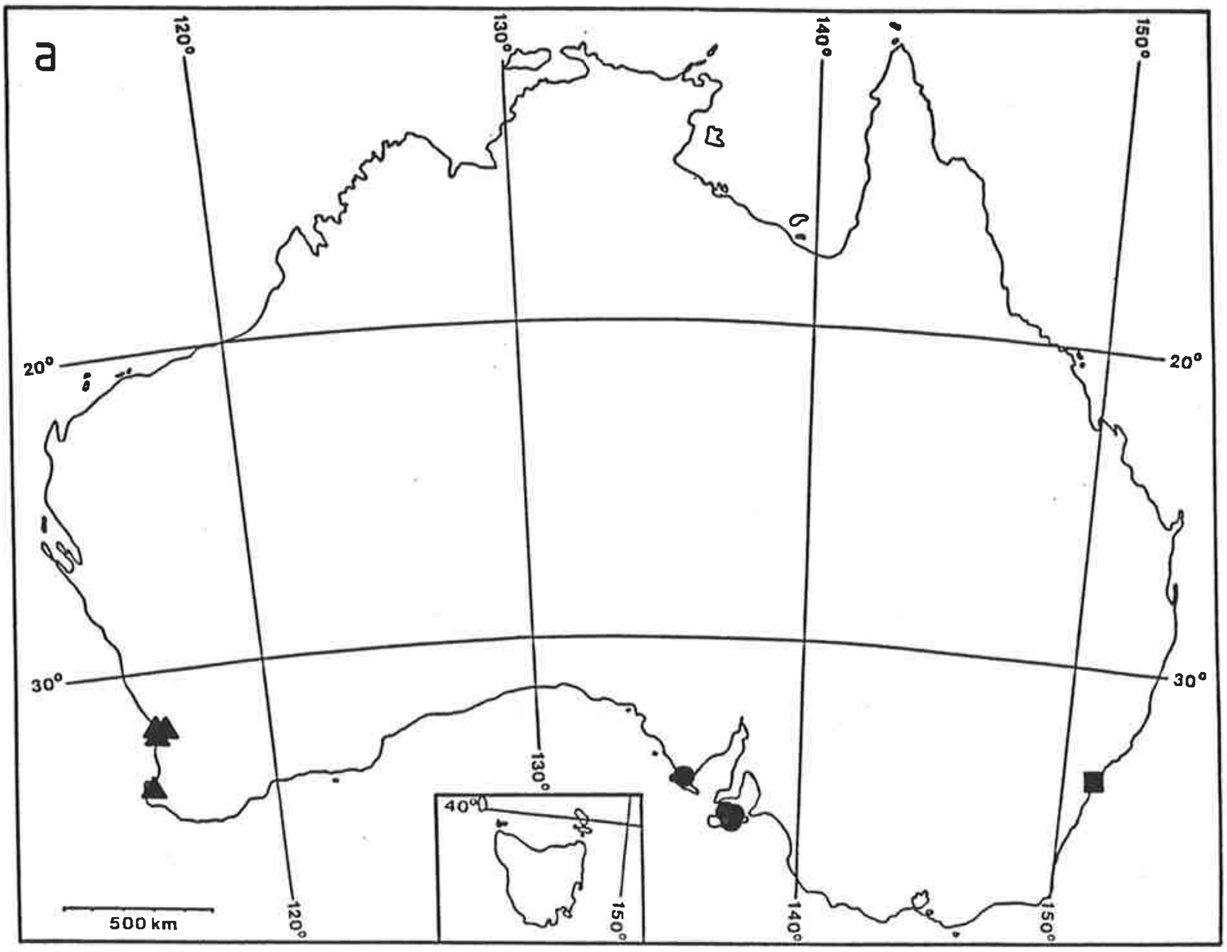

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
40°
150°
120°
140°
150°
500 km

Figure 56a-b. Known distribution of:

(a) *Myrmecia rugosa* Wheeler [▲], *Myrmecia sp.8* (ANIC) [●] and *Myrmecia sp.M1* (GPB) [■]; and

(b) *Myrmecia swalei* Crawley [●] and *Myrmecia sp.M2* (GPB) [▲].


a
120°
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150°
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30°
30°
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120°
140°
150°
40°
150°
500 km

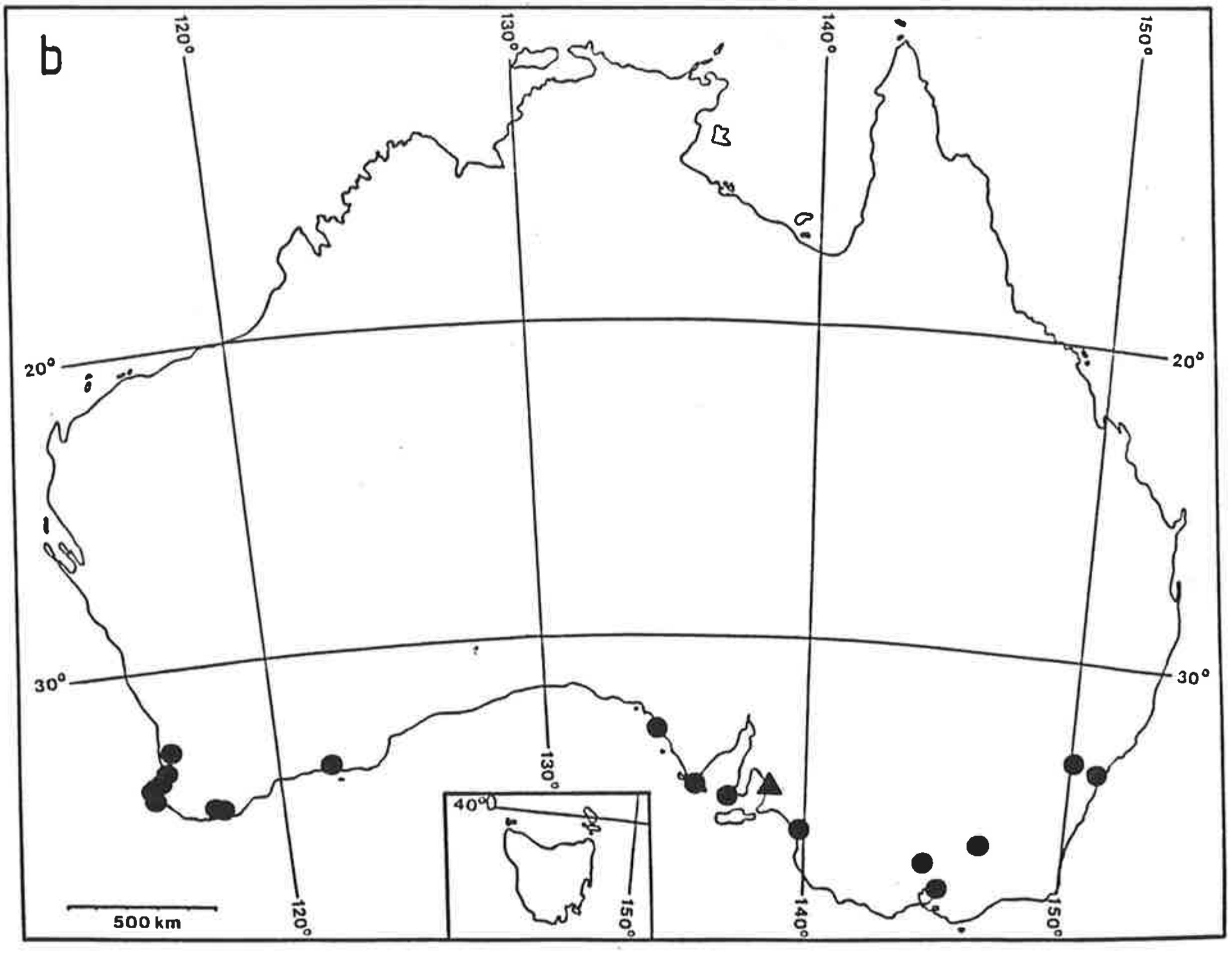
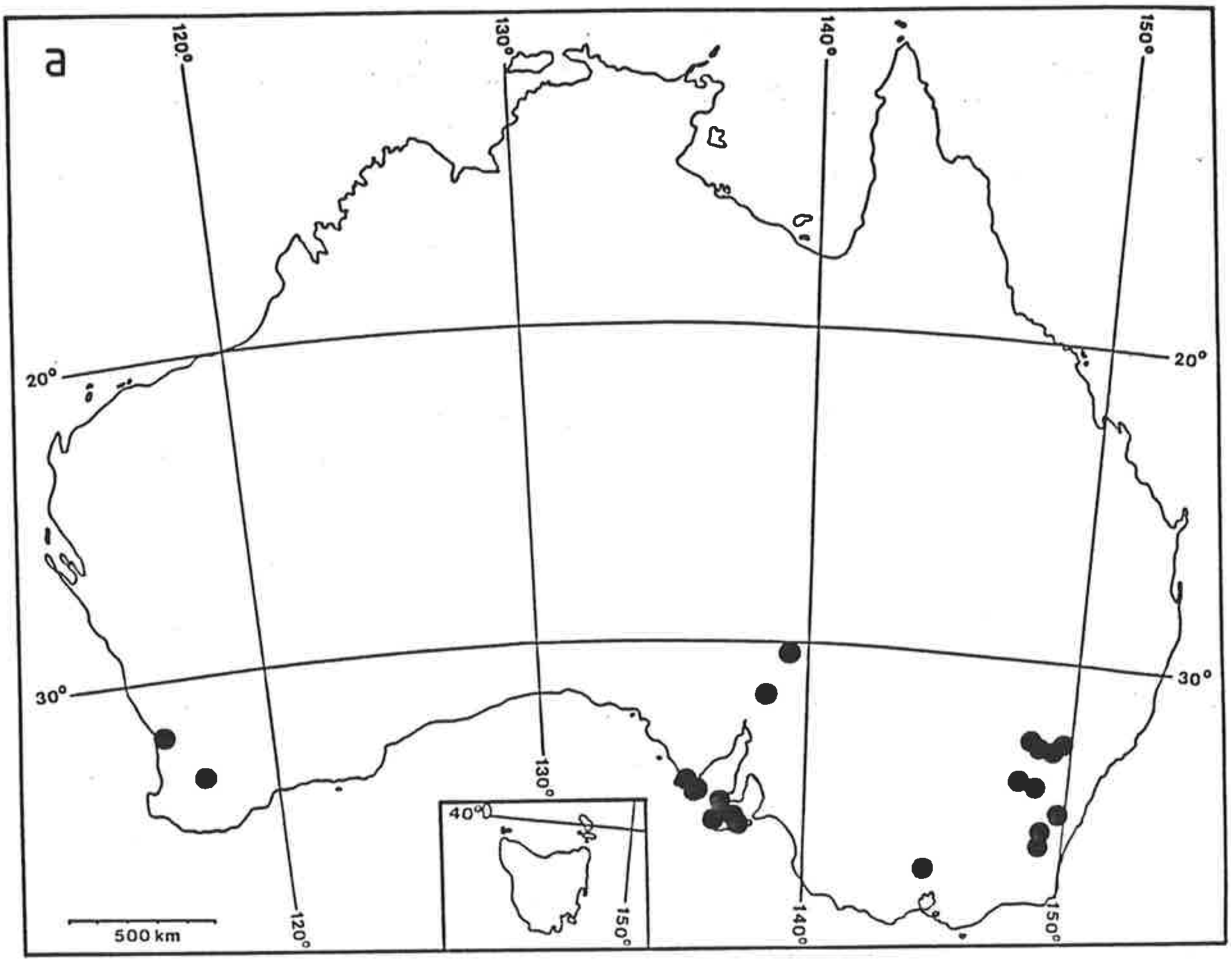

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
120°
140°
150°
40°
150°
500 km

Figure 57a-b. Known distribution of:

(a) *Myrmecia tepperi* Emery; and

(b) *Myrmecia varians* Mayr.


a
120°
130°
140°
150°
20°
30°
40°
500 km

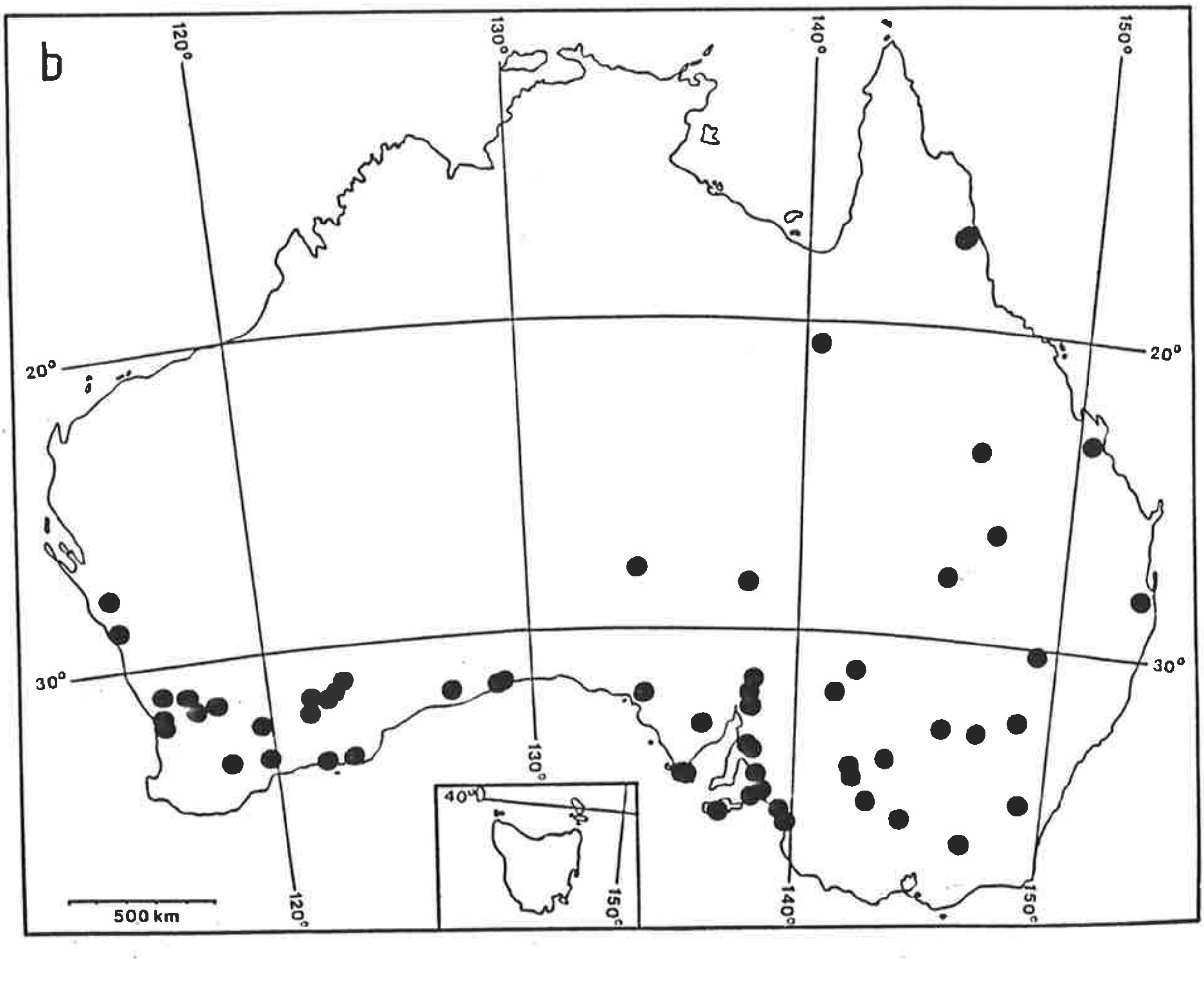
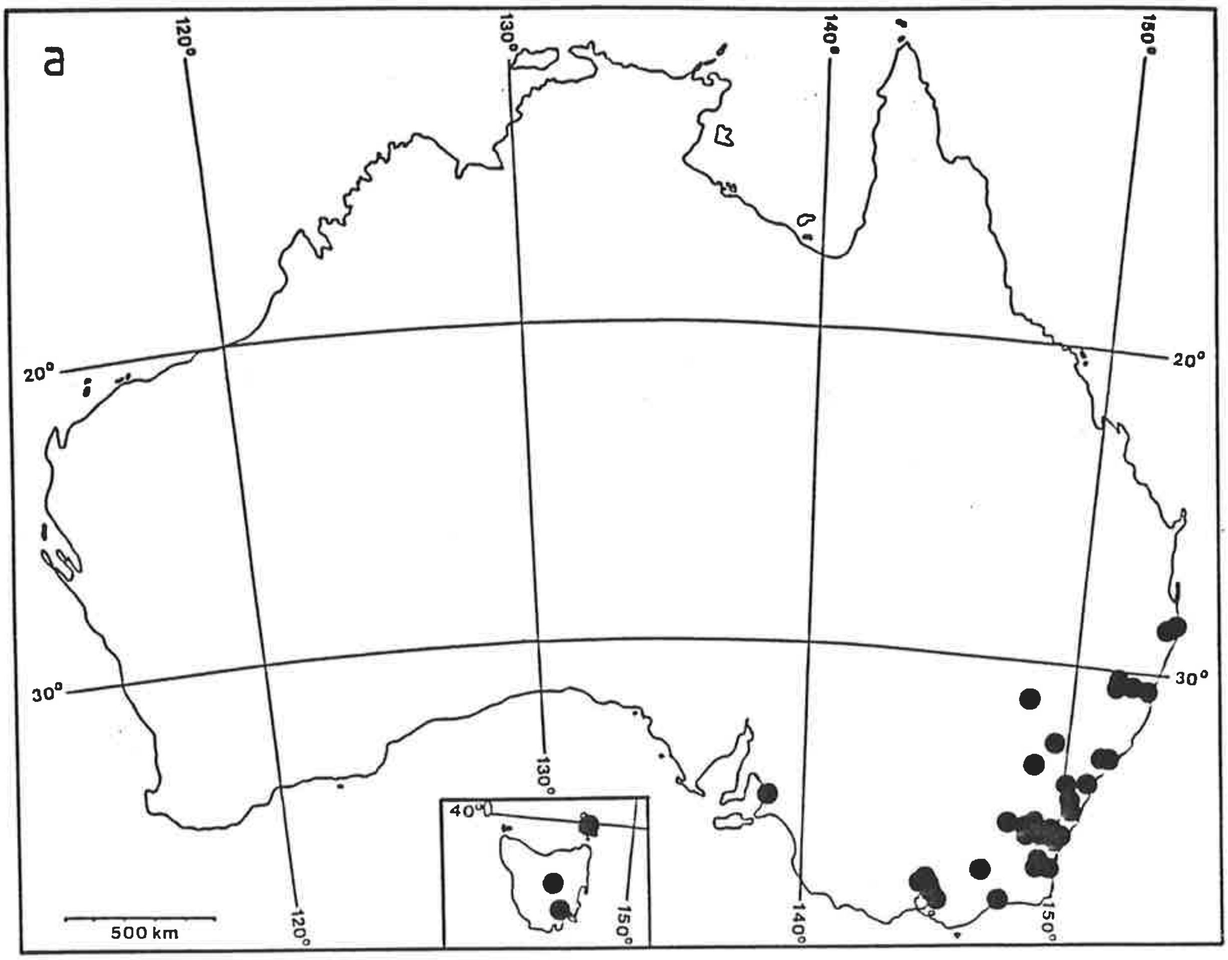

b
120°
130°
140°
150°
20°
30°
40°
500 km

Figure 58a-b. Known distribution of:

(a) *Myrmecia fulvipes* Roger, *s.l.*; and

(b) *Myrmecia fulviculis* Forel [▲], *Myrmecia luteiforceps* (Clark) [■] and *Myrmecia mandibularis* Smith [●].


a
120°
130°
140°
150°
20°
20°
30°
30°
130°
120°
140°
150°
40°
150°
500 km

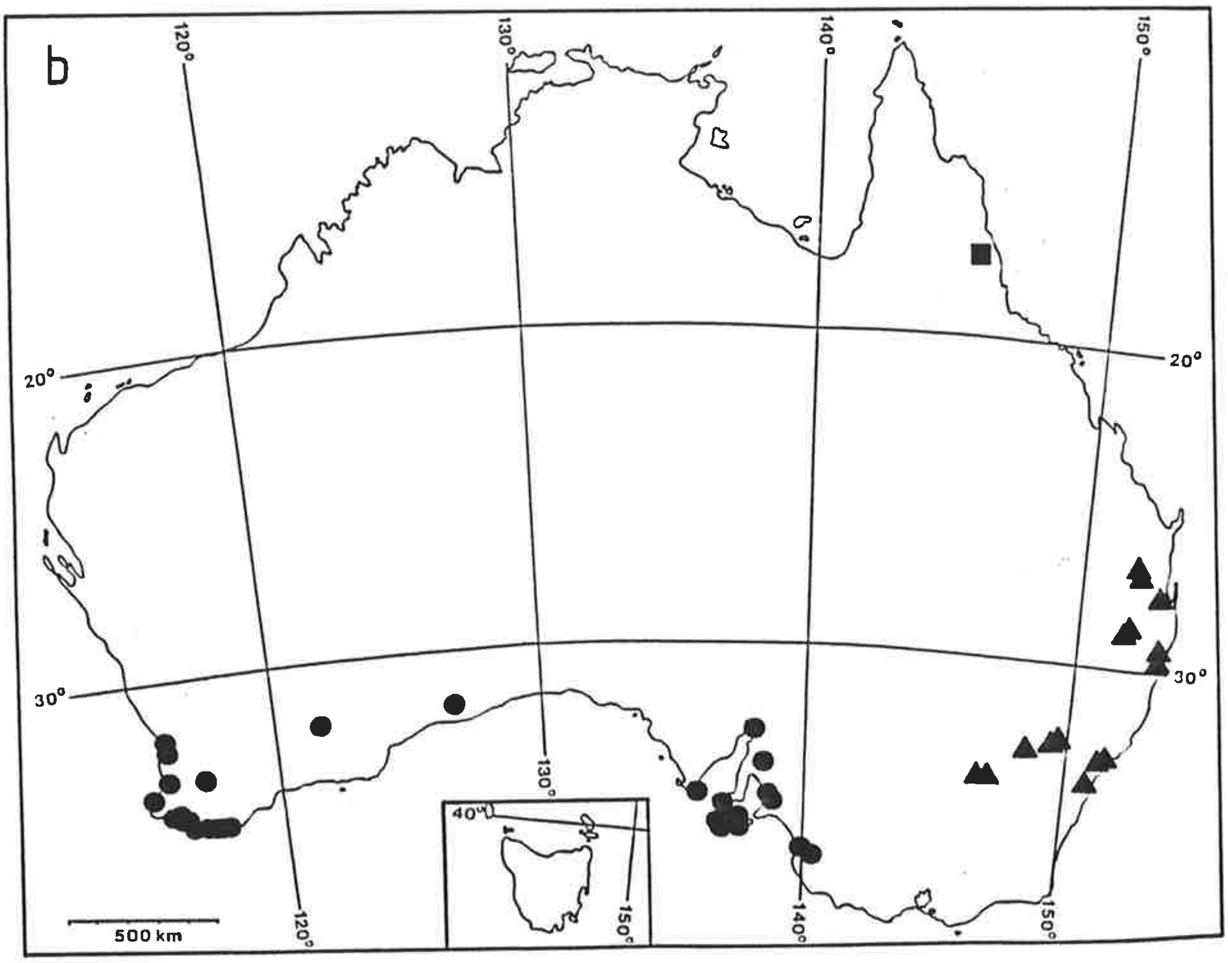

b
120°
130°
140°
150°
20°
20°
30°
30°
130°
120°
140°
150°
40°
150°
500 km

Figure 59a-b. Known distribution of:

(a) *Myrmecia piliventris* Smith, *s.l.* [●] and *Myrmecia fucosa* Clark [▲]; and

(b) *Myrmecia picta* Smith [●] and *Myrmecia sp.15* (ANIC) [▲].

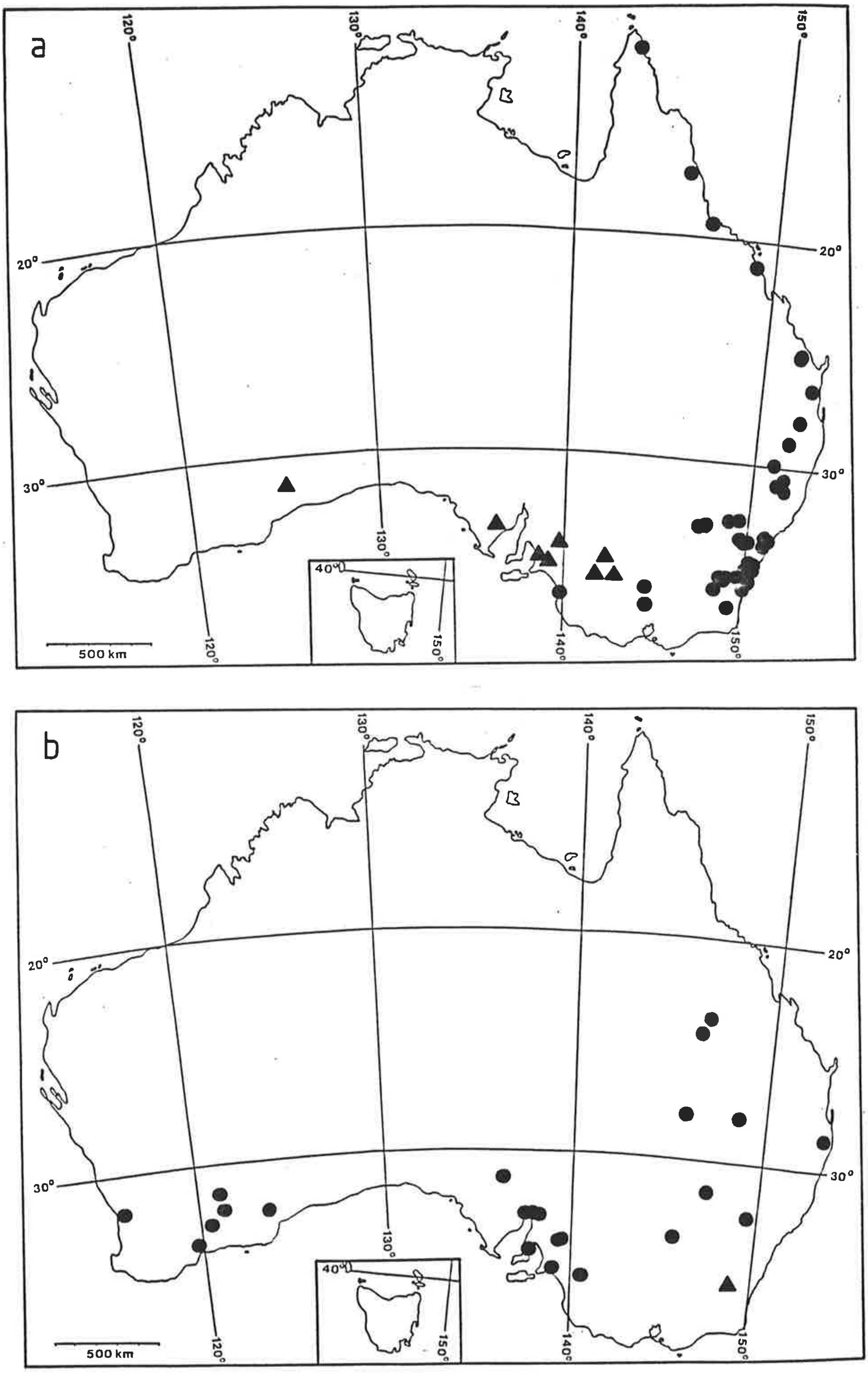

a
120°
130°
140°
150°
20°
30°
40°
500 km
b
120°
130°
140°
150°
20°
30°
40°
500 km

Figure 60. Known distribution of *Myrmecia urens* Lowne.

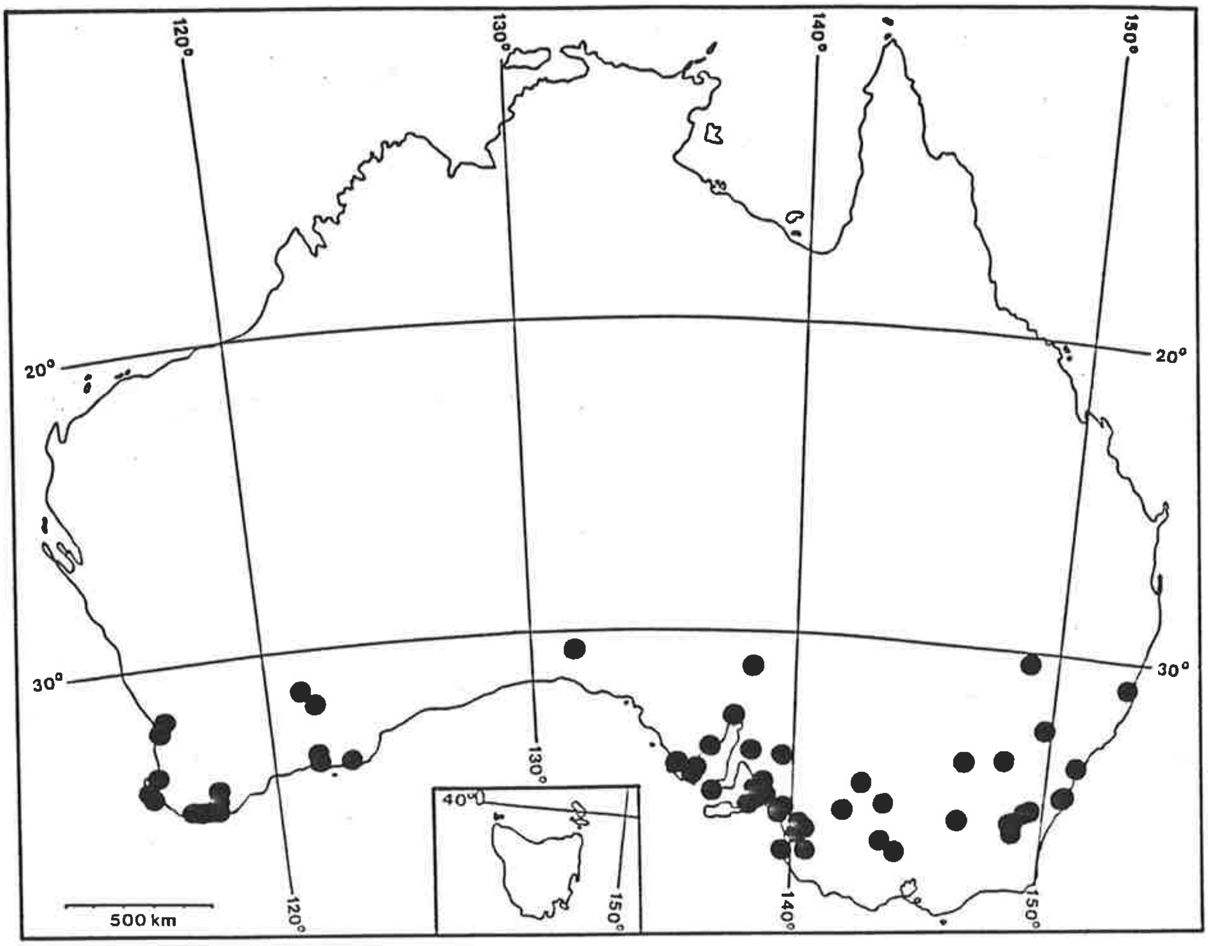

120°
130°
140°
150°
20°
20°
30°
30°
130°
120°
140°
150°
40°
150°
500 km

Figure 61a-c. Male genitalia (intact) of <u>Myrmecia fuscipes</u> Clark, from Port Parham, S.A. [4], (a) dorsal view, (b) ventral view; and (c) lateral view. (BR, basal ring; IV, inner valve; MV, middle valve; OV, outer valve). [From Browning, 1979].

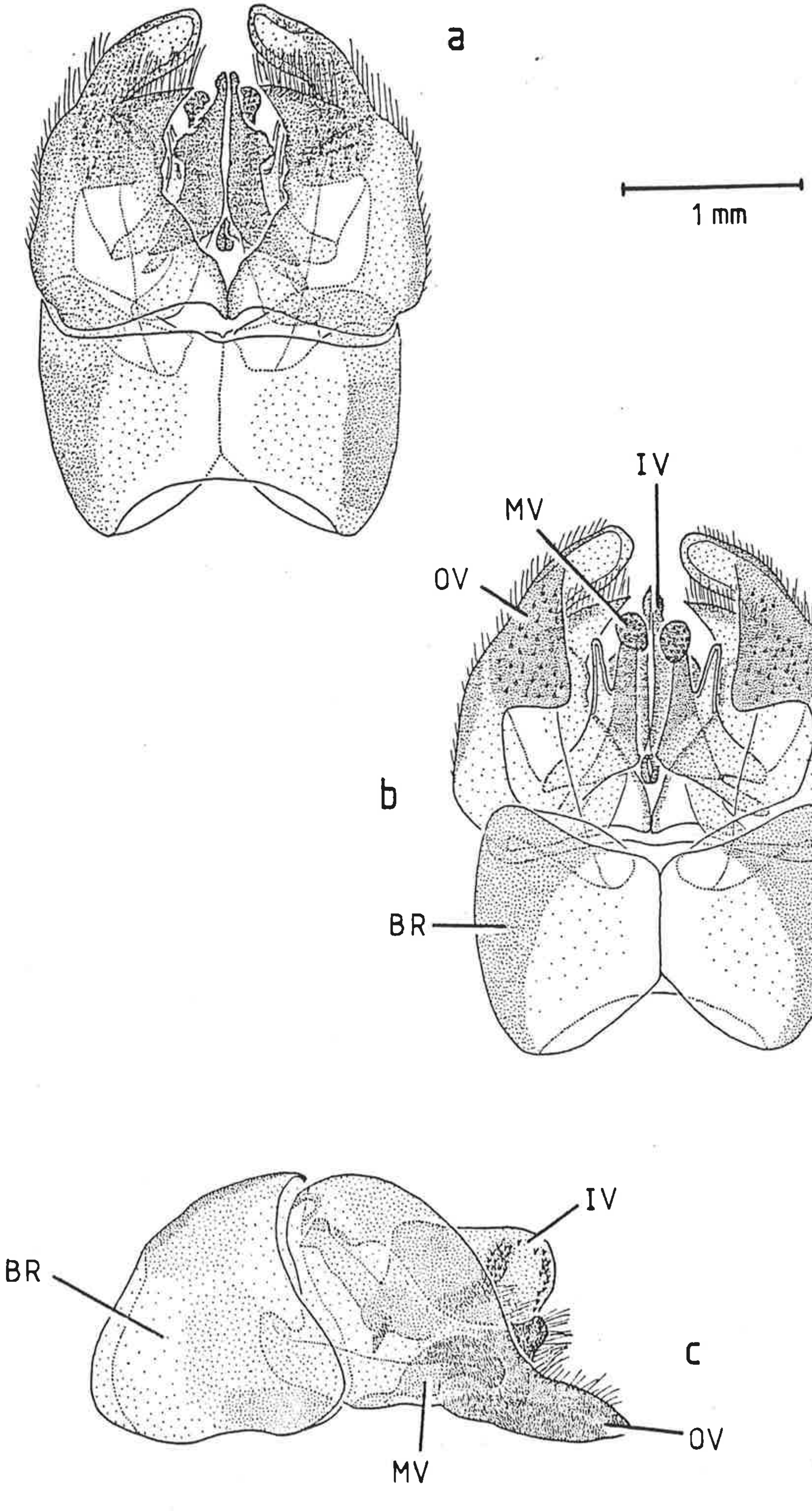
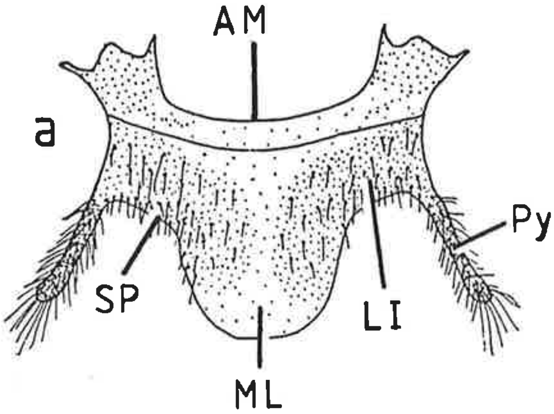
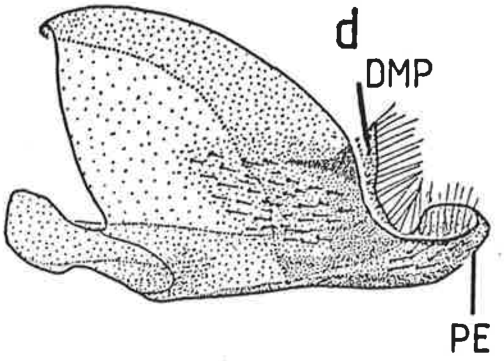
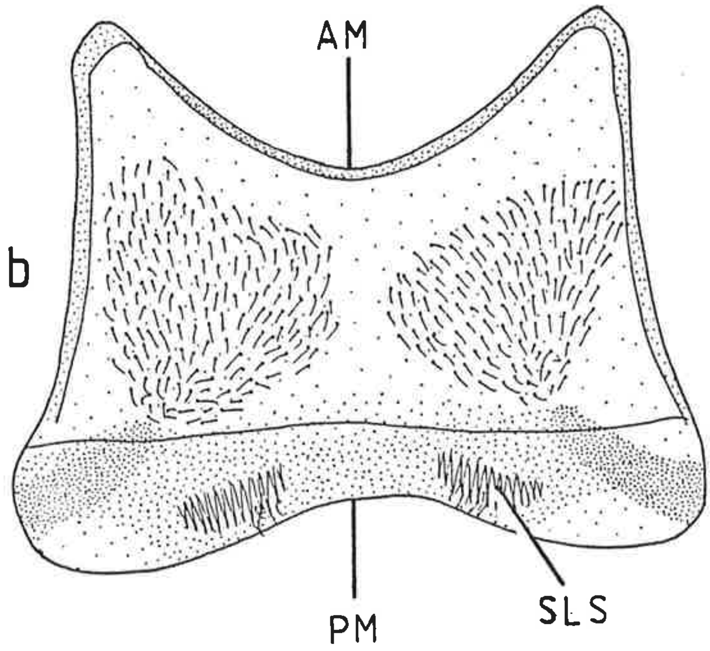
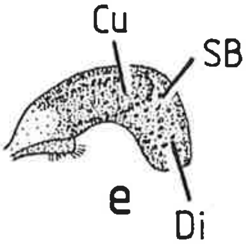

a
1 mm
IV
MV
OV
b
BR
IV
BR
c
MV
OV

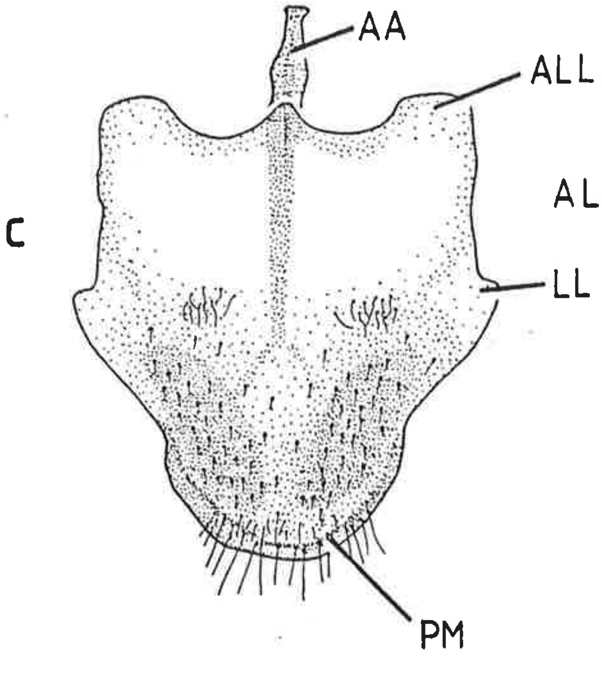
Figure 62a-f. Male terminalia of Myrmecia fuscipes Clark, from Port Parham, S.A. [4], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. (AA, anterior apodeme; ALE, antero-lateral extension of anterior apodeme; ALL, antero-lateral lobe; AM, anterior margin; Cu, cuspis; Di, digitus; DMP, dorsal median projection; LI, lateral indentation; LL, lateral lobe; ML, median lobe; PDM, postero-dorsal margin; PE, posterior end; PM, posterior margin; PVL, postero-ventral lobe; Py, pygostyle; SB, sensilla basiconica; Se, serrations; SLS, serrate longitudinal sculpturing; SP, sensory pits; Sp, spines). [From Browning, 1979].


AM
a
Py
SP
LI
ML


d
DMP
PE


AM
b
PM
SLS


Cu
SB
e
Di


AA
ALL
c
LL
PM

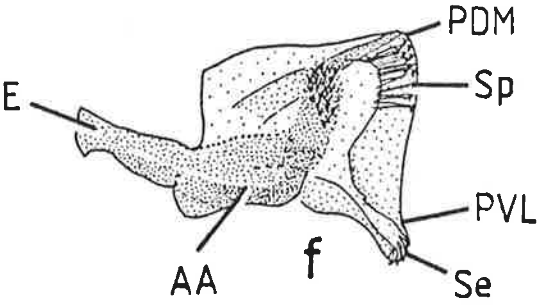
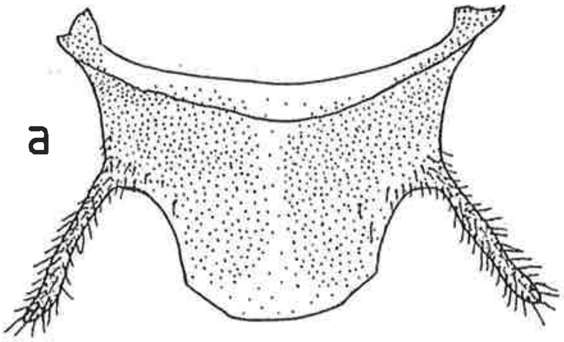
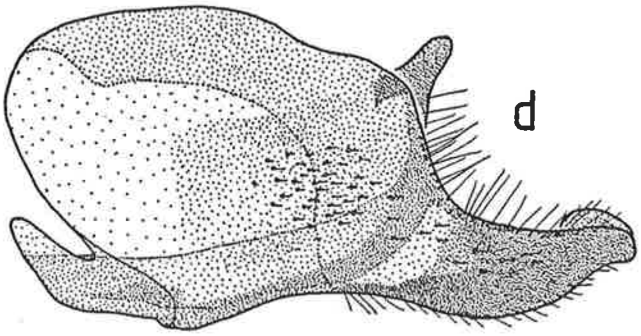

PDM
Sp
ALE
PVL
AA
f
Se

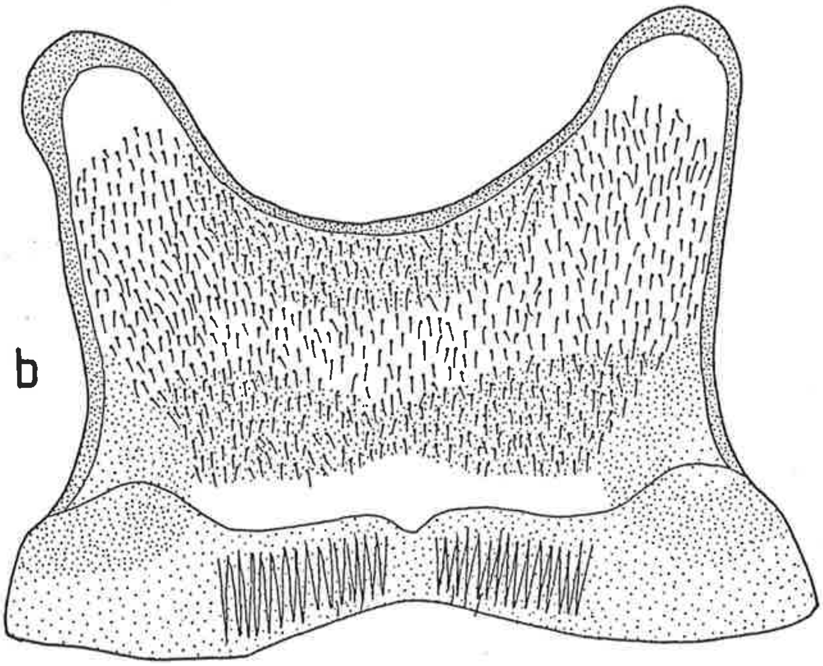
Figure 63a-f. Male terminalia of Myrmecia forceps Roger, from Rocky River H.S., S.A. [31], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. [From Browning, 1979].



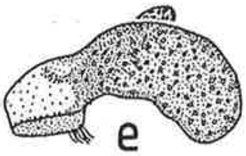
a



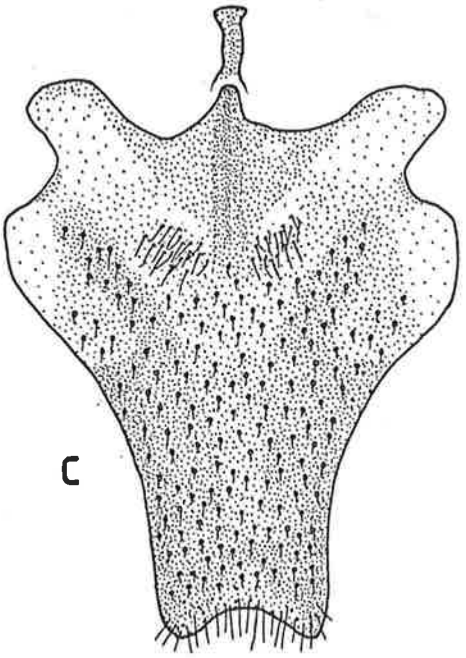
d



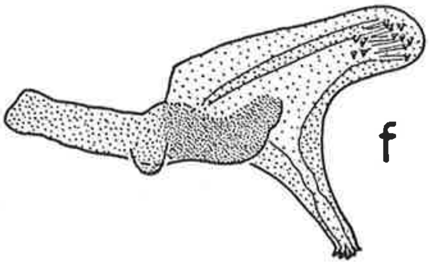
b



e



c

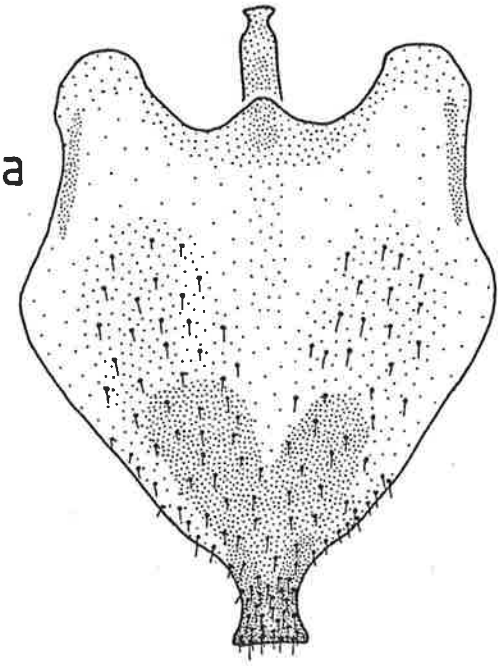


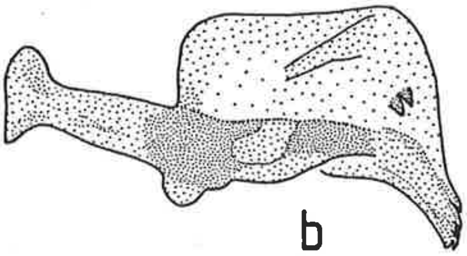
f

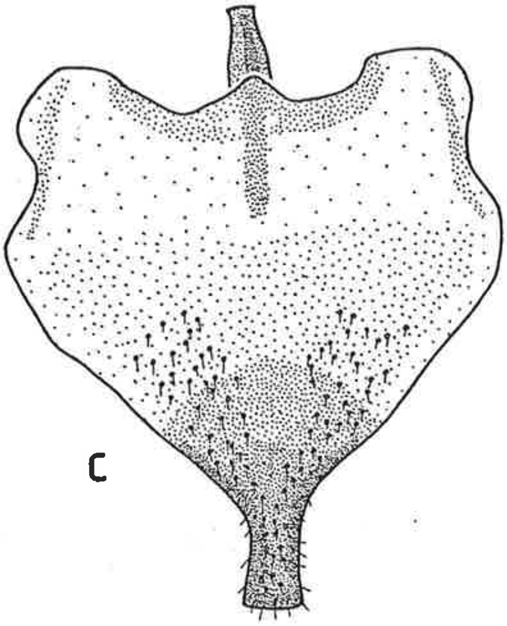
Figure 64a-d. Male terminalia of:

Myrmecia brevinoda Forel, *s.s.*, from Milperra, N.S.W. [63], (a) ninth sternite and (b) inner valve; and

Myrmecia decipiens Clark, from Bungwahl, N.S.W. [61], (c) ninth sternite and (d) inner valve.


a


b


c

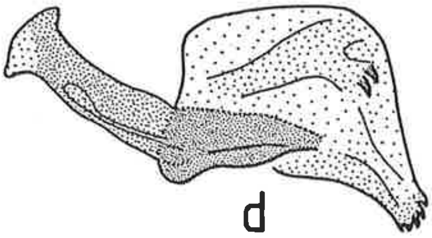
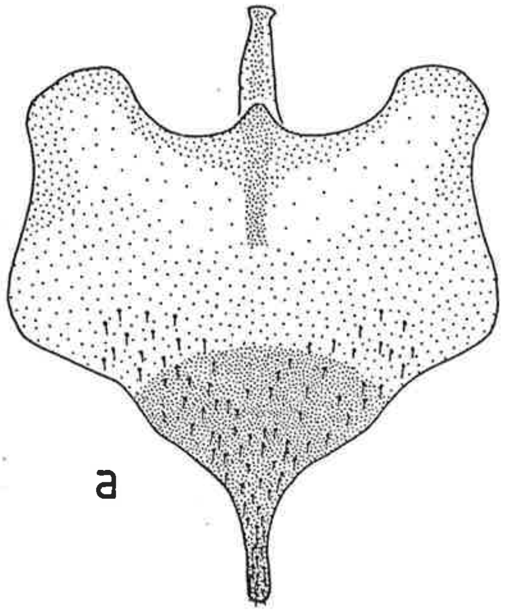
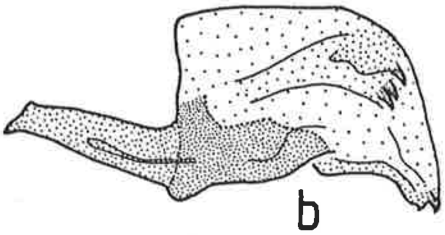

d

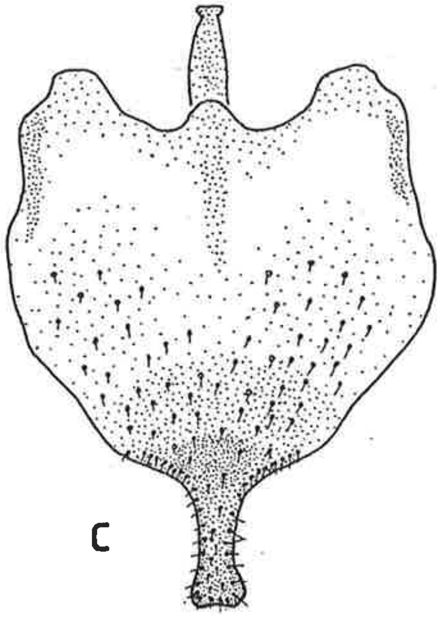
Figure 65a-d. Male terminalia of:

Myrmecia forficata (Fabricius), *s.s.*, from Smokers Gap, A.C.T. [68], (a) ninth sternite and (b) inner valve; and

Myrmecia sp.9 (ANIC), from Rocky River H.S., S.A. [17], (c) ninth sternite and (d) inner valve.


a


b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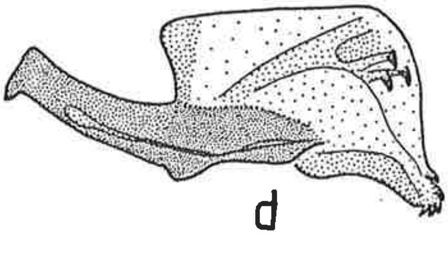
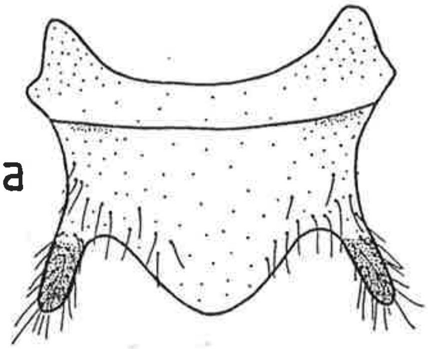
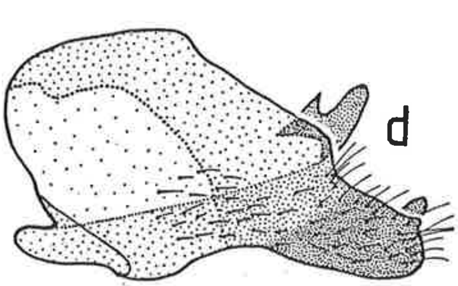
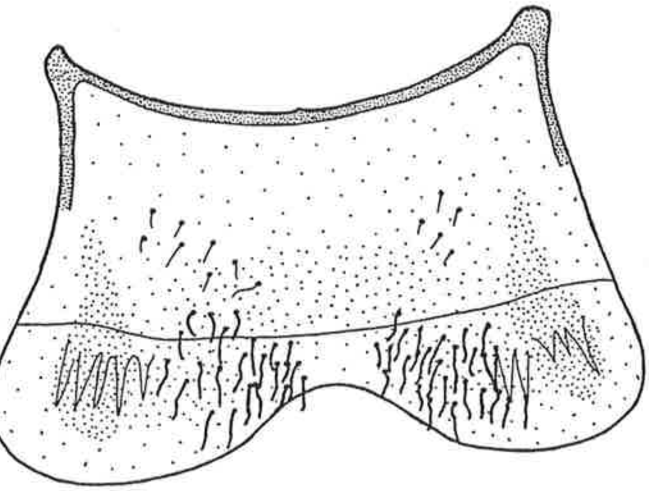
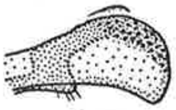

d

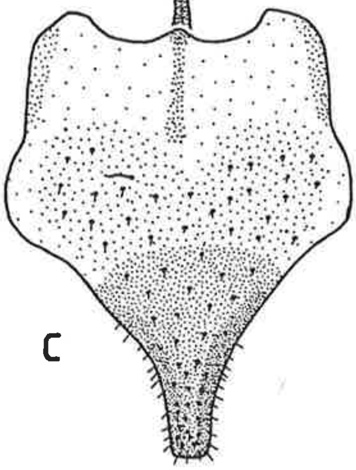
Figure 66a-f. Male terminalia of Myrmecia hirsuta Clark, from Bungwahl, N.S.W. [62], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve.


a


d


b


e


c

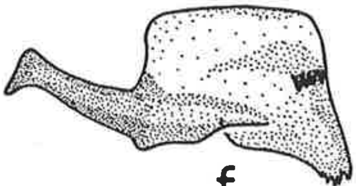

f

Figure 67a-f. Male terminalia of Myrmecia pyriformis Smith, from Upper Hermitage, S.A. [36], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. (DL, dorsal lobe; VL, ventral lobe). [From Browning, 1979].

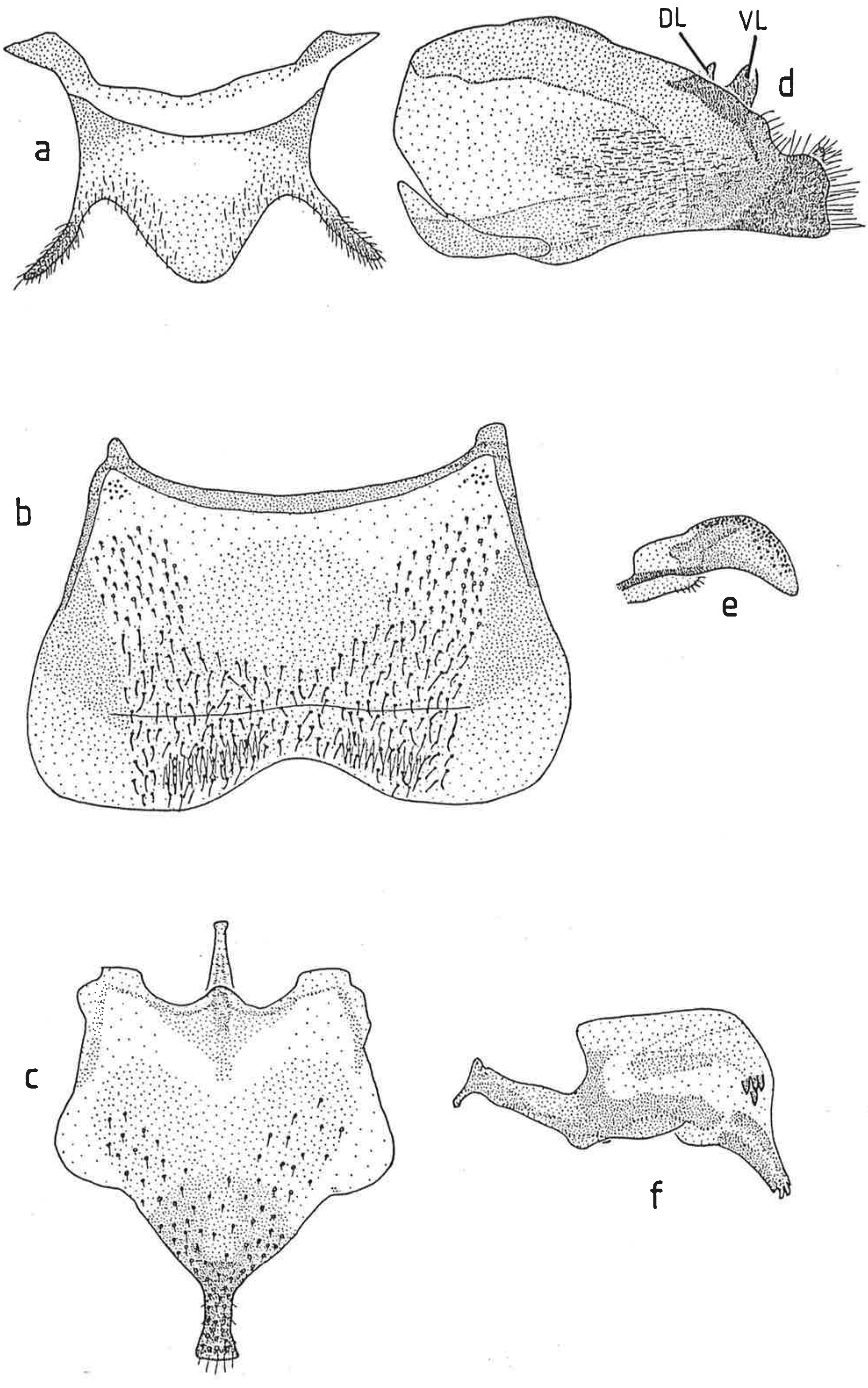

DL
VL
a
d
b
e
c
f

Figure 68a-e. Male terminalia of _Myrmecia_ _regularis_ Crawley, from Augusta, W.A. (WLB; in MCZ), (a) eighth sternite, (b) ninth sternite, (c) outer valve, (d) middle valve and (e) inner valve.

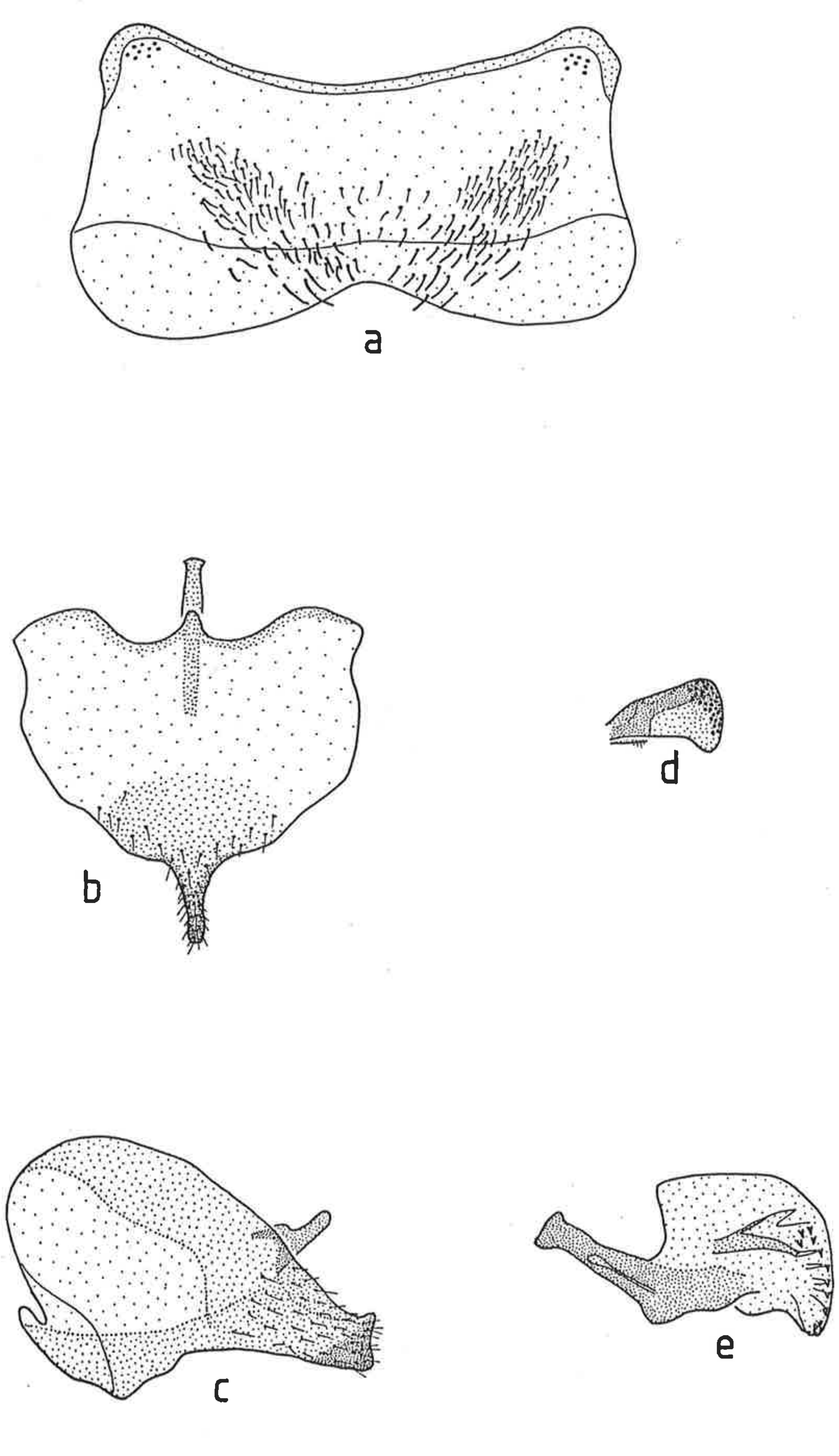
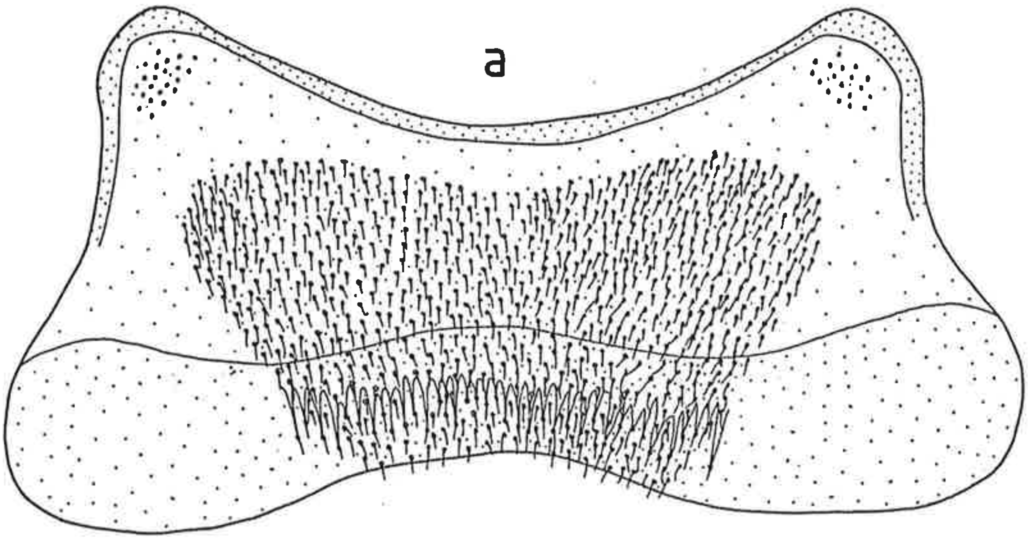
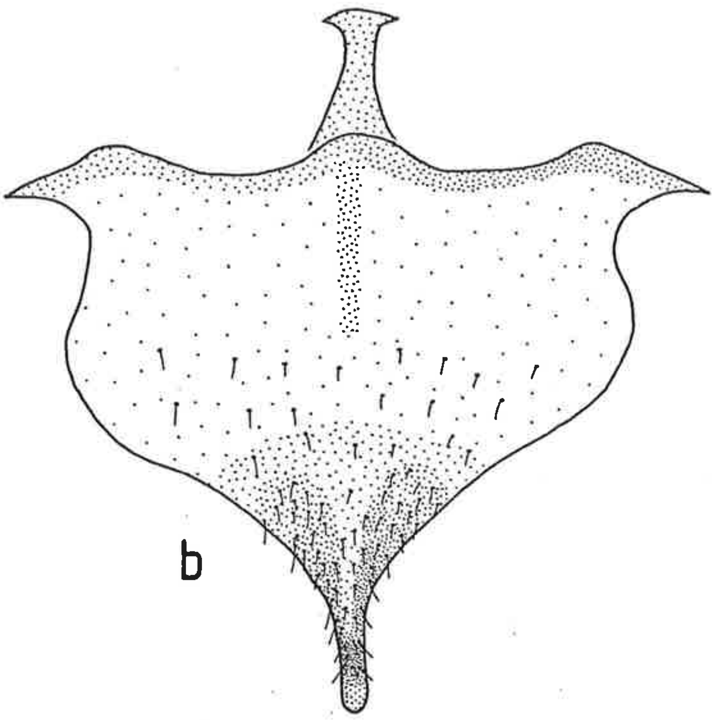
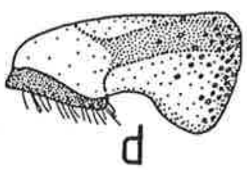
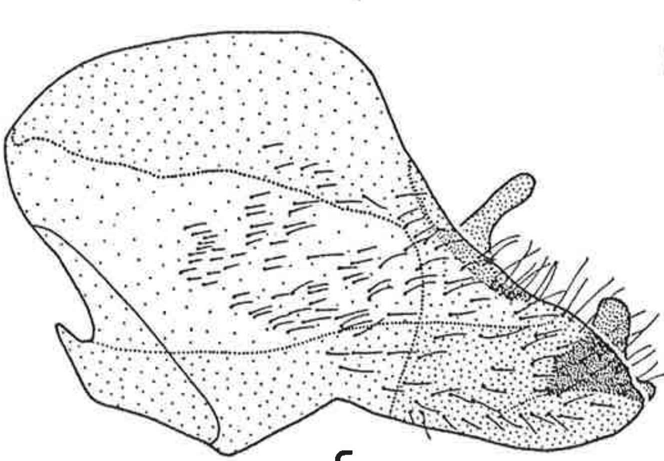

a
b
d
c
e

Figure 69a-e. Male terminalia of Myrmecia mjobergi Forel, from 2 km E of Kuranda, Qld (C&U; in ANIC), (a) eighth sternite, (b) ninth sternite, (c) outer valve, (d) middle valve and (e) inner valve.


a


b


d


c

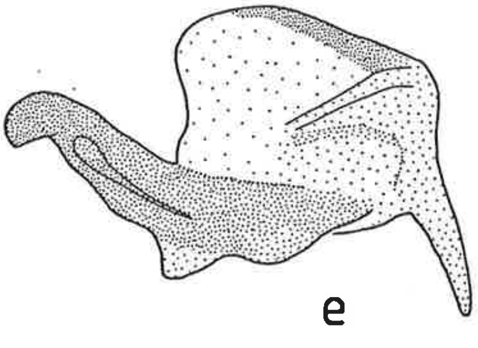
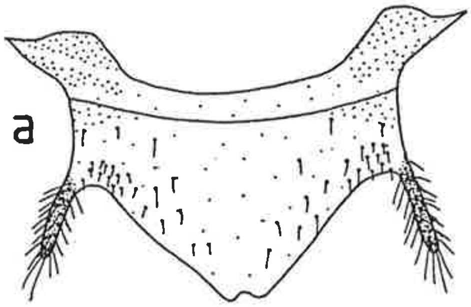
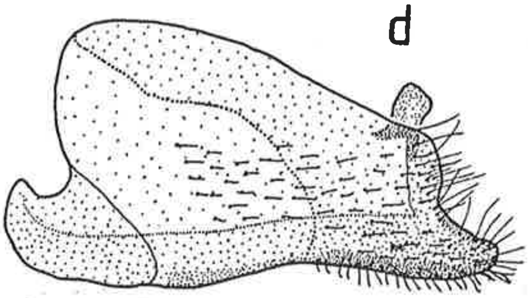

e

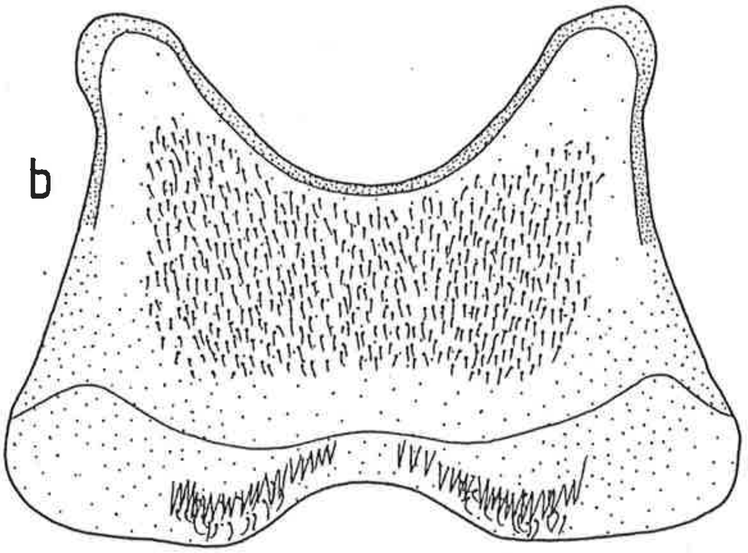
Figure 70a-f. Male terminalia of Myrmecia nigriscapa Roger, from 6 km SW of Cranbourne, Vic. [86], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. [From Browning, 1979].



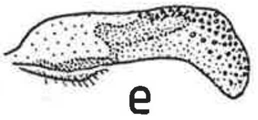
a



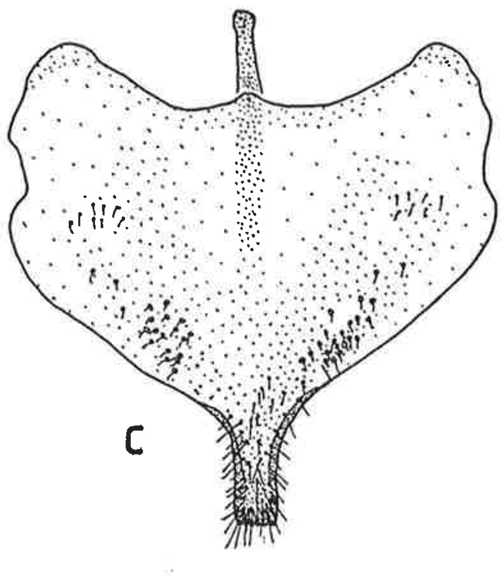
d



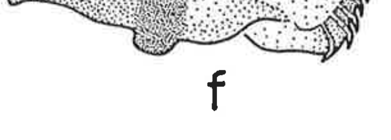
b



e



c



f

Figure 71a-f. Male terminalia of *Myrmecia tarsata* Smith, from 20 km NW of Braidwood, N.S.W. [78], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. [From Browning, 1979].

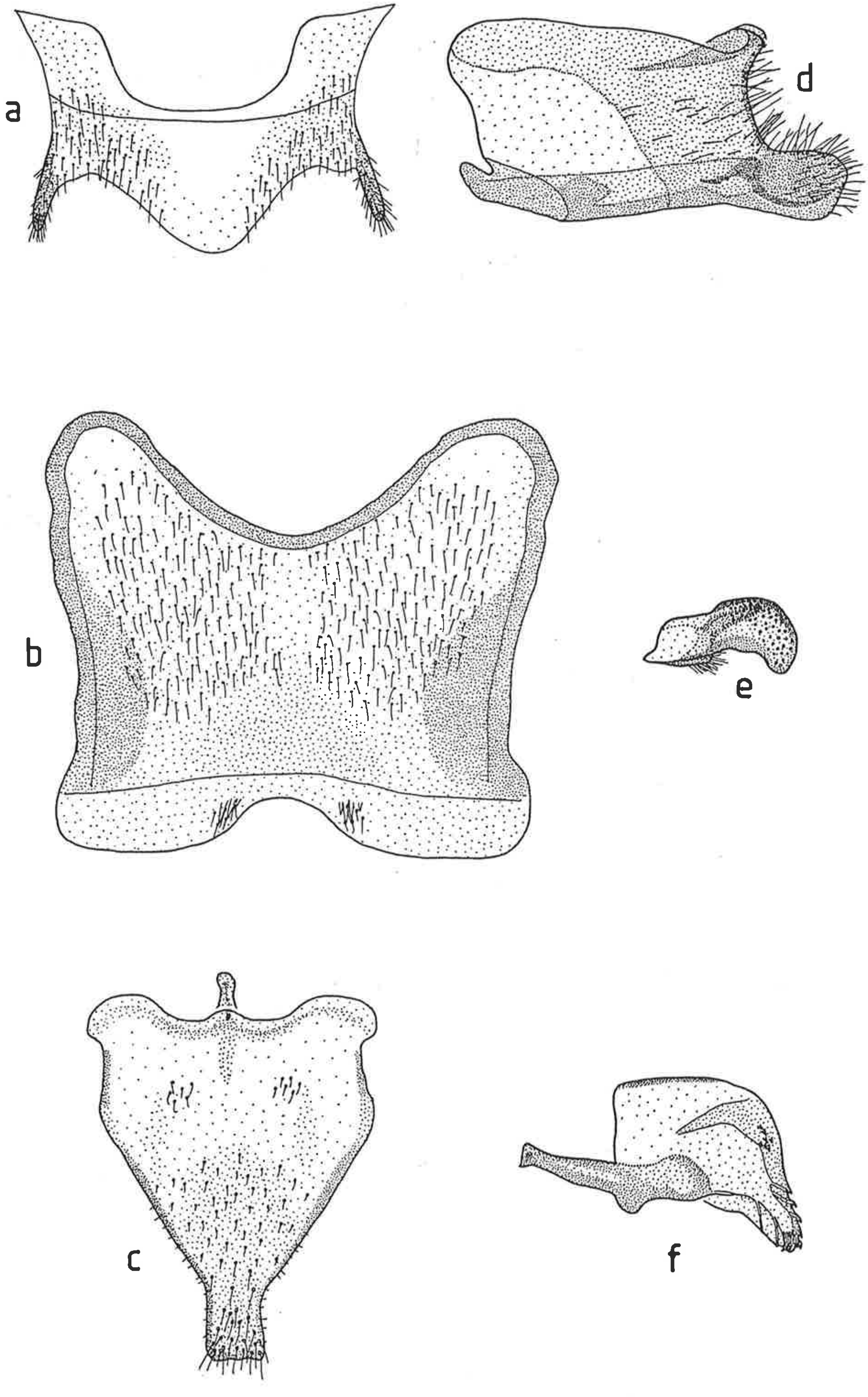

a
d
b
e
c
f

Figure 72a-f. Male terminalia of *Myrmecia flavicoma* Roger, from Mount Jacob, Qld (D*s*; in MCZ), (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. (Sp, spines).

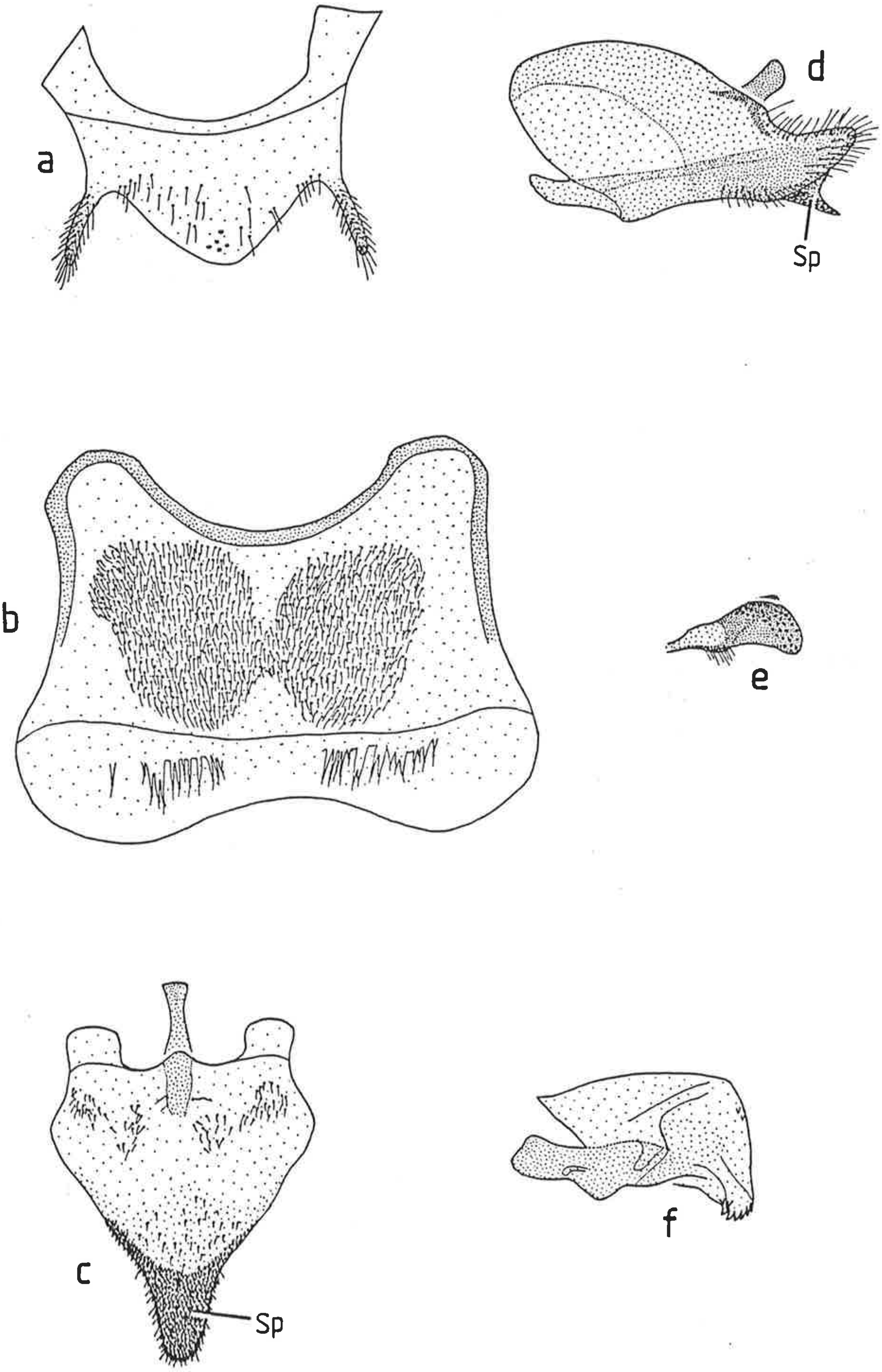
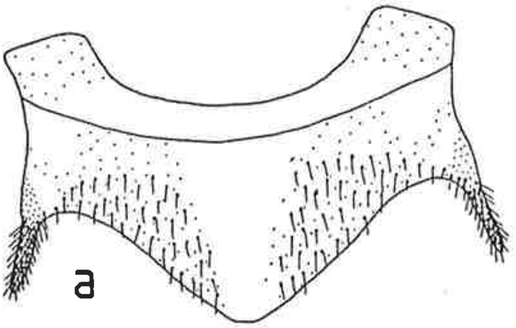
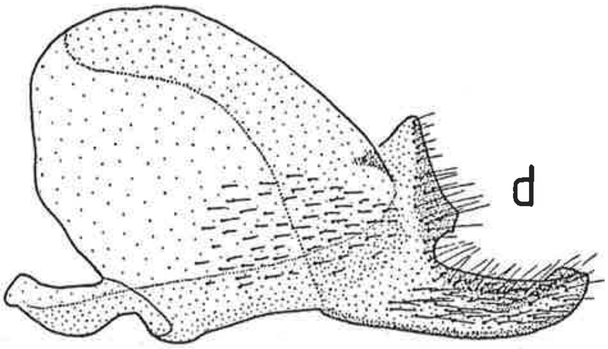

a
d
Sp
b
e
c
Sp
f

Figure 73a-f. Male terminalia of Myrmecia gulosa (Fabricius), from Sydney, N.S.W. [79], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. [From Browning, 1979].


a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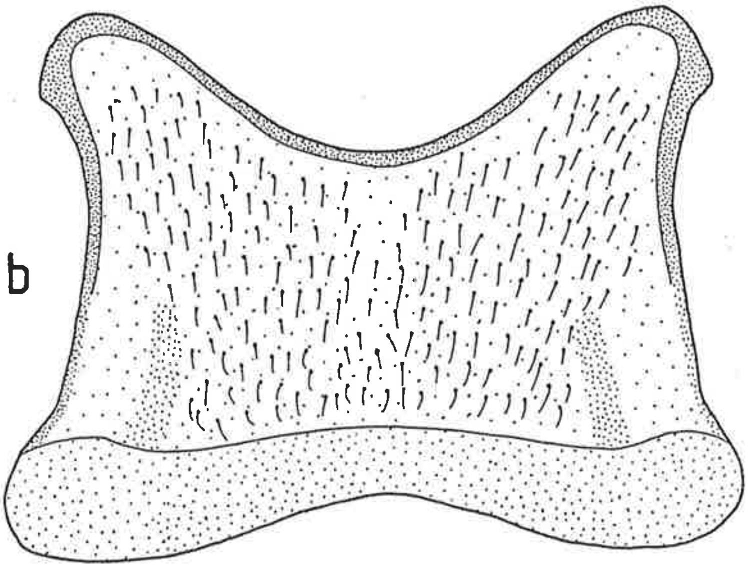
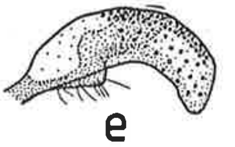

b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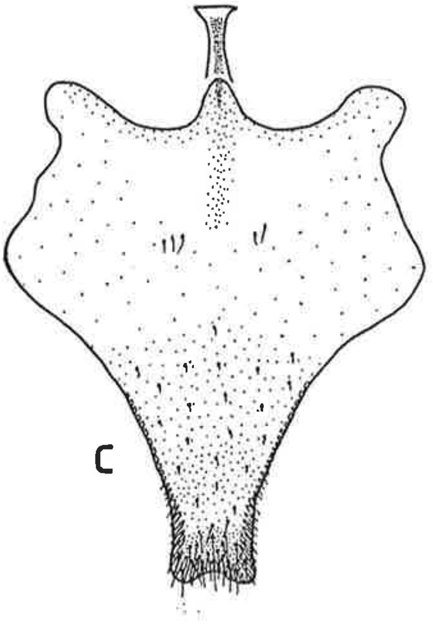
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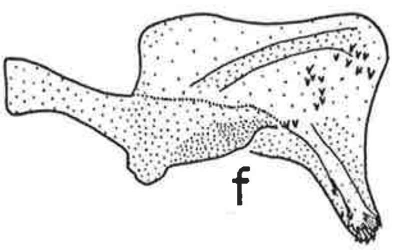
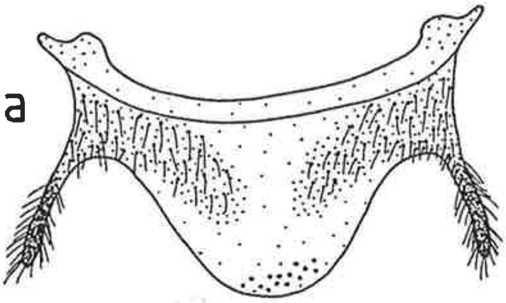
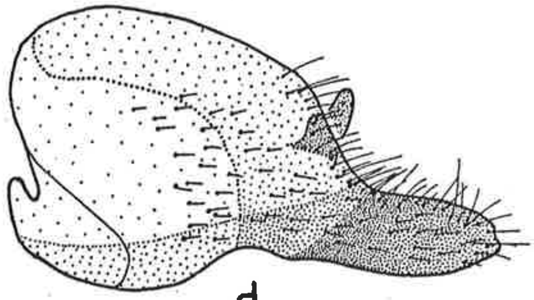

f

Figure 74a-f. Male terminalia of Myrmecia simillima Smith, from Helensburg, N.S.W. [543], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve.


a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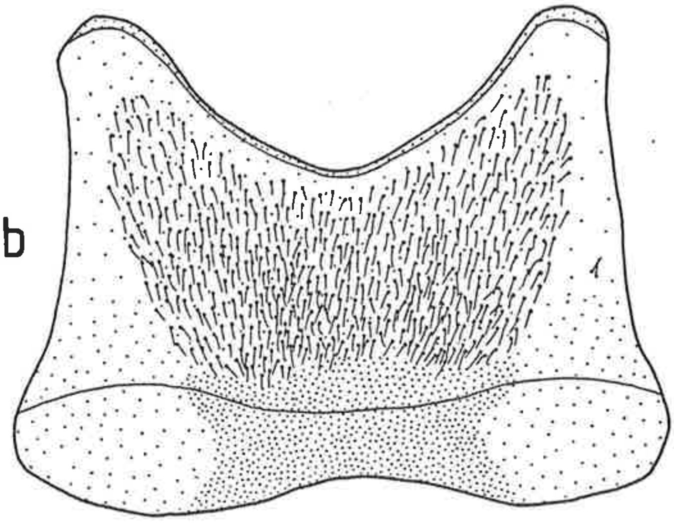
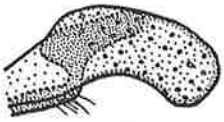
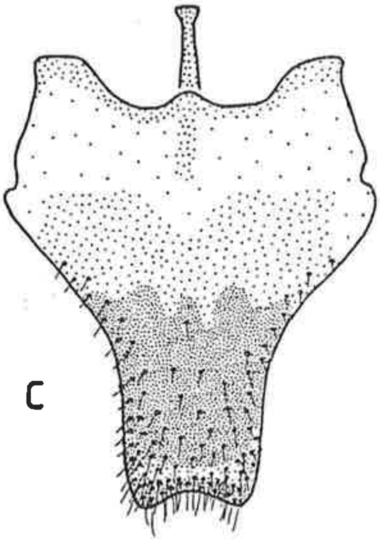

b


e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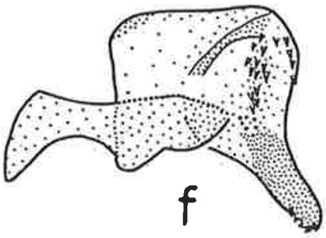
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Figure 75a-f. Male terminalia of Myrmecia arnoldi Clark, from 22 km SW of Tambellup, W.A. [354], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve.

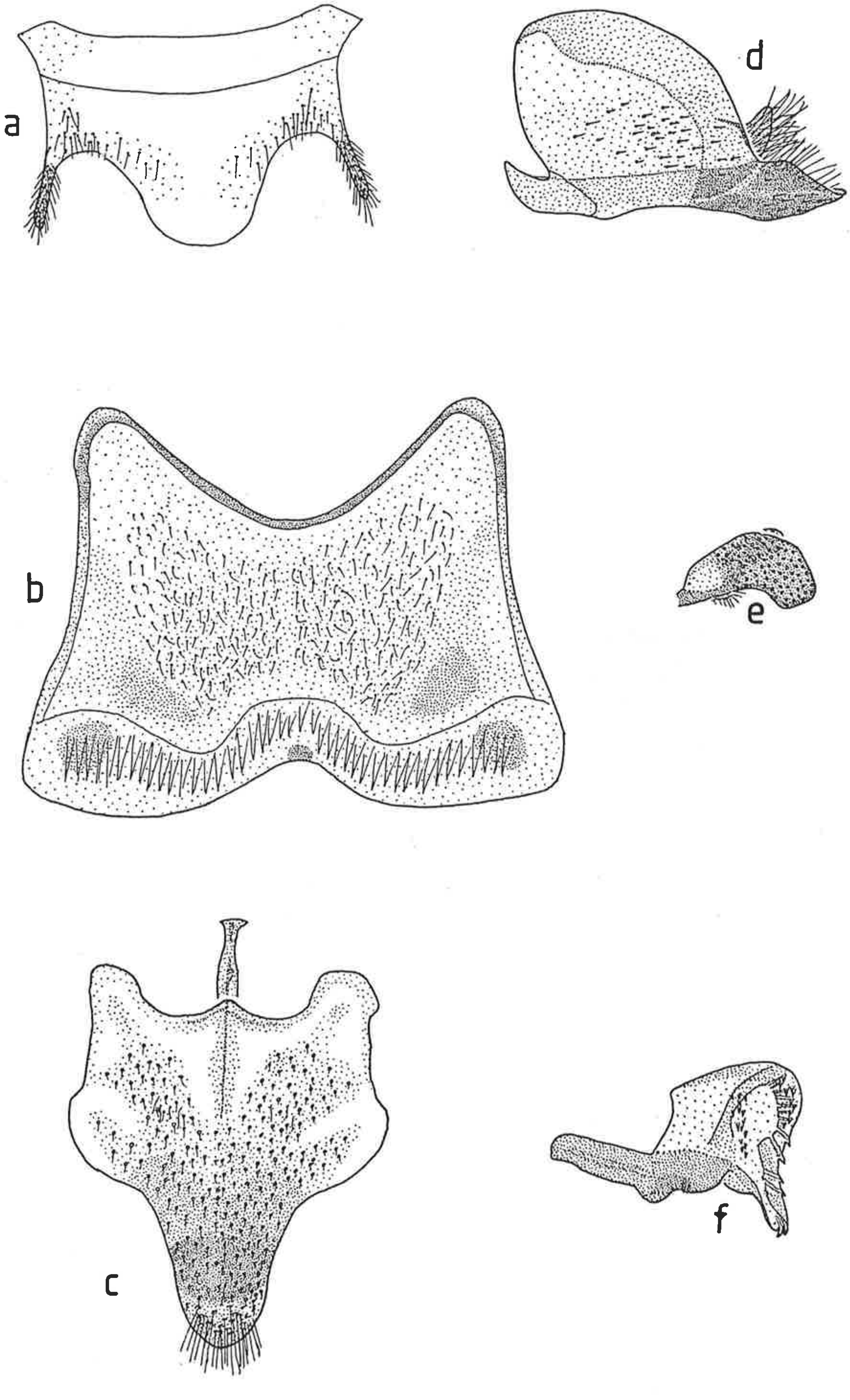
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Figure 76a-f. Male terminalia of <u>Myrmecia</u> <u>rufinodis</u> Smith, from Warrenben C.P., S.A. [60], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. [From Browning, 1979].

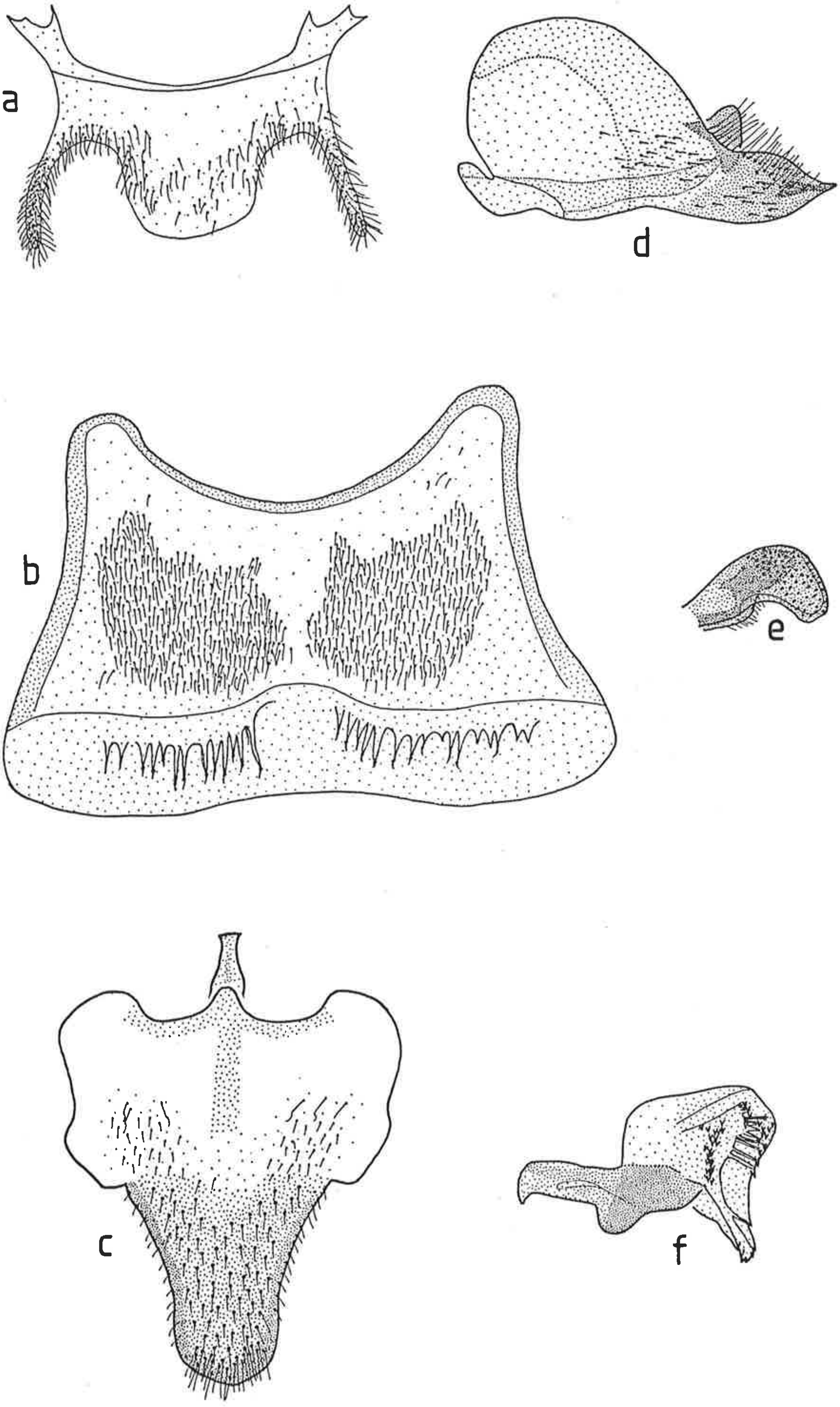
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Figure 77a-f. Male terminalia of Myrmecia vindex Smith, from Rockingham, W.A. [71], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. [From Browning, 1979].

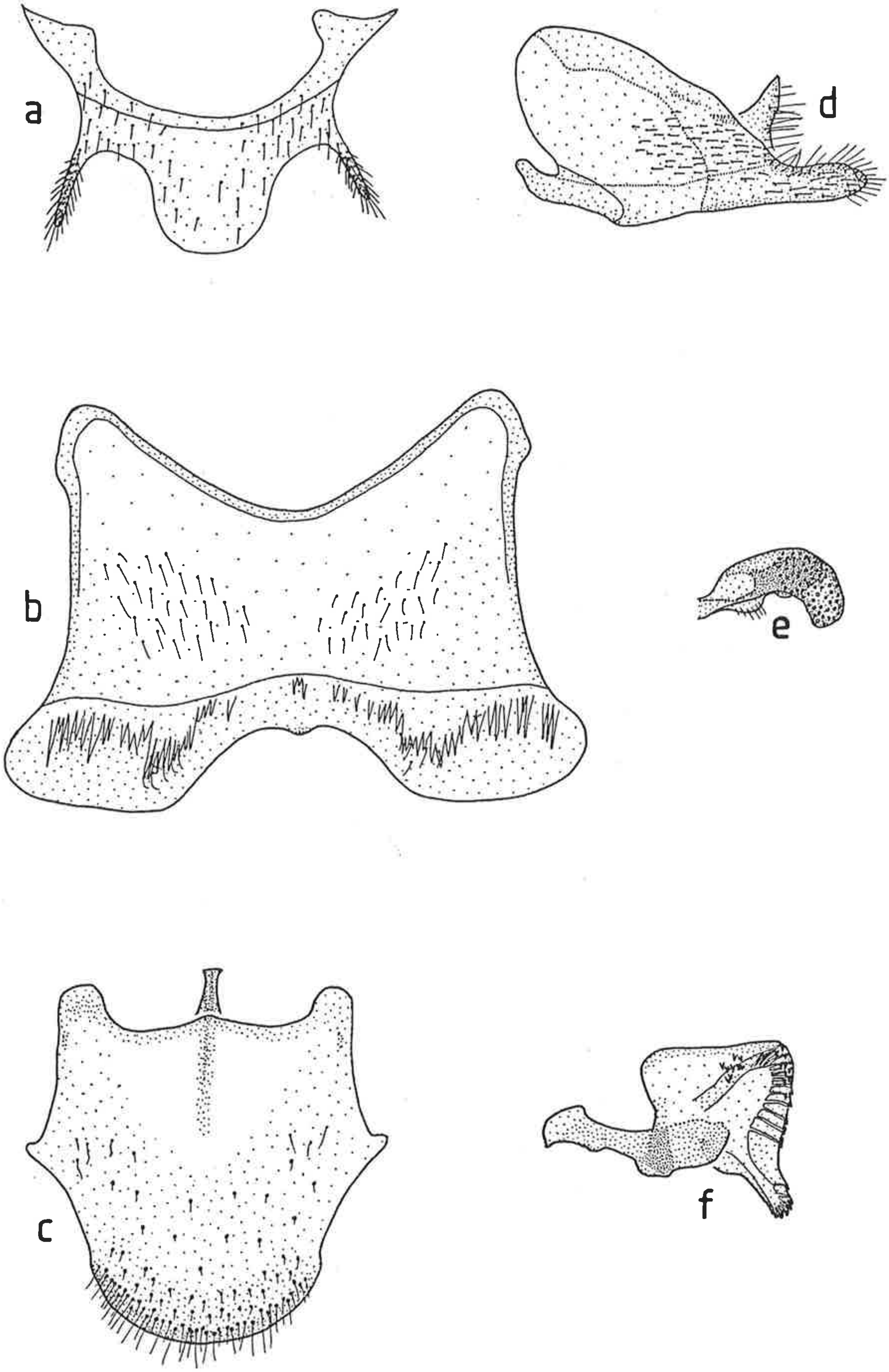
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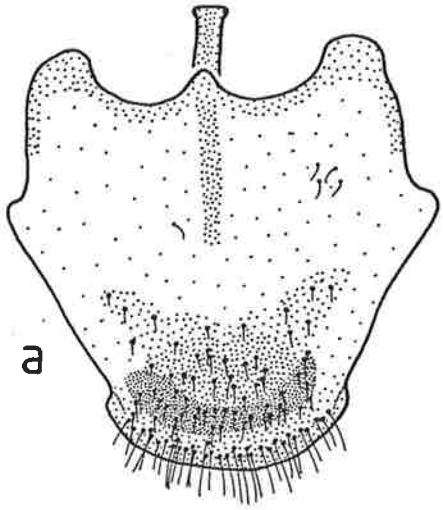
Figure 78a-f. Male terminalia of:

Myrmecia sp.14 (ANIC), from 48 km SE of Pinjarra, W.A. [202], (a) ninth sternite and (b) inner valve;

Myrmecia nigriceps Mayr, s.s., from Lake Gilles C.P., S.A. [133], (c) ninth sternite and (d) inner valve; and

Myrmecia desertorum Wheeler, from Todmorden, S.A. [147], (e) ninth sternite and (f) inner valve.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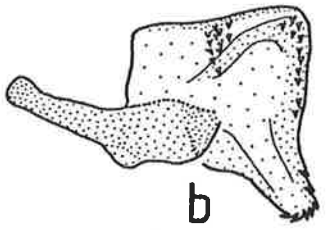
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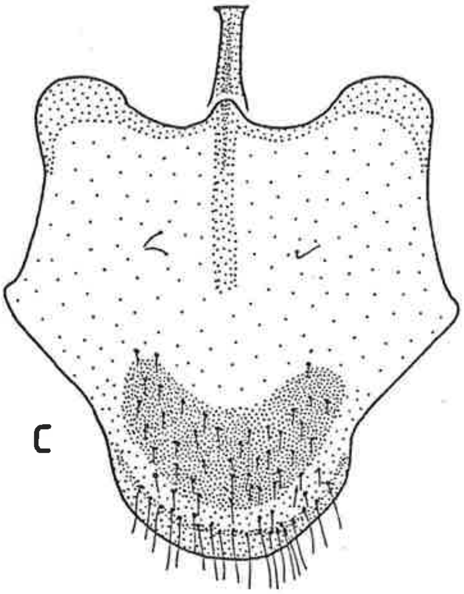
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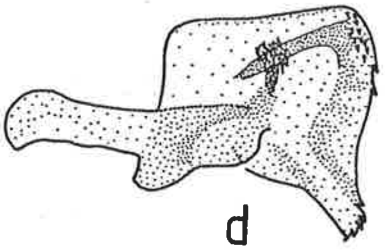
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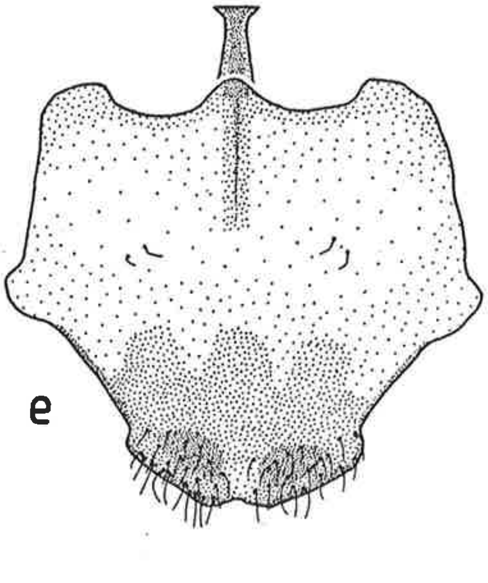
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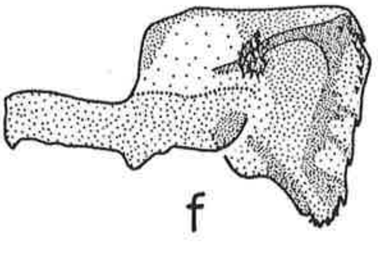
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Figure 79a-f. Male terminalia of:

Myrmecia sp.12 (ANIC), from Port Lincoln, S.A. [162], (a) ninth sternite and (b) inner valve;

Myrmecia sp.11 (ANIC), from Elliston, S.A. [128], (c) ninth sternite and (d) inner valve; and

Myrmecia ferruginea Mayr, from Dalby, Qld (NG; in QM), (e) ninth sternite and (f) inner valve.

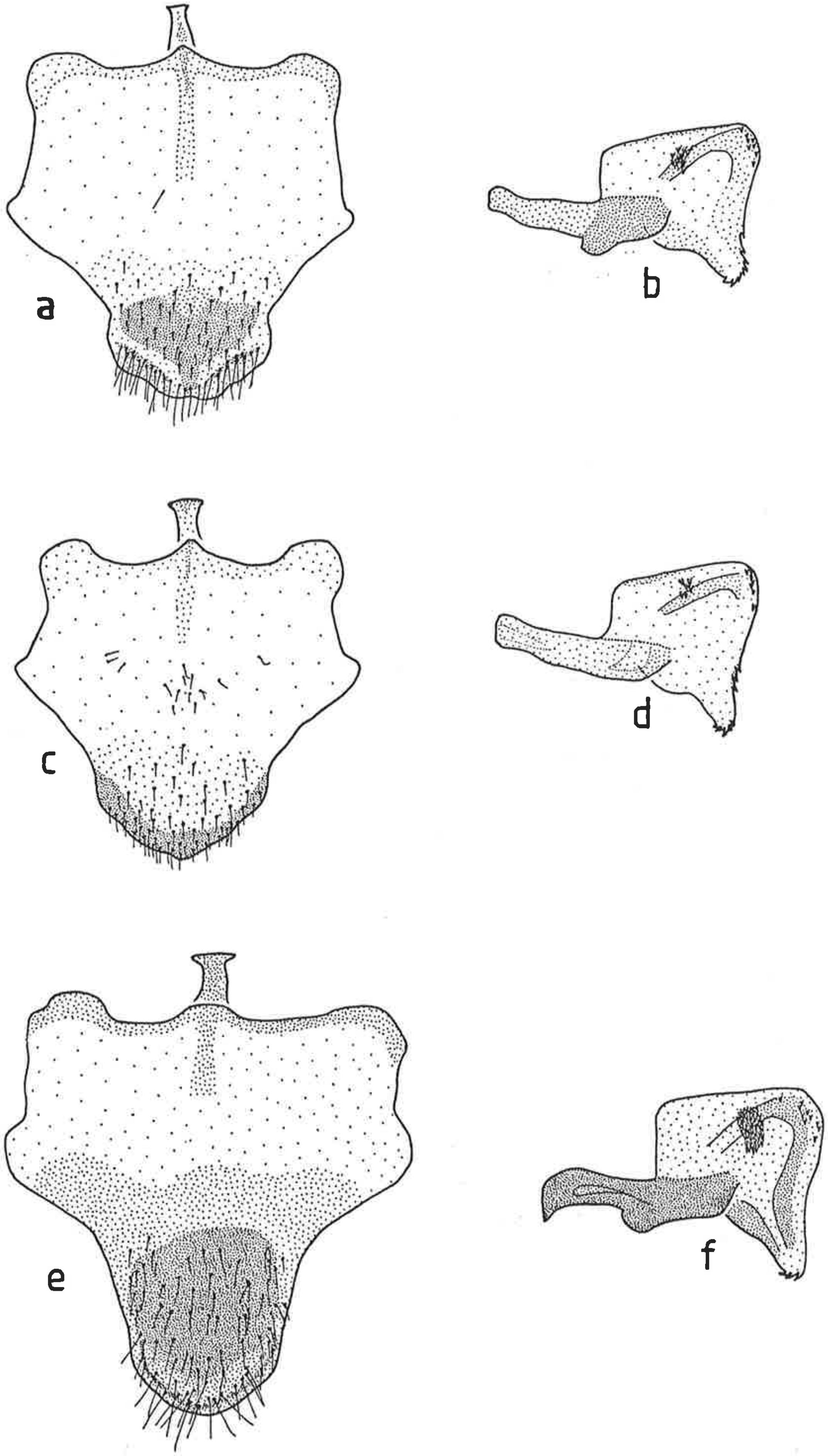
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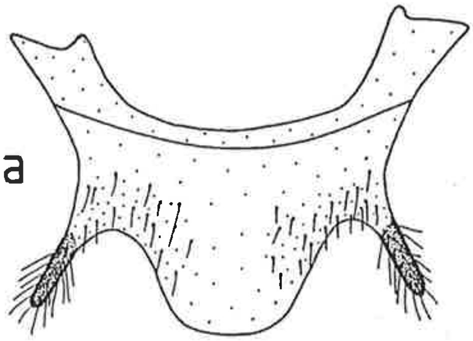
Figure 80a-f. Male terminalia of Myrmecia sp.17 (ANIC), from 5 km NE of Bacchus Marsh, Vic. [87], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve.



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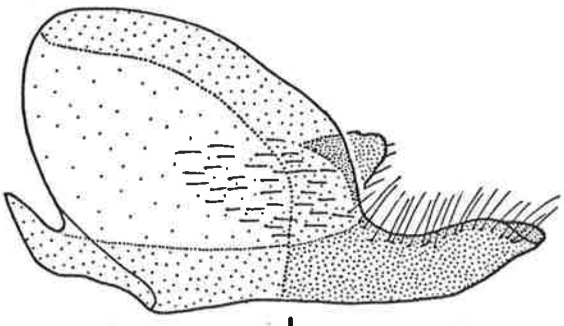

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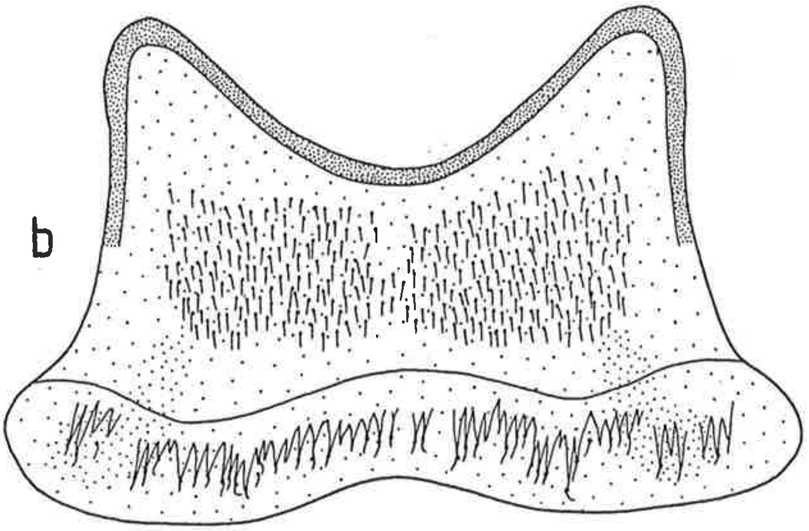

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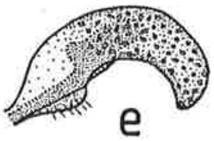

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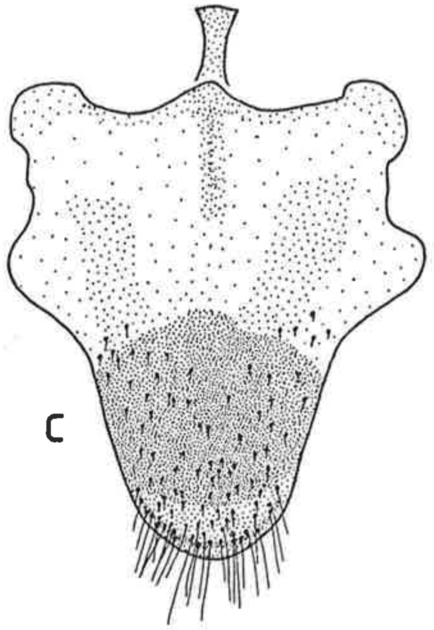

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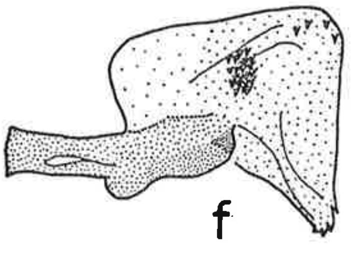

f

Figure 81a-f. Male terminalia of *Myrmecia princeps* Clark, from Calperum, S.A. [161], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve.

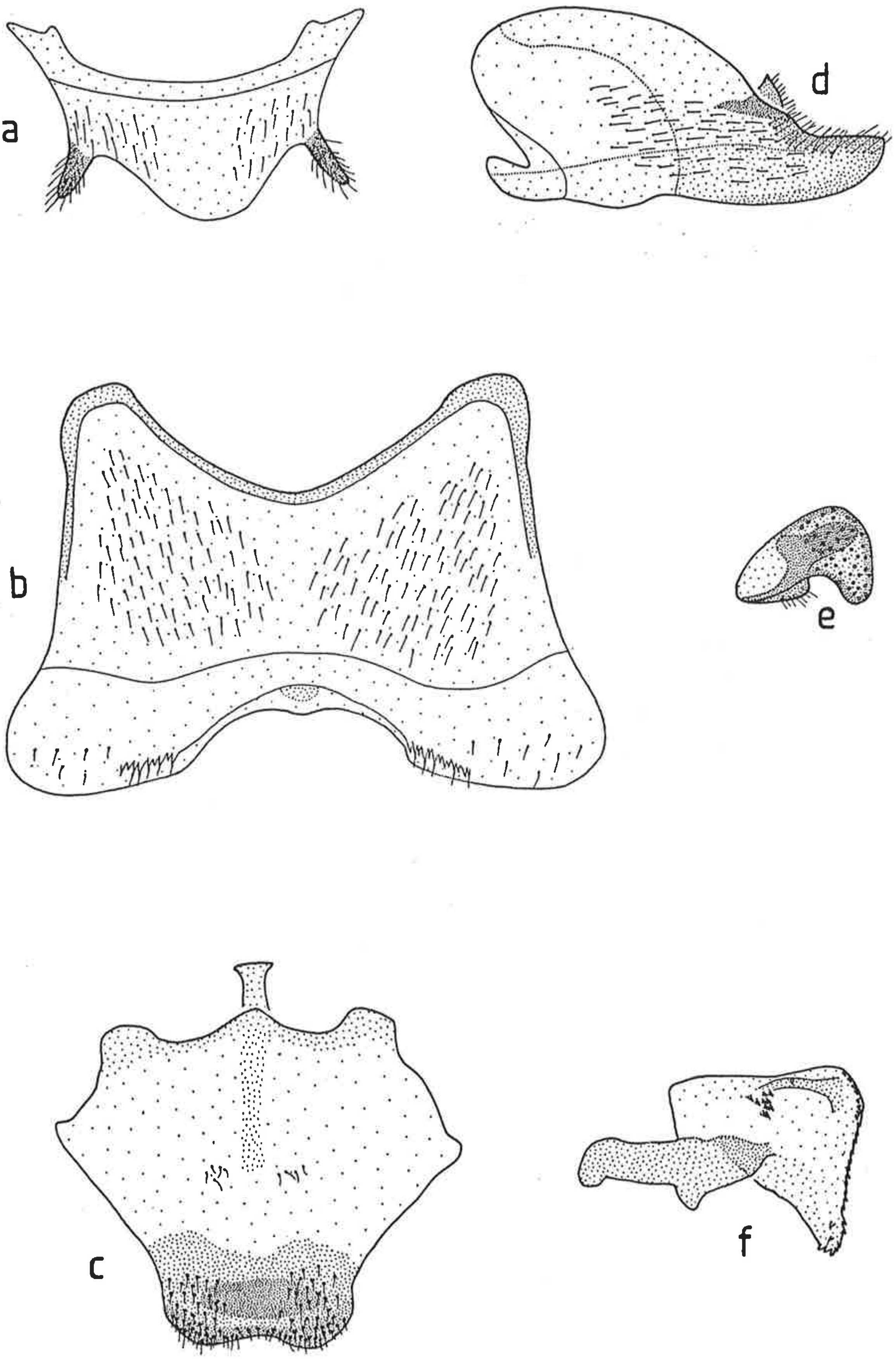
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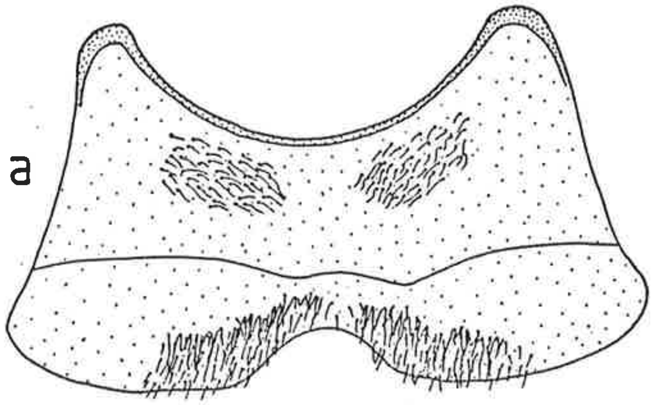
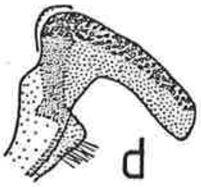
Figure 82a-e. Male terminalia of Myrmecia esuriens Fabricius, from Hobart, Tas. (AML; in MCZ), (a) eighth sternite, (b) ninth sternite, (c) outer valve, (d) middle valve and (e) inner valve. (DL, dorsal lobe; Se, serrations; VL, ventral lobe).


a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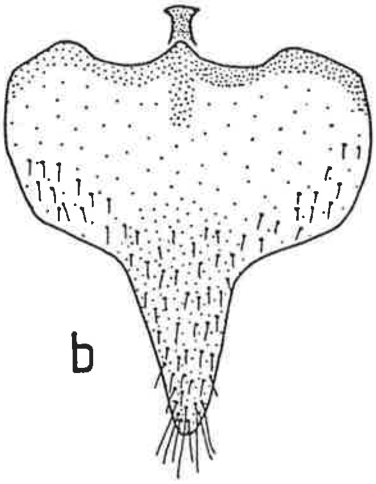
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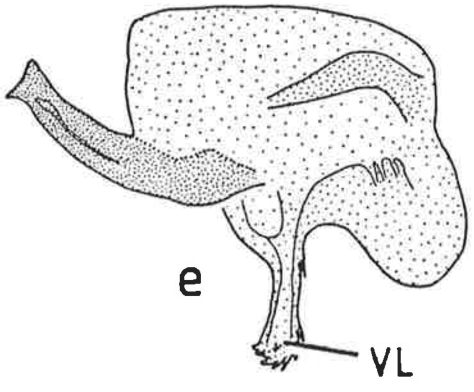
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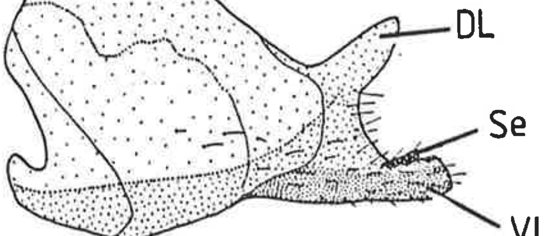
DL
Se
VL
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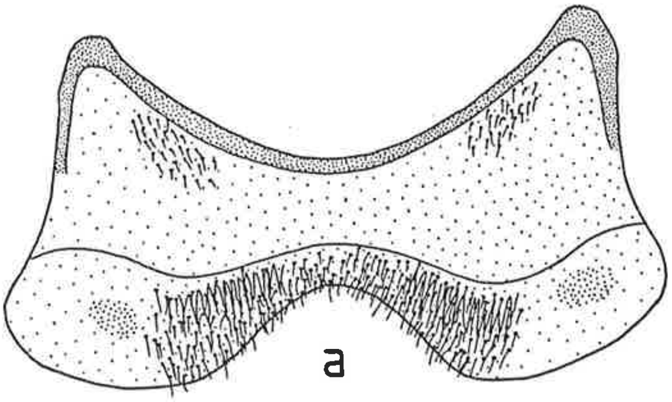
Figure 83a-d. Male terminalia of _Myrmecia midas_ Clark, from Dorrigo, N.S.W. (WH; in MCZ), (a) eighth sternite, (b) ninth sternite, (c) outer valve, and (d) inner valve.



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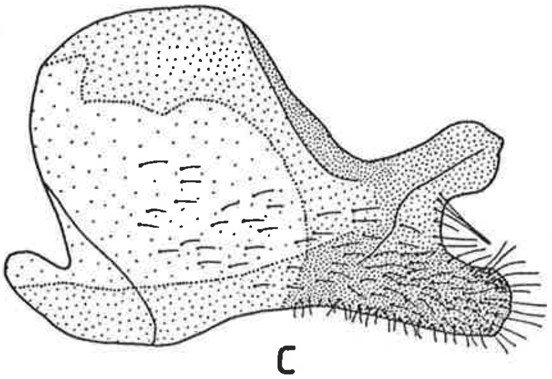

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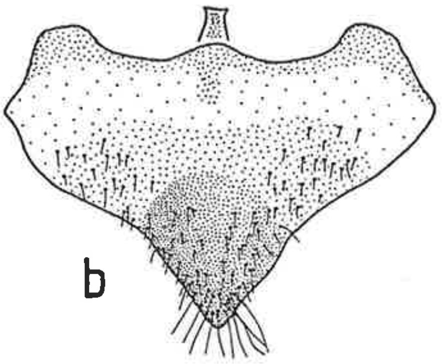

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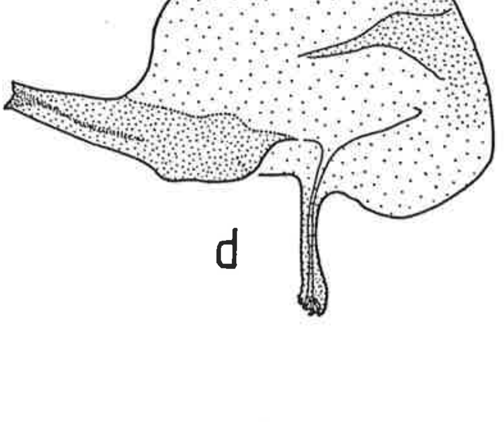

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Figure 84a-f. Male terminalia of Myrmecia pulchra Clark, from Mount Lofty, S.A. [73], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. [From Browning, 1979].

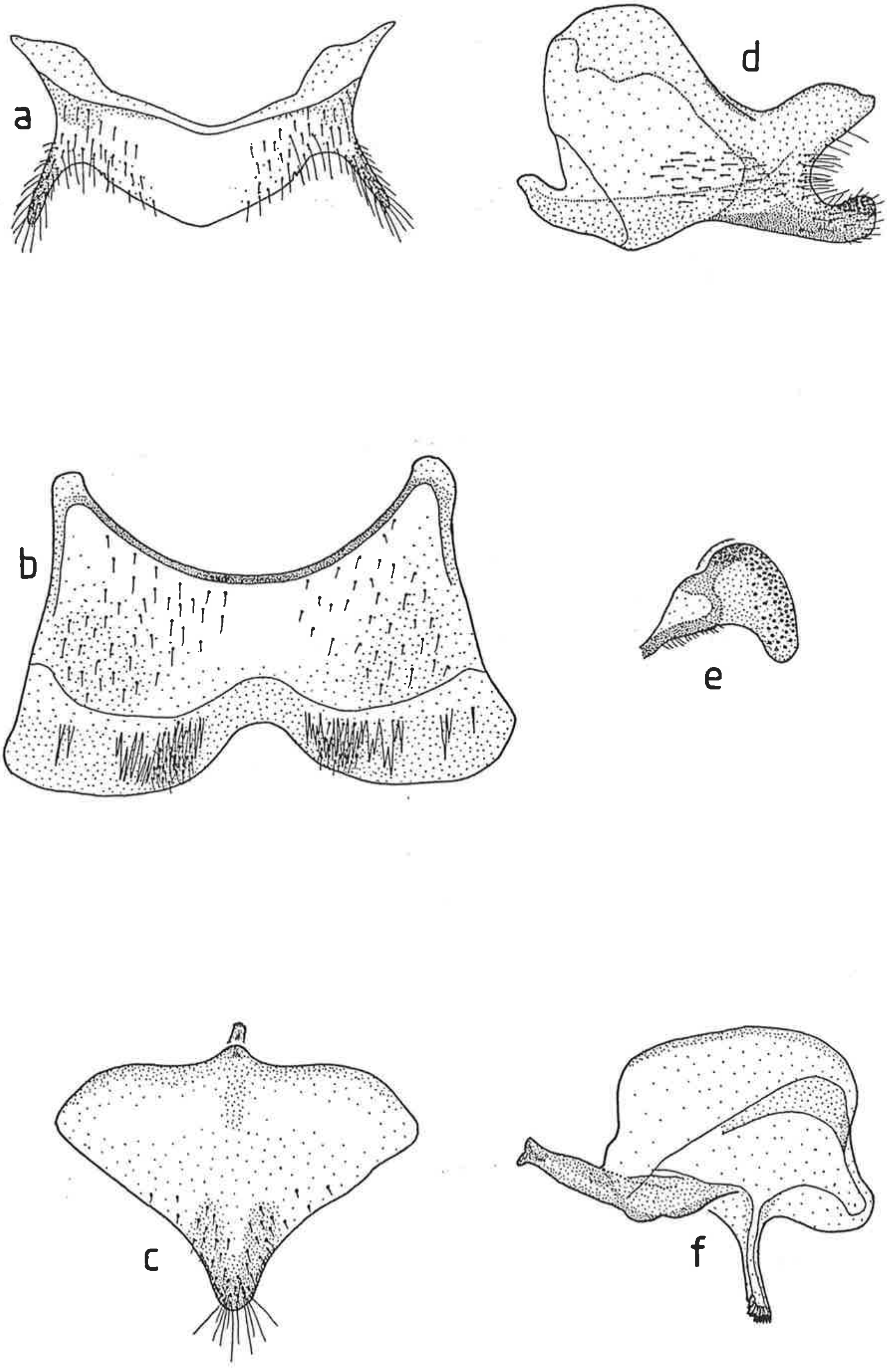
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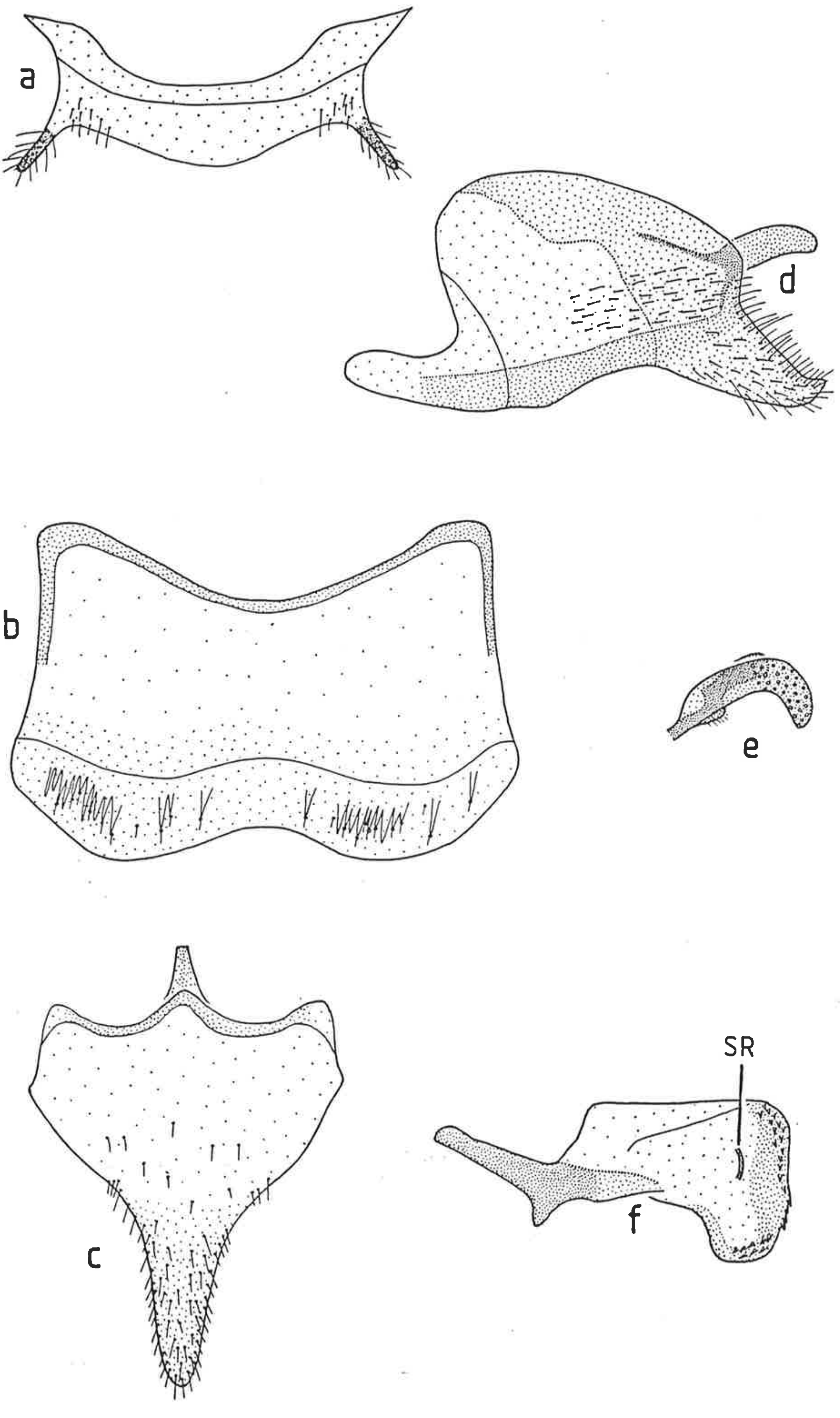
Figure 85a-f. Male terminalia of Myrmecia nigrocincta Smith, from Pymble, N.S.W. [67], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. (SR, sclerotized ridge). [From Browning, 1979].


a
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SR
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Figure 86a-f. Male terminalia of *Myrmecia harderi* Forel, from Bookong S.F., N.S.W. (BBL; in ANIC), (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve.

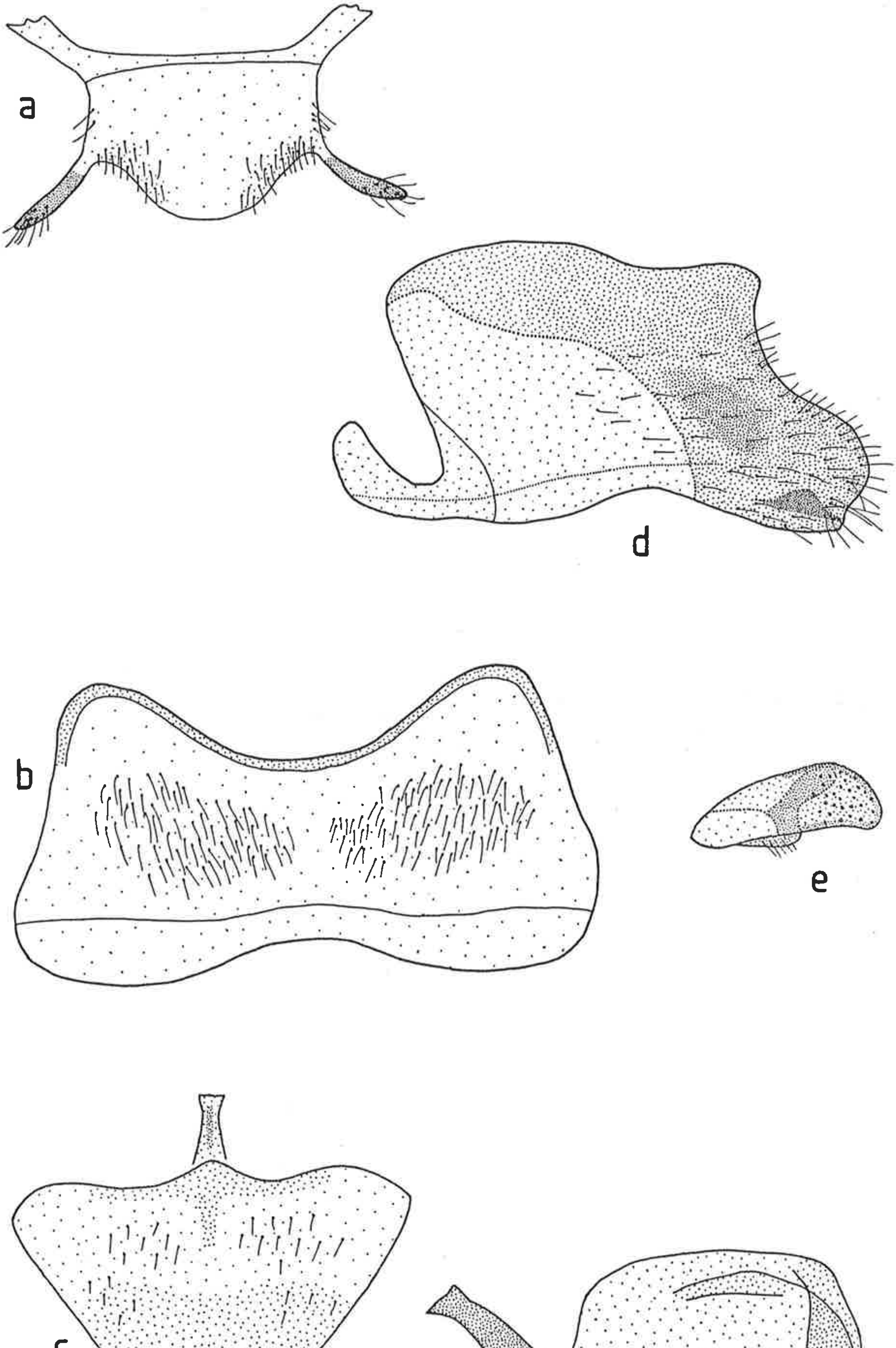
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Figure 87a-e. Male terminalia of Myrmecia aberrans Forel, from Werribee Gorge, Vic. (BBL; in ANIC), (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve and (e) inner valve.

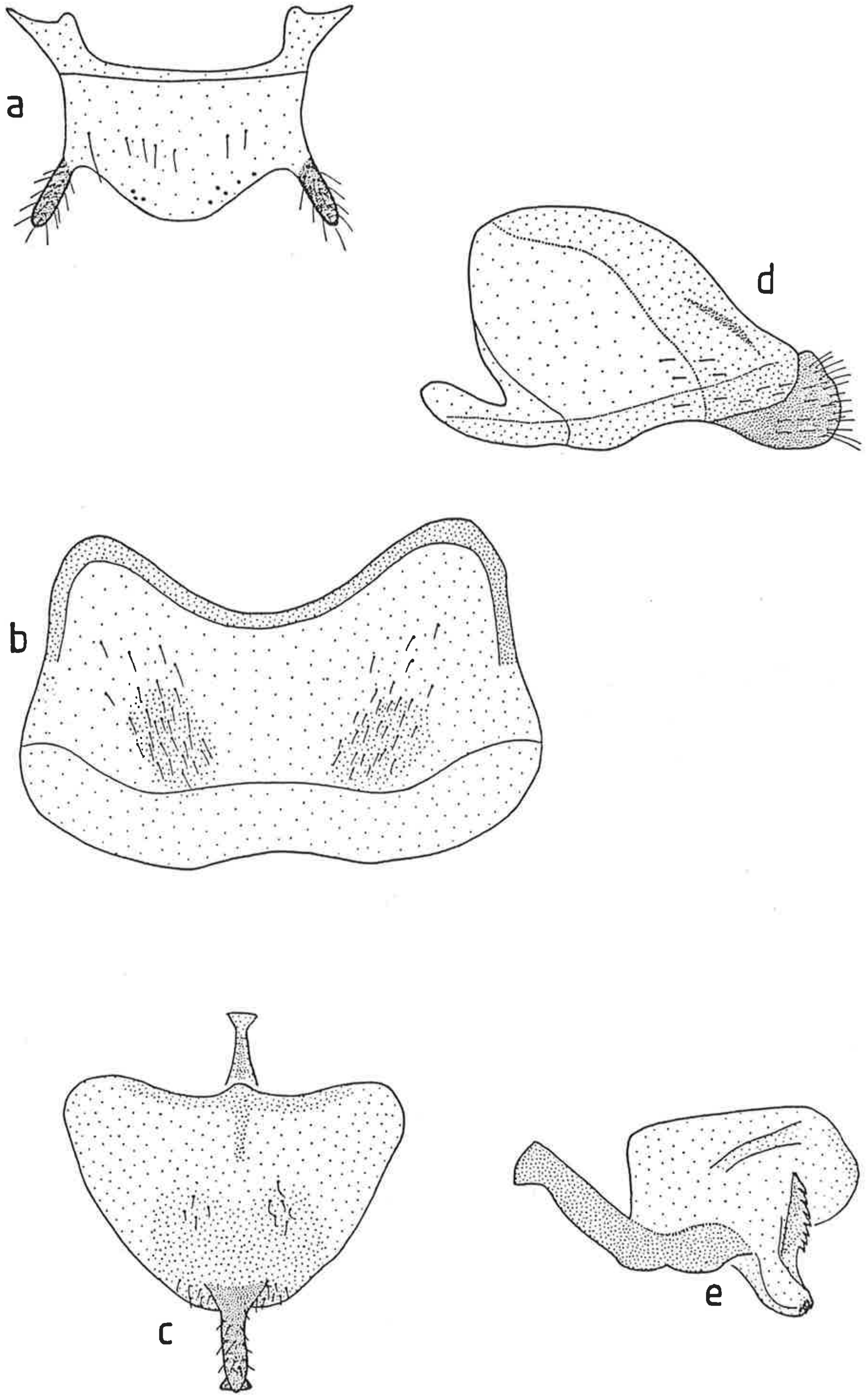
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Figure 88a-g. Male terminalia of:

Myrmecia swalei Crawley, from 10 km N of Denmark, W.A. (BBL; in ANIC), (a) ninth sternite, (b) outer valve and (c) inner valve;

Myrmecia dispar (Clark), probably from Matakana, N.S.W., (d) ninth sternite [from Gray, 1966]; and

Myrmecia cephalotes (Clark), from Black Hill Creek, N.S.W. [511], (e) ninth sternite, (f) outer valve and (g) inner valve.

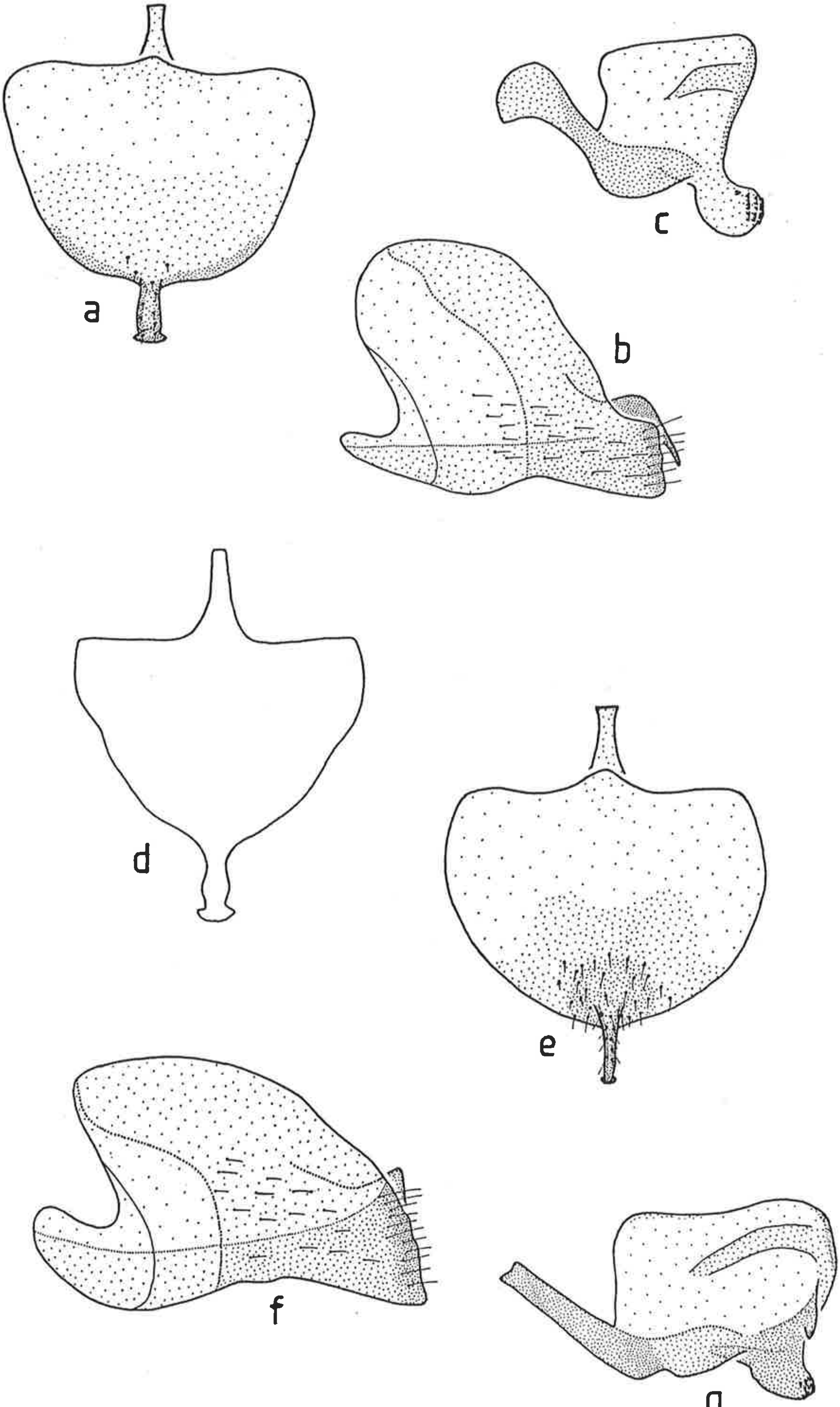
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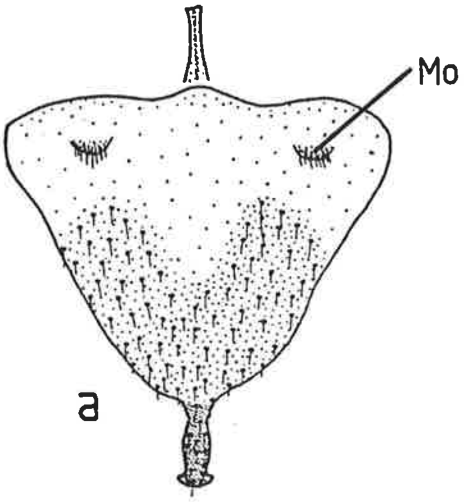
Figure 89a-g. Male terminalia of:

Myrmecia varians Mayr, from Little Dip C.P., S.A. [492], (a) ninth sternite, (b) outer valve and (c) inner valve; and

Myrmecia chasei Forel, from Morley, W.A. (LMO'H; in ANIC), (d) eighth sternite, (e) ninth sternite, (f) outer valve and (g) inner valve. (Mo, mound).



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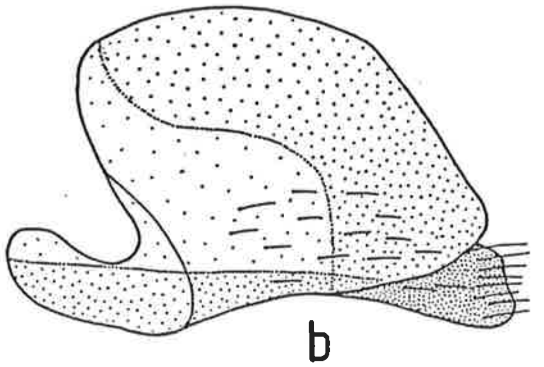

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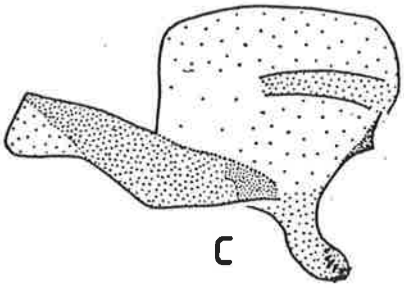

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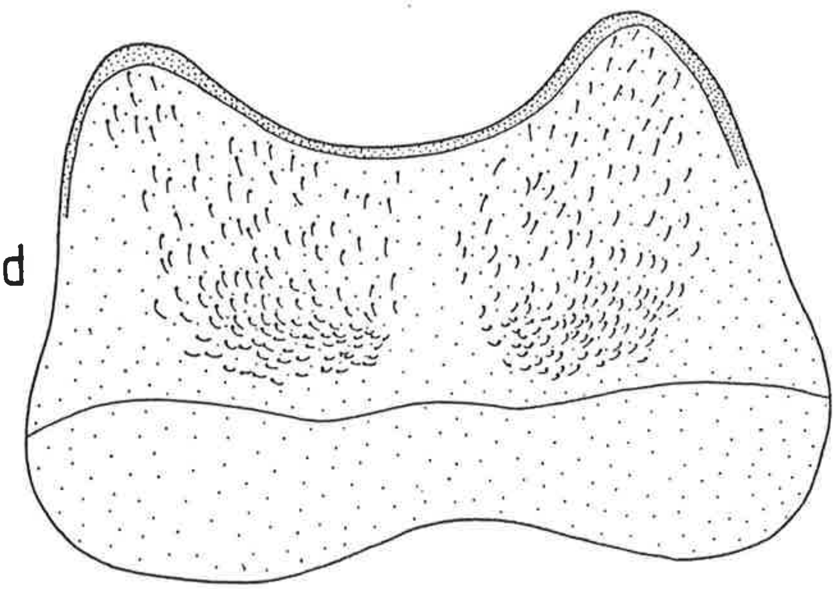

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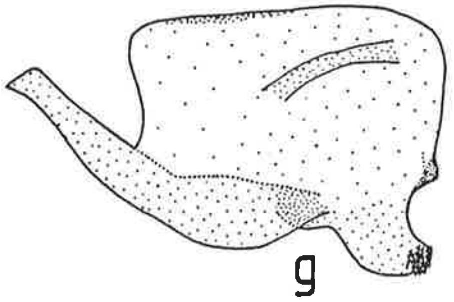

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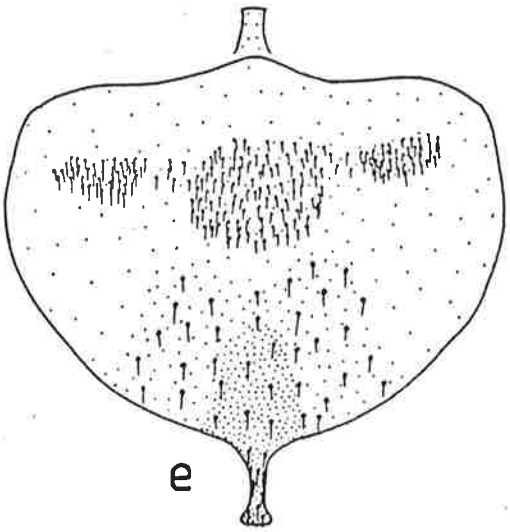

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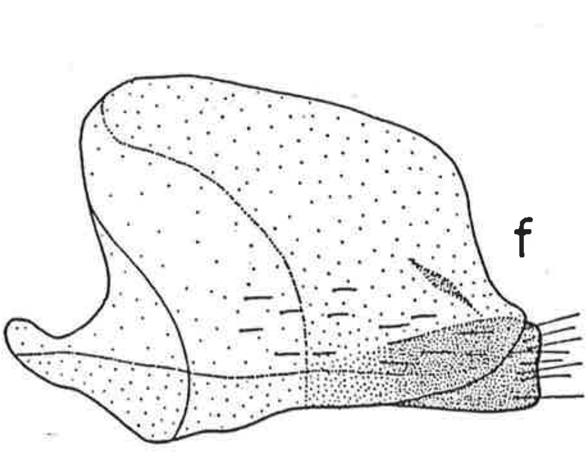
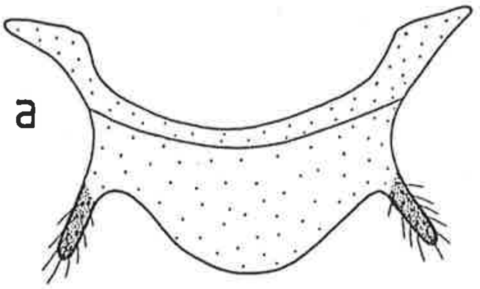


f

Figure 90a-e. Male terminalia of Myrmecia michaelseni Forel, from Cape Le Grand, W.A. [419], (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve and (e) inner valve.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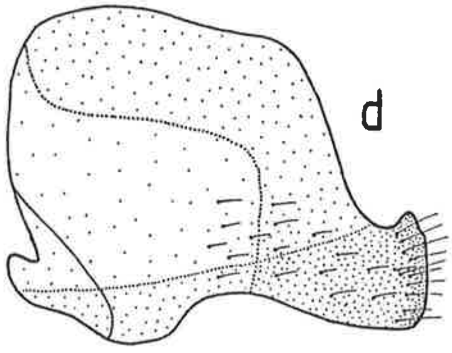
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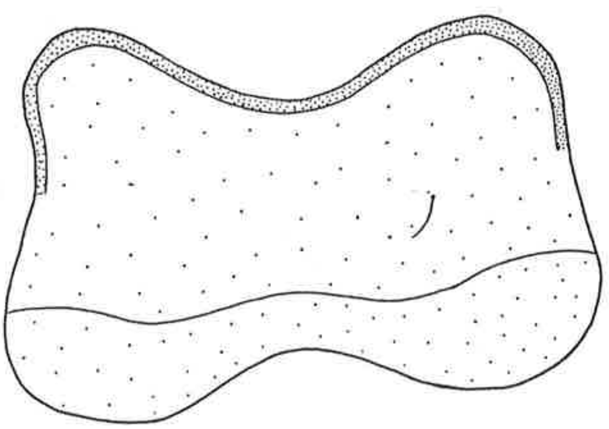
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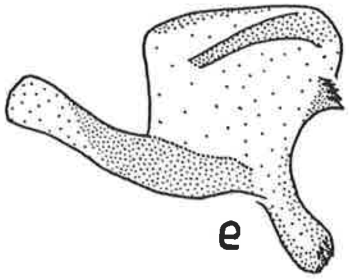
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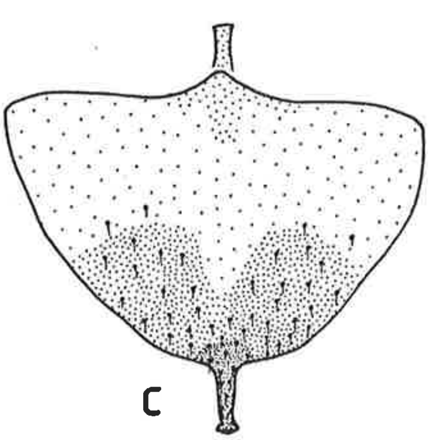
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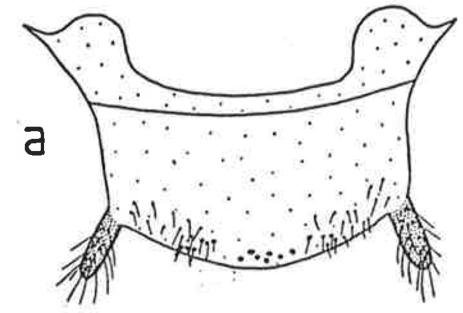
Figure 91a-f. Male terminalia of *Myrmecia pilosula* Smith, *s.l.*, from Rocky River, S.A. [336], and Uraidla, S.A. [46], (a) ninth and tenth tergites [336], (b) eighth sternite [46], (c) ninth sternite [46], (d) outer valve [336], (e) middle valve [336] and (f) inner valve [46]. (BH, barbed hook; VI, ventral indentation).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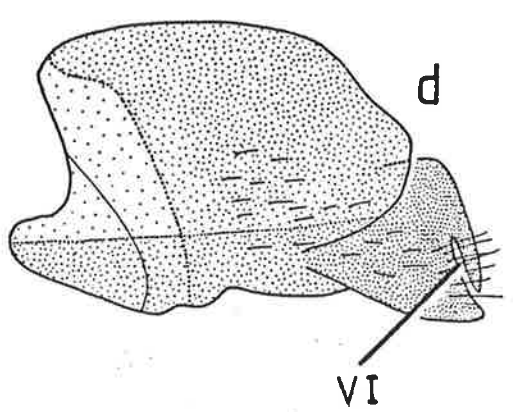
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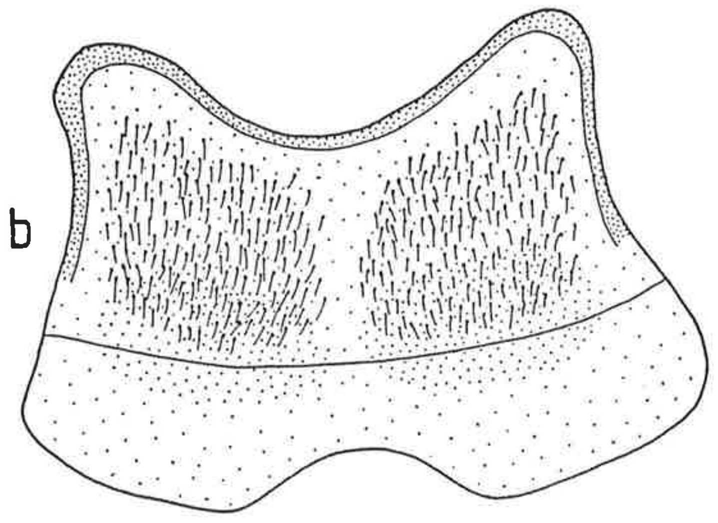
VI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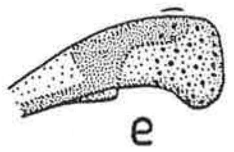
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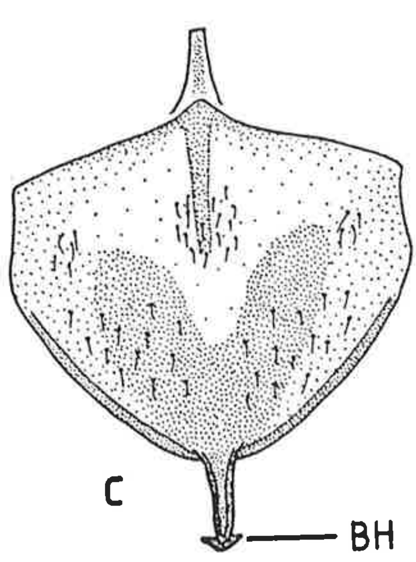
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BH

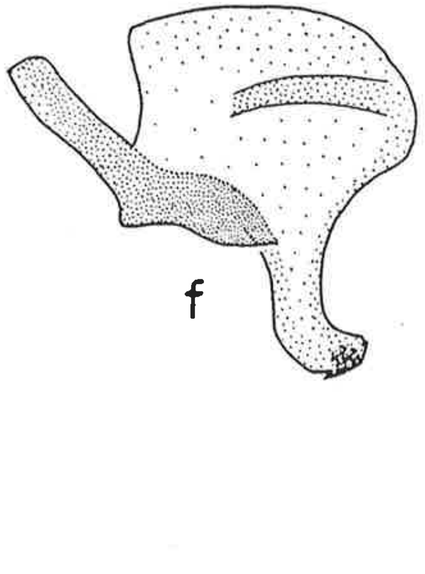
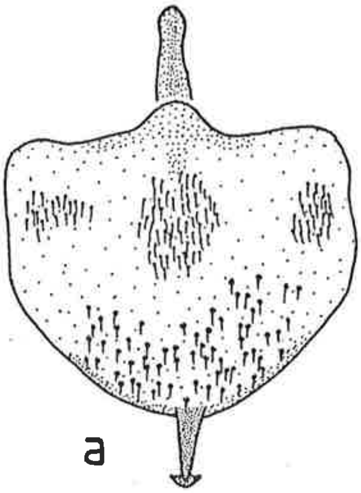

f

Figure 92a-f. Male terminalia of:

Ponera ruginoda Smith HOLOTYPE [= Myrmecia pilosula Smith, s.l.], from Australia (cu; 44.14 in BMNH), (a) ninth sternite and (b) inner valve; and

Myrmecia tepperi Emery, from Inneston, S.A. [271], (c) eighth sternite, (d) ninth sternite, (e) outer valve and (f) inner valve.



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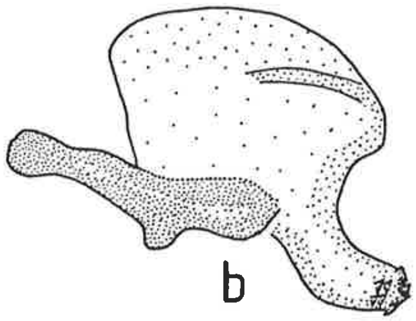

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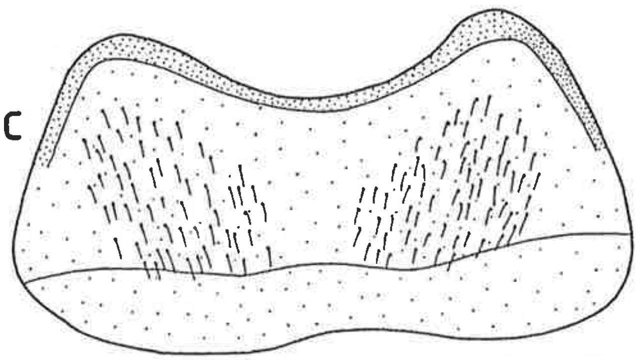

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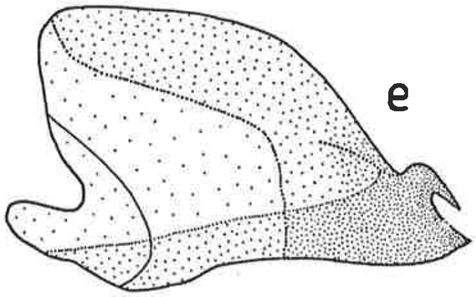

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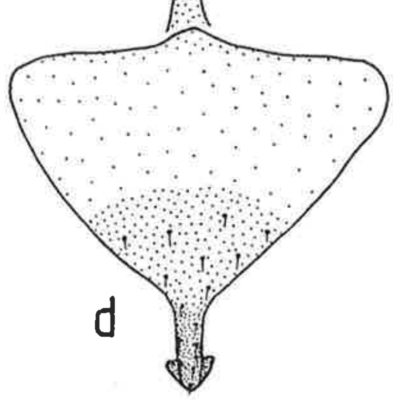
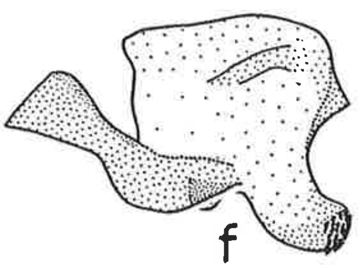
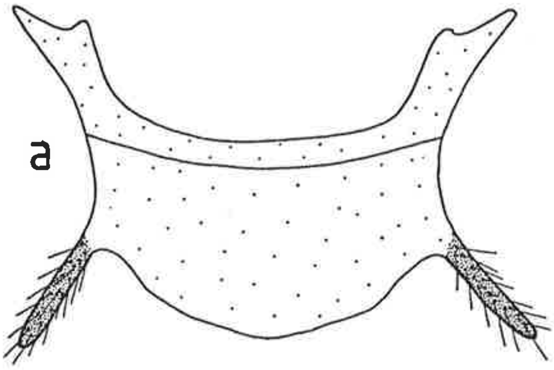


d

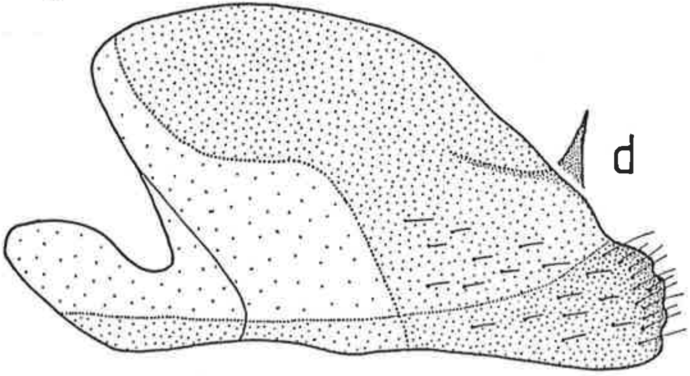


f

Figure 93a-e. Male terminalia of Myrmecia sp.M1 (GPB), from Terrey Hills, N.S.W. (BBL; in ANIC), (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve and (e) inner valve.



a



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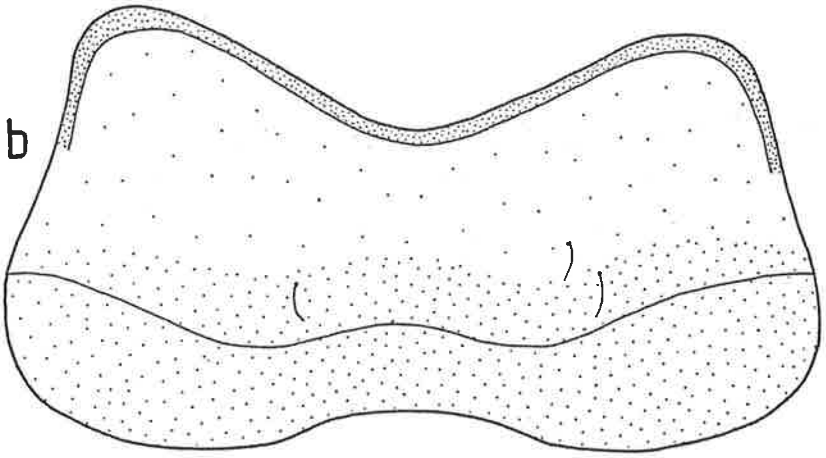

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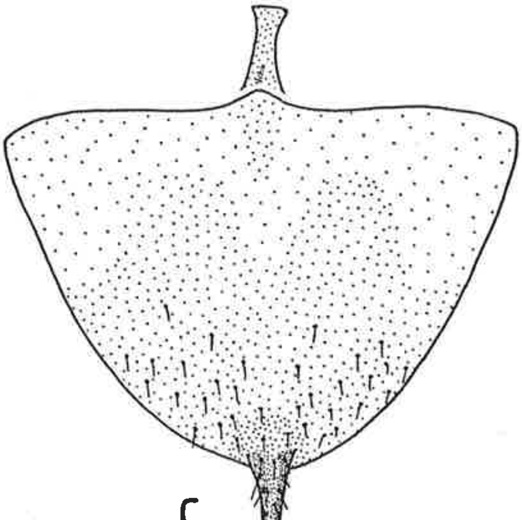

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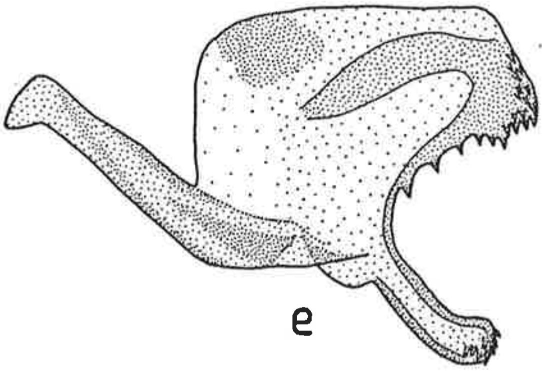
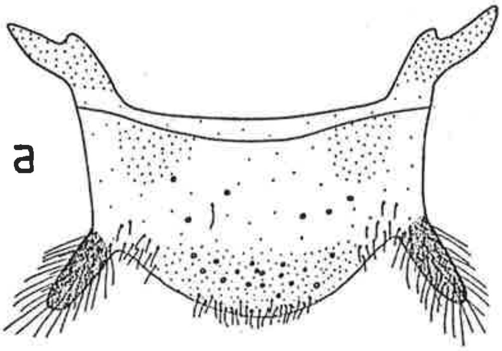


e

Figure 94a-f. Male terminalia of *Myrmecia* *sp*.*M2* (GPB), from Mount Lofty, S.A. (JGOT; in MCZ), (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve.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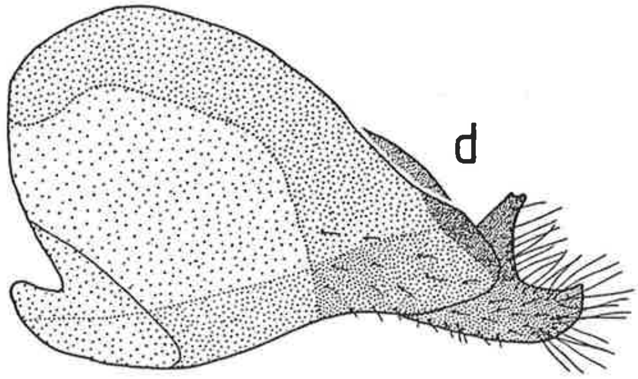
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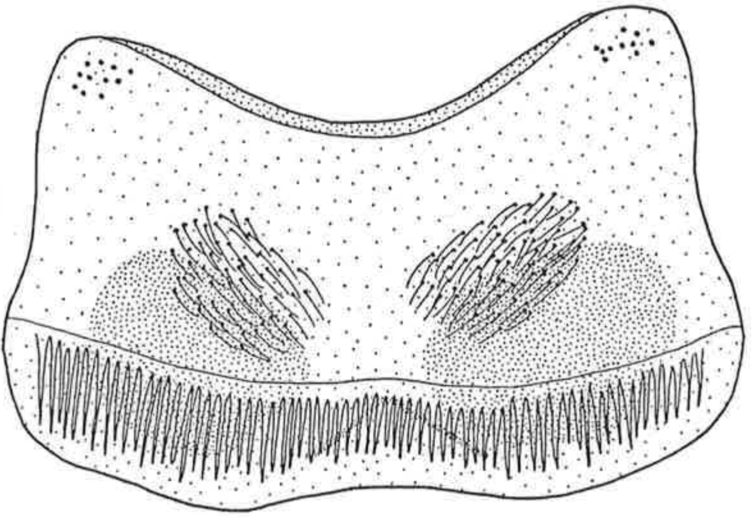
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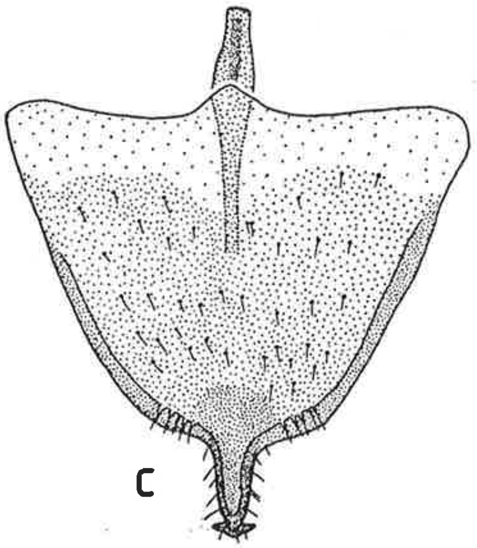
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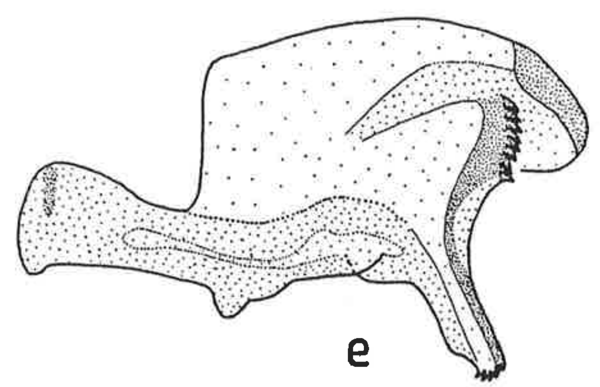
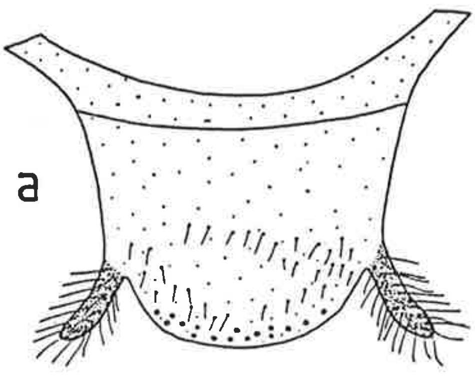

e

Figure 95a-f. Male terminalia of *Myrmecia gilberti* Forel, from 20 km E of Mount Garnet, Qld (cu; in MCZ), (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve. (LI, lateral inclusion).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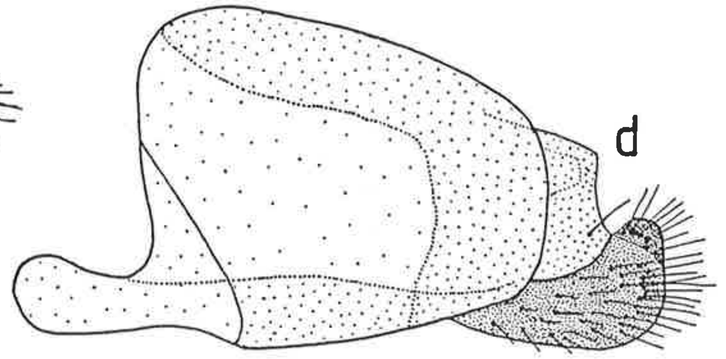
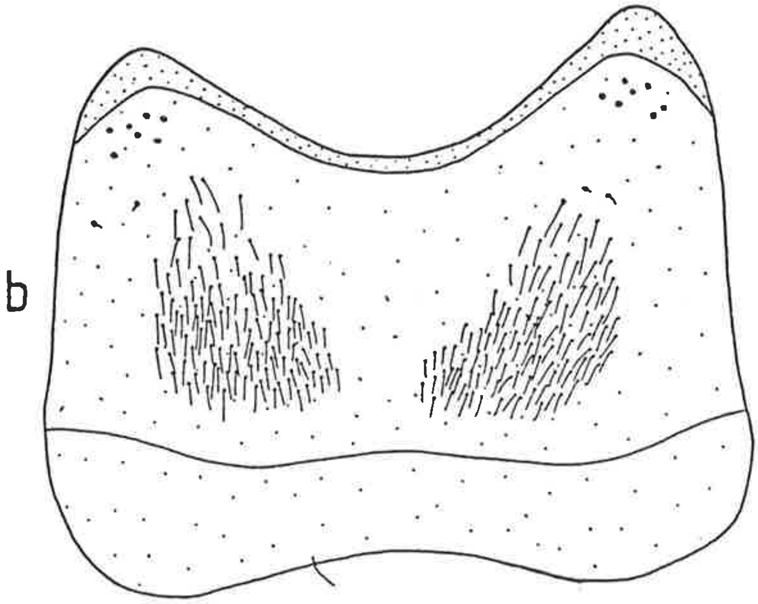

d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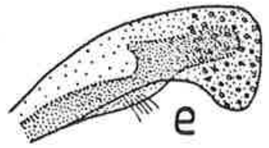
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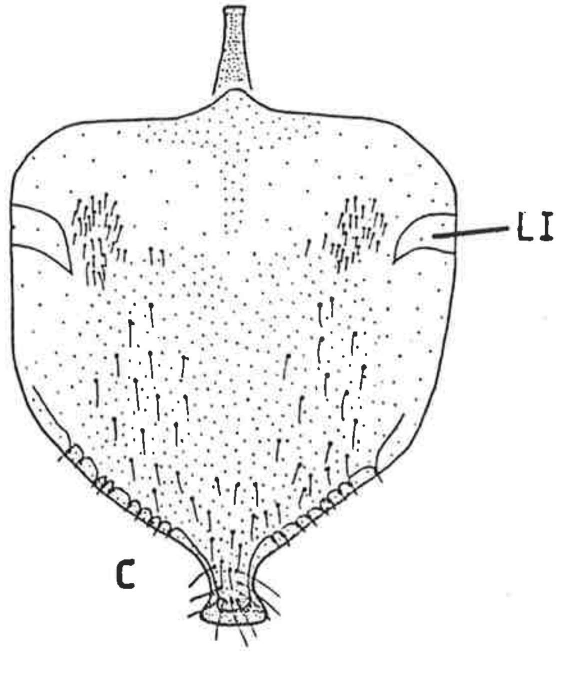
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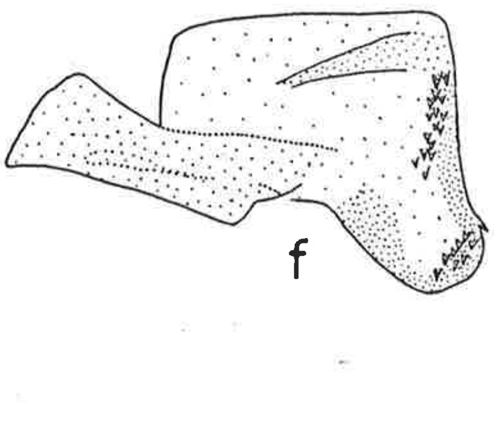
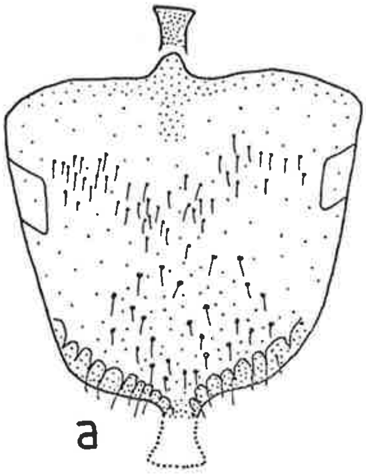

f

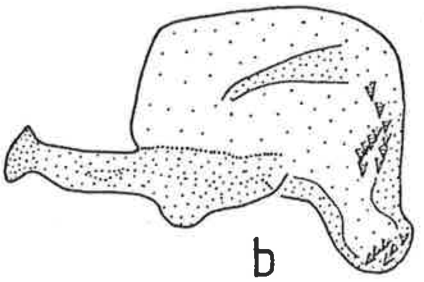
Figure 96a-d. Male terminalia of:

Myrmecia pilosula Smith SYNTYPE [= *Myrmecia gilberti* Forel], from Australia (cu; 50.7 in BMNH), (a) ninth sternite and (b) inner valve; and

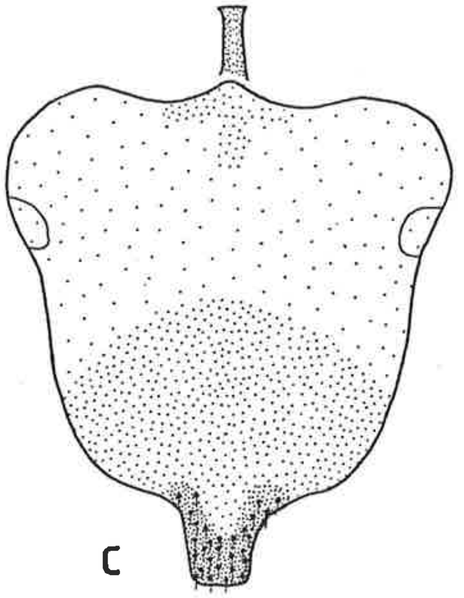
Myrmecia piliventris Smith, *s.s.*, from Black Mountain, A.C.T. (BBL), (c) ninth sternite and (d) inner valve.



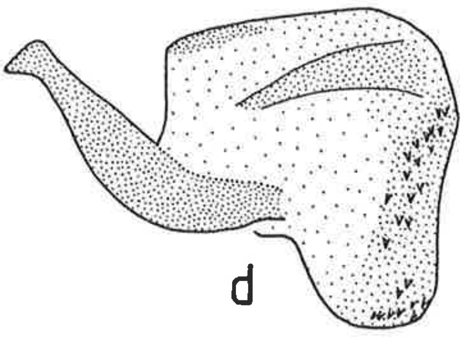
a



b



c

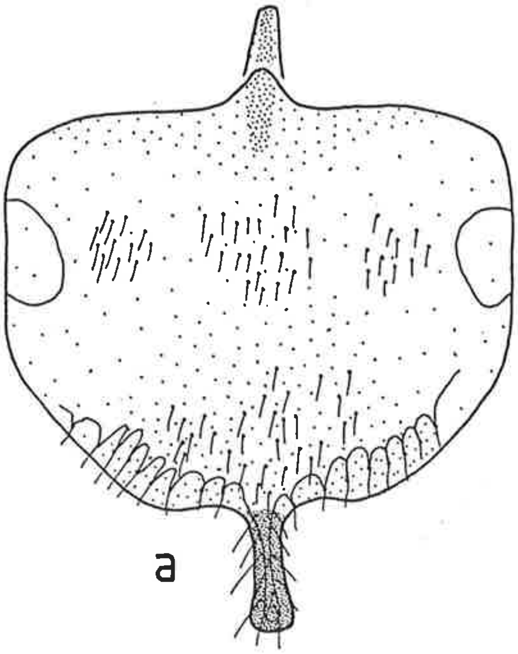


d

Figure 97a-d. Male terminalia of:

Myrmecia mandibularis Smith, from Mount Lofty, S.A. (JGOT; in MCZ), (a) ninth sternite and (b) inner valve; and

Myrmecia fulvipes Roger, *s.l.*, from Mogo S.F., N.S.W. (BBL; in ANIC), (c) ninth sternite and (d) inner valve.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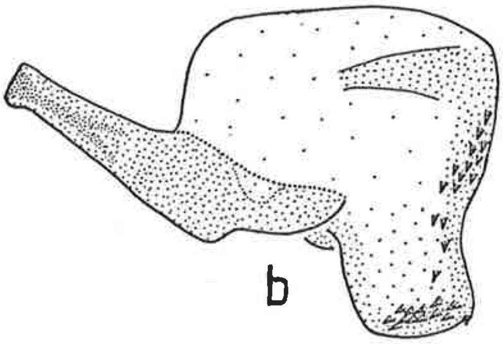
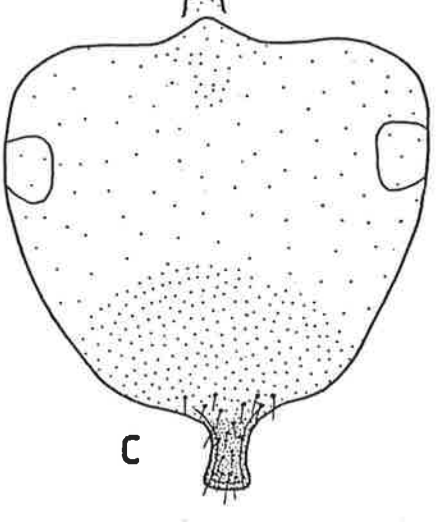

b


c

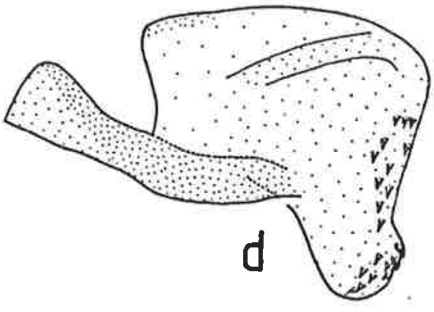
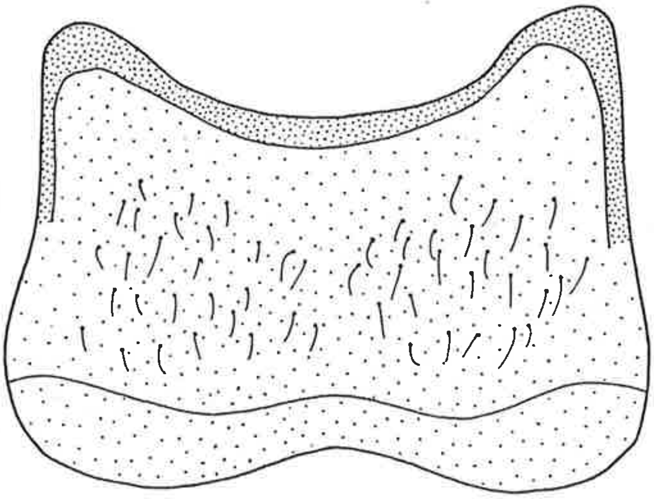
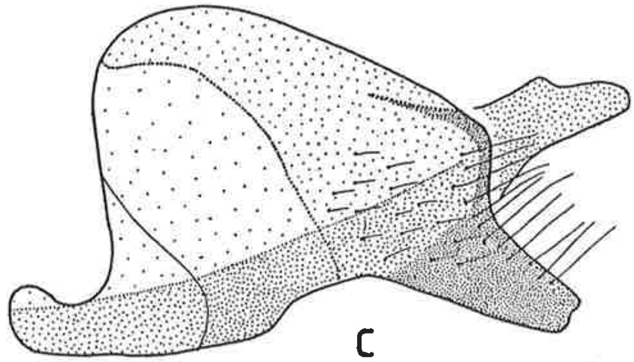

d

Figure 98a-e. Male terminalia of Myrmecia picta Smith, from Mundaring, W.A. (JC1; in ANIC), (a) eighth sternite, (b) ninth sternite, (c) outer valve, (d) middle valve and (e) inner valve.


a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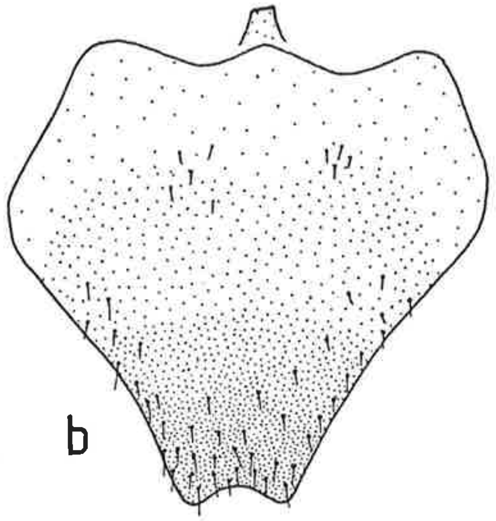
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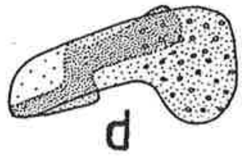

d

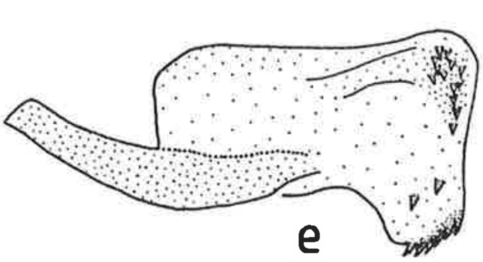

e

Figure 99a-f. Male terminalia of Myrmecia sp.15 (ANIC), from 4 km W of Smokers Gap, A.C.T. (BBL; in ANIC), (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve.

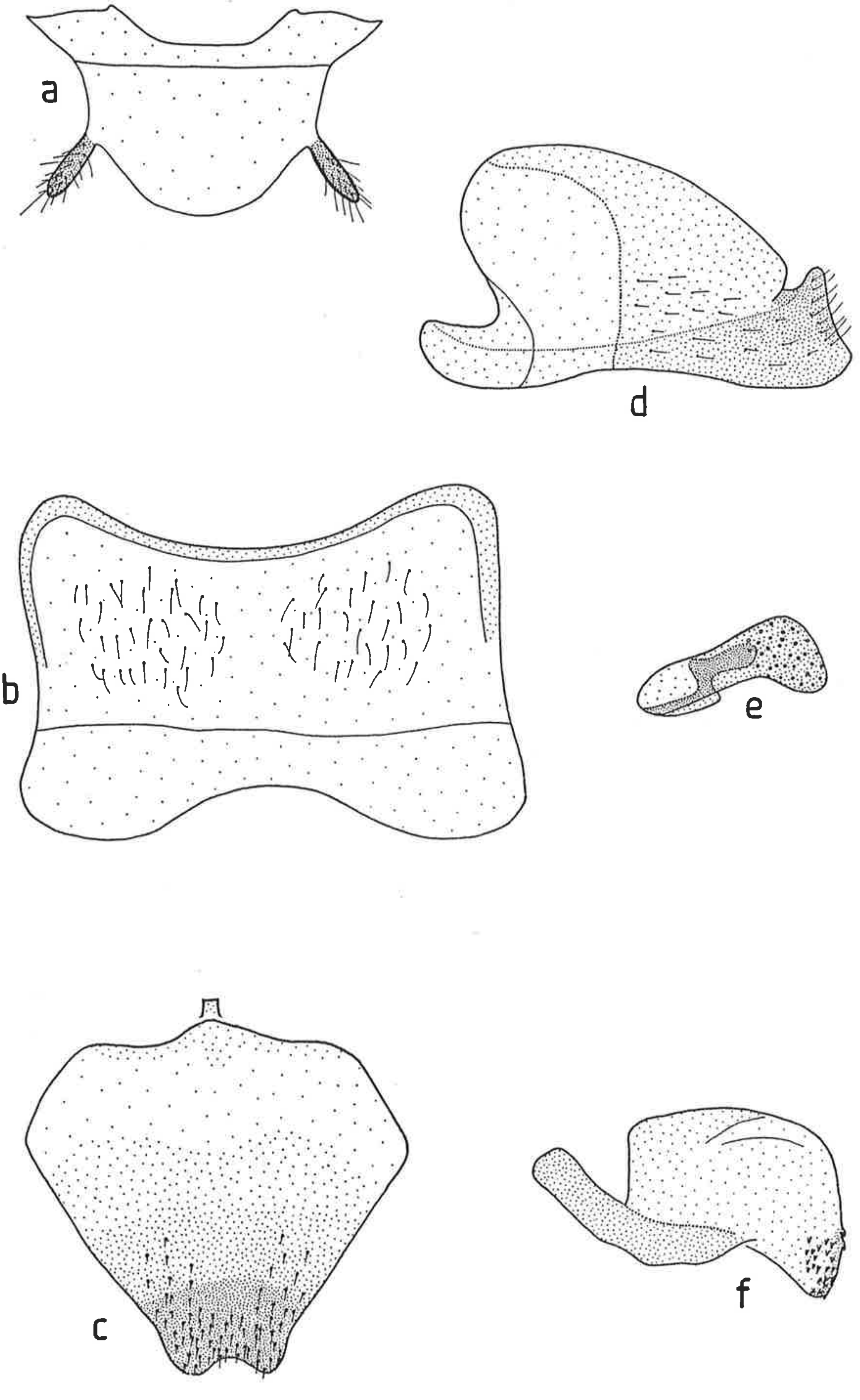
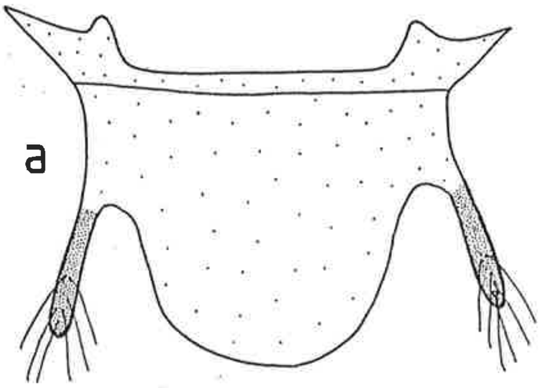
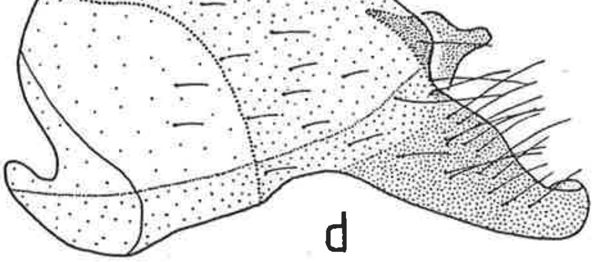
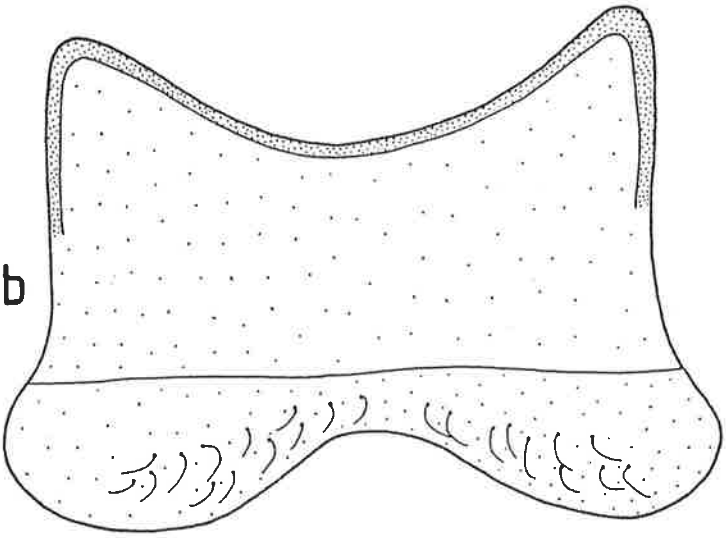
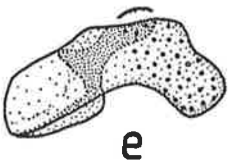

a
d
b
e
c
f

Figure 100a-f. Male terminalia of Myrmecia fucosa Clark, from 19 km SW of Waikerie, S.A. (BBL; in ANIC) and 120 km W of Balladonia, W.A. [525], (a) ninth and tenth tergites [525], (b) eighth sternite (BBL), (c) ninth sternite [525], (d) outer valve [525], (e) middle valve [525] and (f) inner valve (BBL).


a


d


b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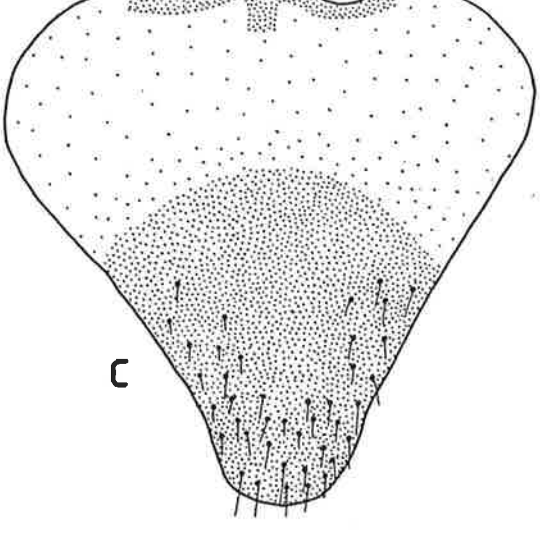
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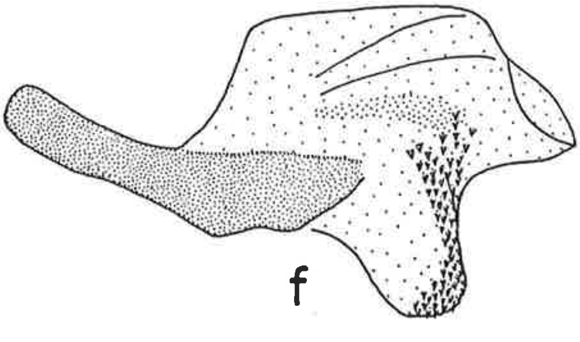
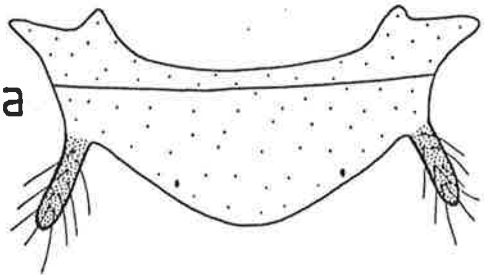
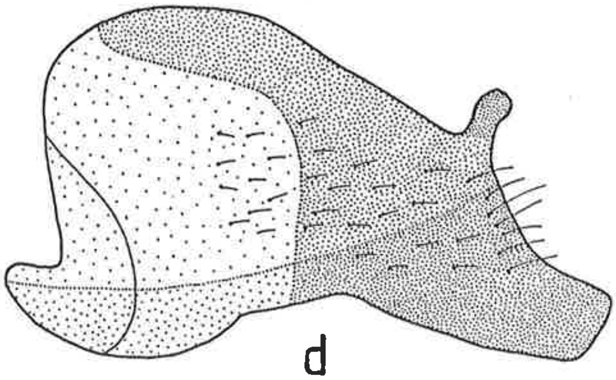

f

Figure 101a-f. Male terminalia of Myrmecia urens Lowne, from 15 km E of Weethalle, N.S.W. (BBL; in ANIC), (a) ninth and tenth tergites, (b) eighth sternite, (c) ninth sternite, (d) outer valve, (e) middle valve and (f) inner valve.


a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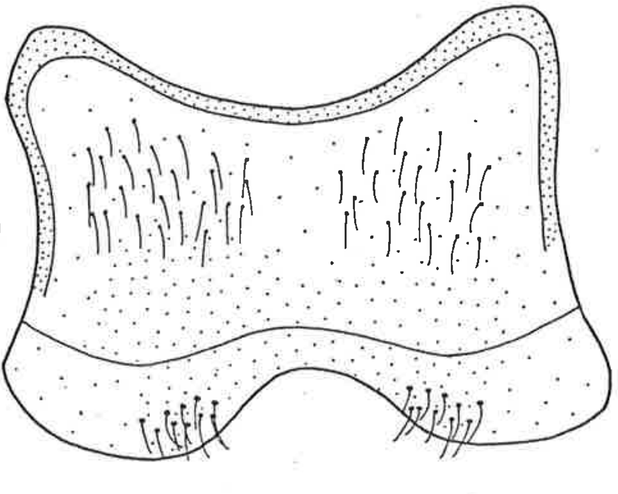
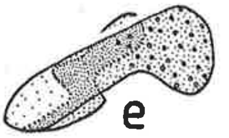
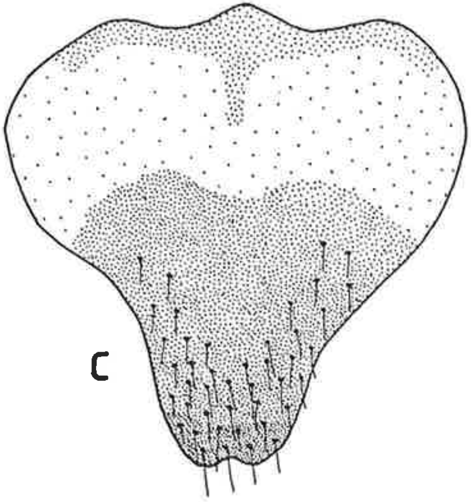

b


e


c

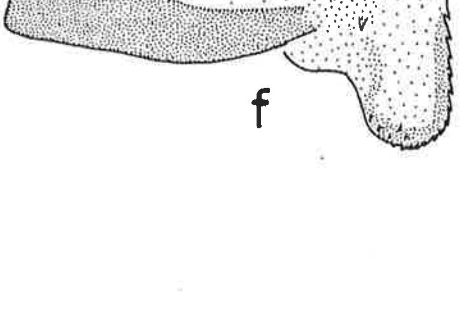

f

Figure 102a-b. Karyograms of:

(a) Myrmecia forceps Roger, from Brownlow, S.A. [140], 2n = 62, N.F. = 62 [open circle indicates chromosome pair which is heterozygous for amount of heterochromatin]; and

(b) Myrmecia pyriformis Smith, from 4 km NW of Ararat, Vic. [495], 2n = 82, N.F. = 82 [open circle indicates chromosome pair which is heterozygous for amount of heterochromatin].

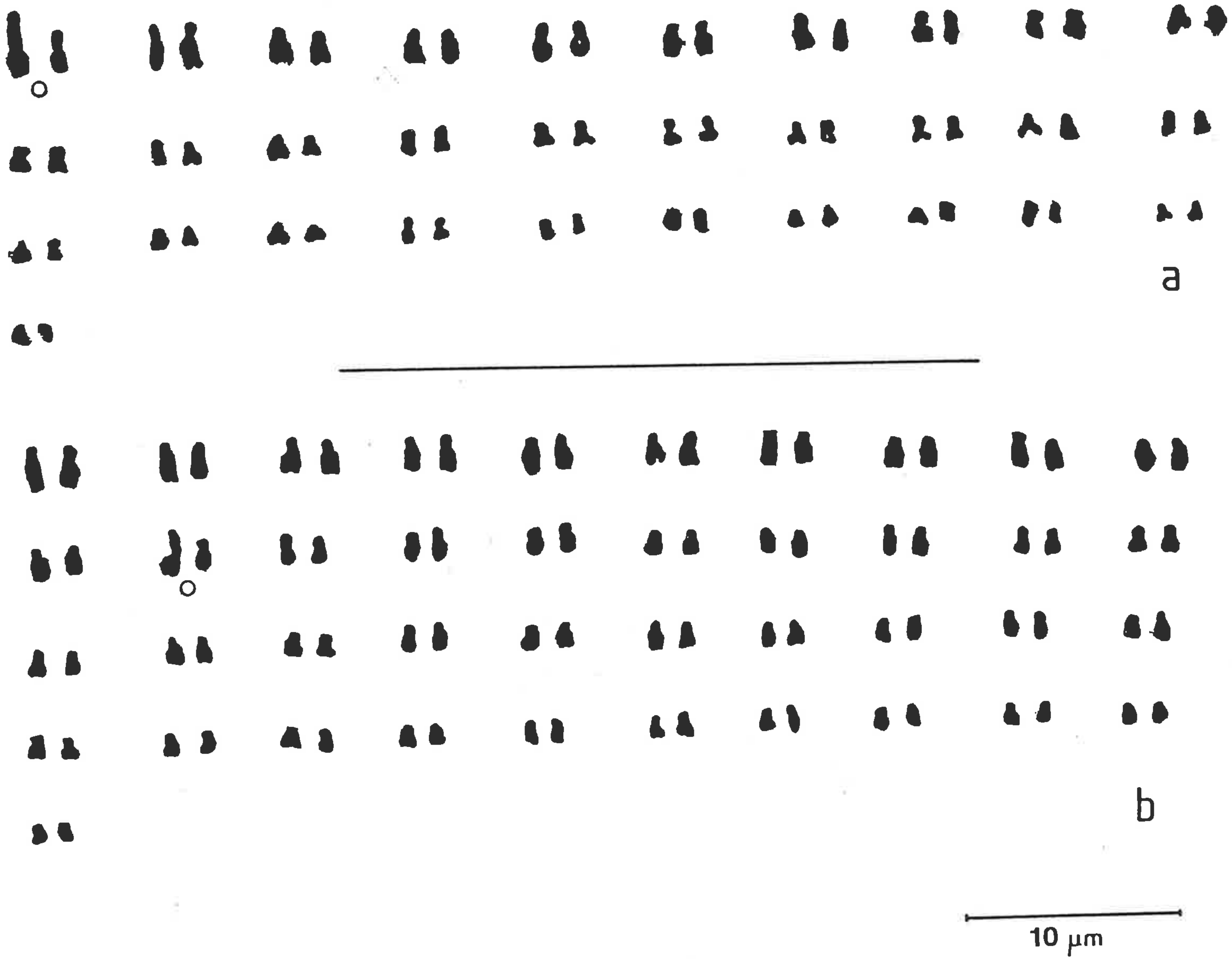

a
b
10 µm

Figure 103a-d. Karyograms of:

(a) Myrmecia arnoldi Clark, from Jerramungup, W.A. [437], 2n = 14, N.F. = 26;

(b) Myrmecia rufinodis Smith, from Marion Bay, S.A. [269], 2n = 10, N.F. = 18;

(c) Myrmecia atrata Clark, from Ravensthorpe, W.A. [240], 2n = 76, N.F. = 77 [boxed chromosomes are unpaired - first three are due to a Robertsonian rearrangement and fourth results from a chromosome deletion]; and

(d) Myrmecia atrata Clark, from Jerramungup, W.A. [227], n = 39, N.F. = 78.

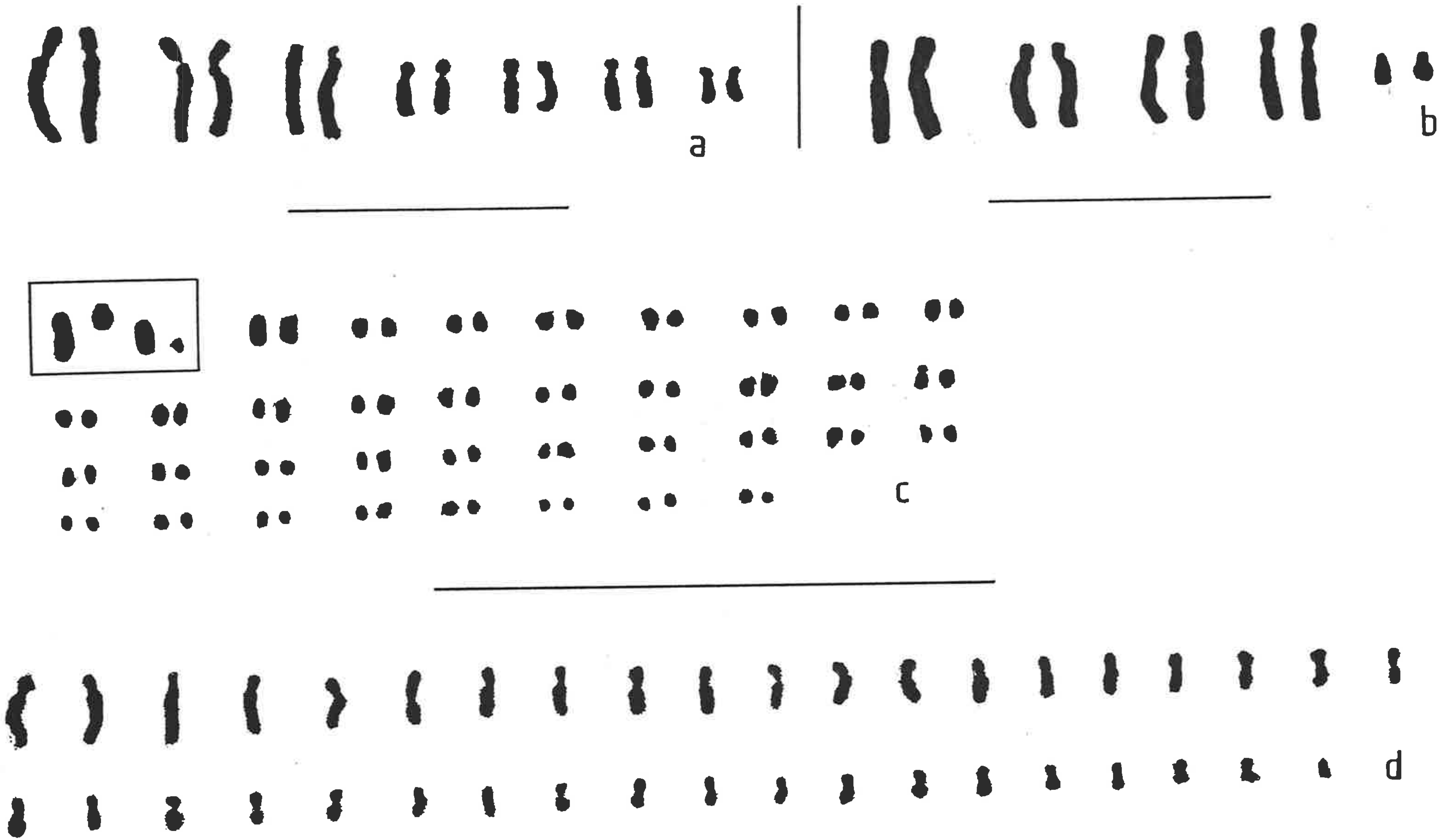

a
b
c
d

Figure 104a-c. Karyograms of:

(a) Myrmecia fulgida Clark, from South Ironcap, W.A. [431], 2n = 40, N.F. = 78;

(b) Myrmecia fuscipes Clark, from Port Parham, S.A. [156], 2n = 76, N.F. = 76; and

(c) Myrmecia fuscipes Clark, from Port Parham, S.A. [159], 2n = 75, N.F. = 76 [boxed chromosomes are unpaired due to a Robertsonian rearrangement].

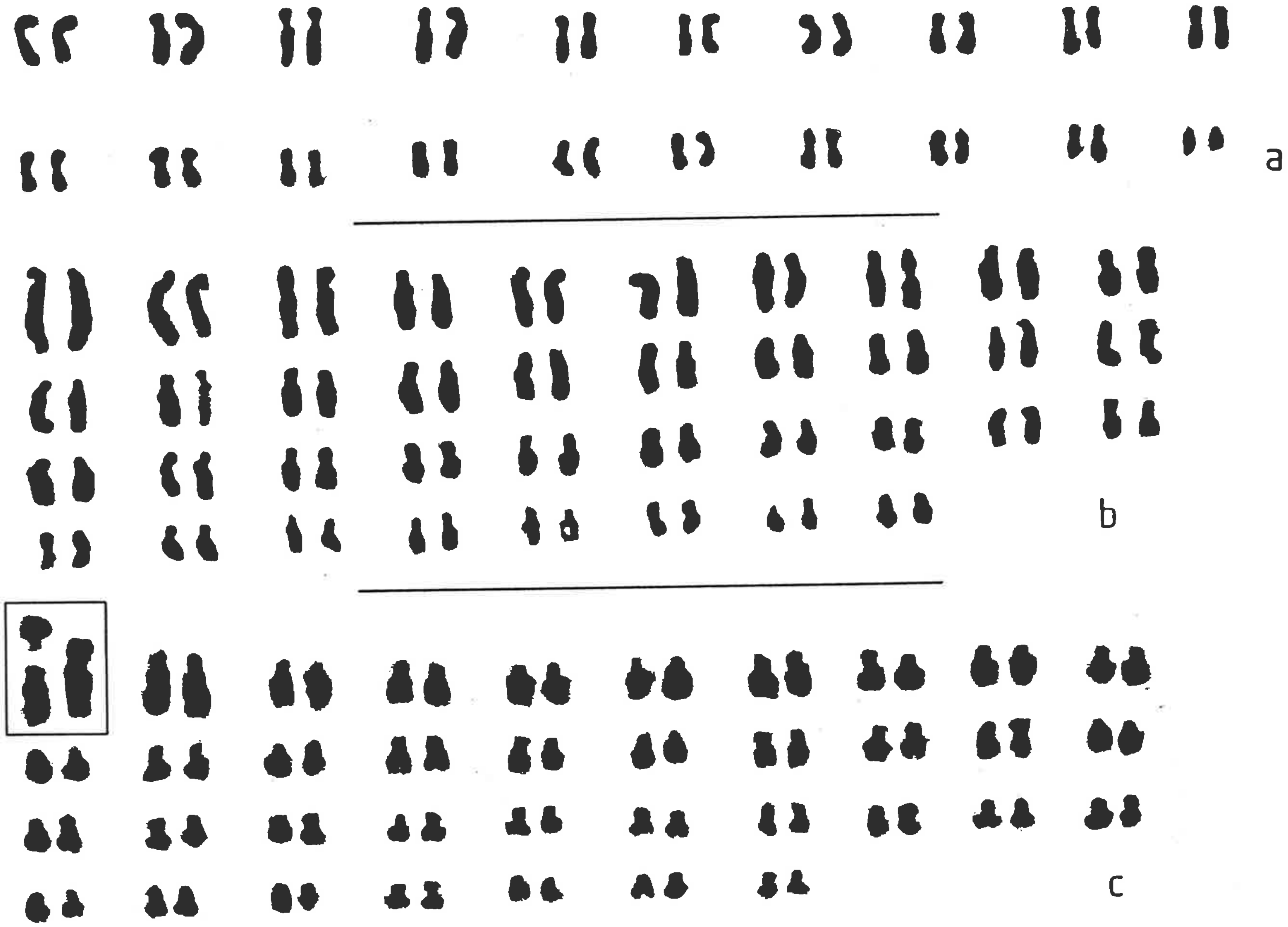

a
b
c

Figure 105a-b. Karyograms of:

(a) Myrmecia fuscipes Clark, from 128 km S of Balladonia, W.A. [413], 2n = 76, N.F. = 76; and

(b) Myrmecia fuscipes Clark, from 2 km S of Peak Charles, W.A. [430], 2n = 76, N.F. = 78.

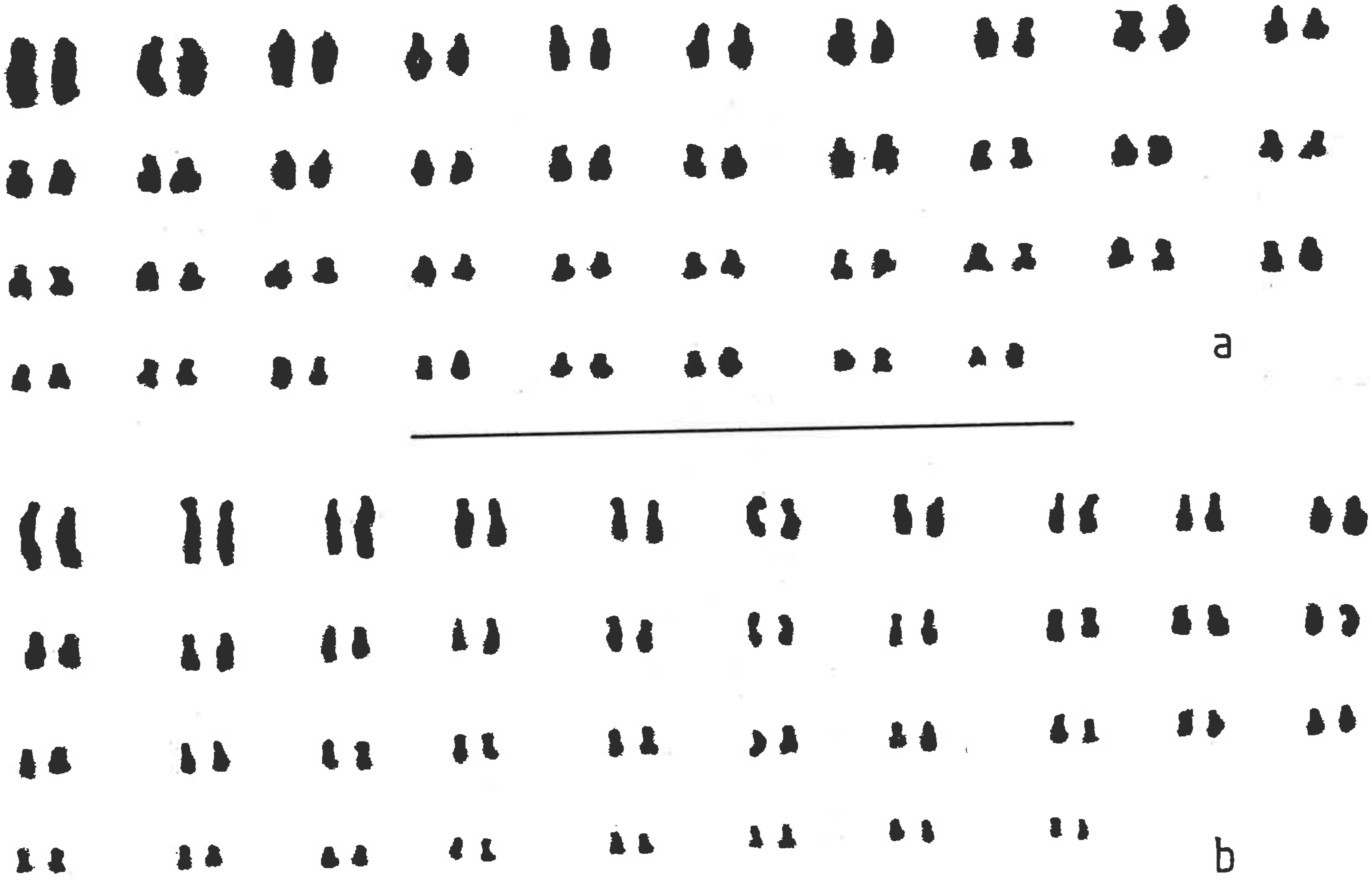

a
b

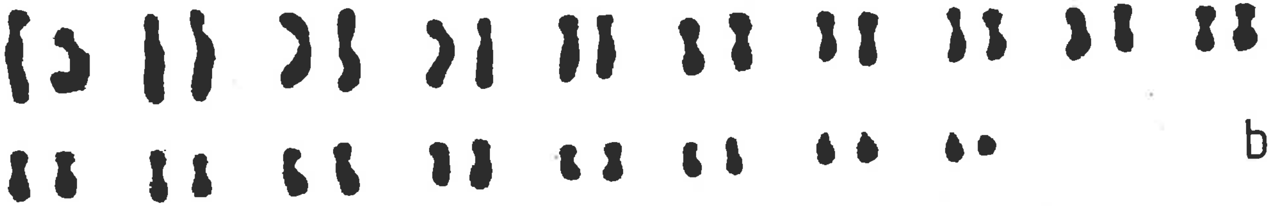
Figure 106a-c. Karyograms of:

(a) Myrmecia fuscipes Clark, from 46 km N of Renmark, S.A. [247], n = 37, N.F. = 80;

(b) Myrmecia sp.11 (ANIC), from Elliston, S.A. [171], 2n = 36, N.F. = 68; and

(c) Myrmecia desertorum Wheeler, from Todmorden, S.A. [147], n = 32, N.F. = 80.

a



b

c

Figure 107a-c. Karyograms of:

(a) *Myrmecia sp.13* (ANIC), from Devlin Pound, S.A. [412], 2n = 40, N.F. = 80;

(b) *Myrmecia sp.13* (ANIC), from 12 km SW of Olympic Dam, S.A. [279], n = 21, N.F. = 80; and

(c) *Myrmecia nigriceps* Mayr, *s.s.*, from Hines Hill, W.A. [466], 2n = 74, N.F. = 78 [boxed chromosomes are unpaired due to two Robertsonian rearrangements].

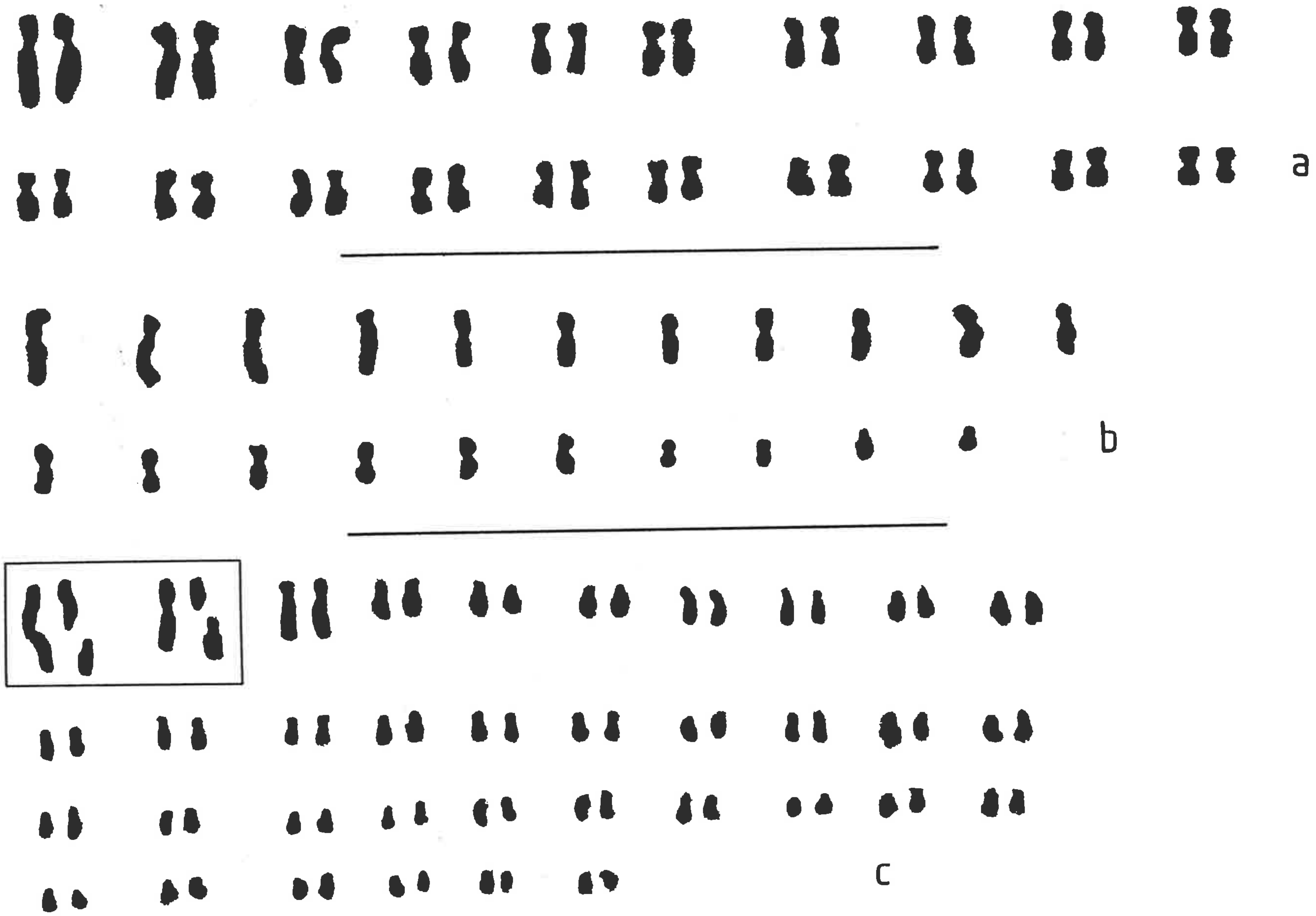

a
b
c

Figure 108a-c. Karyograms of:

(a) Myrmecia nigriceps Mayr, s.s., from 4 km W of Wagin, W.A. [453], n = 36, N.F. = 78;

(b) Myrmecia nigriceps Mayr, s.s., from 4 km W of Wagin, W.A. [453], 2n = 75, N.F. = 78 [boxed chromosomes are unpaired due to a Robertsonian rearrangement]; and

(c) Myrmecia nigriceps Mayr, s.s., from 5 km W of Wagin, W.A. [451], 2n = 70, N.F. = 80.

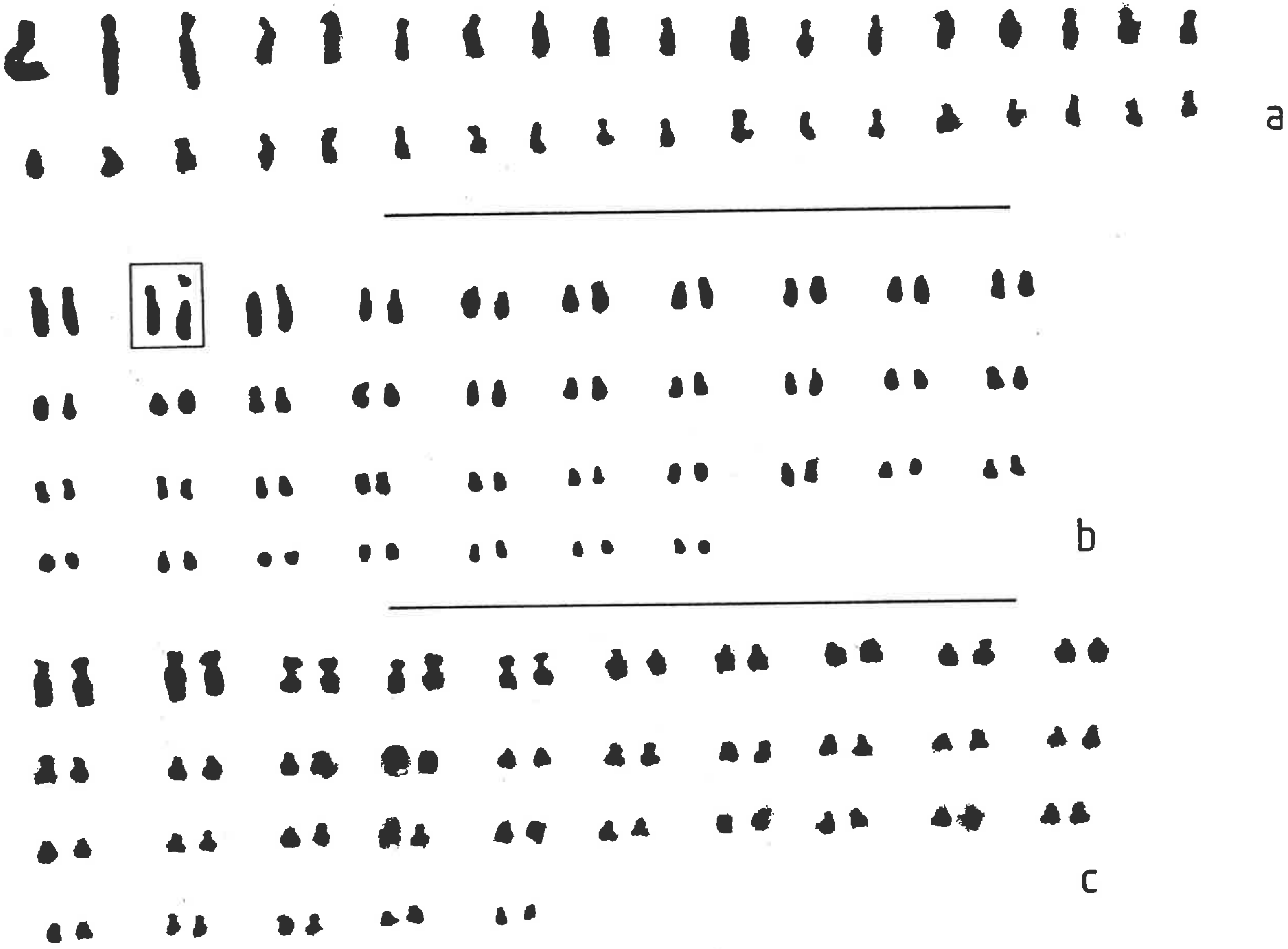
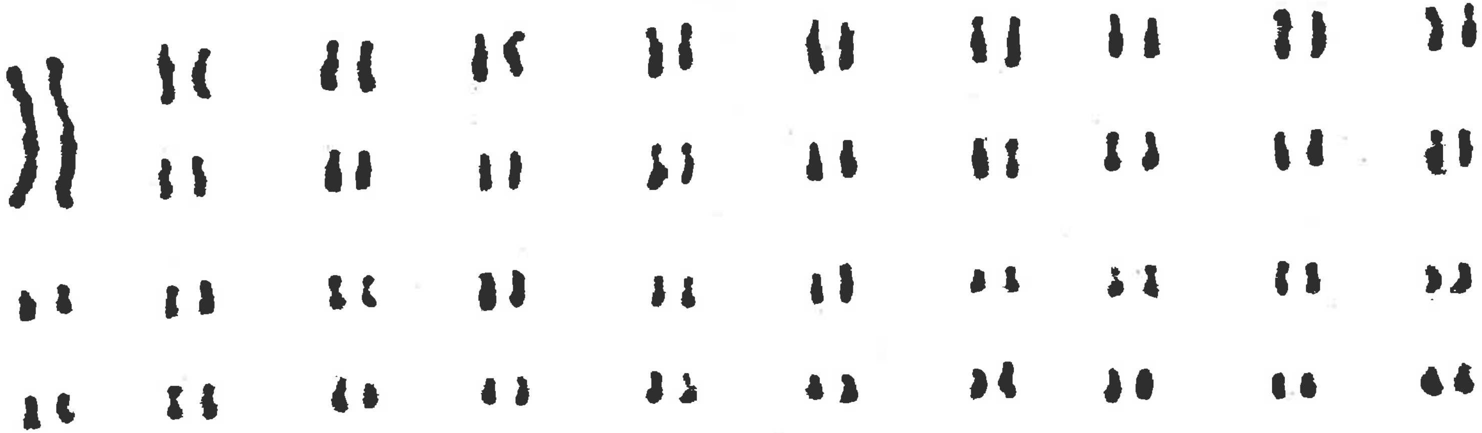

a
b
c

Figure 109a-b. Karyograms of:

(a) Myrmecia nigriceps Mayr, s.s., from Ongerup, W.A. [443], 2n = 74, N.F. = 78; and

(b) Myrmecia nigriceps Mayr, s.s., from 44 km W of Balladonia, W.A. [470], 2n = 78, N.F. = 80.

a



b

Figure 110a-c. Karyograms of:

(a) Myrmecia princeps Clark, from 12 km SW of Olympic Dam, S.A. [487], 2n = 30, N.F. = 50;

(b) Myrmecia princeps Clark, from Calperum, S.A. [161], 2n = 40, N.F. = 56; and

(c) Myrmecia sp.12 (ANIC), from 8 km E of Maitland, S.A. [478], 2n = 74, N.F. = 78.

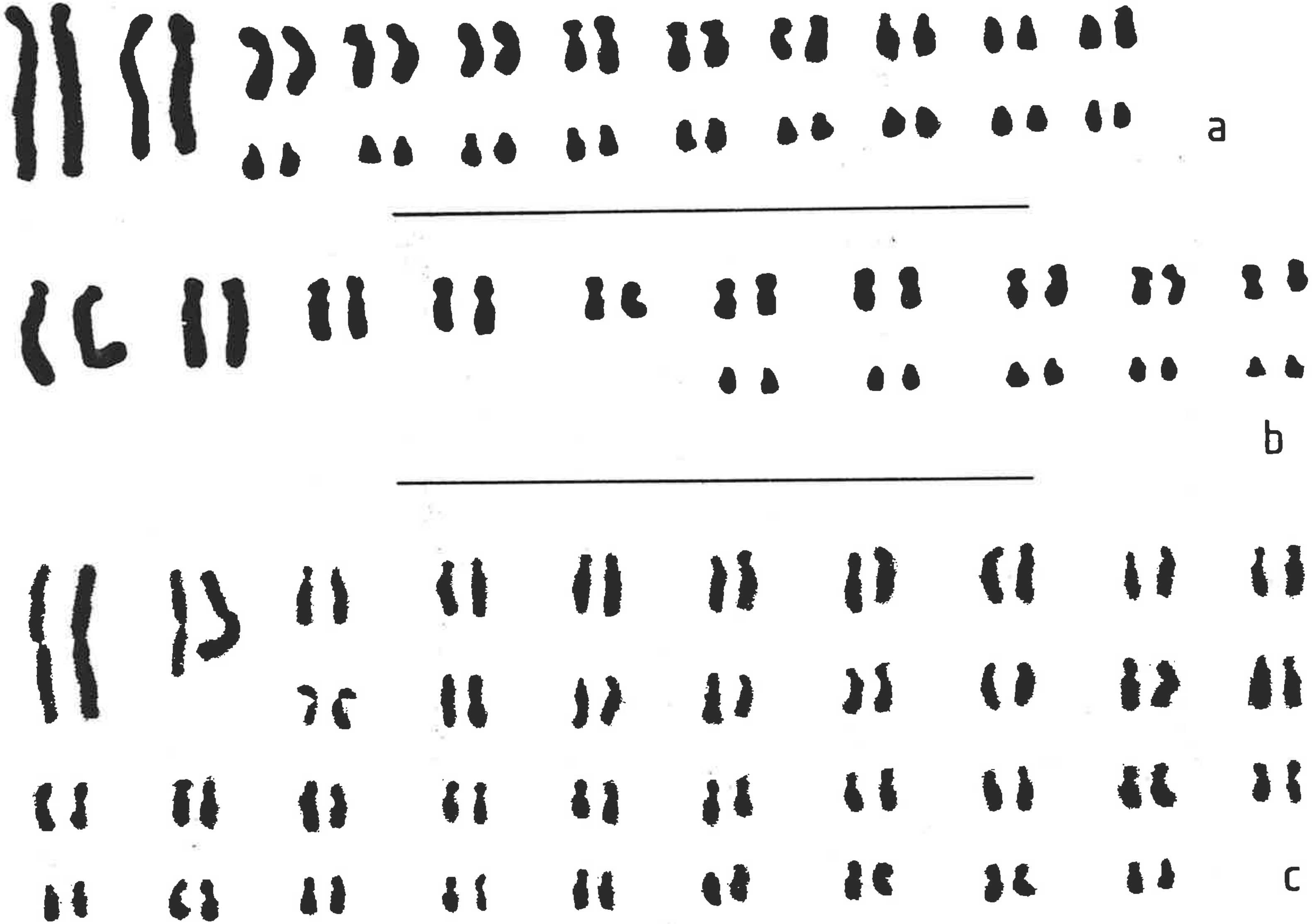

a
b
c

Figure 111a-c. Karyograms of:

(a) Myrmecia vindex Smith, from Kalbarri, W.A. [463], 2n =47, N.F. = 76 [boxed chromosomes are unpaired due to a Robertsonian rearrangement];

(b) Myrmecia vindex Smith, from Le Grand Beach, W.A. [417], 2n = 52, N.F. = 76; and

(c) Myrmecia vindex Smith, from New Norcia, W.A. [465], 2n = 58, N.F. = 78.

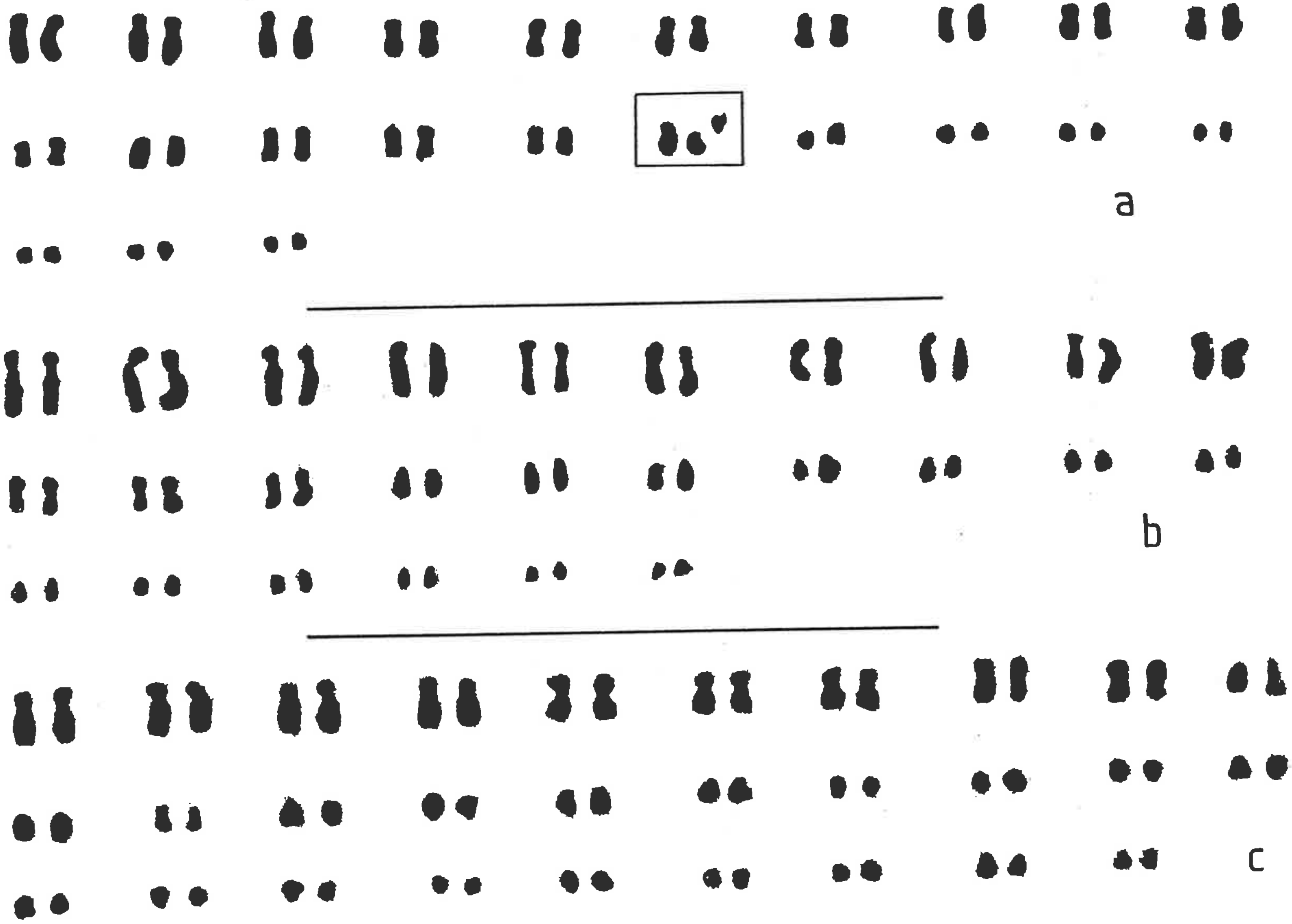

a
b
c

Figure 112a-c. Karyograms of:

(a) Myrmecia sp.14 (ANIC), from 2 km S of Margaret River, W.A. [218], 2n = 56, N.F. = 76;

(b) Myrmecia sp.14 (ANIC), from 48 km SE of Pinjarra, W.A. [202], n = 31, N.F. = 76; and

(c) Myrmecia sp.16 (ANIC), from Four Mile Beach, W.A. [432], 2n = 67, N.F. = 76 [boxed chromosomes are unpaired due to a Robertsonian rearrangement].

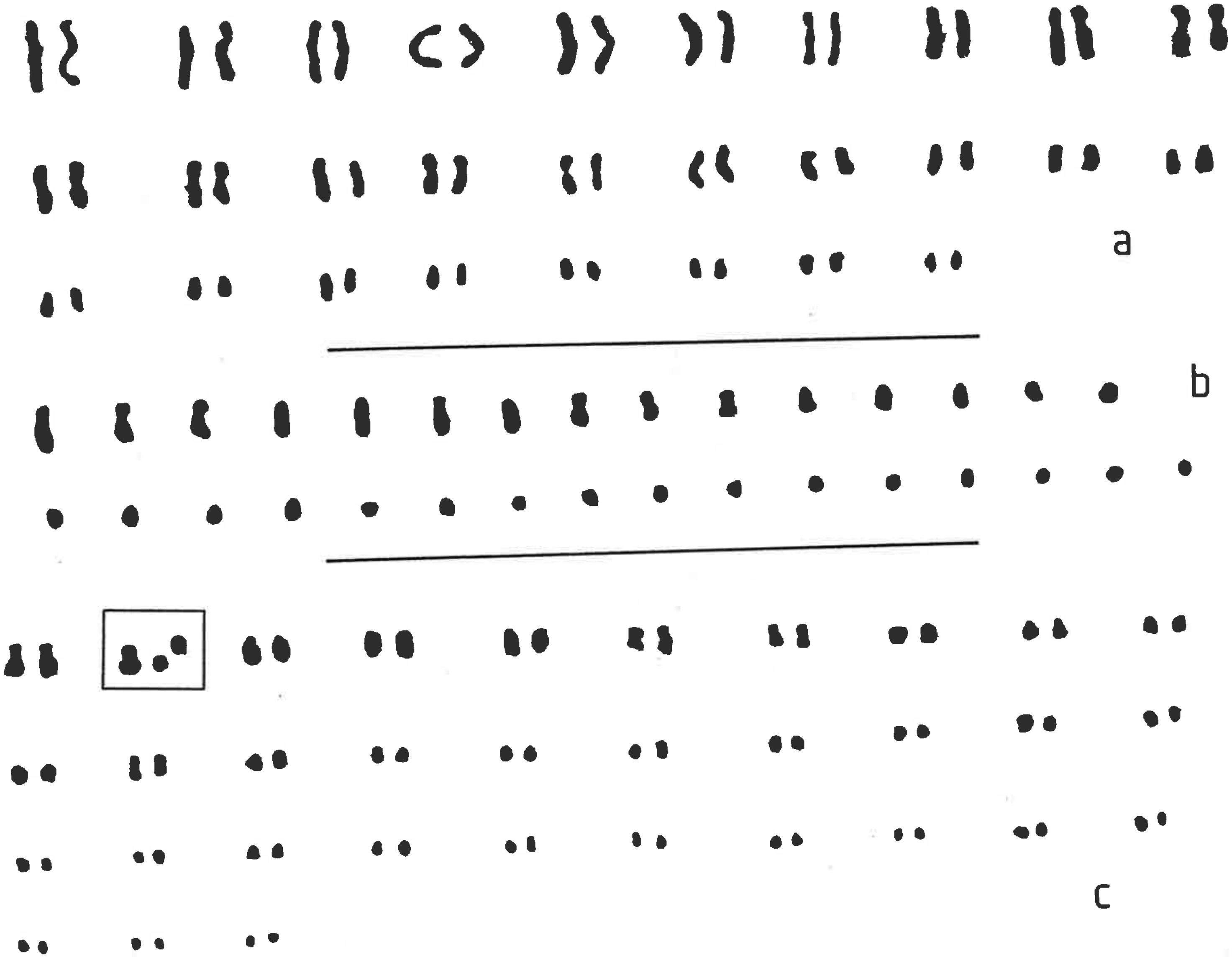
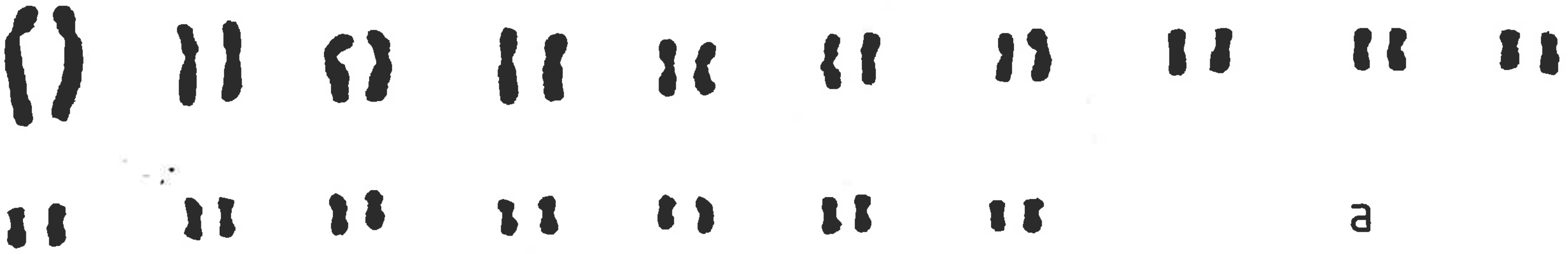

a
b
c

Figure 113a-c. Karyograms of:

(a) Myrmecia sp.17 (ANIC) from 5 km NE of Bacchus Marsh, Vic. [493], 2n = 34, N.F. = 68;

(b) Myrmecia pilosula Smith, s.l., from Western River C.P., S.A. [503], 2n = 16, N.F. = 19 [boxed chromosomes are unpaired due to a complex translocation involving six chromosomes; open circle indicates chromosome pair which has undergone pericentric inversion]; and

(c) Myrmecia pilosula Smith, s.l., from Rocky River H.S., S.A. [324], 2n = 24, N.F. = 32 [boxed chromosomes are unpaired due to a complex translocation involving six chromosomes; open circle indicates chromosome pair which has undergone pericentric inversion].


a

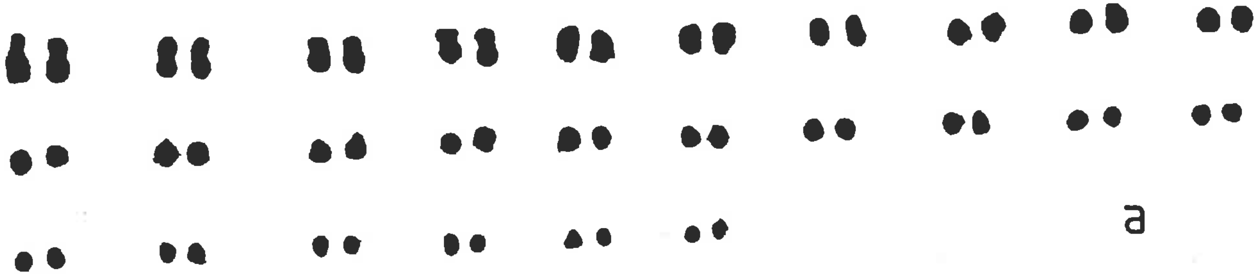

b


c

Figure 114a-b. Karyograms of:

(a) Myrmecia swalei Crawley, from 5 km N of Fishery Bay, S.A. [297], 2n = 52, N.F. = 60; and

(b) Myrmecia tepperi Emery from Inneston, S.A. [271], 2n = 70, N.F. = 70.



a

b

Figure 115a-d. Idiograms of:

(a) *Myrmecia forceps* Roger, from Brownlow, S.A. [140], 2n = 62, N.F. = 62;

(b) *Myrmecia pyriformis* Smith, from 4 km NW of Ararat, Vic. [495], 2n = 82, N.F. = 82;

(c) *Myrmecia arnoldi* Clark, from Jerramungup, W.A. [437], 2n = 14, N.F. = 26; and

(d) *Myrmecia rufinodis* Smith, from Marion Bay, S.A. [269], 2n = 10, N.F. = 18.

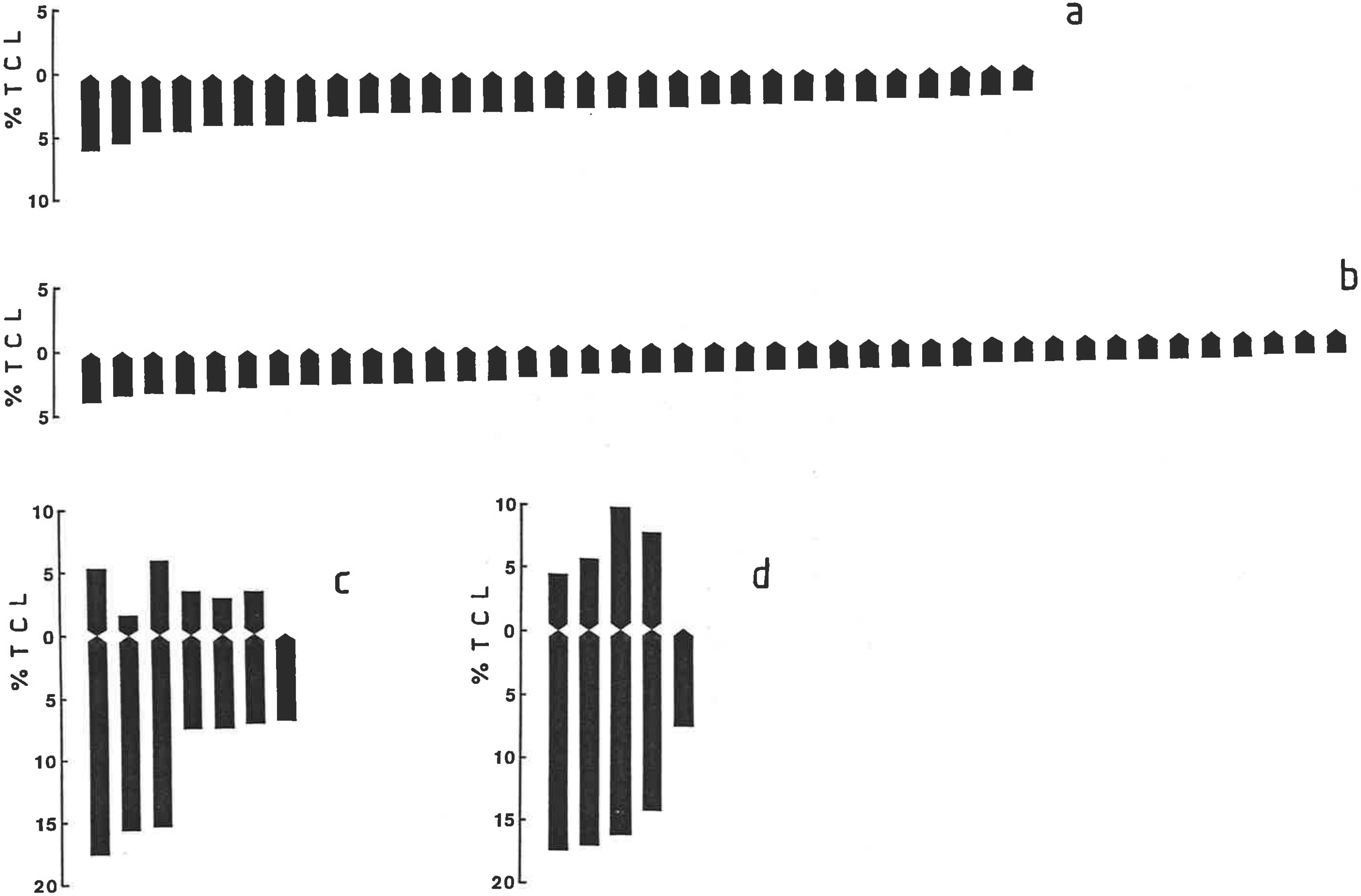

a
% T C L
5
0
5
10
b
% T C L
5
0
5
c
% T C L
10
5
0
5
10
15
20
d
% T C L
10
5
0
5
10
15
20

Figure 116a-c. Idiograms of:

(a) *Myrmecia atrata* Clark, from Ravensthorpe, W.A. [240], 2n = 76, N.F. = 77 [karyotype contains a Robertsonian rearrangement and a chromosome deletion - represented by metacentric beneath rest of complement and open circle respectively];

(b) *Myrmecia atrata* Clark, from Jerramungup, W.A. [227], n = 39, N.F. = 78; and

(c) *Myrmecia fulgida* Clark, from South Ironcap, W.A. [431], 2n = 40, N.F. = 78.

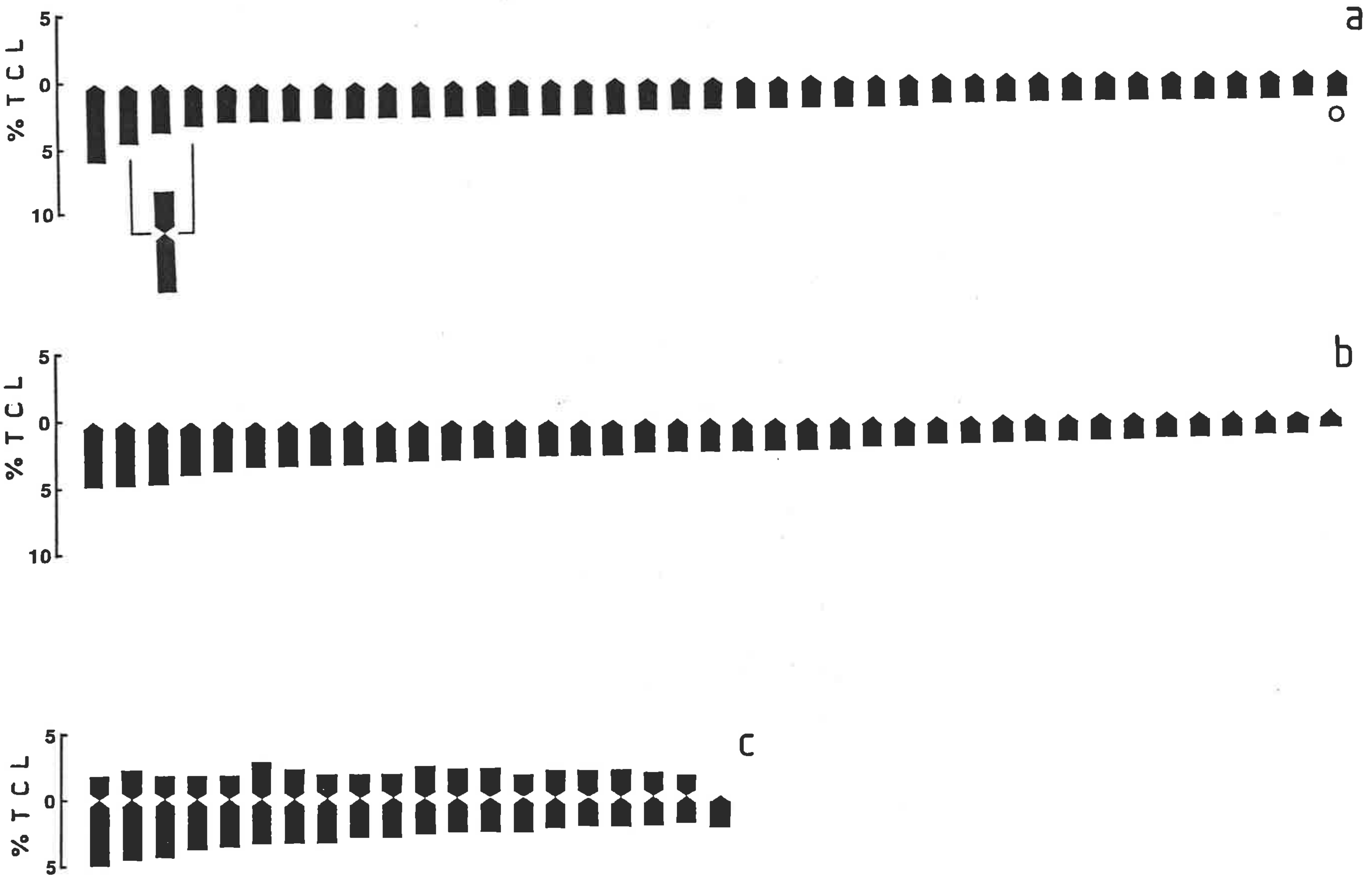

a
% T C L
5
0
5
10
o
b
% T C L
5
0
5
10
c
% T C L
5
0
5

Figure 117a-c. Idiograms of:

(a) Myrmecia fuscipes Clark, from Port Parham, S.A. [156, 159], 2n = 75,76, N.F. = 76 [karyotype includes a Robertsonian rearrangement - represented by metacentric beneath rest of complement];

(b) Myrmecia fuscipes Clark, from 2 km S of Peak Charles, W.A. [430], 2n = 76, N.F. = 78; and

(c) Myrmecia fuscipes Clark, from 46 km N of Renmark, S.A. [247], n = 37, N.F. = 80.

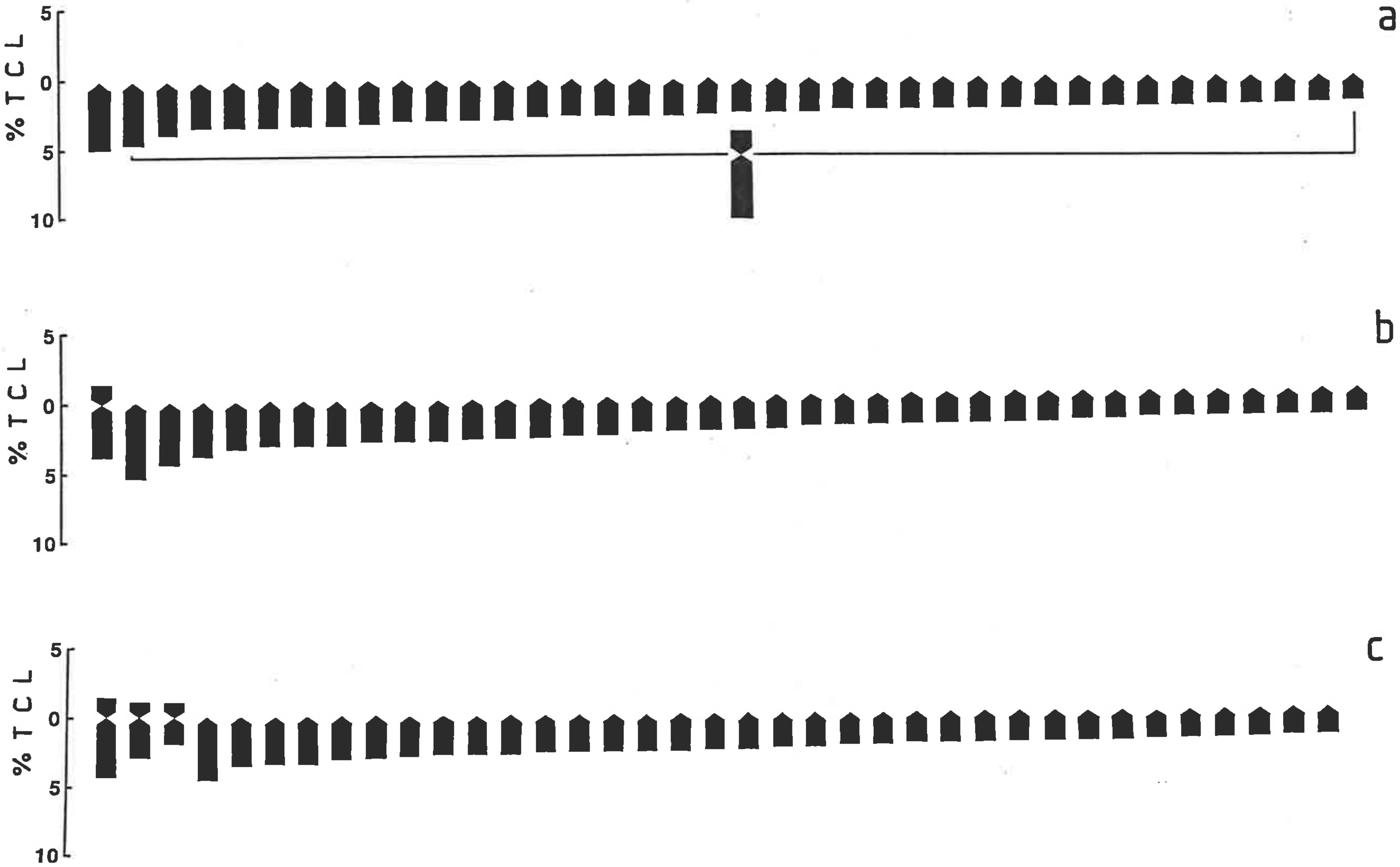

a
b
c
% T C L
5
0
5
10

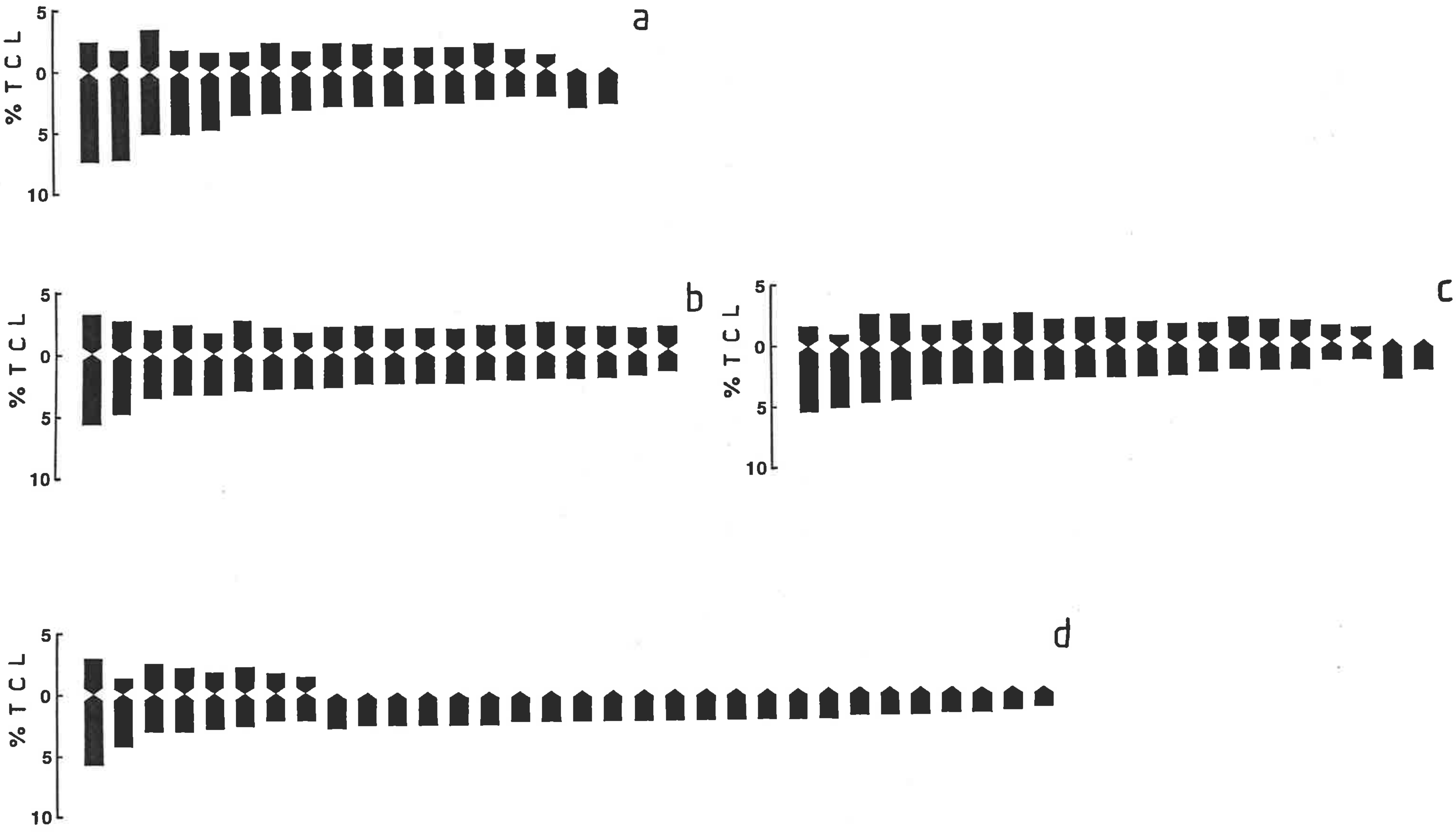
Figure 118a-d. Idiograms of:

(a) Myrmecia sp.11 (ANIC), from Elliston, S.A. [171], 2n = 36, N.F. = 68;

(b) Myrmecia sp.13 (ANIC), from Devlin Pound, S.A. [412], 2n = 40, N.F. = 80;

(c) Myrmecia sp.13 (ANIC), from 12 km SW of Olympic Dam, S.A. [279], n = 21, N.F. = 80; and

(d) Myrmecia desertorum Wheeler, from Todmorden, S.A. [147], n = 32, N.F. = 80.



a
5
0
5
10
% T C L
b
5
0
5
10
% T C L
c
5
0
5
10
% T C L
d
5
0
5
10
% T C L

Figure 119a-c. Idiograms of:

(a) Myrmecia nigriceps Mayr, s.s., from 5 km W of Wagin, W.A. [451], 2n = 70, N.F. = 80;

(b) Myrmecia nigriceps Mayr, s.s., from 4 km W of Wagin, W.A. [453], n = 36, N.F. = 78; and

(c) Myrmecia nigriceps Mayr, s.s., from 4 km W of Wagin, W.A. [453], 2n = 75, N.F. = 78 [karyotype includes a Robertsonian rearrangement - represented by submetacentric beneath rest of complement].

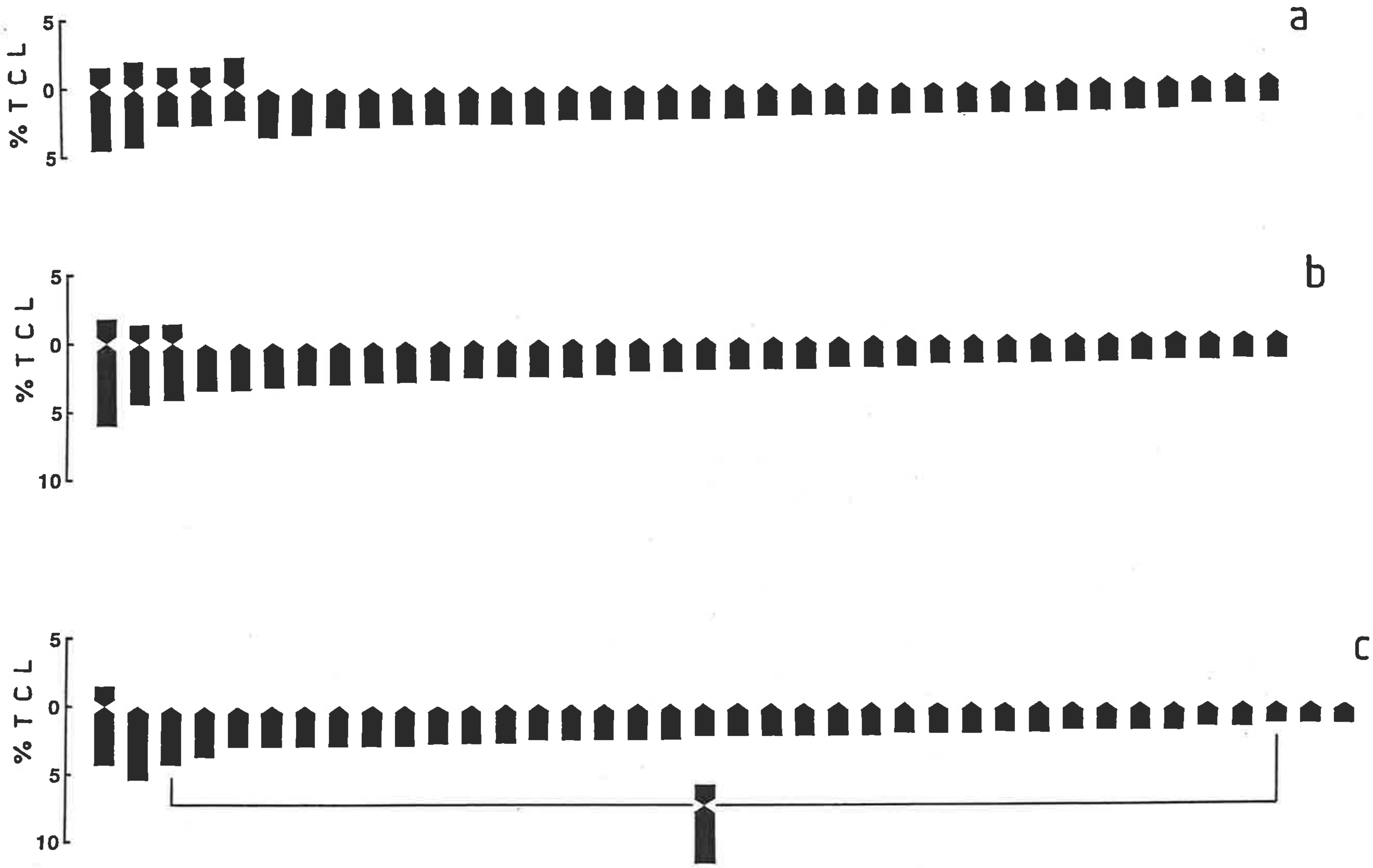

a
5
0
5
% T C L
b
5
0
5
10
% T C L
c
5
0
5
10
% T C L

Figure 120a-c. Idiograms of:

(a) *Myrmecia nigriceps* Mayr, *s.s.*, from Hines Hill, W.A. [466], 2n = 74, N.F. = 78 [karyotype includes two Robertsonian rearrangements - represented by two submetacentrics beneath rest of complement];

(b) *Myrmecia nigriceps* Mayr, *s.s.*, from Ongerup, W.A. [443], 2n = 74, N.F. = 78; and

(c) *Myrmecia nigriceps* Mayr, *s.s.*, from 44 km W of Balladonia, W.A. [470], 2n = 78, N.F. = 80.

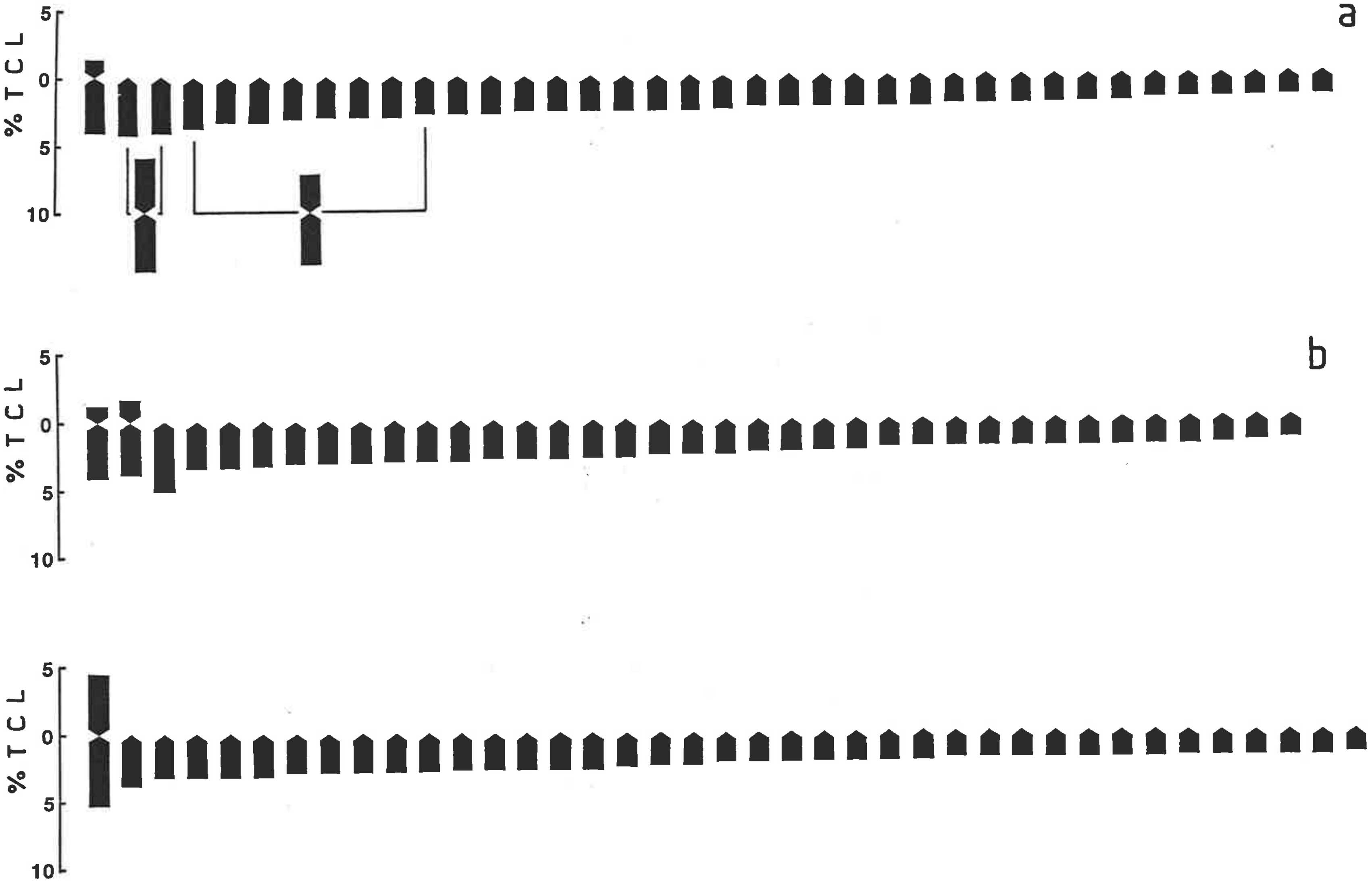
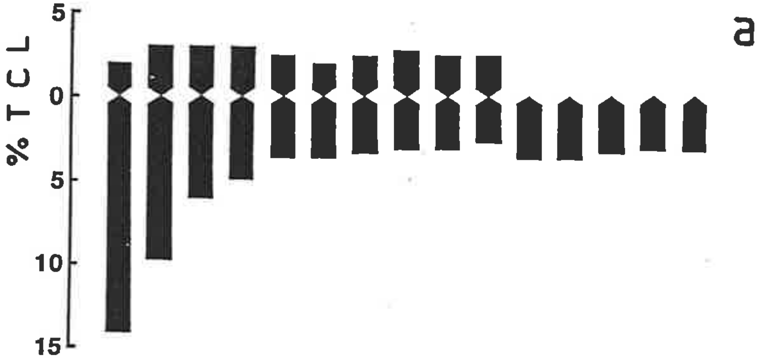

5
0
5
10
% T C L
a
5
0
5
10
% T C L
b
5
0
5
10
% T C L
c

Figure 121a-c. Idiograms of:

(a) *Myrmecia princeps* Clark, from 12 km SW of Olympic Dam, S.A. [487], 2n = 30, N.F. = 50;

(b) *Myrmecia princeps* Clark, from Calperum, S.A. [161], 2n = 40, N.F. = 56; and

(c) *Myrmecia sp.12* (ANIC), from 8 km E of Maitland, S.A. [478], 2n = 74, N.F. = 78.


a
% T C L
5
0
5
10
15


b
% T C L
5
0
5
10
15
20

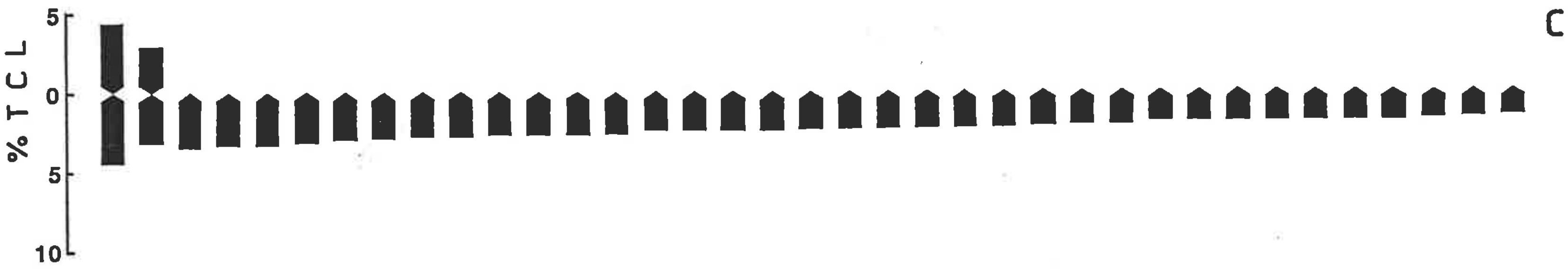

c
% T C L
5
0
5
10

Figure 122a-c. Idiograms of:

(a) Myrmecia vindex Smith, from Kalbarri, W.A. [463], 2n =47, N.F. = 76 [karyotype includes a Robertsonian rearrangement - represented by submetacentric beneath rest of complement];

(b) Myrmecia vindex Smith, from Le Grand Beach, W.A. [417], 2n = 52, N.F. = 76; and

(c) Myrmecia vindex Smith, from New Norcia, W.A. [465], 2n = 58, N.F. = 78.

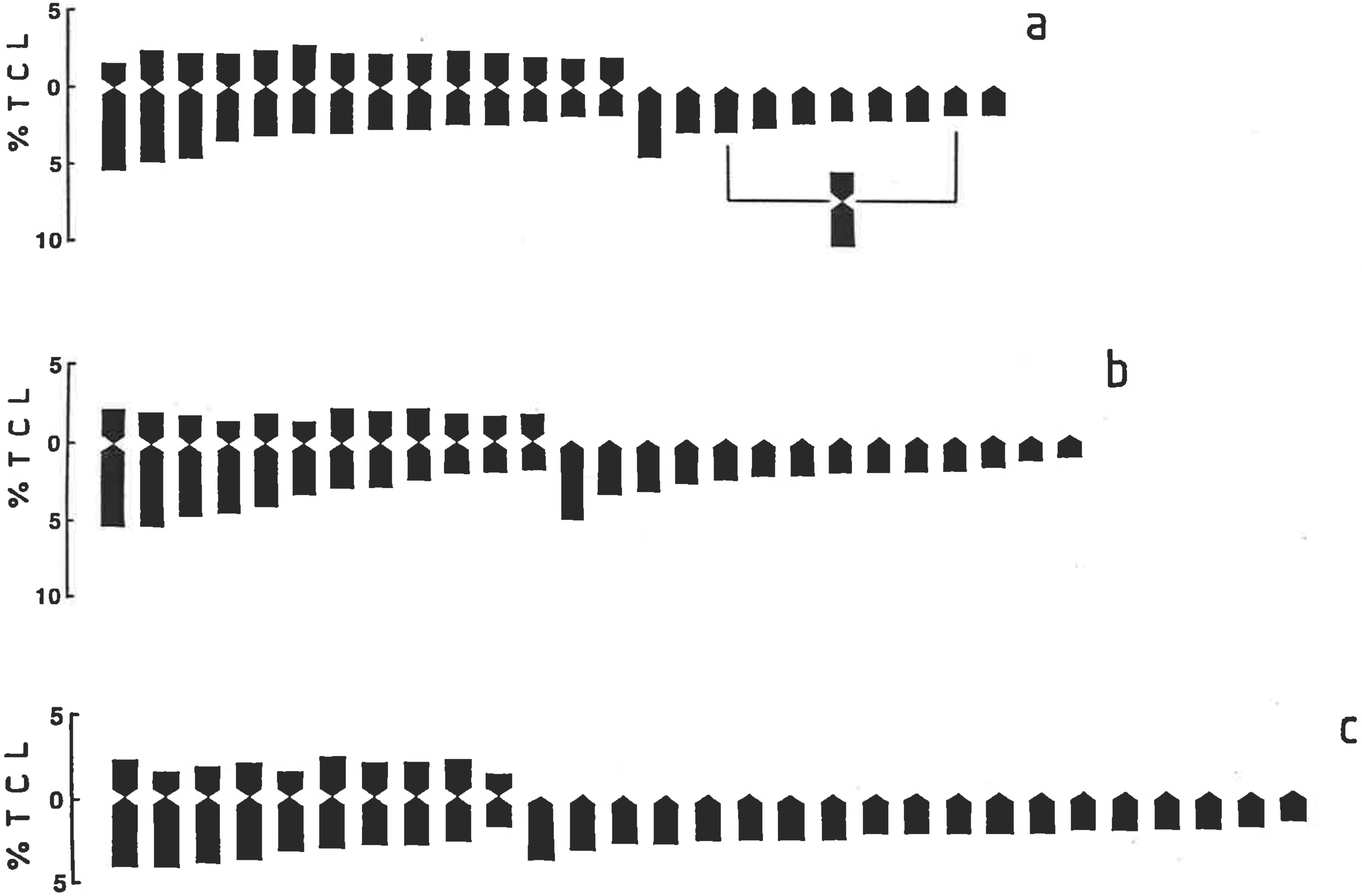

a
% T C L
5
0
5
10
b
% T C L
5
0
5
10
c
% T C L
5
0
5

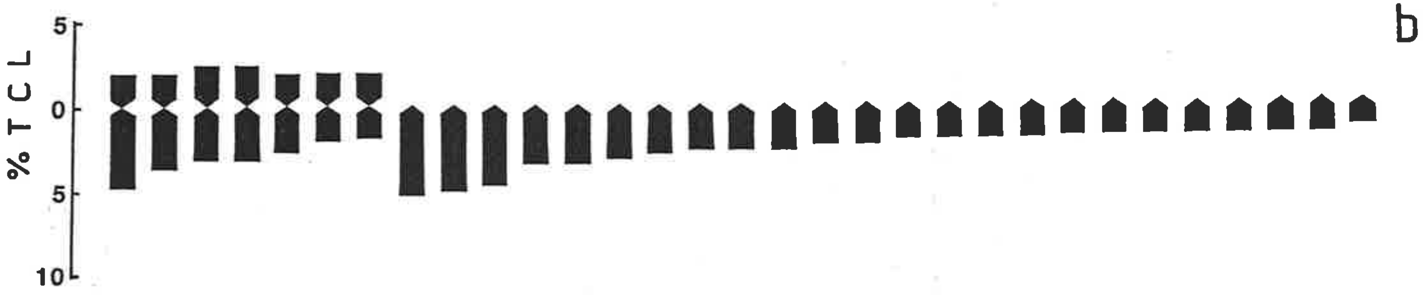
Figure 123a-c. Idiograms of:

(a) Myrmecia sp.14 (ANIC), from 2 km S of Margaret River, W.A. [218], 2n = 56, N.F. = 76;

(b) Myrmecia sp.14 (ANIC), from 48 km SE of Pinjarra, W.A. [202], n = 31, N.F. = 76; and

(c) Myrmecia sp.16 (ANIC), from Four Mile Beach, W.A. [432], 2n = 67, N.F. = 76 [karyotype includes a Robertsonian rearrangement - represented by metacentric beneath rest of complement].


a
% T C L
5
0
5
10


b
% T C L
5
0
5
10

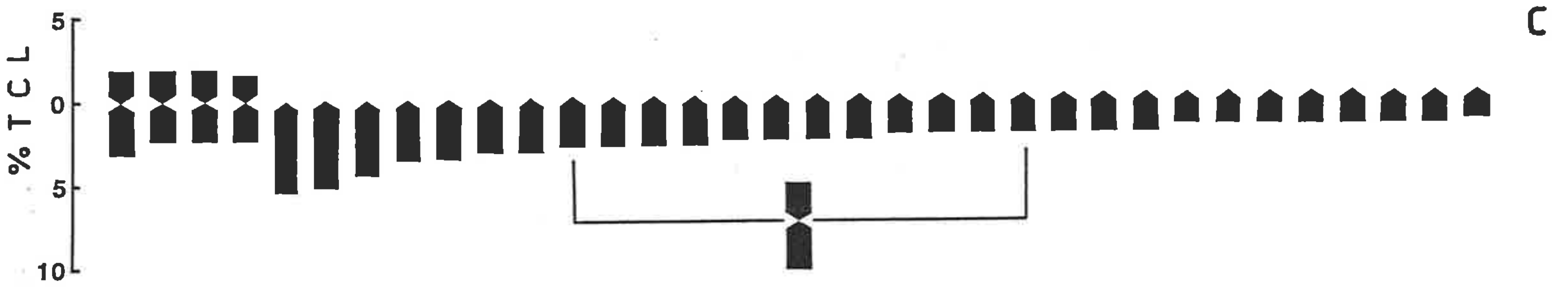
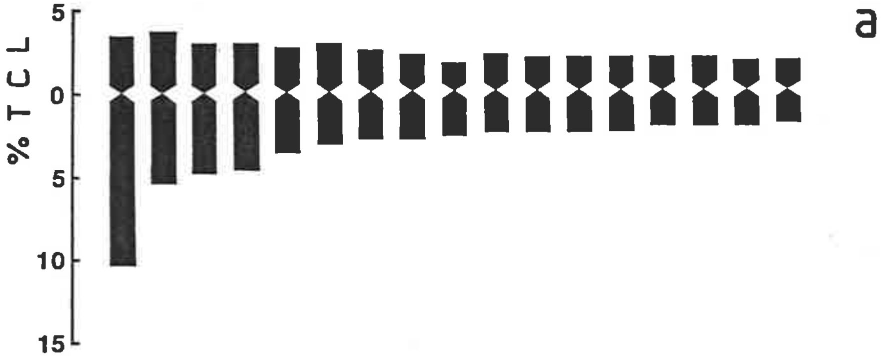

c
% T C L
5
0
5
10

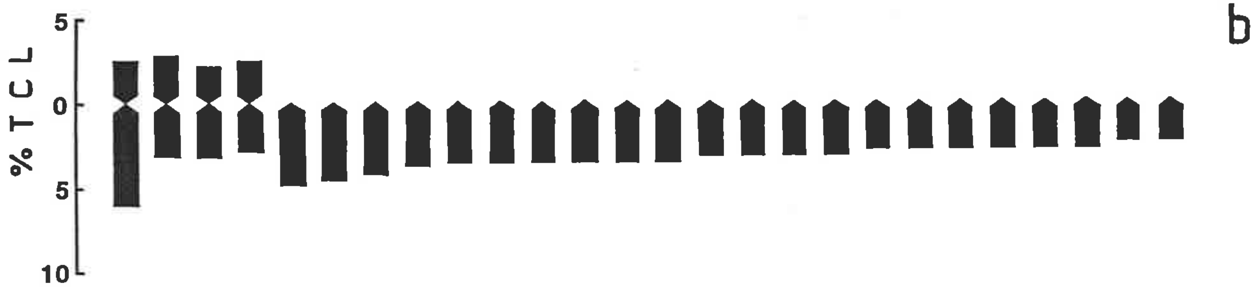
Figure 124a-c. Idiograms of:

(a) Myrmecia sp.17 (ANIC) from 5 km NE of Bacchus Marsh, Vic. [493], 2n = 34, N.F. = 68;

(b) Myrmecia swalei Crawley, from 5 km N of Fishery Bay, S.A. [297], 2n = 52, N.F. = 60; and

(c) Myrmecia tepperi Emery from Inneston, S.A. [271], 2n = 70, N.F. = 70.


a
% T C L
5
0
5
10
15


b
% T C L
5
0
5
10

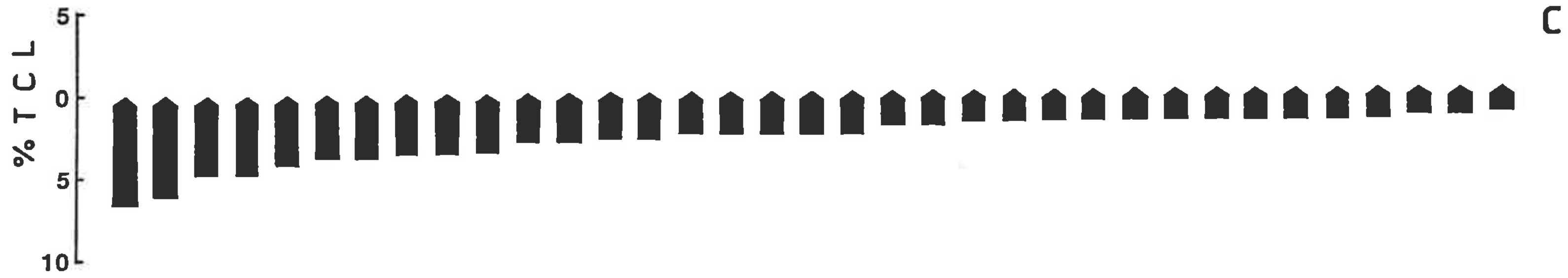

c
% T C L
5
0
5
10

Figure 125a-d. Idiograms of:

(a) Myrmecia pilosula Smith, s.l., from Leumeah, N.S.W., 2n = 10 = 2SM + 6ST + 2A, N.F. = 18 [from karyogram of Imai et al., 1977];

(b) Myrmecia pilosula Smith, s.l., from Leumeah, N.S.W., 2n = 10 = 1M + 2SM + 5ST + 2A, N.F. = 18 [from karyogram of Imai et al., 1977];

(c) Myrmecia pilosula Smith, s.l, from Western River C.P., S.A. [503], 2n = 16, N.F. = 19; and

(d) Myrmecia pilosula Smith, s.l. from Rocky River H.S., S.A. [324], 2n = 24, N.F. = 32.

[Note: These idiograms include all chromosomes from the diploid karyotypes instead of haploid complements as are represented in the previous figures; open circles indicate chromosomes involved in complex translocation; open triangles indicate chromosomes involved in pericentric inversion].

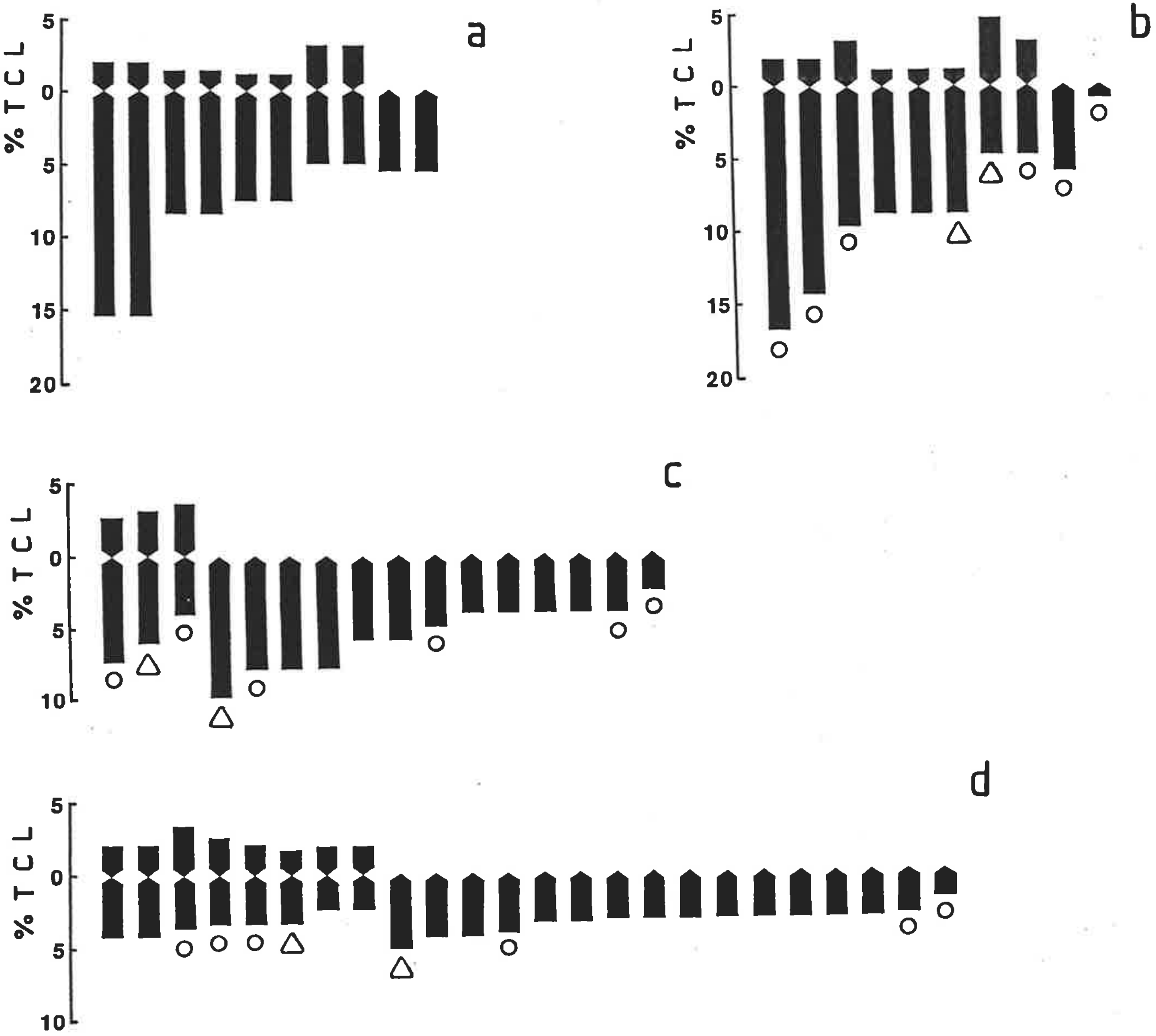
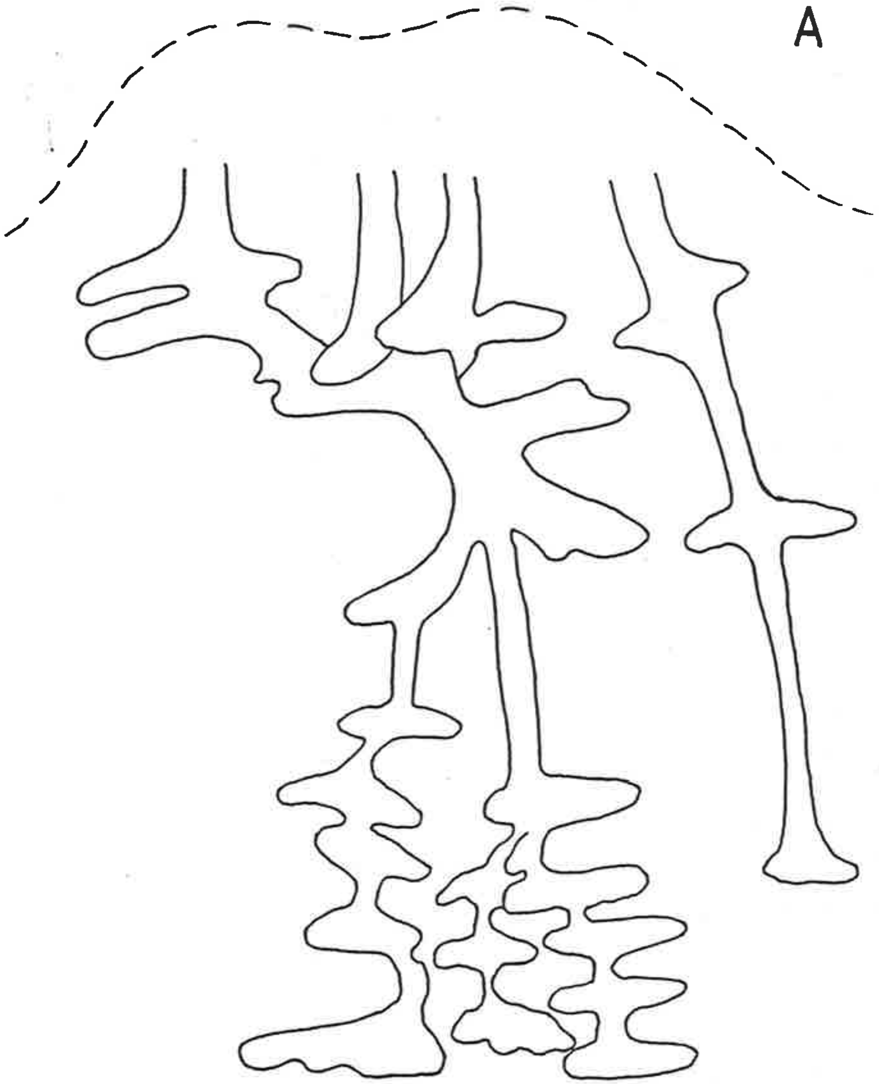
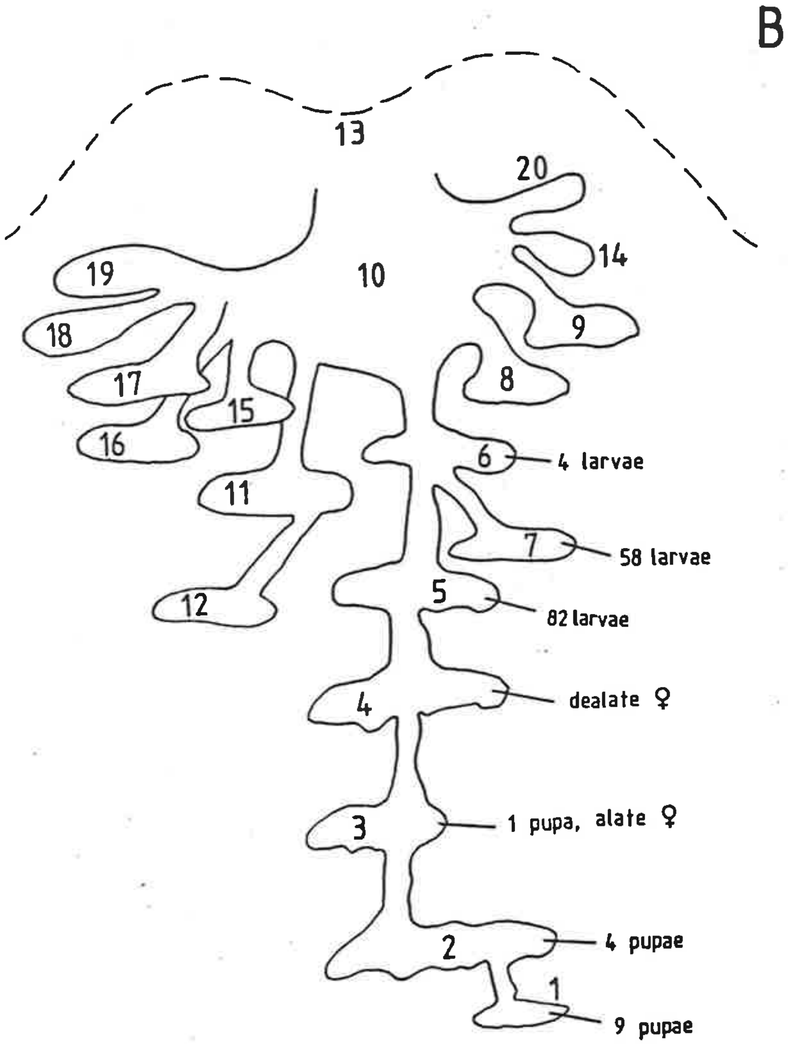

a
b
c
d
% T C L
5
0
5
10
15
20

Figure 126. Sketches of casts from nests A and B in colony 146. The details at the top of the cast are unclear because the mound consists largely of loosely packed twigs and leaves. Consequently, the dashed line at the top only shows the approximate shape of the mound. The chambers in nest B have been numbered as in Table 9.

A



B



13
20
19
10
14
18
9
17
8
15
16
6
4 larvae
11
7
58 larvae
12
5
82 larvae
4
dealate ♀
3
1 pupa, alate ♀
2
4 pupae
1
9 pupae

Figure 127a-d. Scattergrams for colony 146:

(a) mandible length (ML) and head length (HL) [N = 451, ML = -0.67 + 1.27 HL];

(b) log of mandible length (logML) and log of head length (logHL) [N = 451, logML = -0.08 + 1.21 logHL, ML = 0.83 HL $^{1.21}$];

(c) mandible length (ML) and head width (HW) [N = 449, ML = -0.42 + 1.12 HW]; and

(d) log of mandible length (logML) and log of head width (logHW) [N = 449, logML = -0.07 + 1.13 logHW, ML = 0.85 HW $^{1.13}$].

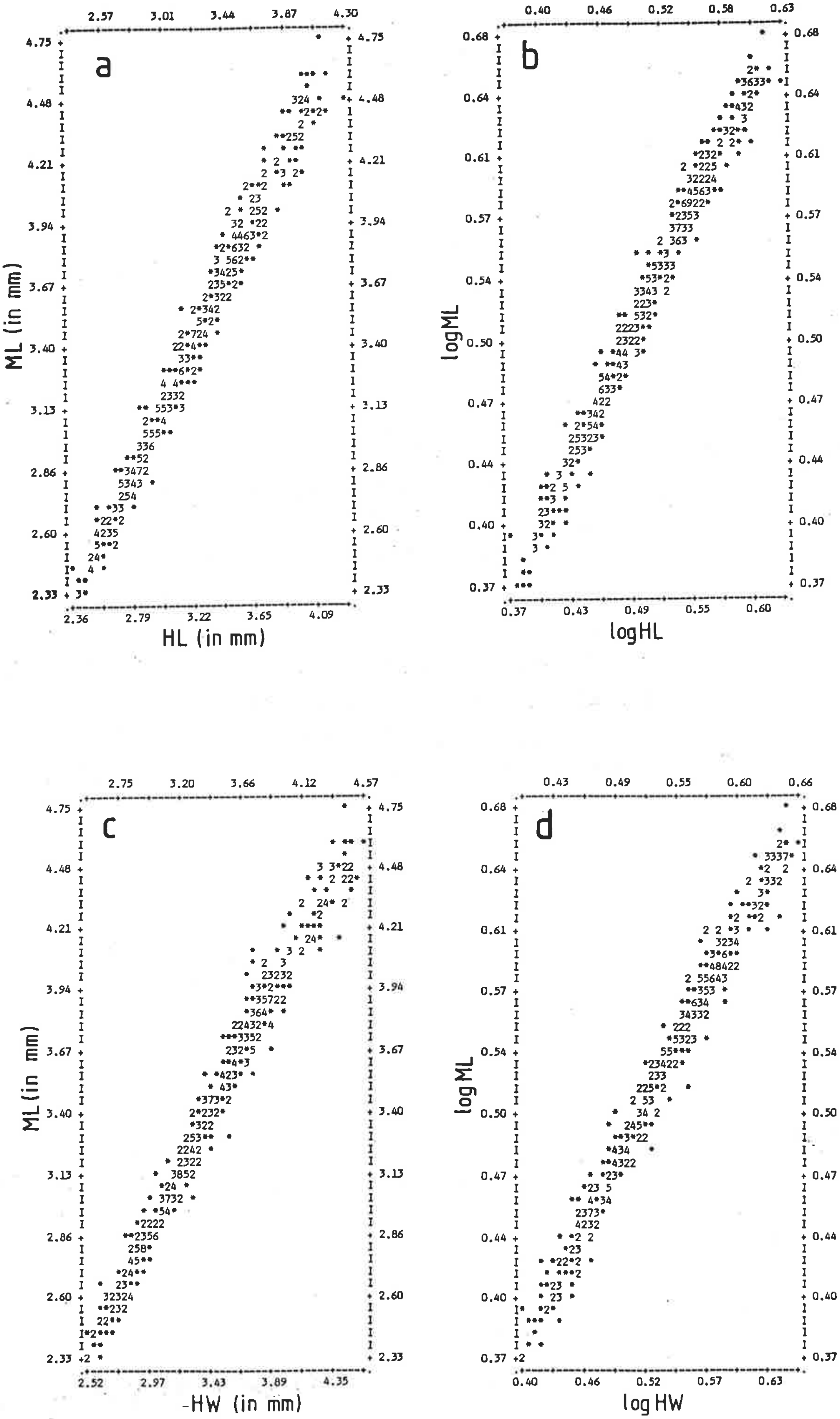

a
ML (in mm)
HL (in mm)
2.57 3.01 3.44 3.87 4.30
4.75 4.48 4.21 3.94 3.67 3.40 3.13 2.86 2.60 2.33
2.36 2.79 3.22 3.65 4.09
b
logML
logHL
0.40 0.46 0.52 0.58 0.63
0.68 0.64 0.61 0.57 0.54 0.50 0.47 0.44 0.40 0.37
0.37 0.43 0.49 0.55 0.60
c
ML (in mm)
HW (in mm)
2.75 3.20 3.66 4.12 4.57
4.75 4.48 4.21 3.94 3.67 3.40 3.13 2.86 2.60 2.33
2.52 2.97 3.43 3.89 4.35
d
logML
log HW
0.43 0.49 0.55 0.60 0.66
0.68 0.64 0.61 0.57 0.54 0.50 0.47 0.44 0.40 0.37
0.40 0.46 0.52 0.57 0.63

Figure 128a-d. Scattergrams for colony 146:

(a) mandible length (ML) and pronotum width (PW) [N = 448, ML = -0.06 + 1.78 PW];

(b) log of mandible length (logML) and log of pronotum width (logPW) [N = 448, logML = 0.23 + 1.04 logPW, ML = 1.70 PW $^{1.04}$];

(c) head length (HL) and head width (HW) [N = 450, HL = 0.21 + 0.88 HW]; and

(d) log of head length (logHL) and log of head width (logHW) [N = 450, logHL = 0.01 + 0.94 logHW, HL = 1.03 HW $^{0.94}$].

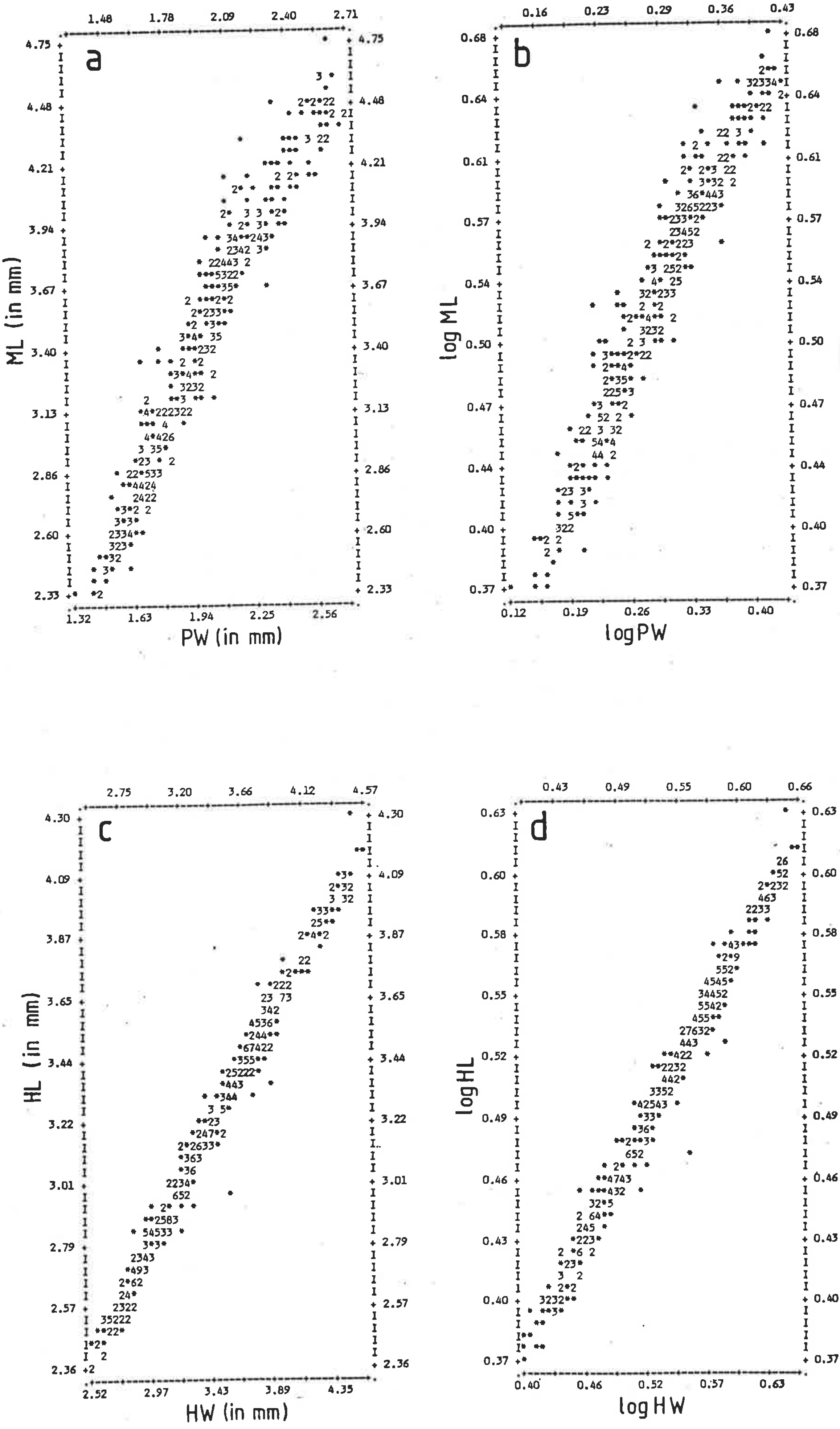

a
ML (in mm)
PW (in mm)
1.48 1.78 2.09 2.40 2.71
4.75 4.48 4.21 3.94 3.67 3.40 3.13 2.86 2.60 2.33
1.32 1.63 1.94 2.25 2.56
b
log ML
log PW
0.16 0.23 0.29 0.36 0.43
0.68 0.64 0.61 0.57 0.54 0.50 0.47 0.44 0.40 0.37
0.12 0.19 0.26 0.33 0.40
c
HL (in mm)
HW (in mm)
2.75 3.20 3.66 4.12 4.57
4.30 4.09 3.87 3.65 3.44 3.22 3.01 2.79 2.57 2.36
2.52 2.97 3.43 3.89 4.35
d
log HL
log HW
0.43 0.49 0.55 0.60 0.66
0.63 0.60 0.58 0.55 0.52 0.49 0.46 0.43 0.40 0.37
0.40 0.46 0.52 0.57 0.63

Figure 129a-d. Scattergrams for colony 146:

(a) head length (HL) and pronotum width (PW) [N = 449, HL = 0.50 + 1.38 PW];

(b) log of head length (logHL) and log of pronotum width (logPW) [N = 449, logHL = 0.26 + 0.86 logPW, $HL = 1.82\ PW^{0.86}$];

(c) head width (HW) and pronotum width (PW) [N = 447, HW = 0.34 + 1.58 PW]; and

(d) log of head width (logHW) and log of pronotum width (logPW) [N = 447, logHW = 0.27 + 0.91 logPW, $HW = 1.86\ PW^{0.91}$].

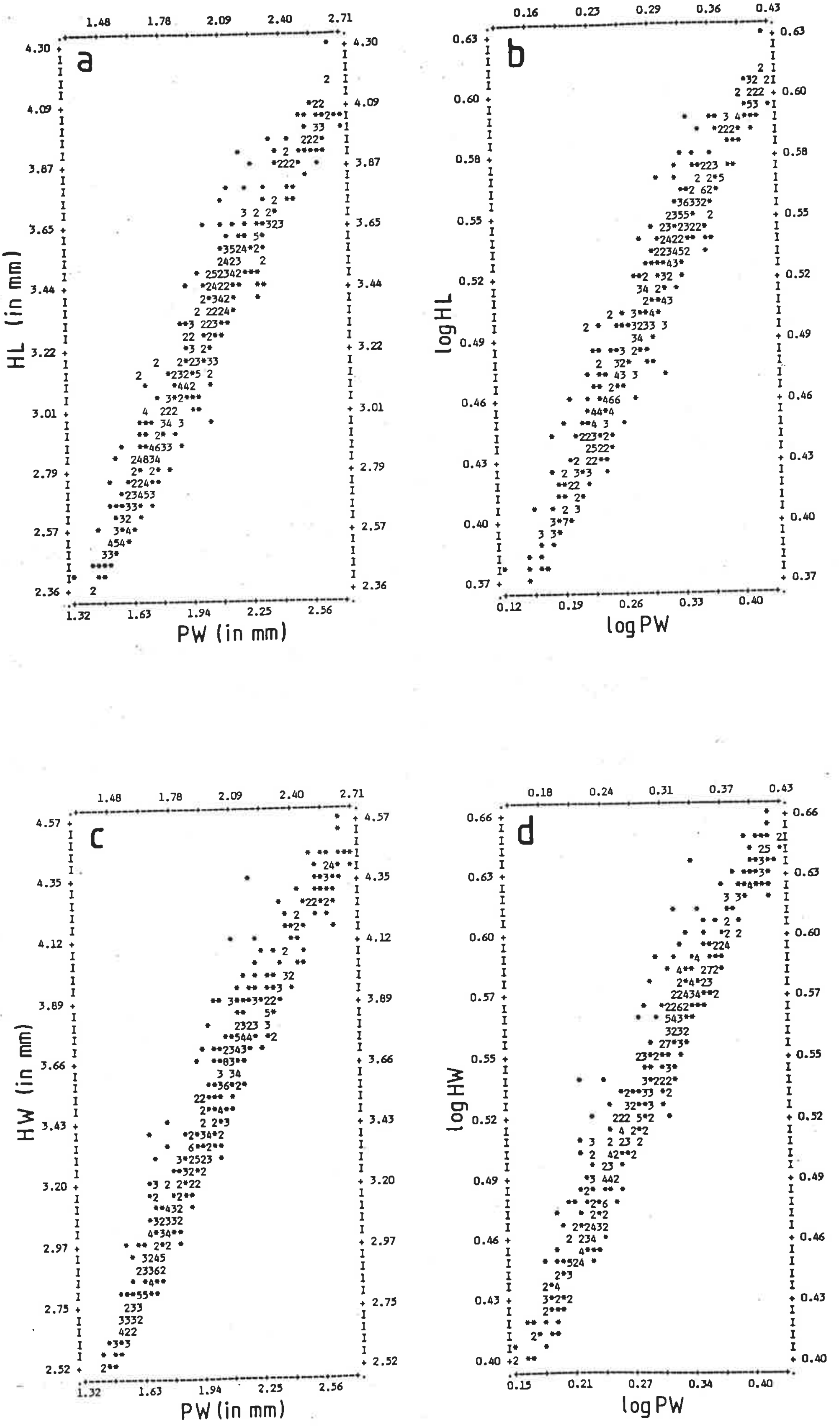

a
HL (in mm)
PW (in mm)
1.48 1.78 2.09 2.40 2.71
4.30 4.09 3.87 3.65 3.44 3.22 3.01 2.79 2.57 2.36
1.32 1.63 1.94 2.25 2.56
b
log HL
log PW
0.16 0.23 0.29 0.36 0.43
0.63 0.60 0.58 0.55 0.52 0.49 0.46 0.43 0.40 0.37
0.12 0.19 0.26 0.33 0.40
c
HW (in mm)
PW (in mm)
1.48 1.78 2.09 2.40 2.71
4.57 4.35 4.12 3.89 3.66 3.43 3.20 2.97 2.75 2.52
1.32 1.63 1.94 2.25 2.56
d
log HW
log PW
0.18 0.24 0.31 0.37 0.43
0.66 0.63 0.60 0.57 0.55 0.52 0.49 0.46 0.43 0.40
0.15 0.21 0.27 0.34 0.40

Figure 130a-d. Size-frequency distributions for colony 146 (0.0125 mm intervals):

(a) mandible length [N = 451, $\bar{x}$ = 3.456, S.D. = 0.576, C.V. = 16.7%];

(b) head length [N = 452, $\bar{x}$ = 3.241, S.D. = 0.449, C.V. = 13.8%];

(c) head width [N = 450, $\bar{x}$ = 3.465, S.D. = 0.506, C.V. = 14.6%]; and

(d) pronotum width [N = 449, $\bar{x}$ = 1.978, S.D. = 0.315, C.V. = 15.9%].

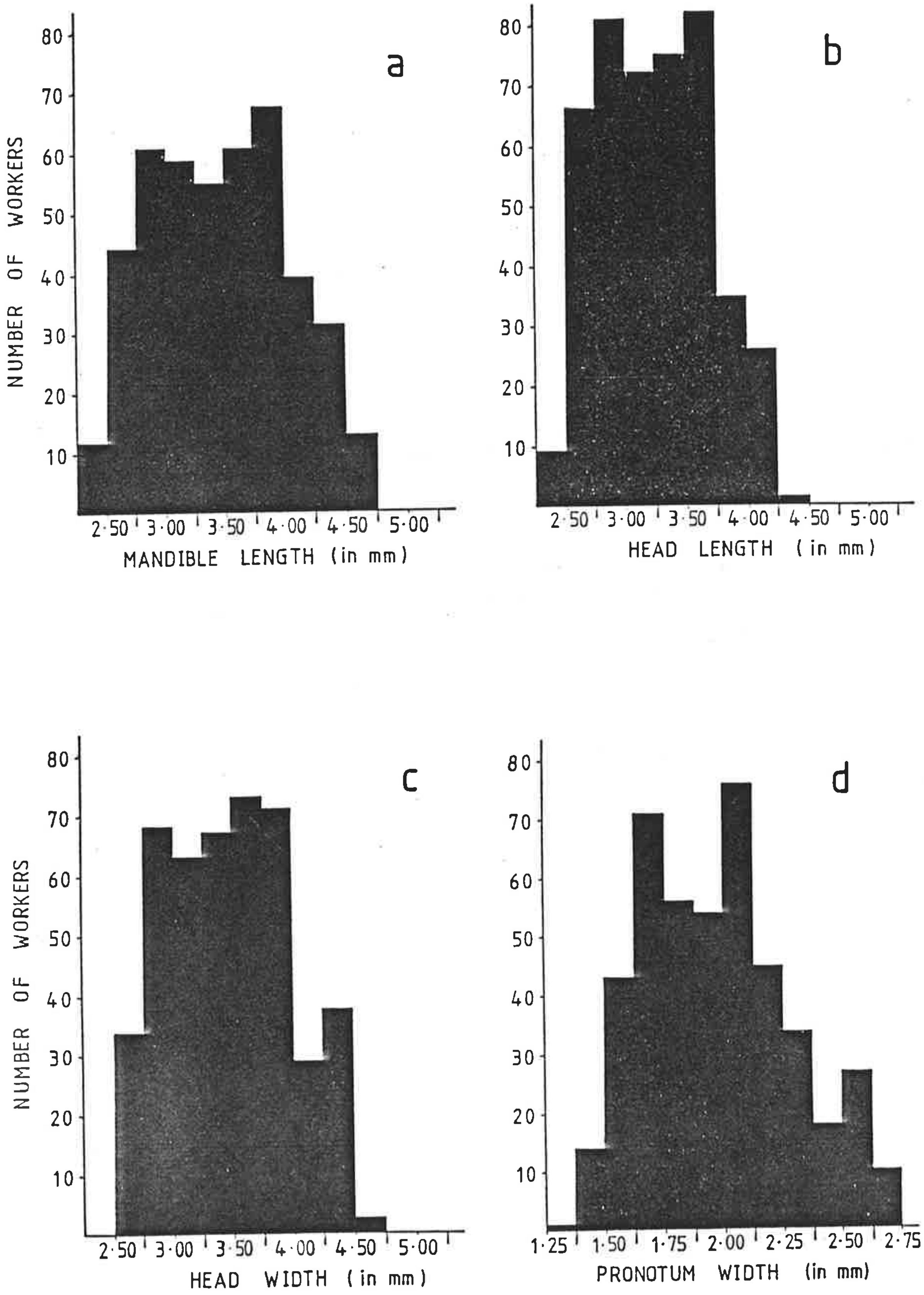

a
NUMBER OF WORKERS
80
70
60
50
40
30
20
10
2·50
3·00
3·50
4·00
4·50
5·00
MANDIBLE LENGTH (in mm)
b
80
70
60
50
40
30
20
10
2·50
3·00
3·50
4·00
4·50
5·00
HEAD LENGTH (in mm)
c
NUMBER OF WORKERS
80
70
60
50
40
30
20
10
2·50
3·00
3·50
4·00
4·50
5·00
HEAD WIDTH (in mm)
d
80
70
60
50
40
30
20
10
1·25
1·50
1·75
2·00
2·25
2·50
2·75
PRONOTUM WIDTH (in mm)

Figure 131a-d. Size-frequency distribution of pronotum width for fuscipes (0.100 mm intervals):

(a) colony 146, from 46 km N of Renmark, S.A. [N = 449, $\bar{x}$ = 1.978, S.D. = 0.315, C.V. = 15.9%];

(b) colony 59, from 46 km N of Renmark, S.A. [N = 533, $\bar{x}$ = 2.132, S.D. = 0.366, C.V. = 17.2%];

(c) Thomas' (1972) colony 21, from Port Parham, S.A. [N = 412, $\bar{x}$ = 1.858, S.D. = 0.282, C.V. = 15.2%]; and

(d) colony 156, from Port Parham, S.A. [N = 209, $\bar{x}$ = 1.749, S.D. = 0.262, C.V. = 15.0%].

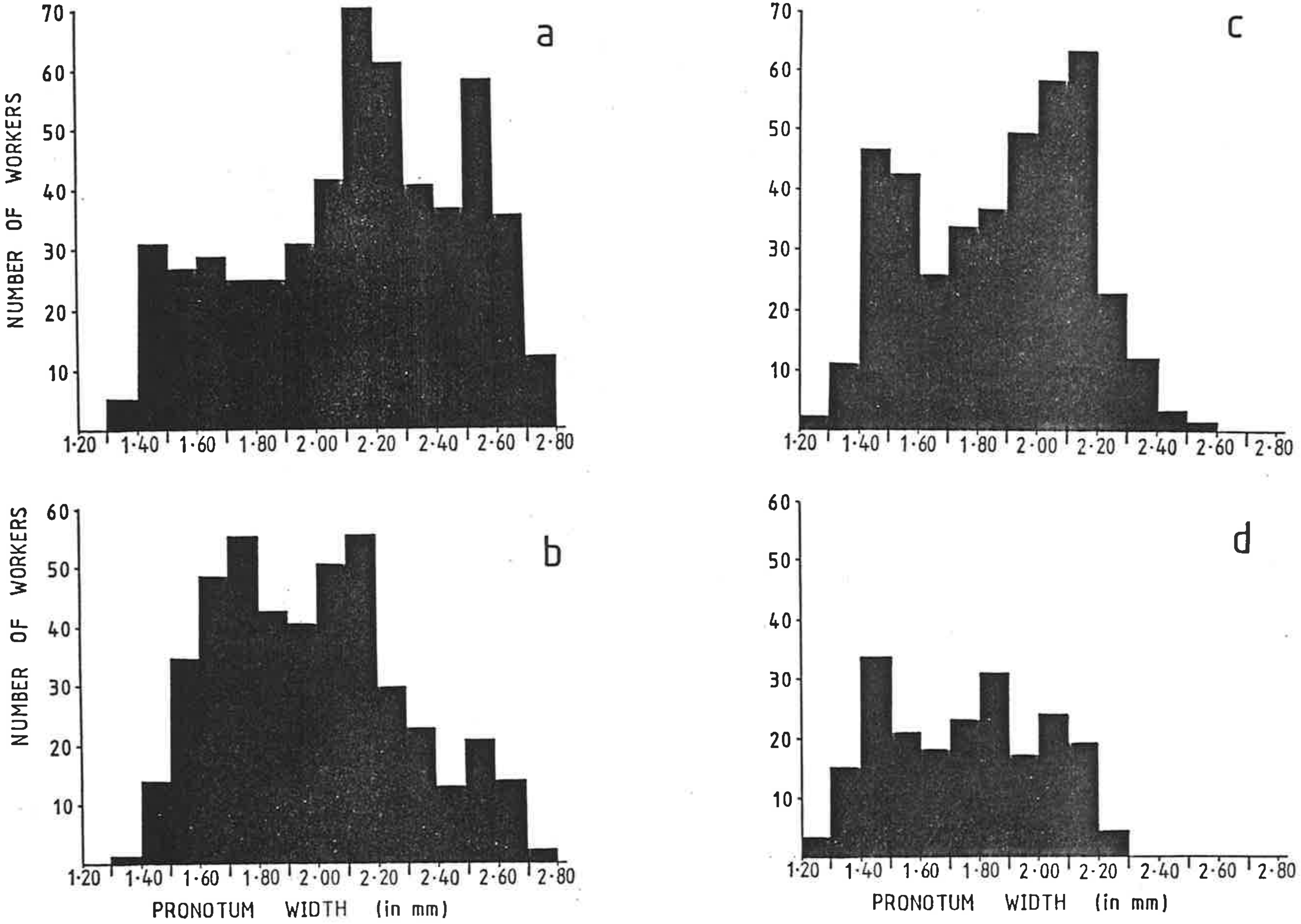

a
b
c
d
NUMBER OF WORKERS
NUMBER OF WORKERS
70
60
50
40
30
20
10
1·20
1·40
1·60
1·80
2·00
2·20
2·40
2·60
2·80
PRONOTUM WIDTH (in mm)
PRONOTUM WIDTH (in mm)

Figure 132a-d. Size-frequency distribution of pronotum width for fuscipes (0.100 mm intervals):

(a) colony 2, from Port Parham, S.A. [N = 132, $\bar{x}$ = 1.923, S.D. = 0.233, C.V. = 12.1%];

(b) colony 3, from Port Parham, S.A. [N = 283, $\bar{x}$ = 1.927, S.D. = 0.298, C.V. = 15.5%];

(c) colony 155, from Port Germein, S.A. [N = 38, $\bar{x}$ = 1.992, S.D. = 0.217, C.V. = 10.9%]; and

(d) colony 131, from Laura Bay C.P., S.A. [N = 188, $\bar{x}$ = 1.981, S.D. = 0.200, C.V. = 10.1%].

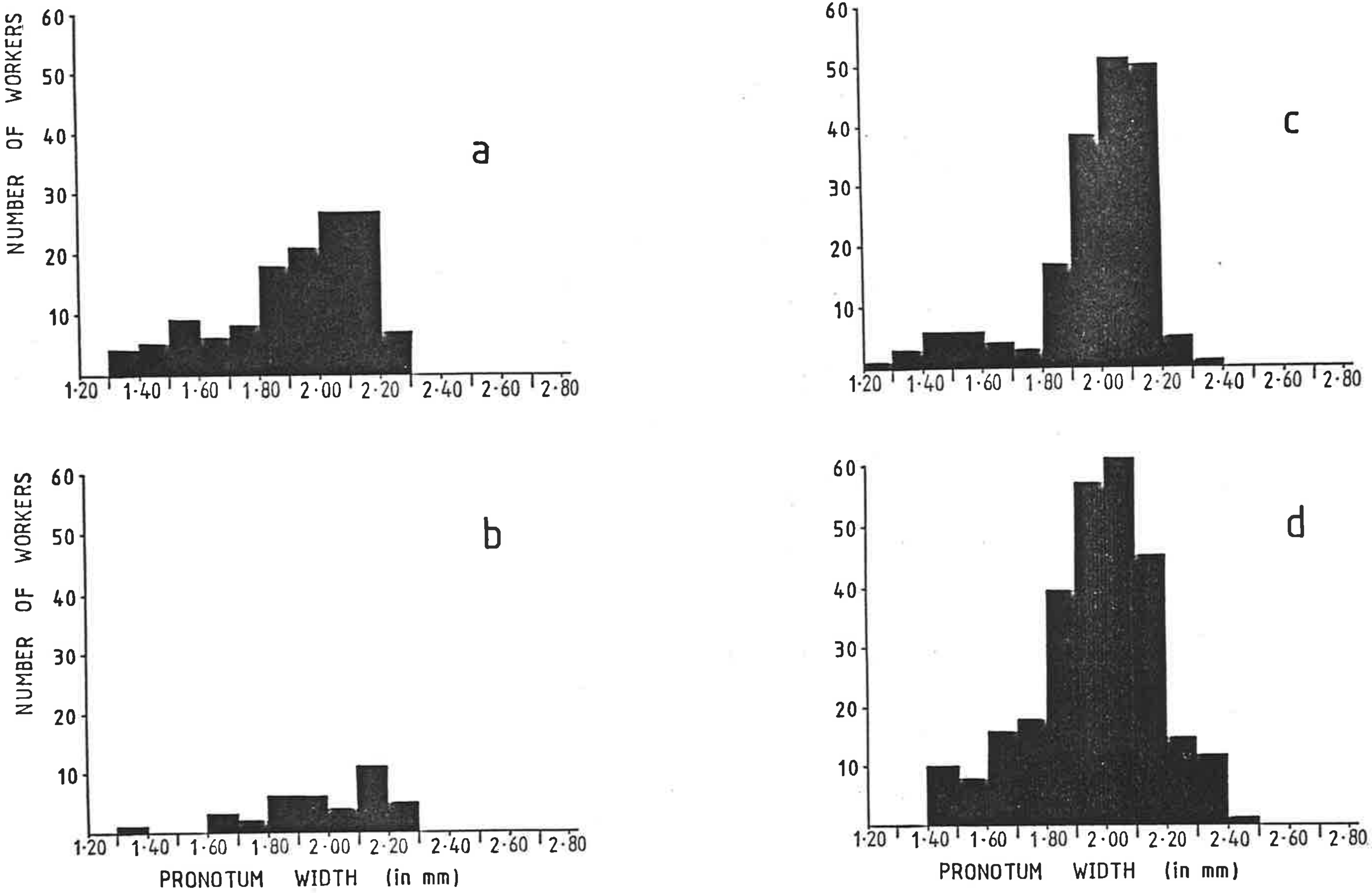

a
b
c
d
NUMBER OF WORKERS
NUMBER OF WORKERS
10
20
30
40
50
60
1·20
1·40
1·60
1·80
2·00
2·20
2·40
2·60
2·80
PRONOTUM WIDTH (in mm)
PRONOTUM WIDTH (in mm)

Figure 133a-d. Size-frequency distribution of pronotum width for fuscipes (0.100 mm intervals):

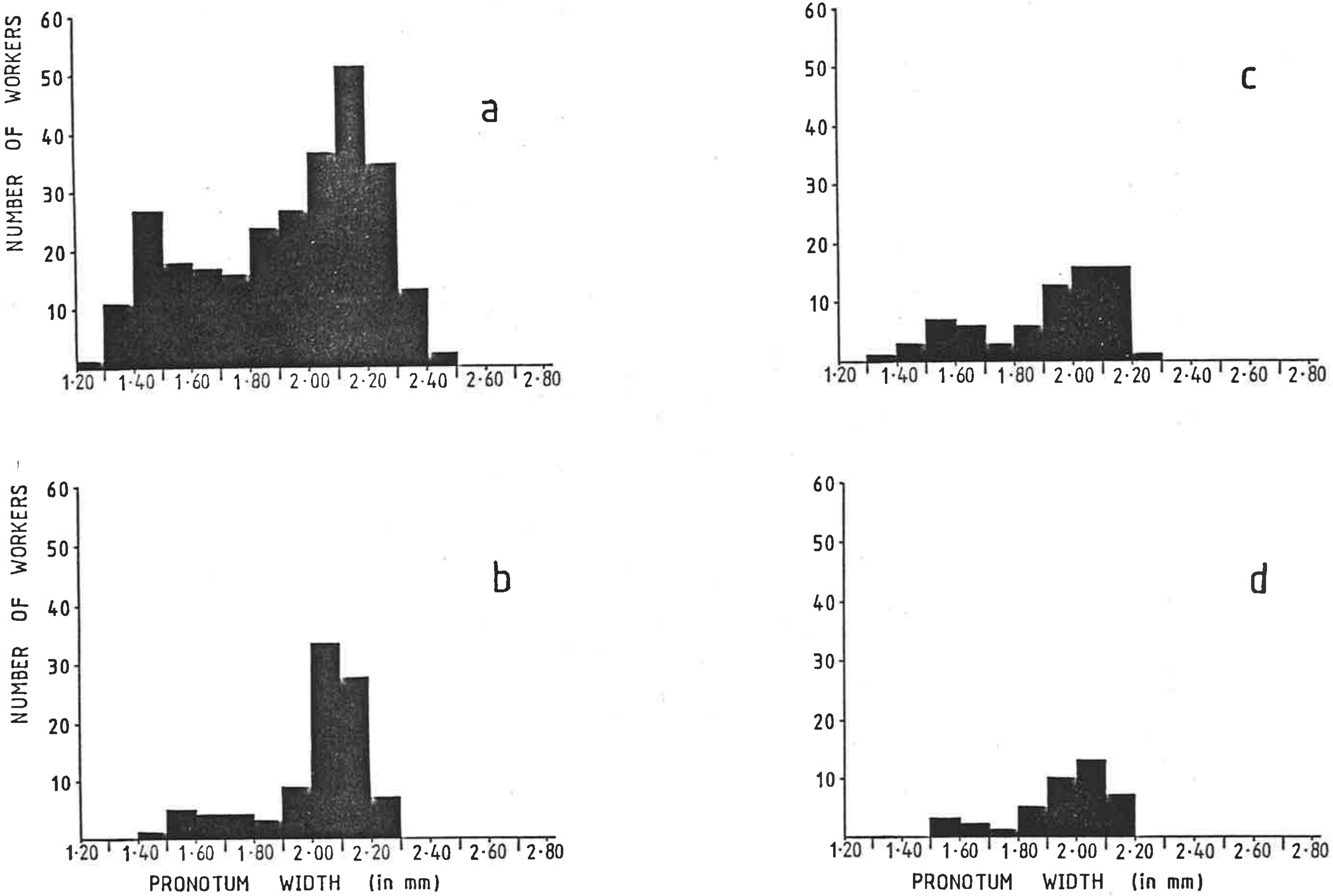
(a) colony 132, from Laura Bay C.P., S.A. [N = 286, $\bar{x}$ = 1.967, S.D. = 0.208, C.V. = 10.6%].

Size-frequency distribution of pronotum width for nigriceps, s.l. (0.100 mm intervals):

(b) colony 10, from Blewitt Springs, S.A. [N = 95, $\bar{x}$ = 2.021, S.D. = 0.186, C.V. = 9.2%];

(c) colony 136, from Blewitt Springs, S.A. [N = 72, $\bar{x}$ = 1.907, S.D. = 0.226, C.V. = 11.9%]; and

(d) colony 160, from Blewitt Springs, S.A. [N = 41, $\bar{x}$ = 1.961, S.D. = 0.164, C.V. = 8.4%].


NUMBER OF WORKERS
60
50
40
30
20
10
a
1·20
1·40
1·60
1·80
2·00
2·20
2·40
2·60
2·80
c
b
d
PRONOTUM WIDTH (in mm)

4. CLADISTIC ANALYSIS

4.1 Introduction

The subgenera and species groups of Myrmecia, described in Chapter 3, are based primarily on morphological features of the workers and male terminalia respectively. It is a phenetic classification, based simply on degrees of resemblance, which does not attempt to express phylogenetic relationships.

There has been much debate during the last two decades about whether classifications should be phenetic, phylogenetic, or a mixture of the two. Pheneticists maintain that the best general classification would be one based on estimates of the overall similarity between organisms, irrespective of degrees of evolutionary relatedness (cf. Sneath and Sokal, 1973). The opposite view is held by phylogeneticists and evolutionists who both advocate classifications based on degrees of evolutionary relationship. However, these schools disagree about how best to represent evolution in classification. Phylogeneticists (cladists) maintain that only cladogenesis should be expressed (cf. Hennig, 1966; Wiley, 1981) while evolutionists insist upon the expression of both cladogenesis and anagenesis (cf. Mayr, 1969, 1974).

The advantages and disadvantages of each type of classification have been discussed at great length (see e.g. 'Systematic Zoology' from 1968) and need not be considered here. In summary, the philosophy I prefer is that of cladism, as derived from the researches of Hennig (1966), because it alone strives to reflect exactly the pattern of evolution and is consistent in approach. Evolution is the general paradigm of comparative biology and a classification expressing the resultant genealogies will provide the best general reference system. Evolutionist taxonomy suffers from inconsistency in the degrees to which anagenesis and cladogenesis are expressed: the mix may vary from worker to worker and from group to group.

To transform the Myrmecia classification of Chapter 3, based on phenetic similarity, into one reflecting phylogenetic relationships, requires a re-examination of the characters used in an attempt to recognize which are apomorphic at each level. 'The likelihood of sufficient recognisable derived conditions evolving undoubtedly varies from group to group and it seems less likely to happen at low taxonomic levels ...' (Arnold, 1981). It is therefore not to be expected that many synapomorphies will be found. Moreover, ants are relatively simple in structure and convergence is therefore quite likely to have occurred. However, with the availability of new taxonomic techniques, it should become increasingly practicable to recognize synapomorphies and produce a phylogenetic classification for ants. This process can begin here with a search for synapomorphies amongst the characters I have used to classify Myrmecia.

The crucial step in identifying synapomorphies is the determination of polarity. The plesiomorphic (relatively primitive) state, that is the state present in the immediate ancestor, must first be identified, then the relationship of the apomorphic (relatively derived) states to it is assessed. Various polarity indicators can be examined, of which the most reliable are: 1) distribution in outgroups; 2) frequency within studied group (commonality); 3) non-coinciding minority states; 4) correlation with states of other characters; 5) ontogenetic clues; 6) functional clues; and 7) fossil evidence (Arnold, 1981). The first two of these will be relied upon heavily to determine plesiomorphic states in Myrmecia. The outgroup used for Myrmecia is the remainder of the Formicidae, since subfamilial classification is in such turmoil that uncertainty exists as to which other subfamily is closest to Myrmecia (Brown, 1954; Wilson et al., 1967a, 1967b; Wilson, 1971; Taylor, 1978b). It is most probably Pseudomyrmecinae, Ponerinae or Nothomyrmeciinae.

The use of frequency within the studied group as a polarity indicator is not recommended by some phylogeneticists (e.g. Stevens, 1980; de Jong, 1980) because in a single lineage with many species the plesiomorphic state could easily be outnumbered by an apomorphic state found throughout. However, broad distribution amongst subgroups increases the probability that an abundant state is plesiomorphic (Arnold, 1981). Therefore, if a character state is found distributed through the species groups of Myrmecia it will tentatively be regarded as plesiomorphic.

The characters chosen for a phylogenetic analysis can be of any kind but for Myrmecia, and many other insect taxa, the best source of characters has proven to be the male terminalia. The preponderance of worker and male terminalic features used in the analysis below does not imply that they are intrinsically more important than other sources (e.g. karyotype, behaviour) but rather that their study has provided more characters which vary between species and species groups.

4.2 Plesiomorphic and apomorphic states of various Myrmecia characters

The plesiomorphic and apomorphic states of various Myrmecia characters and their distribution among species and species groups are listed below. Numbers of apomorphic states include one of the letters W, M, K and B to indicate that the characters are from worker morphology, male terminalia, karyotype or behaviour respectively. They may also be suffixed to indicate that they are derived from an already apomorphic state. For example, apomorphic state M21.1 is a male terminalic character state which is derived from M21.

In a few cases workers, male terminalia or behaviour are so similar between species that, although it is not possible to identify the plesiomorphic and apomorphic states of various characters explicitly, it would be imprudent to suggest other than that the *extreme* similarity is due to synapomorphy. I use these synapomorphies to construct phylogenies only as a last resort and at low taxonomic levels (i.e. within species groups). They are indicated on my phylograms by the circled letters W, M and B.

4.2.1 Worker morphology

4.2.1.1 Worker size

Primitively, all workers in a colony are less than 17 mm long. This is the condition in about 50% of *Myrmecia* species (all the jumpers), in *Nothomyrmecia* and most other genera of ants which are usually considered to be primitive. Apomorphic state is:

W1. Some workers in colonies more than 17 mm long (*forceps* + *forficata* + *mjobergi* + *nigriscapa* + *tarsata* + *flavicoma* + *gulosa* + *simillima* + *vindex* (except *inquilina*) + *esuriens* groups)

4.2.1.2 Worker monomorphism / polymorphism

Primitively, *Myrmecia* workers are monomorphic. This is the condition in about 50% of *Myrmecia* species (including all jumpers), *Nothomyrmecia*, all Ponerinae and the large majority of other ant genera (for full list of monomorphic genera see Oster and Wilson, 1978, pp 4-5). Apomorphic states are:

W2. Mature colonies polymorphic with at least two worker subcastes (*forceps* + *forficata* + *mjobergi* + *tarsata* + *flavicoma* + *nigriscapa* + *gulosa* + *rowlandi* + *simillima* + *vindex* (except *inquilina*) + *esuriens* groups)

W2.1. Mature colonies with no worker caste (social parasite; *inquilina*)

4.2.1.3 Worker colouration

Primitively, worker colouration does not include components which disappear when placed in alcohol. This is the condition in all species of 15 of the 19 species groups of *Myrmecia* and most species of one of the others. Apomorphic states are:

W3. Worker colouration includes blue metallescence which disappears when placed in alcohol (*tarsata* group)

W4. Worker gaster with gold pubescence which disappears when placed in alcohol (*auriventris* group)

W5. Worker gaster with gold pubescence which disappears when placed in alcohol (convergently evolved; *pilosula* (in part) + *mandibularis* groups)

The presence of gold gastric pubescence in the *auriventris* group (of subgenus *Myrmecia*, *s.s.*) and in some *Promyrmecia* (the *mandibularis* group and several species of the *pilosula* group) is due to convergence. Its presence in species of the *pilosula* and *mandibularis* groups appears to be due to incomplete synapomorphy.

4.2.1.4 Worker mandibles, shape

Primitively, the worker mandible is almost uniform in width from base to near apex, with outer border straight or feebly concave and inner border straight with a full complement of erect teeth. This is the condition in at least one and usually all species of 12 of the 19 species groups of *Myrmecia* and some species of two others. Apomorphic states are:

W6. Worker mandibles with outer border strongly convex and inner border having few widely spaced teeth (*forceps* group)

W7. Worker mandibles with outer border noticeably convex and inner border having short basal teeth (*mandibularis* group)

W8. Worker mandibles with straight or slightly concave outer border and inner border with short basal teeth (*tepperi* + *swalei* + *clarki*)

W9. Worker mandibles with strong angulate broadening near base of inner border (*mjobergi* + *forficata* groups)

W9.1. Worker mandibles with backwardly directed teeth (brevinoda, s.l. + hirsuta)

W10. Worker mandibles with slight angulate broadening near base of inner border (convergently evolved; vindex group (except princeps)).

W11. Worker mandibles with noticeable angulate broadening near base of inner border (convergently evolved; picta group)

W12. Worker mandibles very broad or chunky (aberrans)

W13. Worker mandibles with backwardly directed teeth (convergently evolved; varians)

Although angulate broadening near the base of the inner border of the worker mandible is present in four species groups, I conclude that it has evolved three times because the details are not identical in all cases and other characters which support close relationships between any of the groups can only be found for two of them. The picta group has much shorter mandibles with the broadening nearer to the apex than in the other groups, while the vindex group has much slighter broadening than in the forficata and mjobergi groups. The character is probably homologous in the forficata and mjobergi groups because the degree of broadening is similar in both and there are a number of male terminalic characters which suggest that they form a monophyletic group.

Backwardly directed teeth are convergently evolved in some mandibles of the forficata group (brevinoda, s.l. and hirsuta) where they accompany angulate broadening near the base of the inner border, and in those of varians (pilosula group) which have a straight inner border.

4.2.1.5 Worker mandibles, length

Primitively, the worker mandible is about as long as the head. This is the condition in all but three Myrmecia species and in Nothomyrmecia. Apomorphic states are:

W14. Worker mandibles much longer than head (mjobergi group)

W15. Worker mandibles noticeably longer than head (convergently evolved; princeps)

W16. Worker mandibles noticeably shorter than head (aberrans)

Worker mandibles which are longer than the head have evolved convergently because in princeps (vindex group) there is a straight inner border, while in the mjobergi group there is a strong angulate broadening near the base of the inner border. No other characters indicate close relationship between these species.

4.2.1.6 Worker mandibles, colour

Primitively, the worker mandible is yellowish. This is the condition in all species in 16 of the 19 species groups and some species of two others. Apomorphic states are:

W17. Worker mandibles red-brown to brown (forficata group)

W18. Worker mandibles brown to black (mandibularis (in part) + pilosula (in part) groups)

4.2.1.7 Worker head, shape

Primitively, the worker head is only slightly longer than wide. This is the condition in all but one Myrmecia species. Apomorphic state is:

W19. Worker head much longer than wide (mjobergi group)

4.2.1.8 Worker head, frontal setae

Primitively, any setae arising from the frontal area of the head are less than a quarter the length of the mandibles. This is the condition in all but one species group of Myrmecia and all but a few other ant genera. Apomorphic state is:

W20. Workers with four long setae (about half as long as mandibles) arising from frontal area of head and extending into gape of mandibles (mandibularis group)

4.2.1.9 Worker antennae, scape length

Primitively, scapes of worker antennae are short (SI < 94). This is the condition in all species in six of the 19 species groups, most species of another and some species in three others. Furthermore, it is also the case in *Nothomyrmecia*, Pseudomyrmecinae and many Ponerinae. Apomorphic states are:

W21. Scapes of worker antennae long ($94 \leqslant SI \leqslant 129$) (*forceps* + *forficata* + *mjobergi* + *nigriscapa* + *tarsata* + *auriventris* + *flavicoma* + *gulosa* + *simillima* + *vindex* (except *rowlandi*) + *esuriens* (except *esuriens*) groups).

W22. Scapes of worker antennae moderately long ($94 \leqslant SI \leqslant 105$) (convergently evolved; *nigrocincta* group (except *cordata*))

W23. Scapes of worker antennae moderately long ($94 \leqslant SI \leqslant 102$) (convergently evolved; *cephalotes*)

4.2.1.10 Worker petiole, shape

Primitively, the petiolar stalk is noticeably shorter than the petiolar node. This is the condition in all species in 14 of the 19 species groups of *Myrmecia*. Apomorphic states are:

W24. Worker petiolar stalk longer than petiolar node (*gulosa* + *simillima* + *vindex* groups)

W25. Worker petiolar stalk longer than petiolar node (convergently evolved; *forceps* group)

W26. Worker petiolar stalk longer than petiolar node (convergently evolved; *mjobergi* group)

Although long petiolar stalks are found in five groups I consider that they have probably evolved three times. This is only supported by my knowledge of other characters (especially male terminalia) which indicate that *forceps* and *mjobergi* groups are not closely related to each other or the remaining three groups. Several male terminalic characters of *gulosa*, *simillima* and *vindex* groups appear homologous, so it seems likely that this character, being present in each group, is also homologous.

4.2.1.11 Worker postpetiole, sculpturing

Primitively, the worker postpetiole is smooth or very slightly sculptured. This is the condition in all but one species group of *Myrmecia*. Apomorphic states are:

W27. Worker postpetiole heavily sculptured (*harderi* group)

W28. Worker postpetiole heavily sculptured (convergently evolved; *rugosa*)

Although heavily sculptured postpetioles are present in both *harderi* group and *rugosa* (*pilosula* group) I doubt that they are homologous because male terminalia show *rugosa* to be more closely related to other species of the *pilosula* group than to the *harderi* group.

4.2.2. Queen morphology

4.2.2.1 Queen size

Primitively, queens are only slightly larger than the largest workers - the ratio between their lengths being 1.0 - 1.3. This is the condition in all species of *Myrmecia* except one. Apomorphic state is:

Q1. Queen much larger than largest workers - queen about 1.5 times as long as largest workers (*chasei*)

4.2.3 Male terminalia

4.2.3.1 Ninth sternite, spines

Primitively, there are no spines on the ninth sternite. This is the condition in almost all *Myrmecia* and all other ant genera reported previously. Apomorphic state is:

M1. Ninth sternite with spines (*flavicoma* group)

4.2.3.2 Ninth sternite, lateral inclusions

Primitively, there are no lateral inclusions on the ninth sternite. This is the condition in all but one species group of *Myrmecia* and all other ant genera reported previously. Apomorphic state is:

M2. Ninth sternite with lateral inclusions (mandibularis group).

4.2.3.3 Ninth sternite, posterior margin

The plesiomorphic state for shape of the posterior margin of the ninth sternite is uncertain - probably it tapered to a rounded or blunt point. However, several shapes are seen within Myrmecia which are quite distinctive and apomorphic. Apomorphic states are:

M3. Ninth sternite with posterior margin forming posterior extension which is turned dorsally and expanded posteriorly to form a barbed hook (pilosula group)

M4. Ninth sternite with posterior margin forming very narrow posterior extension (mjobergi + forficata (except brevinoda, s.s.) groups)

M4.1. Ninth sternite with posterior margin forming posterior extension which is very narrow, but broadens slightly posteriorly, and is triangular in cross-section (pyriformis + sp.9)

4.2.3.4 Ninth sternite, mounds

Primitively, there are no mounds on the ventral surface of the ninth sternite. This is the condition in all but one Myrmecia species and all other ant genera reported previously. Apomorphic state is:

M5. Ninth sternite with two small mounds near anterior margin, flanking midline, on ventral surface (varians)

4.2.3.5 Eighth sternite, stout setae

Primitively, there are only a few short setae found in the posterior quarter of the eighth sternite. This is the condition in almost all Myrmecia. Apomorphic state is:

M6. Eighth sternite with long, stout setae in posterior quarter (mjobergi + forficata groups)

4.2.3.6 Eighth sternite, anterior margin

Primitively, the anterior margin of the eighth sternite is quite deeply indented. This is the condition in all but two species groups of Myrmecia. Apomorphic state is:

M7. Eighth sternite with anterior margin shallowly and broadly indented (mjobergi + forficata groups).

4.2.3.7 Outer valve, sensilla

Primitively, there are no sensilla on the outer valve. This is the condition in almost all Myrmecia and all other ant genera reported previously. Apomorphic state is:

M8. Outer valve with sensilla posteriorly on dorsal surface (esuriens group)

4.2.3.8 Outer valve, spines

Primitively, there are no spines on the outer valve. This is the condition in almost all Myrmecia and all other ant genera reported previously. Apomorphic state is:

M9. Outer valve with spines (flavicoma group)

4.2.3.9 Outer valve, dorsal median projection

Primitively, the outer valve has a single lobed dorsal median projection. This is the condition in 14 of the 19 species groups of Myrmecia and in Pseudomyrmex (Snodgrass, 1957). Apomorphic states are:

M10. Dorsal median projection lost or very much reduced (pilosula + mandibularis groups)

M11. Dorsal median projection lost (convergently evolved; sp.15 group)

M12. Dorsal median projection lengthened antero-posteriorly (gulosa group)

M13. Dorsal median projection with two lobes (forficata group (except regularis))

Although the dorsal median projection is absent from the outer valve of three groups I consider that it its loss from sp.15 is independent of its loss from the pilosula and mandibularis groups. This is based on other characters of the male terminalia and workers which suggest that the pilosula and mandibularis groups are closely related but neither is close to the sp.15 group.

4.2.3.10 Outer valve, posterior end

Primitively, the posterior end of the outer valve is not divided. This is the condition in most *Myrmecia* and all other ant genera reported previously. Apomorphic states are:

M14. Outer valve with posterior end bifurcate (*pilosula*, *s.l.* + *swalei* + *tepperi*)

M15. Outer valve with posterior end abrupt, Y-shaped in cross-section (*forficata* + *mjobergi* groups)

M16. Outer valve with posterior end divided into two small lobes (*sp.M2*)

4.2.3.11 Inner valve, postero-ventral lobe

Primitively, the inner valve has a postero-ventral lobe bearing spines or serrations. This is the condition in all but three species groups of *Myrmecia*. Apomorphic states are:

M17. Postero-ventral lobe absent (*nigriscapa* group)

M18. Postero-ventral lobe very long and narrow, and shifted anteriorly (*esuriens* group)

M19. Postero-ventral lobe with no spines (*mjobergi* group)

4.2.3.12 Inner valve, spines in dorsal half

Primitively, there are small spines and no ridges in the dorsal half of the inner valve. This is the condition in all species of 15 of the 19 species groups of *Myrmecia* and in one species of another. Apomorphic states are:

M20. Inner valve with a few large spines in dorsal half near posterior margin (*forficata* group (except *regularis*))

M21. Inner valve with small spines in middle of segment additional to those near posterior margin (*gulosa* + *simillima* + *vindex* groups)

M21.1. Inner valve with spines in middle of segment on a large ridge (*simillima* + *vindex* groups)

M21.1.1. Inner valve with spines in middle of segment tightly clustered on a large ridge (*atrata* + *desertorum* + *fuscipes* + *nigriceps*, *s.s.* + *sp.12* + *sp.13* + *sp.16*)

M21.1.2. Inner valve with spines in middle of segment tightly clustered on a large ridge (convergently evolved; *ferruginea* + *sp*.*17*)

M21.1.3. Inner valve with spines in middle of segment spread dorso-ventrally on a large ridge (*simillima* group)

M22. Inner valve with no spines in the dorsal half (*esuriens* group)

M23. Inner valve with no spines in the dorsal half (convergently evolved; *mjobergi* group)

M24. Inner valve with a narrow dorso-ventral ridge in from posterior margin (*nigrocincta* group)

M25. Inner valve with spines in dorsal half replaced by a comb of serrations which may have been subsequently lost (*pilosula* group (except *sp*.*M1*))

M25.1. Inner valve with comb of serrations in dorsal half lost (*pilosula*, *s*.*l*. + *swalei* + *tepperi*)

Spines are absent from the inner valve of the *mjobergi* and *esuriens* groups, but I consider the loss to have been convergent because no other characters from the male terminalia or workers suggest any close relationship between the two.

4.2.3.13 Inner valve, lateral folding

Primitively, the postero-dorsal margin of the inner valve is not folded laterally. This is the condition in all but three species of *Myrmecia* and almost all other ant species. Apomorphic states are:

M26. Inner valve with postero-dorsal margin folded laterally (*harderi* group)

M27. Inner valve with postero-dorsal margin folded laterally (convergently evolved; *sp*.*M2*)

M28. Inner valve with postero-dorsal margin folded laterally (convergently evolved; *fucosa* group)

Folding of the postero-dorsal margin of the inner valve appears to have occurred independently in the *harderi* and *fucosa* groups and *sp*.*M2* (*pilosula* group) because its details vary in each and there is no other evidence to indicate close relationships between any of them.

4.2.4 Karyotype

4.2.4.1 Chromosome number

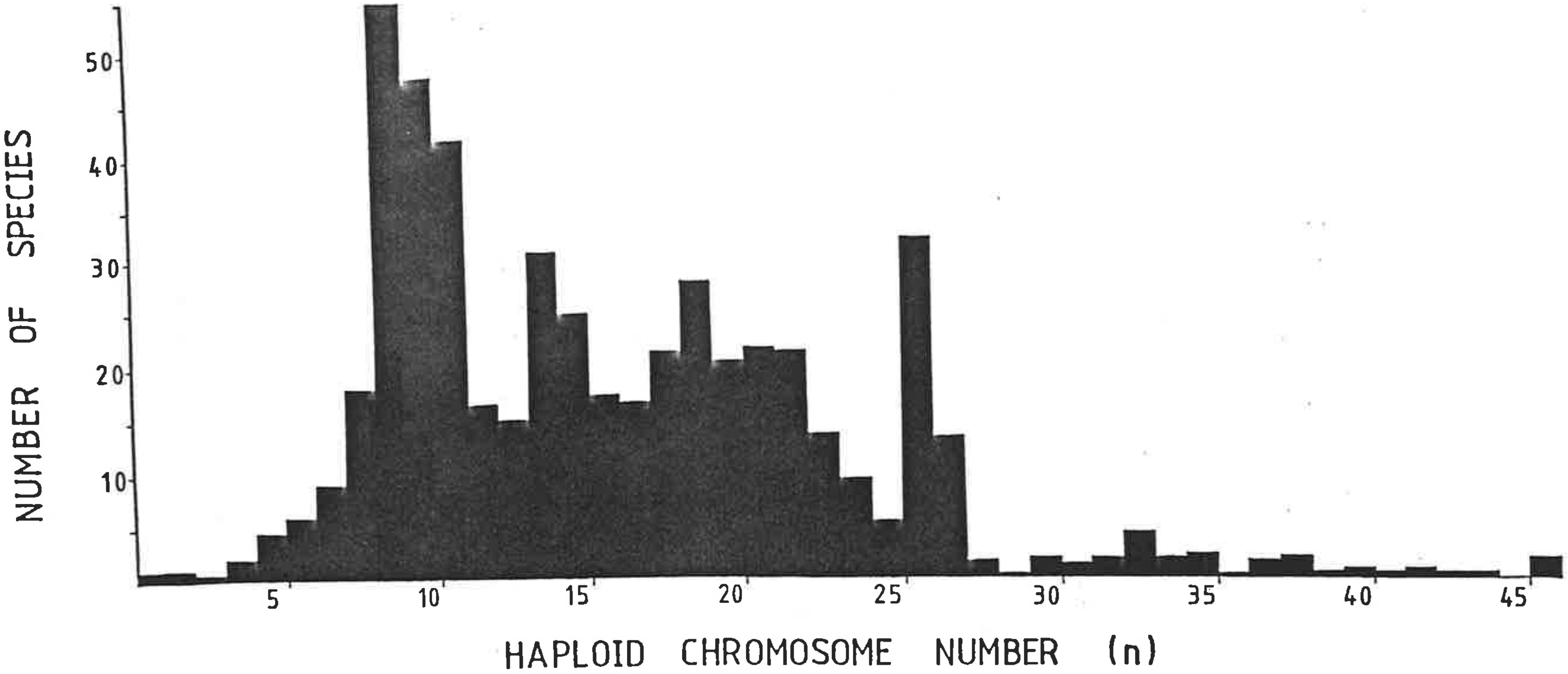
To determine, or at least estimate, the plesiomorphic and apomorphic chromosome numbers for Myrmecia, and ants as a whole, I have sought evidence from four sources: (1) chromosome number ranges in other key taxa (out-group analysis); (2) modal chromosome numbers (in-group analysis); (3) correlation between chromosome numbers and eusociality; and (4) likely directionality of chromosome rearrangements.

4.2.4.1.1 Chromosome number ranges in other key taxa

Chromosome numbers, and their sources, for 521 ant species are listed in Appendix 7. The same data are presented as a frequency distribution in fig. 134. Haploid chromosome numbers range between n = 1 (Myrmecia pilosula, s.l.) and n = 46 (Nothomyrmecia macrops Clark and Probolomyrmex sp.) with a mode of 9, a median of 15 and a mean of 16.4. The number of species karyotyped represents only 3.5 - 4.3 % of the estimated 12,000 - 15,000 ant species (Snelling, 1981) and is biased by emphasis having been placed on determining karyotypes for certain genera in preference to others. However, this histogram is very similar to those prepared by Imai et al. (1977) for 280 species and Crozier (1975) for 178 species. Its ability to retain its form even after the addition of much further data indicates that it provides a firm basis for erecting and evaluating hypotheses about ant karyotype evolution.

A wide range of chromosome numbers is found in all the ant subfamilies which are best-known karyotypically - Myrmeciinae (n = 1-2, 4-8, 11-12, 15-21, 23-26, 29-44), Ponerinae (n = 3, 4, 6-8, 10-15, 17-26, 30, 33, 38, 46), Myrmicinae (n = 4, 6-25, 28, 33-35), Dolichoderinae (n = 5-9, 11-16, 19) and Formicinae (n = 8-10, 12-28). This led Imai et al. (1977) to conclude that the various subfamilies

Figure 134. Frequency distribution of haploid chromosome numbers (n) in 521 ant species. [Note - When species have more than one chromosome number they have been scored as in the following example. *Myrmecia vindex* has n = 23-24, 26, 29, so 0.25 species are added to each of columns 23, 24, 26 and 29.]


NUMBER OF SPECIES
50
40
30
20
10
5
10
15
20
25
30
35
40
45
HAPLOID CHROMOSOME NUMBER (n)

which are well-known karyotypically seem to have been following independent but parallel evolutionary trajectories, but I cannot support this statement because similar ranges could have resulted if karyotypic orthoselection (White 1973, 1975) was acting to increase chromosome number in some subfamilies while decreasing it in others. I maintain that the range of chromosome numbers for the rest of the Formicidae (the out-group of Myrmecia) provides no insight about the plesiomorphic chromosome number of Myrmecia because it is virtually coextensive with its range.

The haploid numbers of 398 hymenopterans, other than ants, are now known and have been listed in Appendices 8 and 9 (for summary see Table 13). They range between n = 3 (Andrena duboisi, Andrenidae) and n = 33 (Polistes exclamans Viereck, Vespidae) which extends the range from n = 5-26 found in Crozier's (1975) list of 127 species. Although no karyotypes are yet known for many hymenopteran families, it is notable that the highest numbers in the non-formicid Hymenoptera are significantly lower than many known from ants. Consequently, it appears that the plesiomorphic ant chromosome number was somewhere in the range n = 3 - 33. If the ancestral ant chromosome number was higher than n = 33, then it would be expected that similarly high numbers would be found amongst the vespoid wasps from which ants are undoubtedly derived. Unfortunately no chromosome numbers are known for the Tiphiidae or Sierolomorphidae, which have been considered closest to the ancestral ant form by Wilson et al. (1967a,b) and Brothers (1975, p. 587) respectively. However, chromosome numbers are known for 18 species from the other vespoid families and these range from n = 6-33. Too few vespoids have been karyotyped to use their range in chromosome numbers to narrow my estimate for the plesiomorphic ant chromosome

Table 13. Range in haploid chromosome number for each family of Hymenoptera.

*Taxon	Number of species karyotyped	Range in haploid chromosome number (n)
ORDER HYMENOPTERA	919	1-46
SUBORDER SYMPHYTA	235	5-22
SIRICOIDEA	5	8-18
Orussidae	0	?
Xiphydriidae	0	?
Siricidae	5	8-18
Syntexidae	0	?
MEGALODONTOIDEA	0	?
Megalodontidae	0	?
TENTHREDINOIDEA	228	5-22
Tenthredinidae	201	5-22
Cimbicidae	0	?
Argidae	1	8
Blasticotomidae	0	?
Diprionidae	26	6-14
Pergidae	0	?
XYELOIDEA	0	?
Xyelidae	0	?
Pamphilidae	0	?
CEPHOIDEA	2	9-26
Cephidae	2	9-26
SUBORDER APOCRITA	684	1-46
MEGALYROIDEA	0	?
Megalyridae	0	?
Stephanidae	0	?
TRIGONALOIDEA	0	?
Trigonalidae	0	?
ICHNEUMONOIDEA	6	10-17
Braconidae	3	10-17
Ichneumonidae	3	10-11
Agriotypidae	0	?
EVANIOIDEA	0	?
Evaniidae	0	?
Aulacidae	0	?
Gasteruptiidae	0	?

Table 13 (cont.)

*Taxon	Number of species karyotyped	Range in haploid chromosome number (n)
SUBORDER APOCRITA (cont.)		
PROCTOTRUPOIDEA	1	10
Heloridae	0	?
Proctotrupidae	0	?
Austroserphidae	0	?
Pelecinidae	0	?
Ceraphronidae	0	?
Platygasteridae	0	?
Scelionidae	1	10
Diapriidae	0	?
CYNIPOIDEA	11	9-10
Liopteridae	0	?
Ibaliidae	0	?
Figitidae	0	?
Cynipidae	11	9-10
CHALCIDOIDEA	31	3-10
Agaonidae	0	?
Trichogrammatidae	5	5
Eulophidae	3	5-6
Mymaridae	0	?
Chalcididae	4	3-6
Eurytomidae	1	10
Torymidae	13	4-6
Pteromalidae	4	5-6
Encyrtidae	1	10
Aphelinidae	1	5
BETHYLOIDEA	0	?
Plumariidae	0	?
Bethylidae	0	?
Scolebythidae	0	?
Cleptidae	0	?
Chrysididae	0	?
Loboscelidiidae	0	?
Dryinidae	0	?
Sclerogibbidae	0	?
Embolemidae	0	?

Table 13 (cont.)

*Taxon	Number of species karyotyped	Range in haploid chromosome number (n)
SUBORDER APOCRITA (cont.)		
SPHECOIDEA	94	3-25
Sphecidae	0	?
Colletidae	3	11-14
Andrenidae	2	3-10
Oxaeidae	0	?
Halictidae	8	6-21
Stenotritidae	0	?
Mellittidae	0	?
Ctenoplectridae	0	?
Megachilidae	13	15-17
Fideliidae	0	?
Anthophoridae	10	6-21
Apidae	58	8-25
VESPOIDEA	541	1-46
Tiphiidae	0	?
Sapygidae	1	25-26
Mutillidae	0	?
Sierolomorphidae	0	?
Rhopalosomatidae	0	?
Pompilidae	0	?
Bradynobaenidae	0	?
Scoliidae	0	?
Masaridae	0	?
Eumenidae	5	6-10
Vespidae	14	6-33
Formicidae	521	1-46

* Classification derived from Riek (1970), except for aculeate superfamilies (BETHYLOIDEA, SPHECOIDEA and VESPOIDEA). Classification of aculeate superfamilies from Snelling (1981) except for Apiformes group (Colletidae, Andrenidae, Oxaeidae, Halictidae, Stenotritidae, Mellittidae, Ctenoplectridae, Megachilidae, Fideliidae, Anthophoridae and Apidae). Classification of Apiformes group from Michener and Greenberg (1980).

number, but when their range is more precisely known it should be possible to do so. Other non-vespoid families of Hymenoptera all have a smaller range of chromosome numbers with lower maximum numbers (e.g. Tenthredinidae, n = 5-22; Diprionidae, n = 6-14; Cynipidae, n = 9-10; Torymidae, n = 4-6; Megachilidae, n = 5-7; Anthophoridae, n = 6-21; Apidae, n = 8-25).

4.2.4.1.2 Modal chromosome numbers

It has often been assumed that in animal taxa phylogenetically primitive subgroups tend to have the modal chromosome number while morphologically specialized subgroups have numbers higher or lower than the mode (Naito, 1982), but there are now many cases known for which the opposite seems to be true. For example, 24 out of 35 Formica Linné species have n = 26 and 11 have n = 27 (see Appendix 7), which would suggest that n = 26 is the plesiomorphic karyotype and n = 27 the apomorphic. However, Hauschteck-Jungen and Jungen (1983) listed the chromosome numbers found in the subgenera of Formica and found that all species with n = 27 belonged to subgenus Serviformica Forel which is considered to have the most plesiomorphic morphology. At best, there appears to be weak correlation between chromosome number change and morphological specialization in ants.

Nevertheless a somewhat similar assumption about modal chromosome numbers does have a place in phylogenetic analysis. This is that the modal chromosome number is likely to be plesiomorphic while apomorphic karyotypes have lower or higher numbers. Generally, the likelihood of the modal chromosome number being plesiomorphic for a taxon increases proportional to the percentage of species with that number, especially if the species are widespread amongst subgroups of the taxon.

Of 41 hymenopteran genera listed in Table 14 (i.e. those for

TABLE 14. Karyotype variability, in terms of variation in haploid number (n) in hymenopteran genera. Data are presented for genera in which five or more species have been examined.

Taxon	No. spp examined	*Modal no.(m)	No. spp with m	$\bar{n}$	S.D.	C.V.
Tenthredinidae						
Aglaostigma	6	-	-	14.83	4.79	32.3
#*Dolerus*	5	8	3	8.40	0.55	6.5
Hemitaxonus	8	6	6	6.25	0.46	7.4
Macrophya	13	10	8	9.62	1.12	11.6
Pachyprotasis	33	10	30	10.09	0.29	2.9
Perineura	5	17	5	17.00	0.00	0.0
Pristophora	5	8	3	7.60	0.55	7.2
Siobla	5	9	5	9.00	0.00	0.0
Strongylogaster	11	9	5	8.18	0.87	10.6
Tenthredo	50	10	37	10.79	2.28	21.1
Tenthredopsis	6	8	4	8.33	0.52	6.2
Diprionidae						
Diprion	7	7	5	7.86	2.73	34.8
Neodiprion	18	7	15	7.17	0.38	5.4
Trichogrammatidae						
Trichogramma	5	5	5	5.00	0.00	0.0
Torymidae						
Torymus	9	6	7	5.78	0.44	7.6
Apidae						
Bombus	17	18	13	18.35	0.70	3.8
#*Melipona*	7	9	7	9.00	0.00	0.0
Trigona	26	17	12	16.38	2.12	12.9
Vespidae						
Polistes	14	-	-	19.61	8.67	44.2
Formicidae						
Myrmeciinae						
Myrmecia	37	-	-	23.78	12.50	52.6
Ponerinae						
Anochetus	7	15	3	15.29	2.21	14.5
Bothroponera	5	24	2	28.40	5.90	20.8
Leptogenys	7	19	2	19.86	4.78	24.1
Rhytidoponera	10	21	5	20.86	4.08	19.6

TABLE 14 (cont.).

Taxon	No. spp examined	*Modal no.(m)	No. spp with m	$\bar{n}$	S.D.	C.V.
Myrmicinae						
Aphaenogaster	23	17	7	17.61	3.42	19.4
Crematogaster	12	18	4	16.00	4.13	25.8
Leptothorax	12	9	5	11.00	2.17	19.8
Meranoplus	6	11	4	10.33	1.21	11.7
Monomorium	17	11	8	14.85	6.60	44.5
Myrmica	8	24	4	24.13	1.64	6.8
Oligomyrmex	7	18,22	2	18.28	3.20	17.5
Pheidole	49	10	34	10.94	3.11	28.4
Solenopsis	9	16	5	14.67	2.92	19.9
Tetramorium	13	-	-	11.19	3.02	27.0
Dolichoderinae						
$*Iridomyrmex*	29	9	20	9.07	1.62	17.9
Tapinoma	8	5	3	7.00	1.77	25.3
Formicinae						
Camponotus	55	-	-	17.07	4.61	27.0
Formica	36	26	24	26.33	0.48	1.8
Lasius	10	15	7	14.70	0.48	3.3
Paratrechina	10	15	4	12.50	3.17	25.4
Polyrhachis	10	21	8	20.80	0.42	2.0

* If modal number is possessed by less than 25% of species there is considered to be no modal number.
\# Excluding polyploid species.
$ Old World *Iridomyrmex* only.

which five or more species have been karyotyped), 24 have 50% or more of their species with the same haploid number, only five have less than 25% with the same number and 10 have more than 75% with the modal number. In *Polyrhachis* Smith, for example, eight out of ten species have n = 21, which, in the absence of evidence to the contrary, I would assume to be its plesiomorphic chromosome number.

Unfortunately, this assumption cannot be invoked for genera such as Myrmecia where the most common chromosome number (n = 20) is present in only three out of 37 species (8.1%). Myrmecia is by far the most variable hymenopteran genus (in terms of haploid chromosome number), with a coefficient of variability (C.V.) of 52.6%. No other hymenopteran genus has C.V. > 45.8% and all but two have C.V. < 34.8%. Furthermore, genus Myrmecia is more variable than any hymenopteran family or any of the other formicid subfamilies (Table 15) and its range of haploid chromosome numbers (n = 1-44) is only just short of the entire range for Hymenoptera (n = 1-46).

When confronted with highly variable genera some authors have chosen to examine subgeneric groups in the hope that they will prove less variable. For example, Hauschteck-Jungen and Jungen (1983), when contemplating karyotype evolution in Camponotus Mayr, found that if the subgenera were examined the most variable subgenus (Tanaemyrmex Ashmead) was much less variable than the genus (C.V. = 8.4%, cf. 27.0% for Camponotus).

However, in Myrmecia, the two subgenera have very high coefficients of variability (39.7% for Myrmecia, s.s. and 73.4% for Promyrmecia; Table 16). If the species groups of Myrmecia, s.s. are examined, slightly less variability is found (28.3% for forficata group and 30.4% for vindex group), but the pilosula and mandibularis groups of Promyrmecia are both extremely variable (70.9% and 90.7% respectively). Therefore, this approach seems to be of little use for determining the plesiomorphic chromosome number in Myrmecia. Nor is it likely to provide much insight into the plesiomorphic chromosome number for Formicidae, because the modal number (n = 9) is present in only 10.6% of ant species.

TABLE 15. Karyotype variability, in terms of variation in haploid number (n) in hymenopteran families and formicid subfamilies. Data are presented for families and subfamilies in which five or more species have been examined.

Taxon	No.genera examined	No.spp examined	*Modal no.(m)	No.spp with m	$\bar{n}$	S.D.	C.V.
Siricidae	2	5	8	3	11.00	4.47	40.7
#Tenthredinidae	43	199	10	87	9.85	2.75	27.8
Diprionidae	3	26	7	21	7.35	1.41	19.2
Cynipidae	9	11	10	10	9.91	0.30	3.0
Trichogrammatidae	1	5	5	5	5.00	0.00	0.0
Torymidae	2	13	6	9	5.62	0.65	11.6
Pteromalidae	4	5	5	4	5.20	0.45	8.6
Halictidae	6	8	-	-	12.63	5.18	41.0
Megachilidae	9	13	16	11	16.00	0.41	2.6
Anthophoridae	8	10	-	-	14.50	5.06	34.9
#Apidae	7	57	18	22	16.25	3.40	20.9
Vespidae	1	14	-	-	19.61	8.67	44.2
Formicidae	92	521	-	-	16.36	7.44	45.5
Myrmeciinae	1	37	-	-	23.78	12.50	52.6
Ponerinae	22	68	-	-	18.54	7.36	39.7
Myrmicinae	37	209	-	-	14.37	5.37	37.4
Dolichoderinae	10	56	9	28	9.66	2.75	28.4
Formicinae	20	147	-	-	18.70	6.24	33.4

* If modal number is possessed by less than 25% of species there is considered to be no modal number.

Excluding polyploid species.

TABLE 16. Karyotype variability, in terms of variation in haploid number (n) in Myrmecia subgenera and species groups. Data are presented for subgenera and species groups in which four or more species have been examined.

Taxon	No. spp examined	$\bar{n}$	S.D.	C.V.
Subgenus Myrmecia, s.s.	23	27.39	10.88	50.6%
forficata group	6	34.08	9.65	28.3%
vindex group	13	29.96	8.51	30.4%
Subgenus Promyrmecia	14	17.86	13.12	73.4%
pilosula group	9	18.56	13.16	70.9%
mandibularis group	4	18.00	16.33	90.7%

4.2.4.1.3 Correlation between high chromosome number and eusociality

Although many eusocial species have low numbers, it is remarkable that all species with $n > 26$ (i.e. three Polistes Latreille and 33 ant spp) are eusocial. Eusociality undoubtedly evolved amongst ancestors which were non-social. Therefore, it seems unlikely that at least two groups of high-numbered non-social ancestors existed and gave rise independently to the paper wasps (including Polistes) and ants, and that these have since become extinct, leaving only low-numbered non-social species today. It is far more appealing to suggest that the non-social ancestors of these groups were low-numbered ($n < 26$) and that the high-numbered eusocial species have been derived from them.

This evidence allows my earlier estimate for the plesiomorphic ant chromosome number to be revised from n = 3 - 33 to n = 3 - 26.

4.2.4.1.4 Likely directionality of chromosome rearrangements

Another method used to estimate the plesiomorphic ant chromosome number was discussed at length by Imai et al. (1977). Based on chromosome numbers of extant species alone, they reasoned that the ancestral ant chromosome number could be expected to fall anywhere in a wide continuum (at least n = 1-46). They attempted to obtain a more precise estimate by erecting three hypotheses, which I have reworded slightly to incorporate karyotypes which were unknown to them: (1) the ancestral species had a high number (n > 40) and ant karyotypes have tended to evolve towards lower numbers (the 'fusion' hypothesis); (2) the ancestral number was low (n ≃ 1) and numbers have tended to increase (the 'fission' hypothesis); and (3) the ancestral number was coincident with the present mode (n ≃ 9) with numbers mainly increasing but also some evolution towards lower numbers (the 'modal' hypothesis).

The modal hypothesis is difficult to distinguish from the fission hypothesis because it, too, involves mainly increasing chromosome number, from a fairly low-numbered ancestor. Therefore the main comparison to be made is between the fusion and fission (including modal) hypotheses.

The procedure used by Imai et al. (1977) to assess these hypotheses, was to examine the types of chromosomal rearrangements found in ants, and then to identify the directionality of the rearrangements which have contributed most during evolution. They found that the following rearrangements were present in ants : (1) Robertsonian rearrangements; (2) pericentric inversions; (3) saltatory changes in constitutive heterochromatin; (4) simple reciprocal translocations;

(5) complex translocations accompanied by the loss of genetic material; (6) supernumerary (B-) chromosomes; and (7) chromosome deletions. Types (1), (5), (6) and (7) change chromosome number, while variation in arm lengths results from (2), (3), (4) and (5). Imai et al. (1977) rejected polyploidy as a significant factor in ant karyotype evolution, after establishing that the mean chromosome size varies inversely with chromosome number, and rearrangements (5), (6) and (7) seem to be rare (see Appendix 7). It can be inferred, therefore, that chromosome number variation in ants is primarily due to Robertsonian rearrangements, as in many other animals. Of the rearrangements which alter arm length, Imai et al. (1977) found pericentric inversions to be the most common.

Robertsonian rearrangements in ants consist primarily or wholly of centric fusions and centric fissions because if centric dissociations had played a significant role, it would be expected that either: (1) a sizeable number of B-chromosome polymorphisms would occur, especially in species with Robertsonian polymorphisms; or (2) acrocentric chromosomes should very often have 'terminal euchromatic caps' to their heterochromatic short arms (Imai et al., 1977). But all acrocentrics observed have totally heterochromatic short arms and only five species have been reported with B-chromosome polymorphisms (see Appendix 7) - none of these in species with Robertsonian polymorphisms. However, the low frequency of B-chromosome polymorphisms in ants should not be given undue weight, because it is likely that B-chromosomes, being small and largely heterochromatic, would be easily lost from karyotypes rather than persisting as polymorphisms.

Centric fusions reduce chromosome number by converting 'acrocentrics' ($\overline{A}$) to 'metacentrics' ($\overline{M}$), while centric fissions increase chromosome number by converting 'metacentrics' to 'acrocentrics'. Here 'acrocentrics' is used in a broad sense to include telocentric (T) and acrocentric (A) chromosomes, while 'metacentrics' involves subtelocentric (ST), submetacentric (SM) and metacentric (M) chromosomes (Imai et al., 1983).

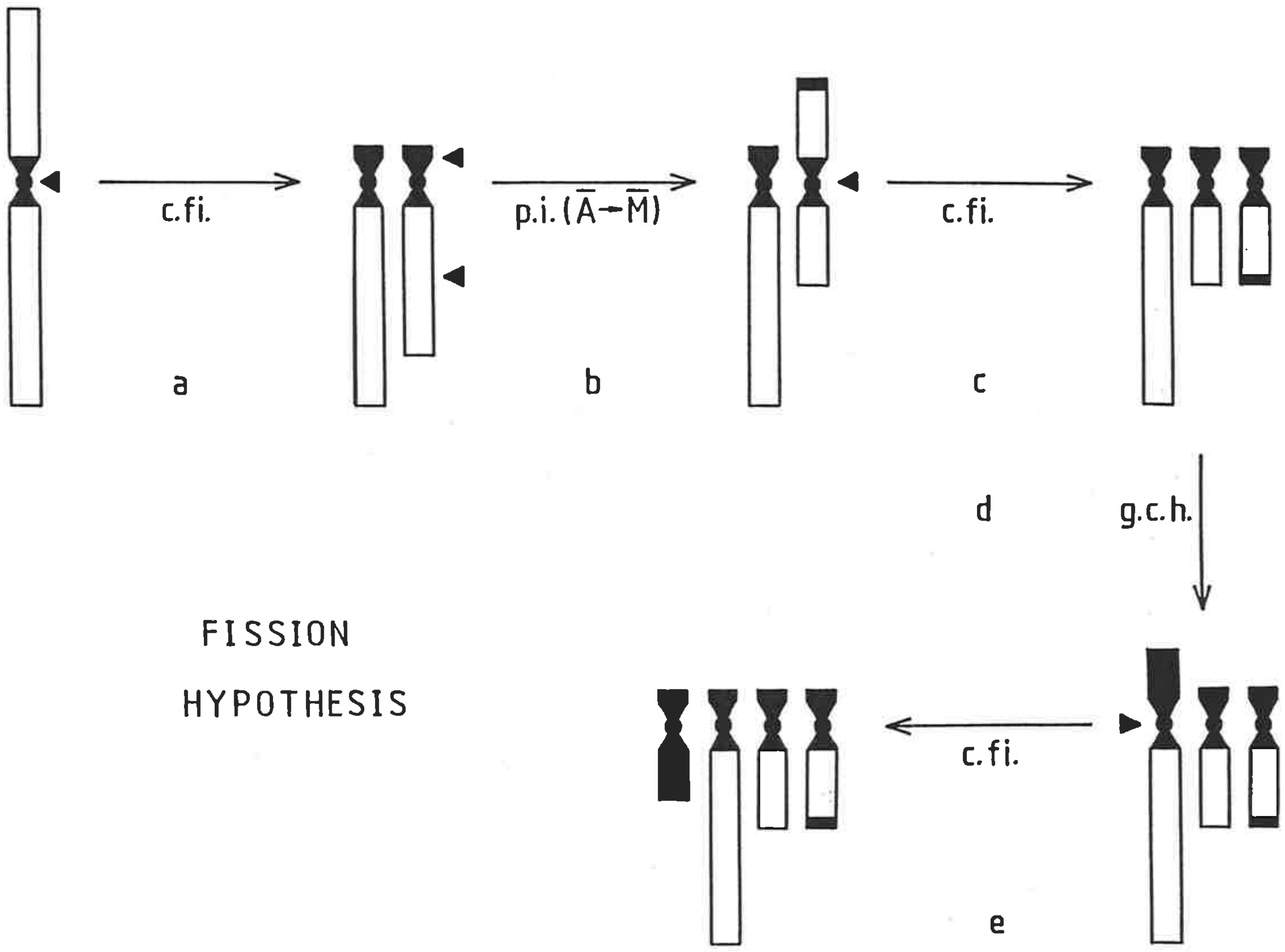
Pericentric inversions can convert 'acrocentrics' to 'metacentrics' by moving the centromere closer to the middle of the chromosome (p.i.($\overline{A}\rightarrow\overline{M}$)) or convert 'metacentrics' to 'acrocentrics' by moving it nearer to one end (p.i.($\overline{M}\rightarrow\overline{A}$)). Other pericentric inversions, which convert 'acrocentrics' to 'acrocentrics' (p.i.($\overline{A}\rightarrow\overline{A}$)) and 'metacentrics' to 'metacentrics' (p.i.($\overline{M}\rightarrow\overline{M}$)), do not alter chromosome morphology in this broad sense and need not be considered further here.

If the fission hypothesis is correct, centric fissions and p.i.($\overline{A}\rightarrow\overline{M}$) will have predominated, but, if the fusion hypothesis is to be preferred, centric fusions and p.i.($\overline{M}\rightarrow\overline{A}$) will have occurred more often. Growth of constitutive heterochromatin is a third important type of rearrangement because, although it can occur under either hypothesis, it particularly facilitates the course of events under the fission hypothesis by providing an additional means for converting 'acrocentrics' into 'metacentrics'. Furthermore, it slows the rate at which chromosome numbers can decrease under the fusion hypothesis, because when it converts 'acrocentrics' to 'metacentrics' it necessitates extra pericentric inversions to change them back to 'acrocentrics', before they can become involved in centric fusion. The two hypotheses and the role played by centric fissions, centric fusions and growth of constitutive heterochromatin are illustrated in Figs 135 and 136.

Direct evidence to show which rearrangements have occurred during ant evolution is lacking because Robertsonian changes and pericentric

Figure 135. Illustration of the fission hypothesis, demonstrating how a large 'metacentric' may be converted into four small 'acrocentrics' without loss of euchromatin: (a) large 'metacentric' undergoes centric fission (c.fi.) to form two 'acrocentrics'; (b) pericentric inversion of one 'acrocentric' converts it into a 'metacentric' (p.i.(A M)); (c) 'metacentric' undergoes centric fission to form two 'acrocentrics'; (d) growth of constitutive heterochromatin (g.c.h.) converts one 'acrocentric' into a 'metacentric'; and (e) 'metacentric' undergoes centric fission to form two 'acrocentrics'.

Solid parts of chromosomes represent heterochromatin and open parts represent euchromatin. Solid arrowheads point at breakage points.



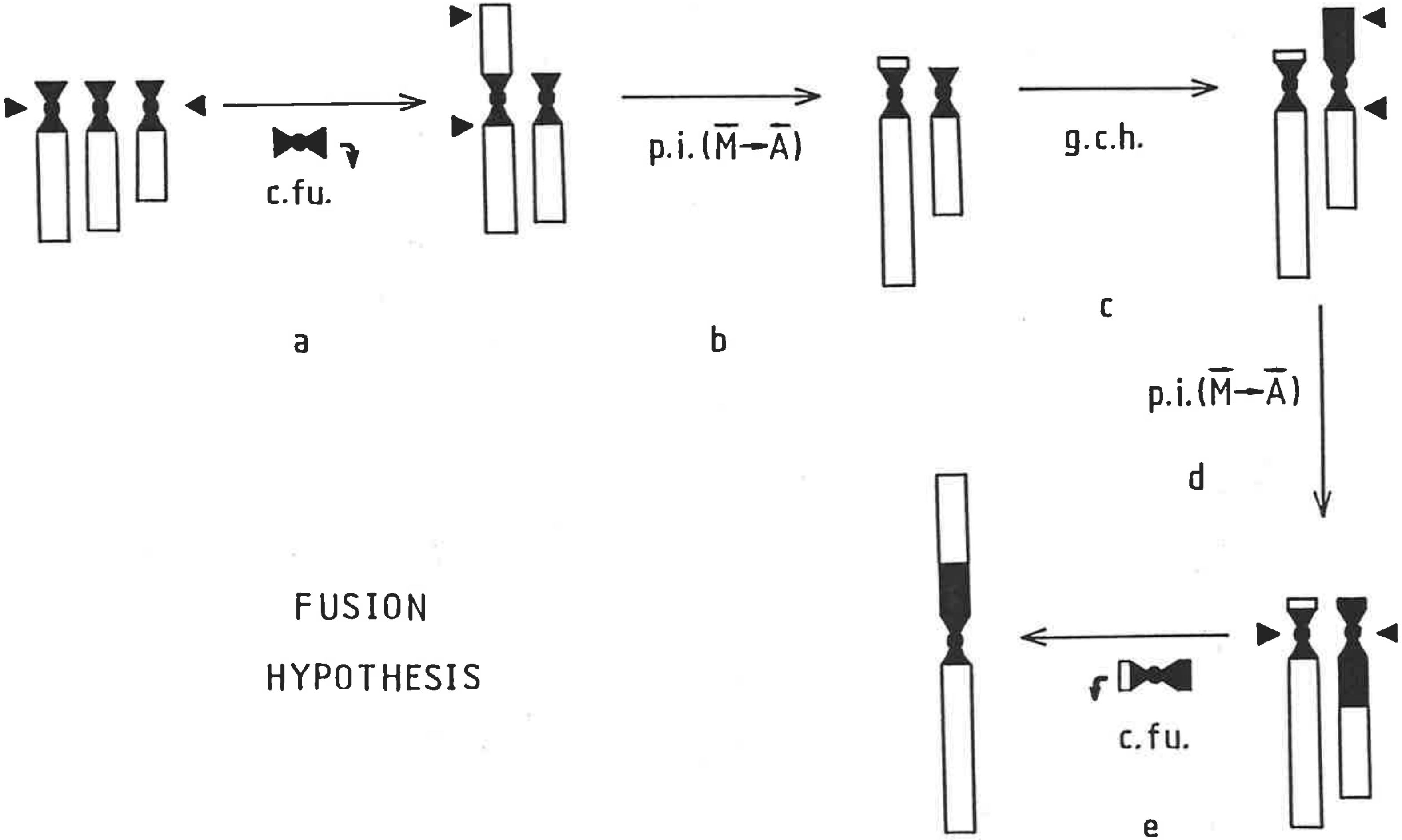
FISSION

HYPOTHESIS

Figure 136. Illustration of the fusion hypothesis, demonstrating how three small 'acrocentrics' may be converted into a large 'metacentric' without loss of euchromatin: (a) two 'acrocentrics' undergo centric fusion (c.fu.) to form a 'metacentric', with loss of a minute chromosome; (b) pericentric inversion converts the 'metacentric' into an 'acrocentric' (p.i.(M A)); (c) growth of constitutive heterochromatin (g.c.h.) converts an 'acrocentric' into a 'metacentric'; (d) pericentric inversion converts a 'metacentric' into an 'acrocentric'; and (e) two 'acrocentrics' undergo centric fusion to form a large 'metacentric'.

[<u>Note</u>: Step (d) is only required to 'undo' the conversion of an 'acrocentric' into a 'metacentric' by growth of constitutive heterochromatin.]

Solid parts of chromosomes represent heterochromatin and open parts represent euchromatin. Solid arrowheads point at breakage points.



FUSION
HYPOTHESIS

inversions can only be *detected* - there is no means of knowing which rearrangements gave rise to them. Consequently, Imai et al. (1977) approached the problem of determining the predominant directionality of chromosome change indirectly by considering (1) the likely directionality of pericentric inversions, and (2) the non-random distribution of Robertsonian and translocation polymorphisms in ants.

They concluded that the likely directionality of pericentric inversions was from 'acrocentrics' to 'metacentrics' because: (1) ant acrocentrics do not have terminal euchromatic caps which are expected when p.i.($\overline{M}\rightarrow\overline{A}$) occurs; (2) statistical considerations strongly indicate that p.i.($\overline{A}\rightarrow\overline{M}$) greatly outnumber those causing the reverse change * (discussed further by Imai and Maruyama, 1978); and (3) their C-banding and comparative karyotype analyses suggested that p.i.($\overline{A}\rightarrow\overline{M}$) have occurred frequently in ant evolution.

The haploid numbers of karyotypes in which Robertsonian and translocation heterozygotes have been found are listed in Appendix 7. The known Robertsonian polymorphisms occur only in high numbered species ($n \geqslant 16$; 20 spp) and translocations only in lower-numbered species ($n \leqslant 16$; 10 spp). Two explanations for this non-random distribution of Robertsonian and translocation polymorphisms have been offered.

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* This is because pericentric inversions involve two breaks, with one break each in the long and short arms of the chromosome. If breaks occur at random along the chromosome, the short arms will usually gain in length. This effect becomes stronger as the centromere is placed nearer the end of the chromosome and should be overwhelming for acrocentrics. However, it is unlikely that all parts of a chromosome will be equally susceptible to breakage.

Imai et al. (1977) interpreted it as follows: '... translocations arise at a constant, although low, rate in all lineages, but ... in those lineages undergoing rapid numerical change, subsequent Robertsonian changes (fissions) soon eliminate any evidence in the form of continued observable heterozygosity for the translocations. In slowly-changing lineages, however, the evidence of translocations will persist longer.' Because translocations are still evident in low-numbered karyotypes, these must represent the slowly-changing and therefore more plesiomorphic lineages, which supports the fission hypothesis.

However, Imai et al. (1984) have recently suggested that translocations may not arise at a constant rate in all lineages. They say instead that because both terminals of bivalents are attached to the nuclear membrane at pachytene (Solari, 1970; Moses, 1977), fundamentally different configurations of chromosomes will arise between karyotypes with a low number of large chromosomes and those with a high number of small chromosomes. The bivalents will be able to interact more freely in the former case and therefore reciprocal translocations will occur more often in low-numbered karyotypes. This second explanation undermines a primary assumption of the first (that translocations occur at a constant rate in all lineages). But it does suggest why chromosome numbers should increase in ants. This is '... to reduce the genetic load due to translocations ...' (Imai et al., 1984).

In summary, evidence from a variety of sources supports the fission hypothesis and contradicts the predictions of the fusion hypothesis. The ancestral ant chromosome number can be assumed to have been low (or at least fairly low), with subsequent increase by a combination of centric fissions, pericentric inversions converting 'acrocentrics' to 'metacentrics', and tandem growth of constitutive heterochromatin. It is expected that centric fusions and p.i.($\overline{M}\rightarrow\overline{A}$) will occur but that these will be significantly outnumbered by those conforming to the fission hypothesis. In other words the overall directionality of ant karyotype evolution is from low-numbered to high-numbered karyotypes but with frequent 'back eddying' towards lower numbers.

In their discussion about overall directionality of chromosome rearrangements, Imai et al. (1977) dealt with chromosome numbers where it would have been preferable to deal with numbers of chromosome arms (*nombre fondamental*, N.F.). However, this was not possible then, nor is it yet possible, because many of the papers citing hymenopteran chromosome numbers do not also document the number of arms. The increase in chromosome number mainly involves centric fissions and p.i.($\overline{A}\rightarrow\overline{M}$) while any decrease, or back-eddying, is mainly via centric fusions and p.i.($\overline{M}\rightarrow\overline{A}$). But, while there are no known reasons why centric fissions should outnumber centric fusions, I have already discussed several reasons to suspect that p.i.($\overline{A}\rightarrow\overline{M}$) are more common than p.i.($\overline{M}\rightarrow\overline{A}$). Thus, the increase in chromosome number is dependent on p.i.($\overline{A}\rightarrow\overline{M}$) but the primary effect of p.i.($\overline{A}\rightarrow\overline{M}$) is to increase the number of chromosome arms. Therefore, it is more accurate to say that the overall directionality has been towards high numbers of chromosome arms. A corollary to the hypothesis that chromosome numbers have tended to increase, is that size of chromosomes has tended to decrease. This can be deduced from Imai et al.'s (1977) demonstration that, in ants, mean chromosome length varies inversely with haploid number.

As a result of the above discussion, I will assume that the plesiomorphic ant chromosome number was near the low end of the n = 3 - 26 range estimated earlier. Extrapolation from this estimate for ants to an estimate for the plesiomorphic *Myrmecia* chromosome number must be done with caution. However, based on (1) the assumption that karyotype evolution in *Myrmecia* has broadly paralleled that in ants, as a whole, and (2) the observation that species in three *Myrmecia* species groups have broadly similar low-numbered karyotypes (i.e. *rufinodis*, n = 5, N.F. = 18; *pilosula*, *s.l.*, n = 5, N.F. = 18; *fulvipes*, *s.l.*, n = 6, N.F. = 22), I will tentatively assume that the plesiomorphic *Myrmecia* karyotype was near n = 5 (N.F. = 20) and that any karyotypes with n > c.26 or N.F. > c.52 (estimated on the basis of an n = 26 karyotype consisting of all 'acrocentrics') are unlikely to be plesiomorphic for their species group. Apomorphic states are:

K1. N.F. ⩾ c.60 (*forficata* group)

K1.1. N.F. ⩾ 82 (*brevinoda*, *s.s.* + *decipiens* + *forficata*, *s.s.* + *pyriformis* + *sp.7*).

K2. N.F. ⩾ 50 (convergently evolved; *vindex* group)

K2.1. N.F. ⩾ 68 (*desertorum* + *fulgida* + *fuscipes* + *nigriceps*, *s.s.* + *vindex* + *sp.11* + *sp.12* + *sp.13* + *sp.14* + *sp.16* + *sp.17*)

K2.1.1. N.F. ⩾ 76 (*desertorum* + *fuscipes* + *nigriceps*, *s.s.* + *sp.12* + *sp.13* + *sp.16*)

K2.1.2. N.F. ⩾ 76 (convergently evolved; *fulgida* + *vindex* + *sp.14*)

K3. N.F. = 76 (convergently evolved; *gulosa* group)

K4. N.F. = 62 (convergently evolved; *forceps* group)

K5. N.F. ⩾ 60 (*pilosula* (in part) + *mandibularis* (in part) groups)

K5.1. N.F. = c.70 (convergently evolved; *michaelseni*)

K5.2. N.F. = 66 (convergently evolved; *cephalotes*)

K5.3. N.F. = c.68 (convergently evolved; *piliventris*, *s.l.* (one population))

4.2.4.2. Complex translocation polymorphism

Primitively, karyotypes do not contain any complex translocation polymorphisms. This is the condition in all but a few *Myrmecia* species and almost all other ants - indeed, almost all other eukaryotes. Apomorphic state is:

K6. Karyotype containing a complex translocation polymorphism involving six chromosomes (*pilosula*, *s.l.* (three populations))

4.2.4.3. Substantial growth of heterochromatin

Primitively, almost all heterochromatin is associated with the centromeres of chromosomes. This is the condition in all but a few *Myrmecia* species, almost all other ants and indeed, almost all other eukaryotes. Apomorphic state is:

K7. Many chromosomes with considerable non-centromeric growth of heterochromatin (*brevinoda*, *s.s.* + *decipiens*)

4.2.5 Behaviour

4.2.5.1 Prosalience

Primitively, *Myrmecia* are incapable of prosalience (forward leaping), and move only by walking (nonsalience). This is the condition in about 50% of *Myrmecia* species and the vast majority of other ant genera. Two other primitive ant genera are prosalient, the ponerine *Harpegnathos* Jerdon and the formicine *Gigantiops* Roger, and according to Wheeler (1922, p. 198) '... it would seem ... that the leaping habit may have been much more general among the most ancient macrophthalmic [large-eyed] Formicidae ...' However, because the majority of extant primitive genera are nonsalient it seems unlikely that *Myrmecia* would have been primitively prosalient. Apomorphic state is:

B1. Workers prosalient (i.e. jumpers; *nigrocincta* + *harderi* + *pilosula* + *mandibularis* + *picta* + *sp.15* + *fucosa* + *urens* groups)

4.2.5.2 Monogyny / polygyny

Primitively, mature colonies are monogynous. This is the condition in all but one *Myrmecia* species. Apomorphic state is:

B2. Mature colonies polygynous (*pilosula*, *s.l.*; possibly not all populations)

4.2.5.3 Monodomy / polydomy

Primitively, colonies are monodomous. This is the condition in all but one *Myrmecia* species. Apomorphic state is:

B3. Polydomous colonies (*fuscipes*)

4.2.5.4 Nest substrate

Primitively, nests are constructed entirely in the ground. This is the condition in all species of 17 out of 19 *Myrmecia* species groups and some species of one other. Apomorphic states are:

B4. Nest constructed in ground but with galleries extending up into a decaying log or constructed in peat of trees (*forficata* (in part) group)

B5. Nest constructed in peat of trees (*mjobergi* group)

[*Note*: State B5 may be derived from state B4.]

4.2.5.5 Nest internal structure

Ascending galleries which end in chambers just beneath the surface are primitively lacking from nests, as in all but one species group of *Myrmecia*. Apomorphic state is:

B6. Nest with ascending galleries which end in chambers just beneath the surface (*nigriscapa* group)

4.2.5.6 Social parasitism

Like the vast majority of ant species, all but two species of *Myrmecia* are not socially parasitic and this is therefore taken to be the plesiomorphic state. Apomorphic states are:

B7. Social parasite (*inquilina*)

B8. Social parasite (convergently evolved; *hirsuta*)

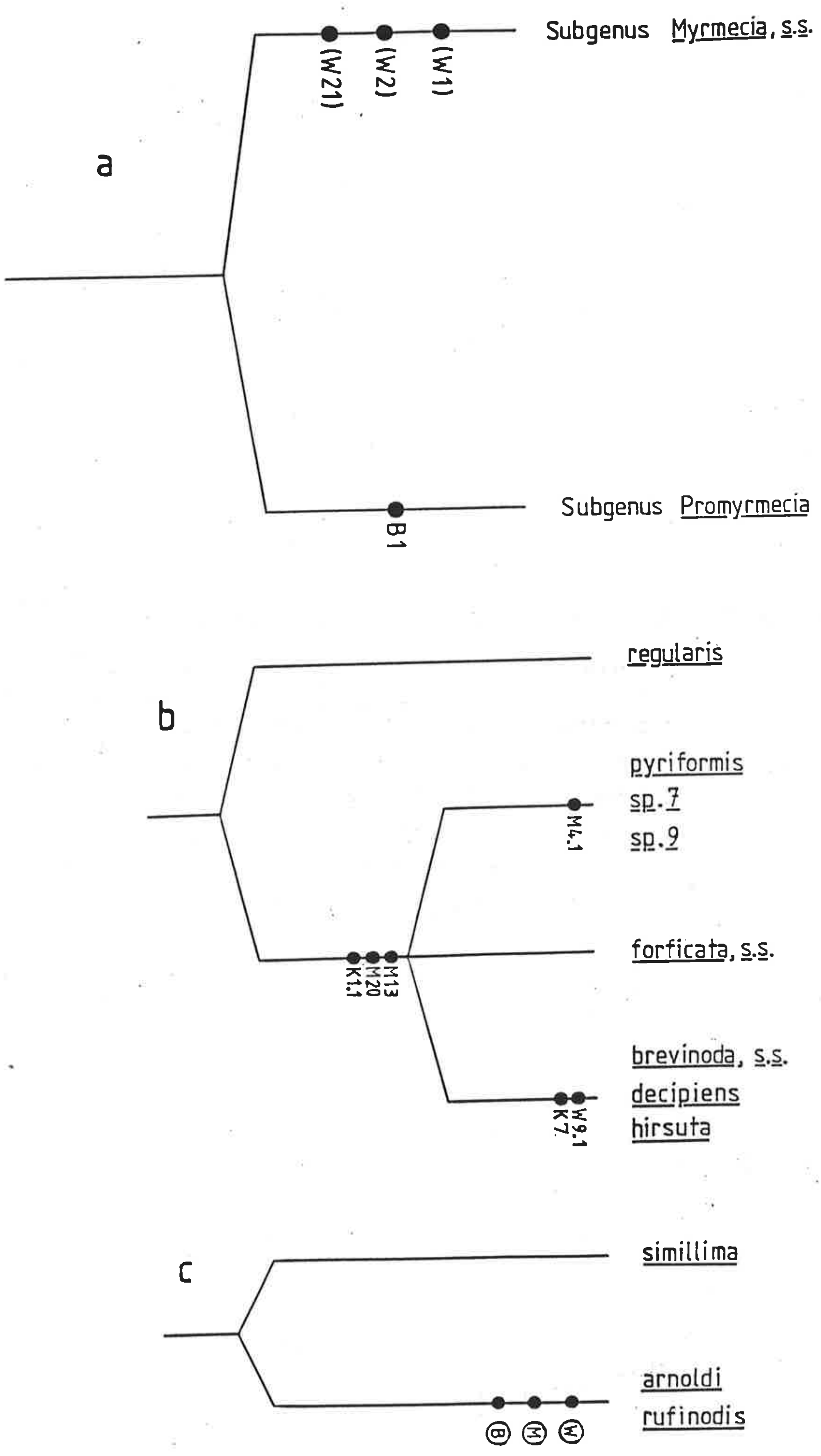
While details of social parasitism by *hirsuta* are not as well documented as the life history of *inquilina* (Douglas and Brown, 1959; Haskins and Haskins, 1964) there are structural differences to suggest marked dissimilarity due to the strategy being evolved convergently. The most obvious of these is that *inquilina* (of the *vindex* group) is workerless, while *hirsuta* (of the *forficata* group) has the usual worker subcastes.

4.3 Splitting *Myrmecia* into subgenera

The ancestral *Myrmecia* was probably: (a) a non-jumper; (b) monomorphic, with workers more or less uniform in size; and (c) relatively small (all workers between about 10 and 18 mm in length). These assumptions have been based upon arguments presented in section 4.2. There are no such species among the extant *Myrmecia*, which probably indicates that for small *Myrmecia* the habit of jumping conveys considerable selective advantage over non-jumping. However, for large *Myrmecia* adoption of jumping as a form of locomotion is probably too expensive energetically. A high energy cost is probably attached to jumping because no species always jump and all are more inclined to do so on warm days and when disturbed. There seems little to differentiate jumpers and non-jumpers morphologically (Wheeler, 1922) and it may be that when large species alight from trees to the ground they are in effect performing a single jump.

From such an ancestor two groups of *Myrmecia* appear to have evolved (fig. 137a) - one group has stayed about the same size and commenced jumping, while the other has become larger and its worker caste has differentiated into two subcastes (the smaller roughly the same size as jumpers). These two groups are recognised as subgenera *Promyrmecia* and *Myrmecia*, *s.s* respectively.

Figure 137. Probable phylogenetic relationships between (a) subgenera of Myrmecia; (b) species of the forficata group; and (c) species of the simillima group. Numbers refer to apomorphic characters listed and discussed in the text. Those placed in parentheses are not present in all species. Note also that some characters may not be known for all species. Circled letters indicate that the species have almost identical characters from that character source (W, worker morphology; M, male terminalia; B, behaviour).


a
Subgenus Myrmecia, s.s.
(W21)
(W2)
(W1)
Subgenus Promyrmecia
B1
b
regularis
pyriformis
sp. 7
sp. 9
M4.1
forficata, s.s.
K1.1
M20
M13
brevinoda, s.s.
decipiens
hirsuta
K7
W9.1
c
simillima
arnoldi
rufinodis
Ⓑ
Ⓜ
Ⓦ

Although this division into subgenera remains somewhat tentative, there are a number of characters, in addition to those mentioned above, which more or less support it. These are listed in Table 17.

It should be noted that no male terminalia or karyotype characters have been found useful for separating the subgenera, but neither do they contradict it in any way. It seems that subsequent evolutionary change in both types of characters may have been sufficient to remove any evidence for separation of the subgenera at a distant point in time.

4.4 Phylogeny of subgenus Myrmecia, s.s.

An hypothesis for the phylogeny of subgenus Myrmecia, s.s. is presented in fig. 138. Seven of the 11 species groups are monotypic, but two (forficata and vindex) are relatively speciose. Monophyly for each of three non-monotypic species groups (forficata, vindex and esuriens) is well supported, but the simillima group is united by a single synapomorphy. My overall impression of the species groups is that they have existed as separate lineages for a considerable period of time because their male terminalia are all very distinctive.

Workers of the esuriens group have a more jumper-like appearance than any of the others, but I am unable to identify any convincing synapomorphies to demonstrate monophyly for the non-esuriens species groups. Such monophyly is nonetheless suggested by their larger size, more slender appearance and very broadly similar inner valves of the male terminalia.

The forficata and mjobergi groups form a monophyletic group, united by six synapomorphies derived from worker morphology, male terminalia and behaviour. However, while monophyly for (gulosa + simillima + vindex) groups is firmly indicated, it is only based on two

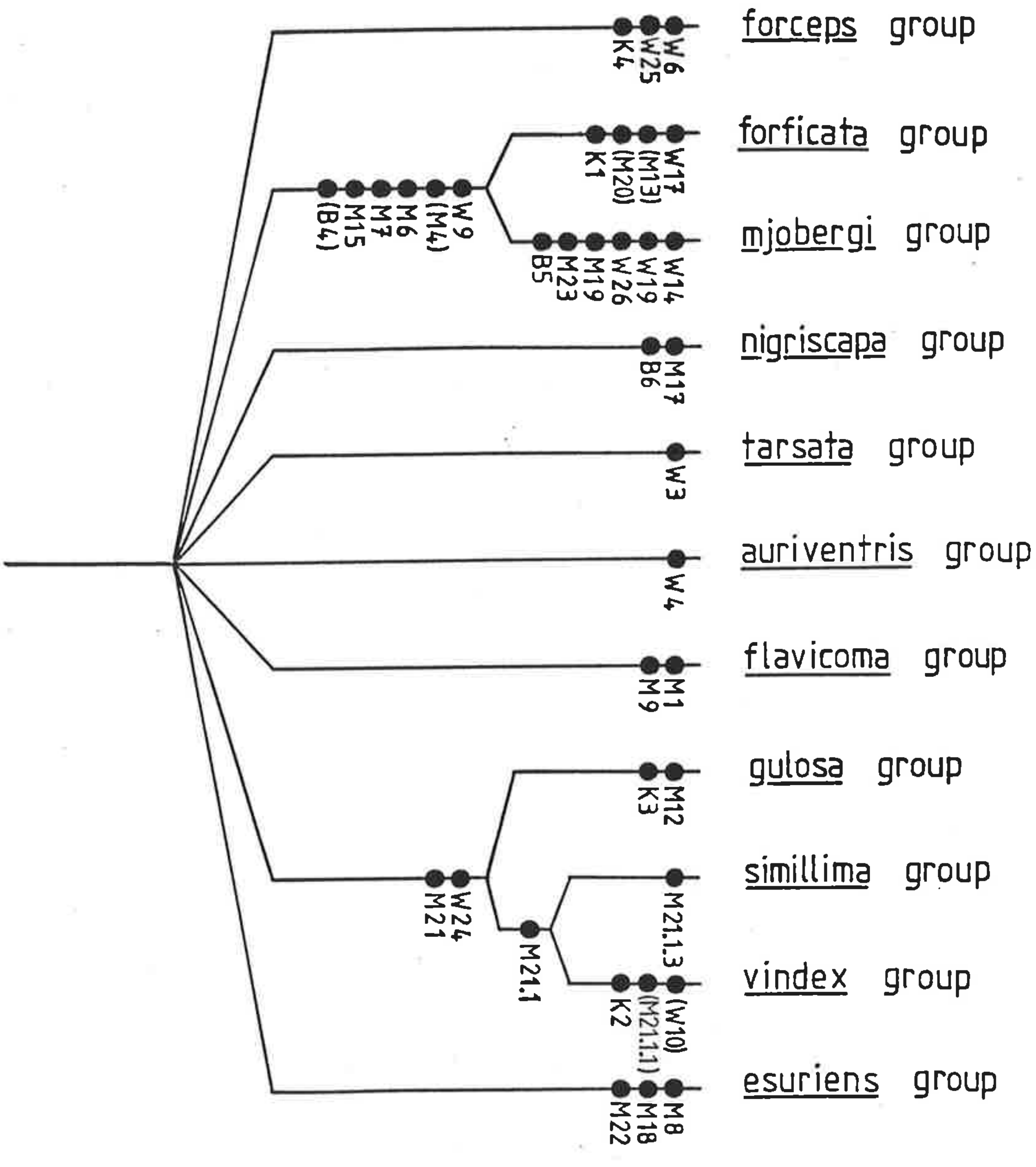


Figure 138. Probable phylogenetic relationships between species groups of subgenus Myrmecia, s.s. Numbers refer to apomorphic characters listed and discussed in the text. Those placed in parentheses are not present in all species. Note also that some characters may not be known for all species.

TABLE 17. Comparison of various characters in subgenera *Myrmecia*, *s.s.* and *Promyrmecia*.

Character	*Myrmecia*, *s.s*	*Promyrmecia*
Queen size (length)	Usually > 20 mm, never < 18mm	Usually < 20 mm, never > 24 mm
Worker size (length)	Always > 17 mm	Always ⩽ 17 mm
Worker size division	Always at least two subcastes	All workers about the same size
Capable of prosalience	No	Yes
Scape length of worker antennae	Long	Short
Mesosoma width of workers	Narrow	Broad
Petiole length of workers	Long	Short
Leg length of workers	Long	Short
Mature colony population	Often > 500 workers	Usually < 200 workers
Mound of nest	Usually large and obvious	Usually small and inconspicuous
Internal nest structure	Usually of Gray's (1974a) diffuse type	Usually of Gray's (1974a) simple type
Aggressiveness	Usually very aggressive when nest disturbed	Tend not to come out of nest when disturbed

synapomorphies. Monophyly of the (*simillima* + *vindex*) group is even more tentative because it is supported by a single synapomorphy. No synapomorphies have been found to suggest monophyly between any combinations of the *forceps*, (*forficata* + *mjobergi*), *nigriscapa*, *tarsata*, *auriventris*, *flavicoma* and (*gulosa* + *simillima* + *vindex*) groups.

4.4.1 Phylogeny of the *forficata* group

My hypothesis for the phylogeny of the *forficata* group (fig. 137b) includes another large monophyletic subgroup, supported by three synapomorphies and including all the species except *regularis*. It appears that *regularis*, with more plesiomorphic male terminalia and chromosome number, has been restricted to a relatively small, high rainfall area of south-west Western Australia, while its relatives in eastern Australia have occupied a much wider geographic area and speciated a number of times. *M. brevinoda*, *s.s.*, *decipiens* and *hirsuta* appear to form a monophyletic subgroup united by two synapomorphies and *pyriformis*, *sp.7* and *sp.9* have tentatively been placed in another on the basis of one synapomorphy.

4.4.2 Phylogeny of the *simillima* group

Although no synapomorphies from section 4.2 can be used to establish monophyly of a species pair within the three-membered *simillima* group, *arnoldi* and *rufinodis* are nearly identical in all aspects of their worker morphology, male terminalia and behaviour so that their monophyly is unquestionable (fig. 137c).

4.4.3. Phylogeny of the *vindex* group

My hypothesis for the phylogeny of the *vindex* group (fig. 139) indicates that, within the *vindex* group, *princeps* is the sister group of the remainder of the species. However, the monophyly of the non-*princeps* subgroup is tentative because it depends upon only one synapomorphy. Furthermore, it includes two species (*inquilina* and *rowlandi*) whose relationships to the remainder of the *vindex* group are uncertain.

Monophyly of the vindex group minus *princeps*, *inquilina* and *rowlandi* (the central block on fig. 139) is well supported by their

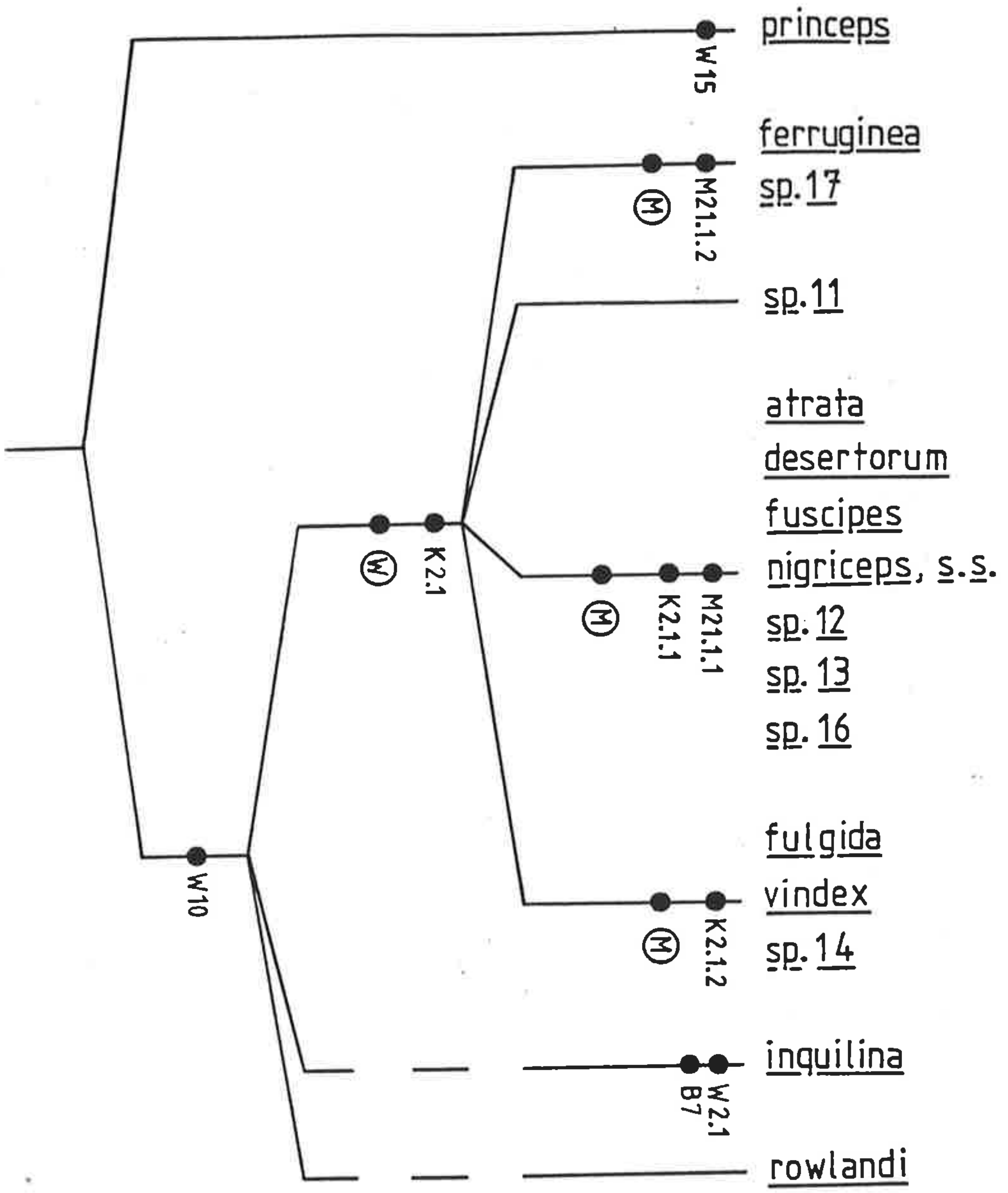


Figure 139. Probable phylogenetic relationships between species of the vindex group. Numbers refer to apomorphic characters listed and discussed in the text. Note that some characters may not be known for all species.

derived karyotypes and workers, which are almost identical except for colouration. It is possible that *inquilina* also belongs to this monophyletic group, but crucial evidence from its male terminalia and karyotype is lacking.

Identification of monophyletic subdivisions within the central subgroup is also tentative, because in this instance male terminalia and karyotypes provide somewhat contradictory evidence. Thus, based on presence of a cluster of spines on the inner valve, it would seem that (*ferruginea* + *sp.17* + *sp.11* + *desertorum* + *fuscipes* + *nigriceps*, *s.s.* + *sp.12*) form a monophyletic group, which probably includes *atrata*, *sp.13* and *sp.16* whose male terminalia are unknown. However, this contradicts evidence from the karyotypes, because *atrata*, *desertorum*, *fuscipes*, *nigriceps*, *s.s.*, *sp.12*, *sp.13*, *sp.16*, *fulgida*, *vindex* and *sp.14* all have higher and more apomorphic *nombres fondamentaux* (N.F. = 76-80) than *ferruginea*, *sp.17* and *sp.11* (N.F. = 68). For the present I have dealt with this contradiction by hypothesizing that the two character states have each evolved twice (i.e. M21.1.1 and M21.1.2, K2.1.1 and K2.1.2). If so, then within the central subgroup there are three monophyletic subdivisions as shown - (*ferruginea* + *sp.17*), (*atrata* + *desertorum* + *fuscipes* + *nigriceps*, *s.s.* + *sp.12* + *sp.13* + *sp.16*) and (*fulgida* + *vindex* + *sp.14*) - and one remaining species (*sp.11*). The male terminalia of species within each subdivision are virtually identical but distinct from those of the other subdivisions.

4.4.4 Phylogeny of the *esuriens* group

Relationships between the three species of the *esuriens* group are unclear. No synapomorphies have been found to suggest affinities between any two species to the exclusion of a third.

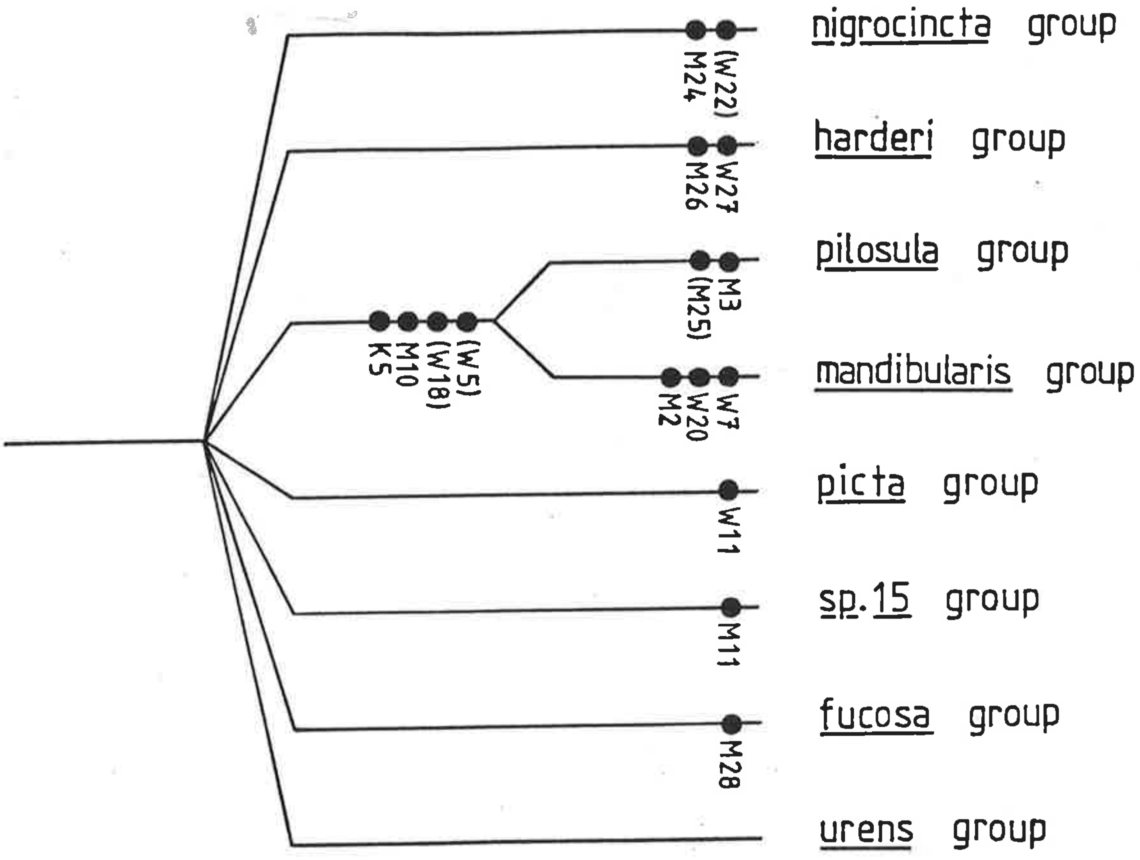


Figure 140. Probable phylogenetic relationships between species groups of subgenus Promyrmecia. Numbers refer to apomorphic characters listed and discussed in the text. Those placed in parentheses are not present in all species. Note also that some characters may not be known for all species.

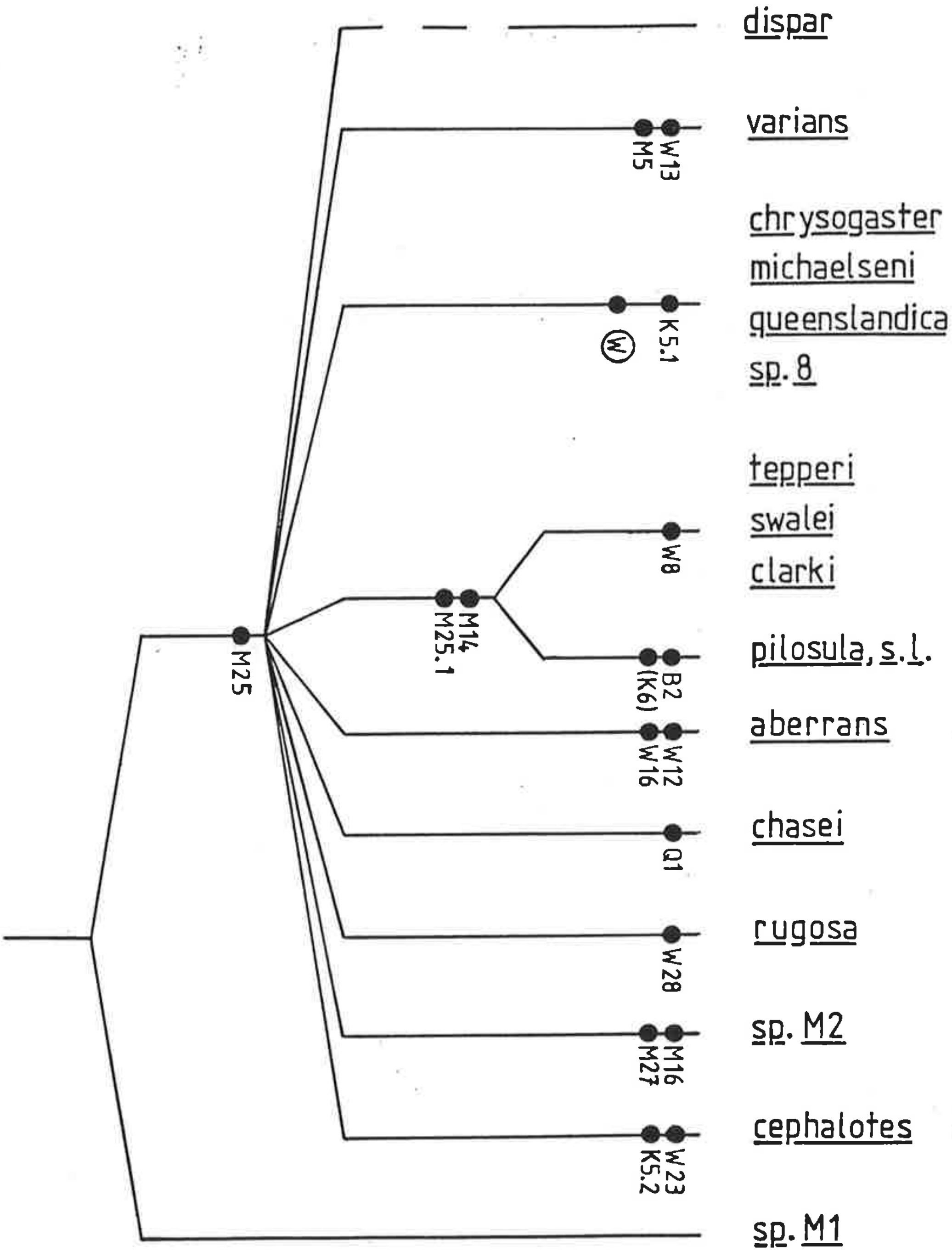


Figure 141. Probable phylogenetic relationships between species of the *pilosula* group. Numbers refer to apomorphic characters listed and discussed in the text. Those placed in parentheses are not present in all species. Note also that some characters may not be known for all species. Circled letters indicate that the species have almost identical characters from that character source (W, worker morphology).

4.5 Phylogeny of subgenus *Promyrmecia*

My hypothesis for the phylogeny of subgenus *Promyrmecia* is shown in fig. 140. Of the eight species groups, five are monotypic, two contain a handful of species (*nigrocincta* and *mandibularis*) and one is relatively speciose (*pilosula*). Monophyly of each of the three non-monotypic species groups is moderately well-supported by two or three synapomorphies. Relationships between the species groups are uncertain. It seems likely that the *pilosula* and *mandibularis* groups together form a monophyletic group, united by three synapomorphies (two of which are not present in all species). At present no other monophyletic groups are recognizable.

4.5.1 Phylogeny of the *nigrocincta* group

Relationships between the five species of the *nigrocincta* group are unclear. My search for synapomorphies in this group was greatly restricted by male terminalia and chromosomes having been examined for only one species.

4.5.2 Phylogeny of the *pilosula* group

Part of my hypothesis for the phylogeny of the *pilosula* group (fig. 141) is that *sp.M1* is a sister group to the remainder of the species. However, monophyly for the non-*sp.M1* species is supported by only one synapomorphy (i.e. M25, loss of spines on the inner valve). *M. chrysogaster*, *michaelseni*, *queenslandica* and *sp.8* form a monophyletic group because their workers are nearly identical. *M. tepperi*, *swalei*, *clarki* and *pilosula*, *s.l.* also appear to form a monophyletic group, based on two synapomorphies in their male terminalia, and within this group the first three appear to form another monophyletic group based mainly on their quite similar, and apomorphic, worker mandibles. Further relationships within the group are unclear.

4.5.3 Phylogeny of the *mandibularis* group

Relationships between the five or so species of the *mandibularis* group are unclear. No synapomorphies have been found which enable me to form subgroups.

5. CONCLUSIONS

The major divisions of bulldog ants and jumpers into genera or subgenera by Emery (1911), Wheeler (1922), Clark (1951) and the present study are broadly similar (figs 1, 142-143). Emery's *Myrmecia*, *s.s.* is the same as mine except for his inclusion of the *nigrocincta* and *pilosula* groups, which Wheeler removed. My subgenus *Promyrmecia* is equivalent to the sum of Emery's *Promyrmecia* and *Pristomyrmecia*, and Wheeler's *Halmamyrmecia*. Clark's genus *Myrmecia* differs from my subgenus *Myrmecia*, *s.s.* only by his inclusion of the *nigrocincta* group, and his genus *Promyrmecia* is identical to my subgenus of the same name, except that he excluded the *nigrocincta* group.

At the species group level, Emery and Clark knew species from 16 of my 19 species groups, yet only two of these groups (*nigrocincta* and *mandibularis*) are common to all three classifications. Emery's *esuriens* group and Clark's *forceps* and *urens* groups are also equivalent to mine, but the rest differ by the inclusion or exclusion of at least one species and sometimes are quite incongruent. For example, Emery's *tarsata* and Clark's *tricolor* groups contain species from seven and nine of my groups respectively, while I have grouped species from five of Clark's groups into my *pilosula* group.

Overall, I consider that my classification is broadly similar to its antecedents and that most improvements are traceable to differentiation between similarity due to synapomorphy and that resulting from parallel evolution (symplesiomorphy) or convergence. While I am still unable to confidently delimit all biological species in *Myrmecia*, my delimitations, which are based on evidence from worker

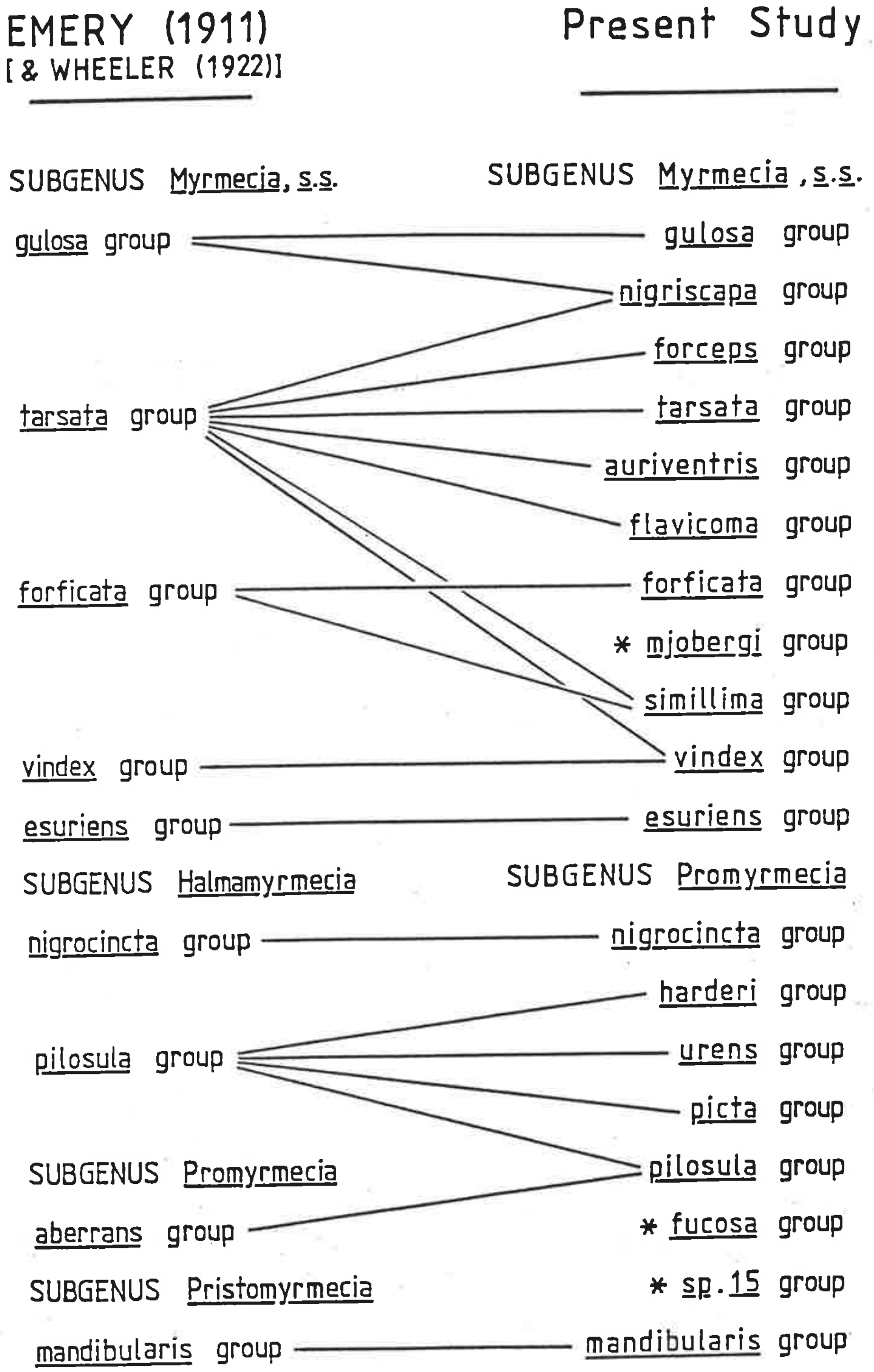


Figure 142. Comparison of the subgeneric classifications for Myrmecia proposed by Emery (1911) and the present study. The Emery classification includes a slight modification by Wheeler (1922), which removed nigrocincta and pilosula groups from subgenus Myrmecia, s.s. and placed them in a new subgenus, Halmamyrmecia. Lines indicate where species from each group of both classifications reside in the opposing classification. Groups asterisked in the present study classification only contain species unknown to Emery.

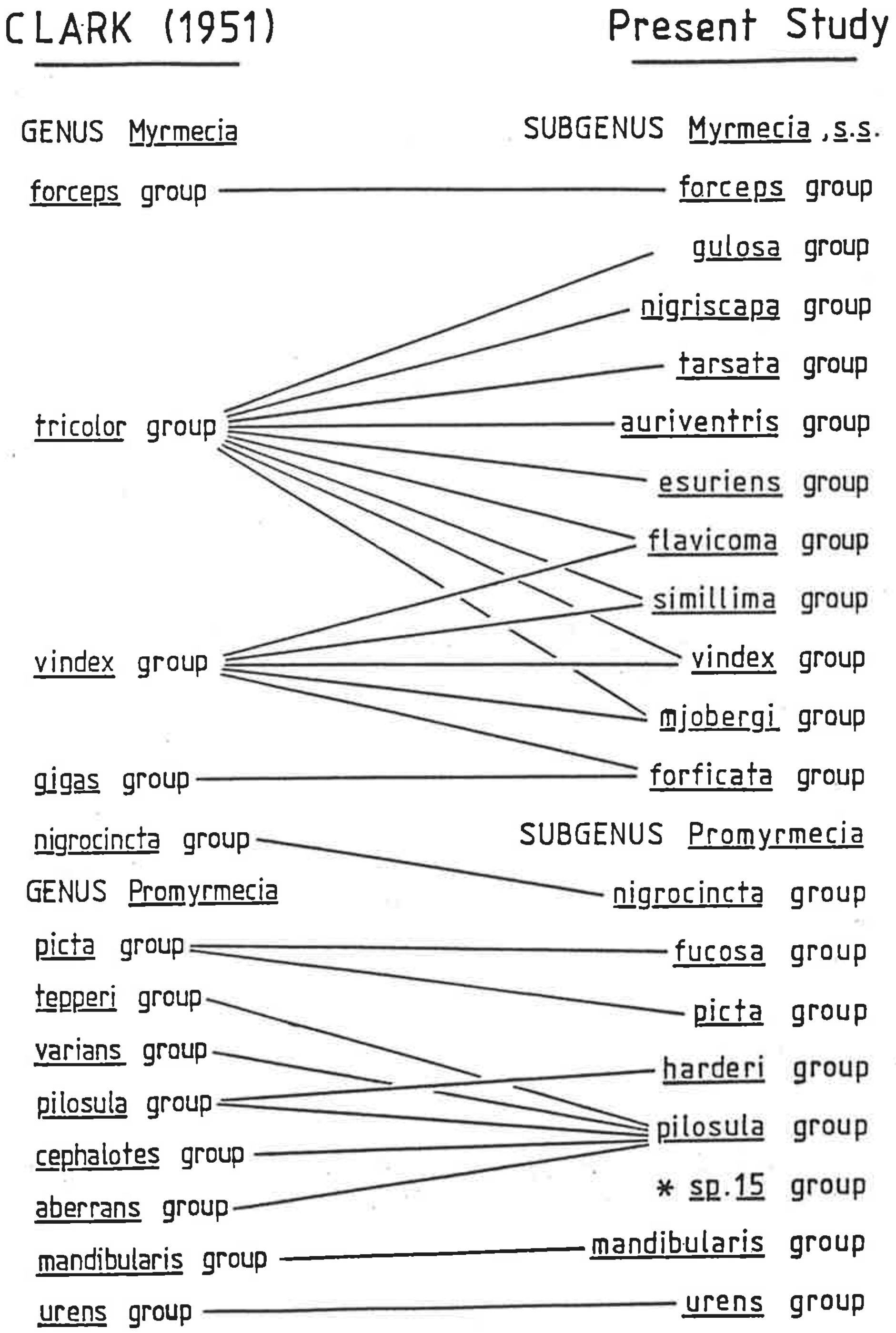


Figure 143. Comparison of the subgeneric classifications for Myrmecia proposed by Clark (1951) and the present study. Lines indicate where species from each group of both classifications reside in the opposing classification. The group asterisked in the present study classification only contains a species unknown to Clark.

morphology, male terminalia, behaviour and karyotype, are naturally more reliable than those of earlier researchers, who often described species based on very small series of workers. Thus this study represents a substantial development of *Myrmecia* taxonomy. The future development of *Myrmecia* taxonomy should involve continued use of the techniques employed here. Males are still unknown for about 20 species and karyotypes have been determined for less than half the known species. Male terminalia have proved to be most valuable for assessing relationships within and between species groups but are also useful for delimiting some sibling species. Karyotypes are generally unsuitable for determining relationships between species groups and will prove more valuable for assessing the status of putative species - particularly when apparent siblings are found to occur sympatrically. Species which should be investigated for sibling species are *forceps*, *brevinoda*, *s.l.*, *forficata*, *s.l.*, *nigriscapa*, *simillima*, *atrata*, *ferruginea*, *fuscipes*, *nigriceps*, *s.l.*, *princeps*, *vindex*, *sp.14*, *pulchra*, *harderi*, *aberrans*, *cephalotes*, *pilosula*, *s.l.*, *queenslandica*, *swalei*, *tepperi*, *varians*, *fulvipes*, *s.l.*, *mandibularis*, *piliventris*, *s.l.*, *picta*, *fucosa* and *urens*. These species all have a widespread distribution, or exhibit inconsistencies in their karyotypes, male terminalia, worker colouration or nest structure. SEM, at the low resolution used in this study for illustrative purposes, is unlikely to be of much further use for delimiting species or identifying relationships, but if it is used to examine workers and other life stages (e.g. larvae, males) at a much higher resolution it should be more valuable. Behavioural studies relating form to function have barely commenced in *Myrmecia* and undoubtedly have the potential to provide more synapomorphies. Morphometric analysis is also likely to provide more insight into the development of worker subcastes in different species, although this may have limited taxonomic applications. It will be interesting to discover whether three worker subcastes as reported here for one population of *fuscipes* are a widespread phenomenon. It seems likely that they will be found in at least one species (*brevinoda*, *s.l.*) which has some enormous workers (36 mm in length). Although no jumpers are yet known to have two worker subcastes it is possible that species such as *chasei* and some from the *mandibularis* group (i.e. those jumpers with the largest queens) may have them.

A number of other, mainly biochemical, techniques which were not used in this study are likely to contribute greatly to development of *Myrmecia* taxonomy. I consider the most promising techniques to be isozyme studies (electrophoresis), analysis of venoms and pheromones, and mitochondrial DNA sequencing. Isozyme studies and analysis of venoms and pheromones will probably provide evidence more suitable for identifying and determining relationships between populations and species within species groups, but could also be useful at higher levels. Mitochondrial DNA sequencing is likely to be less useful at low levels, but invaluable for confirming composition of and relationships between species groups.

A particularly interesting aspect of *Myrmecia* karyotypes is the presence in *pilosula*, *s.l.* of a number of very different cytotypes. How this arose and whether it is related to that species being polygynous is unknown. The observation that ants (especially *Myrmecia*) and other social insects tend to have higher chromosome numbers than their closest non-social relatives (Sherman, 1979) should also be investigated further. I suspect that karyotype evolution in *Myrmecia* and social insects is not fundamentally different to karyotype evolution in other eukaryotes, but that it differs in the speed with which it has been able to proceed. Social insects differ from most other eukaryotes in that they usually live in colonies, which are more or less fixed in space. Therefore it is advantageous for a colony to maintain a home range, within which it will not allow other colonies to become established, because they would provide competition for resources. Such behaviour has been observed in Myrmecia by Muir (1975, pp 103-105), who found that workers of several species will seek out, and destroy, incipient nests of the same species if they occur within a certain radius of their home nests. The establishment of home ranges by such inter-colony aggression means that new colonies will usually begin in space unoccupied by that species. If a new colony is founded far enough away from other colonies of the same species, then its queen, which may live for an estimated 20-30 years, and probably is fertilized only once, will be able to saturate the surrounding area with her progeny. Thus, any chromosome polymorphisms she may possess will rapidly become fixed.

Essentially what I am proposing is the 'founder principle' of Mayr (1942). According to White (1978), 'theoretically, a newly founded colony [in a non-social sense], whether derived from a small number of immigrants or a single gravid female, will at the start be more homozygous and less polymorphic than the original population. If the colony survives, however, mutation is expected to restore the level of polymorphism rather soon to approximately the original value, although the alleles may not be exactly the same as the original ones, and their frequencies would certainly be different. Moreover, in the initial stages of its existence, unless the colony exhibits "inbreeding depression", the population size is likely to increase rapidly, as a result of temporary absence of competitors and controlling agents. During this phase of expansion the chances of survival of new mutations are much greater than in a population of stable size.' Hence, deleterious rearrangements will be quickly eliminated from the population while advantageous ones, if they occur in a colony-founding queen or the male which fertilizes her, will quickly become established as polymorphisms in the population. Consequently, rapid and extensive changes in chromosome number and _nombres fondamentaux_, and speciation without gross morphological change, are likely to be occur commonly in _Myrmecia_ in particular, but also in other social insects, because they invest the ability to reproduce in a relatively small number of individuals. Rapid speciation has been associated with small effective population size and close inbreeding in such diverse groups as horses (Bush et al., 1977) and parasitic Hymenoptera (Goodpasture, 1975a). An investigation of speciation mechanisms in social insects would provide valuable insight into speciation of eukaryotic organisms.

Other interesting avenues for research on _Myrmecia_ include examining the role of worker subcastes found by morphometric analysis, effects of venom on various animals (including humans), investigating the predators and prey of _Myrmecia_, understanding the movements of workers and brood within the nest in response to moisture and temperature gradients, investigation of life cycles of protozoan, wasp and other parasites, and investigation of coloural convergence between species.

Undoubtedly, exploration of the avenues outlined above would lead to a far superior understanding of the phylogenetic relationships and general biology of this extraordinary genus.

6. APPENDICES

APPENDIX 1. COLLECTION DATA

Colony	Species	Lat.S Long.E	Locality	State	Date Collected	Collected by
1.	*pyriformis*	34°55' 138°45'	Marble Hill	SA	26.ii.79	GPB
2.	*fuscipes*	34°26' 138°16'	Port Parham	SA	27.ii.79	GPB,PC
3.	*fuscipes*	34°26' 138°16'	Port Parham	SA	27.ii.79	GPB,PC
4.	*fuscipes*	34°26' 138°16'	Port Parham	SA	27.ii.79	GPB,PC
5.	*fuscipes*	34°26' 138°16'	Port Parham	SA	3.iii.79	GPB
6.	*fuscipes*	34°26' 138°16'	Port Parham	SA	3.iii.79	GPB
7.	*fuscipes*	34°31' 138°20'	Port Prime	SA	3.iii.79	GPB
8.	*nigriceps*, *s.l.*	35°10' 138°34'	Manning Reserve, Blewitt Springs	SA	6.iii.79	GPB
9.	*nigriceps*, *s.l.*	35°10' 138°34'	Manning Reserve, Blewitt Springs	SA	6.iii.79	GPB,DAD
10.	*nigriceps*, *s.l.*	35°10' 138°34'	Manning Reserve, Blewitt Springs	SA	6.iii.79	GPB
11.	*nigriscapa*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	17.iii.79	GPB
12.	*sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	18.iii.79	GPB
13.	*sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	18.iii.79	GPB
14.	*sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	19.iii.79	GPB
15.	*nigriscapa*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	19.iii.79	GPB
16.	*sp.9*	35°48' 136°37'	Ravine de Casoars, Flinders Chase NP	SA	20.iii.79	GPB

APPENDIX 1 (cont.).

17. *sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	20.iii.79	GPB
18. *sp.9*	35°57' 136°40'	4 km W of Rocky River HS, Flinders Chase NP	SA	21.iii.79	GPB
19. *sp.9*	35°57' 136°40'	4 km W of Rocky River HS, Flinders Chase NP	SA	21.iii.79	GPB
20. *sp.9*	35°57' 136°40'	4 km W of Rocky River HS, Flinders Chase NP	SA	21.iii.79	GPB
21. *sp.9*	35°54' 136°44'	6 km N of Rocky River HS, Flinders Chase NP	SA	21.iii.79	GPB
22. *sp.9*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	21.iii.79	GPB
23. *pilosula*, *s.l.*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	21.iii.79	GPB
24. *nigriceps*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	21.iii.79	GPB
25. *sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	22.iii.79	GPB
26. *nigriceps*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	22.iii.79	GPB
27. *nigriceps*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	22.iii.79	GPB
28. *sp.9*	35°37' 136°44'	Rocky River HS, Flinders Chase NP	SA	22.iii.79	GPB
29. *sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	22.iii.79	GPB
30. *sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	22.iii.79	GPB
31. *forceps*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	22.iii.79	GPB
32. *sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	22.iii.79	GPB
33. *sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	22.iii.79	GPB

APPENDIX 1 (cont.).

34. *sp.9*	35°48' 137°12'	Parndana CP	SA	23.iii.79	GPB
35. *rufinodis*	35°39' 137°38'	7 km S of Kingscote	SA	23.iii.79	GPB
36. *pyriformis*	34°47' 138°47'	Upper Hermitage	SA	29.iii.79	GPB
37. *pyriformis*	34°58' 138°42'	Greenhill	SA	3.iv.79	GPB
38. *pyriformis*	35°01' 138°37'	Blackwood	SA	4.iv.79	GPB
39. *pyriformis*	35°00' 138°38'	Belair	SA	4.iv.79	GPB
40. *pyriformis*	35°00' 138°38'	Belair	SA	4.iv.79	GPB
41. *pyriformis*	34°57' 138°45'	Uraidla	SA	6.iv.79	GPB,PC
42. *pyriformis*	34°57' 138°45'	Uraidla	SA	6.iv.79	GPB,PC
43. *pyriformis*	34°57' 138°45'	Uraidla	SA	6.iv.79	GPB,PC
44. *pyriformis*	34°57' 138°45'	Uraidla	SA	6.iv.79	GPB,PC
45. *pilosula*, *s.l.*	34°57' 138°45'	Uraidla	SA	6.iv.79	GPB,PC
46. *pilosula*, *s.l.*	34°57' 138°45'	Uraidla	SA	6.iv.79	GPB,PC
47. *pilosula*, *s.l.*	34°57' 138°45'	Uraidla	SA	6.iv.79	GPB,PC
48. *pilosula*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	20.iii.79	GPB
49. *nigriscapa*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	18.iii.79	GPB
50. *nigriceps*, *s.l.*	35°10' 138°34'	Manning Reserve, Blewitt Springs	SA	6.iii.79	GPB,DAD
51. *pilosula*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	17.iii.79	GPB

APPENDIX 1 (cont.).

52.	*sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	18.iii.79	GPB
53.	*pilosula*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	18.iii.79	GPB
54.	*pilosula*, *s.l.*	34°55' 138°46'	Cherryville	SA	26.ii.79	GPB
55.	*queenslandica*	34°36' 138°53'	Sandy Creek CP	SA	12.iii.79	GPB
56.	*pilosula*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	7.iii.79	MBT
57.	*fuscipes*	34°39' 139°37'	Ridley CP	SA	12.v.79	PC
58.	*fuscipes*	33°53' 140°57'	46 km N of Renmark	SA	7.vi.79	GPB,PC, MBT
59.	*fuscipes*	33°53' 140°57'	46 km N of Renmark	SA	7.vi.79	GPB,PC, MBT
60.	*rufinodis*	35°08' 137°07'	Warrenben CP	SA	14.iv.79	PC
61.	*brevinoda*, *s.l.*	32°24' 152°26'	Smith's Lake, Bungwahl	NSW	2.xii.78	ADB
62.	*hirsuta*	32°24' 152°26'	Smith's Lake, Bungwahl	NSW	13.xii.78	ADB
63.	*brevinoda*, *s.l.*	33°58' 151°02'	Deepwater Park, Milperra	NSW	11.ii.79	ADB
64.	*brevinoda*, *s.l.*	32°24' 152°26'	Smith's Lake, Bungwahl	NSW	13.xii.78	ADB
65.	*pyriformis*	33°50' 138°37'	Clare	SA	10.iii.57	BBL
66.	*nigriceps*, *s.l.*	33°39' 134°53'	Elliston	SA	30.viii.74	BBL
67.	*nigrocincta*	33°45' 151°09'	Pymble	NSW	10.x.56	BBL
68.	*forficata*, *s.l.*	35°31' 148°55'	Smoker's Gap	ACT	19.ii.79	BBL
69.	*forficata*, *s.l.*	35°40' 148°30'	Sawpit Creek, Kosciusko NP	NSW	12.iii.79	BBL

APPENDIX 1 (cont.).

70.	*forficata*, *s.l.*	35°22' 148°49'	Picadilly Circus	ACT	26.ii.79	BBL
71.	*vindex*	32°17' 115°43'	Rockingham	WA	11.ii.62	AMD
72.	*pulchra*	35°31' 148°55'	Smoker's Gap	ACT	7.ii.78	BBL
73.	*pulchra*	34°59' 138°43'	Mt Lofty Range	SA	23.iii.69	BBL
74.	*pyriformis*	35°27' 149°48'	Braidwood	NSW	6.iii.79	BBL
75.	*forficata*, *s.l.*	35°40' 148°30'	Sawpit Creek, Kosciusko NP	NSW	12.iii.79	BBL
76.	*pyriformis*	33°36' 151°10'	Cowan	NSW	5.iv.56	BBL
77.	*vindex*	30°17' 115°19'	Hill River	WA	9.iv.55	AMD
78.	*tarsata*	35°18' 149°44'	20 km NW of Braidwood	NSW	6.iii.79	BBL
79.	*gulosa*	33°53' 151°13'	Lane Cove, Sydney	NSW	25.ii.66	BBL
80.	*nigriceps*, *s.l.*	34°18' 117°33'	Cranbrook	WA	25.ii.62	AMD
81.	*nigriceps*, *s.l.*	32°20' 142°20'	Lake Menindee	NSW	5.vi.60	BBL
82.	*nigriceps*, *s.l.*	26°36' 118°28'	Meekatharra	WA	19.v.67	CTM
83.	*nigriceps*, *s.l.*	33°19' 117°20'	Wagin	WA	17.ii.62	AMD
84.	*nigriceps*, *s.l.*	33°21' 117°02'	Arthur River	WA	17.vi.62	AMD
85.	*nigriceps*, *s.l.*	27°59' 119°18'	Sandstone	WA	29.iii.75	AMD
86.	*nigriscapa*	38°10' 145°19'	6 km SW of Cranbourne	Vic	29.iii.74	PC,PMey
87.	*sp.17*	37°40' 144°23'	5 km NE of Bacchus Marsh	Vic	27.ii.75	PC

APPENDIX 1 (cont.).

88. *fuscipes*	34°26' 138°16'	Port Parham	SA	8.x.79	GPB,DGB
89. *nigriceps*, *s.l.*	37°40' 144°23'	6 km NE of Bacchus Marsh	Vic	1.iii.75	PC
90. *rufinodis*	35°08' 137°07'	Warrenben CP	SA	19.iv.80	GPB,JJP PJW
91. *rufinodis*	35°08' 137°07'	Warrenben CP	SA	20.iv.80	GPB,JJP, PJW
92. *pyriformis*	35°00' 138°38'	Belair	SA	17.viii.80	JG
93. *fuscipes*	33°53' 140°57'	46 km N of Renmark	SA	21.viii.80	GPB,BRS
94. *nigriceps*, *s.l.*	34°13' 140°27'	Lake Bonney	SA	22.viii.80	GPB,BRS
95. *pyriformis*	34°55' 138°45'	Marble Hill	SA	12.ix.80	GPB
96. *fuscipes*	34°31' 138°20'	Port Prime	SA	26.ix.80	GPB
97. *fuscipes*	34°31' 138°20'	Port Prime	SA	18.x.80	GPB
98. *fuscipes*	34°31' 138°20'	Port Prime	SA	18.x.80	GPB
99. *sp.9*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC
100. *pilosula*, *s.l.*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC
101. *nigriceps*, *s.l.*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC
102. *sp.9*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC
103. *sp.9*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC
104. *nigriscapa*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC
105. *nigriscapa*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC

APPENDIX 1 (cont.).

106. *sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	5.xi.80	GPB,PC
107. *sp.9*	36°02' 136°44'	Hanson Bay	SA	5.xi.80	GPB,PC
108. *nigriceps*, *s.l.*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	8.xi.80	GPB,PC
109. *sp.9*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	7.xi.80	GPB,PC
110. *nigriceps*, *s.l.*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	8.xi.80	GPB,PC
111. *nigriceps*, *s.l.*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	8.xi.80	GPB,PC
112. *nigriceps*, *s.l.*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	8.xi.80	GPB,PC
113. *nigriceps*, *s.l.*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC
114. *pilosula*, *s.l.*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC
115. *nigriscapa*	36°02' 136°51'	Hanson Bay	SA	5.xi.80	GPB,PC
116. *nigriceps*, *s.l.*	34°29' 139°36'	Castle's Landing, 15 km S of Blanchetown	SA	28.i.80	GPB,MAR
117. *nigriceps*, *s.l.*	30°15' 139°05'	Aroona Valley, Flinders Ranges	SA	April '80	DGB,JJP, BRS
118. *pyriformis*	33°55' 138°40'	Spring Gully CP	SA	21.xi.80	LP
119. *rufinodis*	34°49' 135°52'	Lincoln NP	SA	5.xii.80	GPB
120. *fuscipes*	33°39' 134°53'	Elliston	SA	6.xii.80	GPB
121. *fuscipes*	33°01' 138°00'	Port Germein	SA	8.xii.80	GPB
122. *pyriformis*	35°00' 138°38'	Belair RP	SA	14.xii.80	GPB

APPENDIX 1 (cont.).

123.	*sp.12*	34°49' 135°49'	Kurrara, Port Lincoln	SA	19.i.81	GPB
124.	*sp.12*	34°46' 135°34'	Uley-Wanilla PS	SA	19.i.81	GPB
125.	*sp.12*	34°46' 135°34'	Uley-Wanilla PS	SA	19.i.81	GPB
126.	*nigriceps*, *s.l.*	33°39' 134°53'	Elliston	SA	19.i.81	GPB
127.	*nigriceps*, *s.l.*	33°39' 134°53'	Elliston	SA	20.i.81	GPB
128.	*nigriceps*, *s.l.*	33°39' 134°53'	Elliston	SA	20.i.81	GPB
129.	*nigriceps*, *s.l.*	33°39' 134°53'	Elliston	SA	20.i.81	GPB
130.	*fuscipes*	33°10' 134°41'	Port Kenny	SA	21.i.81	GPB
131.	*fuscipes*	32°14' 133°50'	Laura Bay CP	SA	22.i.81	GPB
132.	*fuscipes*	32°14' 133°50'	Laura Bay CP	SA	22.i.81	GPB
133.	*nigriceps*, *s.l.*	33°07' 136°41'	Lake Gilles CP	SA	23.i.81	GPB
134.	*fuscipes*	33°01' 138°00'	Port Germein	SA	24.i.81	GPB
135.	*nigriceps*, *s.l.*	35°10' 138°34'	Manning Reserve, Blewitt Springs	SA	4.ii.81	GPB
136.	*nigriceps*, *s.l.*	35°10' 138°34'	Manning Reserve, Blewitt Springs	SA	4.ii.81	GPB
137.	*fuscipes*	34°31' 138°20'	Port Prime	SA	10.ii.81	GPB
138.	*forficata*, *s.l.*	38°31' 143°59'	4 km N of Lorne	Vic	7.ii.81	MBT
139.	*vindex*	31 59' 115°41'	King's Park, Perth	WA	30.xii.74	cu
140.	*forceps*	35°40' 137°37'	Brownlow	SA	23.iii.81	CS

APPENDIX 1 (cont.).

141. *forficata*, *s.l.*	38°33' 145°28'	Kilcunda	Vic	20.iv.81	PC
142. *varians*	35°36' 138°32'	Waitpinga	SA	29.iv.81	GPB,PC
143. *pyriformis*	35°36' 138°32'	Waitpinga	SA	29.iv.81	GPB,PC
144. *pyriformis*	35°38' 138°27'	Parson's Beach	SA	29.iv.81	GPB,PC
145. *forficata*, *s.l.*	35°38' 138°27'	Parson's Beach	SA	29.iv.81	GPB,PC
146. *fuscipes*	33°53' 140°57'	46 km N of Renmark	SA	26.v.81	GPB,BRS
147. *nigriceps*, *s.l.*	27°08' 134°45'	Alberga River, Todmorden	SA	7.viii.81	GPB,BRS
148. *nigriceps*, *s.l.*	27°08' 134°45'	Alberga River, Todmorden	SA	7.viii.81	GPB,BRS
149. *nigriceps*, *s.l.*	27°08' 134°45'	Alberga River, Todmorden	SA	9.viii.81	GPB,BRS
150. *nigriceps*, *s.l.*	27°08' 134°45'	Alberga River, Todmorden	SA	9.viii.81	GPB,BRS
151. *nigriceps*, *s.l.*	27°08' 134°45'	Alberga River, Todmorden	SA	9.viii.81	GPB,BRS
152. *fuscipes*	31°08' 136°23'	Lake Hart	SA	13.viii.81	GPB,BRS
153. *fuscipes*	31°08' 136°23'	Lake Hart	SA	13.viii.81	GPB,BRS
154. *nigriceps*, *s.l.*	31°31' 137°07'	41 km S of Pimba	SA	13.viii.81	GPB,BRS
155. *fuscipes*	33°01' 138°00'	Port Germein	SA	14.viii.81	GPB,BRS
156. *fuscipes*	34°26' 138°16'	Port Parham	SA	28.viii.81	GPB
157. *fuscipes*	34°26' 138°16'	Port Parham	SA	17.x.81	GPB
158. *fuscipes*	34°26' 138°16'	Port Parham	SA	17.x.81	GPB

APPENDIX 1 (cont.).

159. fuscipes	34°26' 138°16'	Port Parham	SA	31.x.81	GPB
160. nigriceps, s.l.	35°10' 138°34'	Manning Reserve, Blewitt Springs	SA	10.xi.81	GPB
161. princeps	34°15' 140°40'	Calperum	SA	18.xi.81	GPB
162. sp.12	34°49' 135°49'	Kurrara, Port Lincoln	SA	8.xii.81	GPB
163. sp.12	34°49' 135°49'	Kurrara, Port Lincoln	SA	8.xii.81	GPB
164. varians	34°54' 135°57'	Sleaford Bay	SA	9.xii.81	GPB
165. sp.12	34°38' 135°40'	Uley-Wanilla PS	SA	9.xii.81	GPB
166. sp.12	34°38' 135°40'	Uley-Wanilla PS	SA	10.xii.81	GPB
167. nigriscapa	34°33' 135°36'	3 km NE of Coffin Bay	SA	10.xii.81	GPB
168. sp.12	34°33' 135°36'	3 km NE of Coffin Bay	SA	10.xii.81	GPB
169. sp.12	34°33' 135°36'	3 km NE of Coffin Bay	SA	11.xii.81	GPB
170. nigriceps, s.l.	33°39' 134°53'	Elliston	SA	12.xii.81	GPB
171. nigriceps, s.l.	33°39' 134°53'	Elliston	SA	12.xii.81	GPB
172. nigriceps, s.l.	33°39' 134°53'	Elliston	SA	12.xii.81	GPB
173. nigriceps, s.l.	33°39' 134°53'	Elliston	SA	12.xii.81	GPB
174. fuscipes	33°39' 134°53'	Elliston	SA	13.xii.81	GPB
175. fuscipes	32°14' 133°50'	Laura Bay CP	SA	14.xii.81	GPB
176. fuscipes	32°14' 133°50'	Laura Bay CP	SA	14.xii.81	GPB

APPENDIX 1 (cont.).

177.	forficata, s.l.	33°07' 136°41'	Lake Gilles CP	SA	15.xii.81	GPB
178.	NOT USED					
179.	nigriceps, s.l.	34°21' 139°37'	S of Blanchetown	SA	Nov '81	CS
180.	nigriceps, s.l.	36°02' 136°51'	Hanson Bay	SA	10.ii.82	GPB
181.	nigriceps, s.l.	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	11.ii.82	GPB
182.	nigriceps, s.l.	36°02' 136°51'	Hanson Bay	SA	12.ii.82	GPB
183.	nigriceps, s.l.	36°02' 136°51'	Hanson Bay	SA	12.ii.82	GPB
184.	nigriceps, s.l.	36°02' 136°51'	Hanson Bay	SA	12.ii.82	GPB
185.	nigriceps, s.l.	36°02' 136°51'	Hanson Bay	SA	13.ii.82	GPB
186.	nigriceps, s.l.	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	14.ii.82	GPB
187.	nigriceps, s.l.	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	14.ii.82	GPB
188.	fulgida	32°37' 119°47'	Middle Ironcap	WA	17.ii.82	JG
189.	fuscipes	32°31' 136°29'	13 km W of Nonning HS	SA	13.viii.82	JP
190.	NOT USED					
191	fuscipes	31°48' 121°40'	52 km N of Norseman	WA	9.x.82	GPB
192.	fuscipes	30°47' 121°26'	4 km SW of Kalgoorlie	WA	10.x.82	GPB
193.	fuscipes	30°48' 121°23'	8 km SW of Kalgoorlie	WA	10.x.82	GPB
194.	nigriceps, s.l.	30°37' 121°25'	15 km N of Kalgoorlie	WA	11.x.82	GPB

APPENDIX 1 (cont.).

195. nigriceps, s.l.	30°20' 121°21'	13 km N of Broad Arrow	WA	11.x.82	GPB
196. nigriceps, s.l.	29°09' 121°20'	64 km N of Menzies	WA	11.x.82	GPB
197. nigriceps, s.l.	28°47' 121°14'	13 km NW of Leonora	WA	12.x.82	GPB
198. nigriceps, s.l.	28°47' 121°14'	13 km NW of Leonora	WA	12.x.82	GPB
199. vindex	31°57' 116°10'	Mundaring Weir	WA	17.x.82	GPB
200. vindex	32°02' 115°52'	Canning River, Perth	WA	19.x.82	GPB
201. sp.14	32°48' 116°16'	48 km SE of Pinjarra	WA	19.x.82	GPB
202. sp.14	32°48' 116°16'	48 km SE of Pinjarra	WA	19.x.82	GPB
203. nigriceps, s.l.	32°46' 116°35'	12 km E of Boddington	WA	19.x.82	GPB
204. vindex	33°00' 117°13'	6 km S of Narrogin	WA	20.x.82	GPB
205. nigriceps, s.l.	33°00' 117°13'	7 km S of Narrogin	WA	20.x.82	GPB
206. vindex	33°02' 117°14'	13 km S of Narrogin	WA	20.x.82	GPB
207. vindex	33°14' 117°17'	35 km S of Narrogin	WA	20.x.82	GPB
208. nigriceps, s.l.	33°19' 117°17'	5 km W of Wagin	WA	20.x.82	GPB
209. nigriceps, s.l.	33°19' 117°17'	5 km W of Wagin	WA	20.x.82	GPB
210. nigriceps, s.l.	33°19' 117°17'	5 km W of Wagin	WA	21.x.82	GPB
211. nigriceps, s.l.	33°19' 117°17'	5 km W of Wagin	WA	21.x.82	GPB
212. nigriceps, s.l.	33°23' 116°54'	43 km W of Wagin	WA	21.x.82	GPB

APPENDIX 1 (cont.).

213. *nigriceps*, *s.l.*	33°24' 116°32'	49 km E of Collie	WA	21.x.82	GPB
214. *nigriscapa*	33°37' 115°28'	2 km S of Ludlow	WA	21.x.82	GPB
215. *vindex*	33°39' 115°25'	9 km N of Busselton	WA	21.x.82	GPB
216. *nigriscapa*	33°39' 115°25'	9 km N of Busselton	WA	21.x.82	GPB
217. *sp.14*	34°00' 115°05'	2 km S of Margaret River	WA	22.x.82	GPB
218. *sp.14*	34°00' 115°05'	2 km S of Margaret River	WA	22.x.82	GPB
219. *sp.14*	34°00' 115°05'	2 km S of Margaret River	WA	22.x.82	GPB
220. *regularis*	35°07' 117°22'	10 km N of Denmark	WA	23.x.82	GPB
221. *pilosula*, *s.l.*	34°53' 117°23'	12 km N of Denmark	WA	23.x.82	GPB
222. *regularis*	34°53' 117°23'	12 km N of Denmark	WA	23.x.82	GPB
223. *nigriceps*, *s.l.*	34°41' 117°56'	Porongorup NP	WA	23.x.82	GPB
224. *vindex*	31°50' 116°05'	Darlington	WA	14.x.82	GPB
225. *atrata*	33°57' 118°54'	Jerramungup	WA	24.x.82	GPB
226. *atrata*	33°57' 118°54'	Jerramungup	WA	24.x.82	GPB
227. *atrata*	33°57' 118°54'	Jerramungup	WA	24.x.82	GPB
228. *chasei*	33°57' 118°54'	Jerramungup	WA	24.x.82	GPB
229. *arnoldi*	34°00' 119°23'	Twertup, Fitzgerald River NP	WA	25.x.82	GPB
230. *forceps*	34°00' 119°23'	Twertup, Fitzgerald River NP	WA	25.x.82	GPB

APPENDIX 1 (cont.).

231.	*atrata*	33°57' 118°54'	Jerramungup	WA	25.x.82	GPB
232.	*nigriceps*, *s.l.*	33°57' 118°51'	6 km W of Jerramungup	WA	25.x.82	GPB
233.	*arnoldi*	33°57' 118°54'	Jerramungup	WA	26.x.82	GPB
234.	*nigriceps*, *s.l.*	33°57' 118°49'	9 km W of Jerramungup	WA	27.x.82	GPB
235.	*nigriceps*, *s.l.*	33°57' 118°49'	9 km W of Jerramungup	WA	27.x.82	GPB
236.	*nigriceps*, *s.l.*	33°57' 118°49'	9 km W of Jerramungup	WA	27.x.82	GPB
237.	*vindex*	34°23' 119°23'	Bremer Bay	WA	28.x.82	GPB
238.	*vindex*	34°23' 119°23'	Bremer Bay	WA	28.x.82	GPB
239.	*atrata*	34°08' 118°52'	20 km SW of Jerramungup	WA	29.x.82	GPB
240.	*atrata*	33°35' 120°02'	Ravensthorpe	WA	29.x.82	GPB
241.	*atrata*	33°35' 120°02'	Ravensthorpe	WA	29.x.82	GPB
242.	*atrata*	33°35' 120°02'	Ravensthorpe	WA	29.x.82	GPB
243.	*atrata*	33°35' 120°02'	Ravensthorpe	WA	30.x.82	GPB
244.	*atrata*	33°35' 120°02'	Ravensthorpe	WA	30.x.82	GPB
245.	*chasei*	33°35' 121°46'	8 km N of Gibson	WA	30.x.82	GPB
246.	*nigriceps*, *s.l.*	27°26' 140°09'	Tirrawarra WH	SA	24.ix.82	PH
247.	*fuscipes*	33°53' 140°57'	46 km N of Renmark	SA	9.xii.82	GPB,MAR, DRBa
248.	*pyriformis*	35°36' 137°32'	3 km S of Emu Bay	SA	12.xii.82	CS

APPENDIX 1 (cont.).

249. *mandibularis*	35°37' 137°33'	Bay of Shoals	SA	12.xii.82	CS
250. *rufinodis*	35°36' 137°32'	3 km S of Emu Bay	SA	12.xii.82	CS
251. *rufinodis*	35°36' 137°32'	3 km S of Emu Bay	SA	12.xii.82	CS
252. *nigriscapa*	35°46' 137°34'	18 km S of Kingscote	SA	12.xii.82	CS
253. *forceps*	35°36' 137°32'	3 km S of Emu Bay	SA	12.xii.82	CS
254. *pyriformis*	35°48' 137°45'	3 km SW of American River	SA	12.xii.82	CS
255. *rufinodis*	35°36' 137°32'	3 km S of Emu Bay	SA	12.xii.82	CS
256. *rufinodis*	35°56' 137°18'	Little Sahara	SA	12.xii.82	CS
257. *nigriceps*, *s.l.*	35°49' 137°43'	6 km SW of American River	SA	12.xii.82	CS
258. *nigriscapa*	35°44' 138°01'	10 km E of Penneshaw	SA	12.xii.82	CS
259. *pyriformis*	34°57' 138°45'	Uraidla	SA	22.xii.82	GPB,DLGW
260. *princeps*	33°04' 136°10'	Pinkawillinie Crown Land	SA	11.x.81	MJS
261. *princeps*	33°04' 136°10'	Pinkawillinie Crown Land	SA	11.x.81	MJS
262. *nigriscapa*	37°14' 139°48'	Little Dip CP	SA	28.xii.82	JG
263. *princeps*	30°42' 136°46'	Roxby Downs	SA	Sept '81	LP
264. *nigriceps*, *s.l.*	26°32' 139°17'	Andrewilla WH	SA	29.ix.82	JP,LP
265. *forficata*, *s.l.*	34°12' 140°27'	Pelican Point, Lake Bonney	SA	2.iv.81	MBT
266. *nigrocincta*	27°29' 152°57'	Mt Coot-tha,	Qld	13.v.81	GPB

APPENDIX 1 (cont.).

267. *fuscipes*	33°56' 137°46'	6 km NW of Kadina	SA	9.i.83	GPB,KC
268. *rufinodis*	35°11' 137°15'	Foul Bay	SA	13.i.83	GPB
269. *rufinodis*	35°14' 137°02'	Marion Bay	SA	13.i.83	GPB
270. *nigriceps*, *s.l.*	35°16' 136°54'	Inneston, Innes NP	SA	13.i.83	GPB
271. *tepperi*	35°16' 136°54'	Inneston, Innes NP	SA	13.i.83	GPB
272. *nigriceps*, *s.l.*	35°16' 136°54'	Inneston, Innes NP	SA	13.i.83	GPB
273. *urens*	35°16' 136°54'	Inneston, Innes NP	SA	13.i.83	GPB
274. *sp.12*	33°17' 138°16'	9 km W of Gladstone	SA	18.i.83	JP
275. *fuscipes*	32°44' 137°24'	Honeymoon Paddock, Roopeena	SA	28.i.83	GPB, MS-S
276. *nigriceps*, *s.l.*	31°31' 137°07'	40 km S of Pimba	SA	28.i.83	GPB,CS
277. *princeps*	30°38' 136°55'	20 km S of Olympic Dam	SA	28.i.83	GPB,CS
278. *princeps*	30°34' 136°52'	12 km SW of Olympic Dam	SA	29.i.83	GPB,CS
279. *nigriceps*, *s.l.*	30°34' 136°52'	12 km SW of Olympic Dam	SA	29.i.83	GPB,CS
280. *fuscipes*	31°08' 136°23'	Lake Hart	SA	30.i.83	GPB,CS
281. *forceps*	33°07' 136°41'	Lake Gilles CP	SA	1.ii.83	GPB,CS
282. *varians*	33°07' 136°41'	Lake Gilles CP	SA	1.ii.83	GPB,CS
283. *nigriceps*, *s.l.*	33°28' 138°32'	Bundaleer Reservoir	SA	2.ii.83	GPB,BBL
284. *sp.12*	33°28' 138°32'	Bundaleer Reservoir	SA	2.ii.83	GPB,BBL

APPENDIX 1 (cont.).

285.	chasei	33°51' 122°08'	18 km N of Cape Le Grand	WA	26.ii.83	GPB,SB, HV
286.	vindex	34°01' 122°12'	Thistle Bay, Cape Le Grand NP	WA	26.ii.83	GPB,SB, HV
287.	michaelseni	33°59' 122°07'	Le Grand Beach, Cape Le Grand NP	WA	26.ii.83	GPB,SB, HV
288.	clarki	33°45' 122°32'	Condingup	WA	27.ii.83	GPB,SB, HV
289.	sp.16	33°45' 122°32'	Condingup	WA	27.ii.83	GPB,SB, HV
290.	fuscipes	32°42' 121°32'	34 km N of Salmon Gums	WA	28.ii.83	GPB,SB, HV
291.	vindex	33°59' 122°07'	Le Grand Beach, Cape Le Grand NP	WA	26.ii.83	GPB,SB, HV
292.	fuscipes	32°05' 122°03'	26 km E of Norseman	WA	28.ii.83	GPB,SB, HV
293.	fuscipes	33°06' 123°20'	Breeborinia Rocks	WA	1.iii.83	GPB,SB, HV
294.	fuscipes	31°27' 130°52'	4 km W of Nullarbor	SA	2.iii.83	GPB,SB, HV
295.	esuriens	43°14' 148°00'	Cape Pillar NP	Tas	27.i.83	HV,SB
296.	forficata, s.l.	42°48' 146°01'	Strathgordan- Pedder NP	Tas	29.i.83	HV,SB
297.	swalei	34°52' 135°42'	5 km N of Fishery Bay	SA	17.iii.83	GPB,RMD
298.	mandibularis	34°55' 135°41'	Fishery Bay	SA	17.iii.83	GPB,RMD
299.	rufinodis	34°48' 135°53'	Lincoln NP	SA	17.iii.83	GPB,RMD
300.	rufinodis	34°48' 135°53'	Lincoln NP	SA	17.iii.83	GPB,RMD
301.	tepperi	34°48' 135°53'	Lincoln NP	SA	17.iii.83	GPB,RMD
302.	forceps	34°57' 136°26'	Taylor's Landing, Lincoln NP	SA	18.iii.83	GPB,RMD

APPENDIX 1 (cont.).

303. *sp.12*	34°57' 136°26'	Taylor's Landing, Lincoln NP	SA	18.iii.83	GPB,RMD
304. *rufinodis*	34°57' 136°26'	Taylor's Landing, Lincoln NP	SA	18.iii.83	GPB,RMD
305. *nigriscapa*	34°41' 135°19'	Point Avoid, Coffin Bay NP	SA	19.iii.83	GPB,RMD
306. *sp.12*	34°33' 135°36'	3 km NE of Coffin Bay	SA	20.iii.83	GPB,RMD
307. *sp.12*	34°05' 135°20'	83 km S of Elliston	SA	20.iii.83	GPB,RMD
308. *nigriceps*, *s.l.*	33°39' 134°53'	Elliston	SA	20.iii.83	GPB,RMD
309. *rufinodis*	35°40' 137°35'	5 km NW of Kingscote	SA	1.iv.83	GPB
310. *nigriscapa*	35°40' 137°35'	5 km NW of Kingscote	SA	1.iv.83	GPB
311. *tepperi*	35°40' 137°35'	5 km NW of Kingscote	SA	1.iv.83	GPB
312. *pyriformis*	35°40' 137°35'	5 km NW of Kingscote	SA	1.iv.83	GPB
313. *tepperi*	35°40' 137°35'	5 km NW of Kingscote	SA	1.iv.83	GPB
314. *pyriformis*	35°40' 137°35'	5 km NW of Kingscote	SA	1.iv.83	GPB
315. *pilosula*, *s.l.*	36°04' 136°41'	Admiral's Arch, Flinders Chase NP	SA	2.iv.83	GPB
316. *mandibularis*	36°04' 136°41'	Admiral's Arch, Flinders Chase NP	SA	2.iv.83	GPB
317. *nigriscapa*	36°04' 136°42'	Cape du Couedic, Flinders Chase NP	SA	2.iv.83	GPB
318. *mandibularis*	36°04' 136°41'	Admiral's Arch, Flinders Chase NP	SA	2.iv.83	GPB
319. *mandibularis*	36°04' 136°41'	Admiral's Arch, Flinders Chase NP	SA	2.iv.83	GPB
320. *pilosula*, *s.l.*	36°04' 136°41'	Admiral's Arch, Flinders Chase NP	SA	2.iv.83	GPB

APPENDIX 1 (cont.).

321. *pilosula*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	2.iv.83	GPB
322. *pilosula*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	2.iv.83	GPB
323. *sp.9*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	2.iv.83	GPB
324. *pilosula*, *s.l.*	35°57' 136°44'	Rocky River HS, Flinders Chase NP	SA	2.iv.83	GPB
325. *mandibularis*	36°04' 136°41'	Admiral's Arch, Flinders Chase NP	SA	2.iv.83	GPB
326. *sp.9*	35°54' 136°32'	West Bay, Flinders Chase NP	SA	3.iv.83	GPB
327. *nigriceps*, *s.l.*	35°54' 136°32'	West Bay, Flinders Chase NP	SA	3.iv.83	GPB
328. *nigriscapa*	36°12' 136°37'	Ravine de Casoars, Flinders Chase NP	SA	3.iv.83	GPB
329. *tepperi*	36°12' 136°37'	Ravine de Casoars, Flinders Chase NP	SA	3.iv.83	GPB
330. *mandibularis*	36°12' 136°37'	Ravine de Casoars, Flinders Chase NP	SA	3.iv.83	GPB
331. *nigriscapa*	36°12' 136°37'	Ravine de Casoars, Flinders Chase NP	SA	3.iv.83	GPB
332. *pilosula*, *s.l.*	35°54' 136°32'	West Bay, Flinders Chase NP	SA	3.iv.83	GPB
333. *mandibularis*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	4.iv.83	GPB
334. *sp.9*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	4.iv.83	GPB
335. *pulchra*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	4.iv.83	GPB
336. *pilosula*, *s.l.*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	4.iv.83	GPB
337. *mandibularis*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	4.iv.83	GPB
338. *sp.9*	35°55' 136°47'	Rocky River, Flinders Chase NP	SA	4.iv.83	GPB

APPENDIX 1 (cont.).

339. *nigriceps*, *s.l.*	36°02' 136°51'	Hanson Bay	SA	4.iv.83	GPB
340. *nigriscapa*	35°59' 137°11'	Vivonne Bay	SA	5.iv.83	GPB,DTB
341. *pyriformis*	35°59' 137°11'	Vivonne Bay	SA	5.iv.83	GPB,DTB
342. *forceps*	35°59' 137°11'	Vivonne Bay	SA	5.iv.83	GPB,DTB
343. *pilosula*, *s.l.*	35°59' 137°11'	Vivonne Bay	SA	5.iv.83	GPB,DTB
344. *nigriceps*, *s.l.*	36°00' 137°20'	Seal Bay	SA	5.iv.83	GPB,RMD
345. *mandibularis*	35°55' 137°34'	4 km E of D'Estrees Bay	SA	5.iv.83	GPB
346. *tepperi*	35°52' 137°34'	10 km NE of D'Estrees Bay	SA	5.iv.83	GPB
347. *sp.8*	35°52' 137°34'	10 km NE of D'Estrees Bay	SA	5.iv.83	GPB,RMD
348. *rufinodis*	35°43' 137°34'	5 km SE of Kingscote Aerodrome	SA	5.iv.83	GPB,DTB
349. *nigriceps*, *s.l.*	31°31' 138°37'	Wilpena Station	SA	24.iv.83	DTB
350. *nigriceps*, *s.l.*	31°34' 138°35'	Wilpena Pound	SA	24.iv.83	DTB
351. *pyriformis*	34°47' 138°43'	Surrey Downs	SA	21.iv.83	CS
352. *vindex*	32°17' 115°43'	Rockingham	WA	11.ii.62	AMD
353. *nigriceps*, *s.l.*	32°48' 138°05'	Mt Remarkable NP	SA	15.v.83	MBT
354. *arnoldi*	34°14' 117°39'	22 km SW of Tambellup	WA	17.vi.62	AMD
355. *princeps*	33°27' 140°57'	Danggali CP	SA	June '83	SC
356. *fuscipes*	34°31' 138°20'	Port Prime	SA	12.vi.83	CS

APPENDIX 1 (cont.).

357.	*pyriformis*	37°40' 144°23'	6 km NE of Bacchus Marsh	Vic	14.vii.83	GPB
358.	*sp.17*	37°40' 144°23'	6 km NE of Bacchus Marsh	Vic	14.vii.83	GPB
359.	*sp.17*	37°40' 144°23'	6 km NE of Bacchus Marsh	Vic	14.vii.83	GPB
360.	*simillima*	33°17' 151°14'	3 km N of Peats Ridge	NSW	20.vii.83	GPB
361.	*brevinoda*, *s.l.*	32°54' 151°25'	4 km SE of Kearsley	NSW	20.vii.83	GPB
362.	*gulosa*	32°54' 151°25'	4 km SE of Kearsley	NSW	20.vii.83	GPB
363.	*brevinoda*, *s.l.*	32°52' 151°19'	Bellbird	NSW	20.vii.83	GPB
364.	*gulosa*	32°52' 151°19'	Bellbird	NSW	20.vii.83	GPB
365.	*sp.17*	32°52' 151°19'	Bellbird	NSW	20.vii.83	GPB
366.	*gulosa*	28°18' 152°02'	10 km S of Warwick	Qld	27.vii.83	GPB
367.	*gulosa*	28°18' 152°02'	10 km S of Warwick	Qld	27.vii.83	GPB
368.	*pilosula*, *s.l.*	28°40' 151°56'	Stanthorpe	Qld	27.vii.83	GPB
369.	*ferruginea*	28°40' 151°56'	Stanthorpe	Qld	27.vii.83	GPB
370.	*nigriceps*, *s.l.*	29°59' 138°17'	11 km N of Farina	SA	24.vii.83	JP
371.	*forficata*, *s.l.*	36°48' 147°43'	20 km N of Benambra	Vic	16.i.82	AW
372.	*forficata*, *s.l.*	37°40' 145°11'	Wattle Glen	Vic	29.xii.80	RJKa
373.	*pyriformis*	37°30' 145°18'	Kinglake NP	Vic	30.xii.80	RJKa
374.	*gulosa*	28°54' 151°55'	10 km S of Girraween NP	Qld	29.x.81	DC

APPENDIX 1 (cont.).

375. *nigriceps*, *s.l.*	34°00' 140°46'	Lake Merreti	SA	May '83	JR
376. *princeps*	33°27' 140°57'	Danggali CP	SA	10.iv.77	PC
377. *princeps*	34°11' 140°36'	12 km W of Renmark	SA	25.iv.82	VS
378. *sp.12*	32°50' 137°59'	Mambray Creek	SA	1.v.82	DS
379. *sp.12*	31°34' 138°35'	Wilpena	SA	22.iv.82	ECy
380. *sp.12*	34°23' 137°40'	Maitland	SA	14.iv.78	cu
381. *nigriscapa*	35°38' 139°07'	Kundaten	SA	22.viii.83	MBT
382. *pyriformis*	35°38' 139°07'	Kundaten	SA	22.viii.83	MBT
383. *sp.12*	34°40' 138°53'	Williamstown	SA	25.iv.83	DRBr
384. *nigriceps*, *s.l.*	29°35' 139°25'	St Mary Pool	SA	Sept '82	CS
385. *nigriceps*, *s.l.*	36°58' 140°45'	Naracoorte	SA	12.iv.82	RC
386. *rufinodis*	35°10' 136°55'	4 km NE of Browns Beach	SA	22.iv.82	DC,MK
387. *rufinodis*	35°17' 136°57'	Stenhouse Bay	SA	15.iv.79	PD
388. *pulchra*	35°00' 138°38'	Belair	SA	12.iii.78	cu
389. *pilosula*, *s.l.*	35°23' 138°28'	Myponga	SA	April '82	SW
390. *tepperi*	30°10' 139°17'	Yudnamutana	SA	9.ix.70	BBL
391. *nigriscapa*	37°10' 140°33'	Mary Seymour CP	SA	12.x.82	MBT,DTB
392. *nigriscapa*	37°10' 139°45'	Robe	SA	17.iv.82	MDB

APPENDIX 1 (cont.).

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393. *nigriscapa*	38°24' 145°06'	Merrick Beach	Vic	3.i.83	DTB
394. *nigriscapa*	35°04' 138°52'	Mt Barker	SA	18.iv.83	MJB
395. *forficata*, *s.l.*	38°26' 145°03'	Shoreham	Vic	8.i.83	DTB
396. *harderi*	30°10' 139°17'	Yudnamutana	SA	9.ix.70	BBL
397. *mandibularis*	32°10' 121°47'	5 km E of Norseman	WA	17.x.82	SB
398. *mandibularis*	36°02' 136°51'	Hanson Bay	SA	27.xi.80	CH
399. *pyriformis*	37°56' 145°07'	Clayton	Vic	22.iv.82	UJ
400. *pyriformis*	34°32' 138°58'	Tanunda	SA	10.iv.83	GJT
401. *pyriformis*	34°56' 138°33'	Lockleys, Adelaide	SA	20.iv.80	RR
402. *pyriformis*	34°56' 138°33'	Fulham Gardens, Adelaide	SA	30.iv.80	RR
403. *forceps*	34°44' 135°52'	Port Lincoln	SA	14.iv.79	THK
404. *forceps*	36°02' 136°51'	Hanson Bay	SA	27.xi.80	CH
405. *aberrans*	35°36' 138°32'	Waitpinga	SA	19.iv.80	PC
406. *aberrans*	34°59' 138°37'	Brownhill Creek	SA	26.iii.81	CM
407. *gulosa*	33°40' 151°15'	Ku-ring-gai Chase NP	NSW	1.ix.83	JG
408. *vindex*	31°53' 116°05'	John Forrest NP	WA	31.viii.83	CS
409. *nigriceps*, *s.l.*	31°53' 116°05'	John Forrest NP	WA	31.viii.83	CS
410. *pyriformis*	34°55' 138°45'	Montacute CP	SA	18.ix.83	GJM

APPENDIX 1 (cont.).

411. *nigriceps*, *s.l.*	34°09' 140°20'	Overland Corner	SA	20.ix.83	BW
412. *nigriceps*, *s.l.*	34°10' 140°11'	Devlin Pound	SA	20.ix.83	BW
413. *fuscipes*	33°26' 123°25'	128 km S of Balladonia	WA	3.x.83	GPB,GJM
414. *fuscipes*	33°37' 123°53'	Israelite Bay	WA	5.x.83	GPB,GJM
415. *chasei*	33°45' 122°55'	105 km W of Israelite Bay	WA	6.x.83	GPB,GJM
416. *sp.16*	33°45' 122°55'	105 km W of Israelite Bay	WA	6.x.83	GPB,GJM
417. *vindex*	33°59' 122°07'	Le Grand Beach, Cape le Grand NP	WA	6.x.83	GPB,GJM
418. *vindex*	33°59' 122°07'	Le Grand Beach, Cape le Grand NP	WA	6.x.83	GPB,GJM
419. *michaelseni*	33°59' 122°07'	Le Grand Beach, Cape le Grand NP	WA	6.x.83	GPB,GJM
420. *vindex*	33°59' 122°07'	Le Grand Beach, Cape le Grand NP	WA	6.x.83	GPB,GJM
421. *vindex*	33°52' 121°54'	Esperance	WA	7.x.83	GPB,GJM
422. *vindex*	33°52' 121°54'	Esperance	WA	7.x.83	GPB,GJM
423. *arnoldi*	33°52' 121°54'	Esperance	WA	7.x.83	GPB,GJM
424. *nigriscapa*	33°52' 121°54'	Esperance	WA	7.x.83	GPB,GJM
425. *pilosula*, *s.l.*	33°52' 121°54'	Esperance	WA	7.x.83	GPB,GJM
426. *nigriscapa*	33°52' 121°54'	Esperance	WA	7.x.83	GPB,GJM
427. *vindex*	33°52' 121°54'	Esperance	WA	7.x.83	GPB,GJM
428. *vindex*	33°52' 121°54'	Esperance	WA	7.x.83	GPB,GJM

APPENDIX 1 (cont.).

429. *vindex*	33°52' 121°54'	Esperance	WA	7.x.83	GPB,GJM
430. *fuscipes*	32°53' 121°10'	2 km S of Peak Charles	WA	8.x.83	GPB,GJM
431. *fulgida*	32°41' 119°47'	South Ironcap	WA	9.x.83	GPB,GJM
432. *sp.16*	33°56' 120°04'	Four Mile Beach, Fitzgerald River NP	WA	10.x.83	GPB,GJM
433. *chasei*	33°55' 120°02'	East Mt Barren, Fitzgerald River NP	WA	10.x.83	GPB,GJM
434. *atrata*	33°35' 120°02'	Ravensthorpe	WA	10.x.83	GPB,GJM
435. *atrata*	33°35' 120°02'	Ravensthorpe	WA	10.x.83	GPB,GJM
436. *atrata*	33°35' 120°02'	Ravensthorpe	WA	10.x.83	GPB,GJM
437. *arnoldi*	33°57' 118°54'	Jerramungup	WA	10.x.83	GPB,GJM
438. *atrata*	33°57' 118°54'	Jerramungup	WA	11.x.83	GPB,GJM
439. *atrata*	33°57' 118°54'	Jerramungup	WA	11.x.83	GPB,GJM
440. *chasei*	33°57' 118°54'	Jerramungup	WA	11.x.83	GPB,GJM
441. *nigriceps*, *s.l.*	33°57' 118°49'	9 km W of Jerramungup	WA	11.x.83	GPB,GJM
442. *atrata*	33°57' 118°38'	24 km W of Jerramungup	WA	11.x.83	GPB,GJM
443. *nigriceps*, *s.l.*	33°58' 118°29'	Ongerup	WA	11.x.83	GPB,GJM
444. *vindex*	34°00' 118°25'	8 km W of Ongerup	WA	11.x.83	GPB,GJM
445. *atrata*	34°19' 118°12'	Stirling Ranges NP	WA	12.x.83	GPB,GJM
446. *atrata*	34°20' 117°57'	Stirling Ranges NP	WA	12.x.83	GPB,GJM

APPENDIX 1 (cont.).

447. atrata	34°21' 117°47'	Stirling Ranges NP	WA	12.x.83	GPB,GJM
448. atrata	34°24' 117°54'	Stirling Ranges NP	WA	12.x.83	GPB,GJM
449. regularis	34°59' 116°44'	Coalmine Beach, Walpole	WA	13.x.83	GPB,GJM
450. sp.14	34°00' 115°05'	2 km S of Margaret River	WA	15.x.83	GPB,GJM
451. nigriceps, s.l.	33°19' 117°17'	5 km W of Wagin	WA	15.x.83	GPB,GJM
452. nigriceps, s.l.	33°19' 117°17'	5 km W of Wagin	WA	15.x.83	GPB,GJM
453. nigriceps, s.l.	33°19' 117°17'	4 km W of Wagin	WA	16.x.83	GPB,GJM
454. tepperi	33°19' 117°17'	4 km W of Wagin	WA	16.x.83	GPB,GJM
455. mandibularis	33°19' 117°17'	4 km W of Wagin	WA	16.x.83	GPB,GJM
456. vindex	33°10' 117°16'	23 km S of Narrogin	WA	16.x.83	GPB,GJM
457. vindex	33°10' 117°16'	23 km S of Narrogin	WA	16.x.83	GPB,GJM
458. forceps	33°00' 117°13'	6 km S of Narrogin	WA	16.x.83	GPB,GJM
459. nigriceps, s.l.	32°18' 116°37'	Crossman	WA	16.x.83	GPB,GJM
460. sp.14	32°34' 116°26'	71 km NE of Williams	WA	16.x.83	GPB,GJM
461. nigriceps, s.l.	30°43' 115°31'	Cataby Brook	WA	18.x.83	GPB,GJM
462. vindex	30°25' 115°21'	35 km E of Cervantes	WA	18.x.83	GPB,GJM
463. vindex	27°42' 114°12'	Kalbarri	WA	21.x.83	GPB,GJM
464. nigriceps, s.l.	30°38' 116°00'	Moora	WA	22.x.83	GPB,GJM

APPENDIX 1 (cont.).

465. *vindex*	30°58' 116°13'	New Norcia	WA	22.x.83	GPB,GJM
466. *nigriceps*, *s.l.*	31°32' 118°04'	Hines Hill	WA	24.x.83	GPB
467. *nigriceps*, *s.l.*	31°32' 118°04'	Hines Hill	WA	24.x.83	GPB
468. *fuscipes*	30°58' 121°14'	7 km SE of Coolgardie	WA	25.x.83	GPB
469. *fuscipes*	32°05' 122°28'	66 km E of Norseman	WA	25.x.83	GPB
470. *nigriceps*, *s.l.*	32°10' 123°12'	44 km W of Balladonia	WA	25.x.83	GPB
471. *fuscipes*	31°27' 130°52'	4 km W of Nullarbor	SA	26.x.83	GPB
472. *cephalotes*	32°23' 119°46'	Lake Cronin	WA	1981	WFH
473. *varians*	32°23' 119°46'	Lake Cronin	WA	1981	WFH
474. *vindex*	32°23' 119°46'	Lake Cronin	WA	Feb '81	WFH
475. *fuscipes*	33°56' 137°46'	6 km NW of Kadina	SA	20.xi.83	GPB
476. *sp.12*	34°24' 134°45'	8 km E of Maitland	SA	27.xi.83	GPB
477. *sp.12*	34°24' 134°45'	8 km E of Maitland	SA	27.xi.83	GPB
478. *sp.12*	34°24' 134°45'	8 km E of Maitland	SA	27.xi.83	GPB
479. *nigriscapa*	35°30' 138°44'	Scott CP	SA	29.xi.83	GPB,DJH
480. *sp.12*	35°30' 138°44'	Scott CP	SA	29.xi.83	GPB,DJH
481. *pyriformis*	35°00' 138°42'	Crafers	SA	1.xii.83	PGK
482. *princeps*	30°40' 136°55'	25 km S of Olympic Dam	SA	18.i.84	GPB,ARD

APPENDIX 1 (cont.).

483. *princeps*	30°35' 136°55'	15 km S of Olympic Dam	SA	18.i.84	GPB,ARD
484. *nigriceps*, *s.l.*	30°34' 136°52'	12 km SW of Olympic Dam	SA	19.i.84	GPB,ARD
485. *nigriceps*, *s.l.*	30°34' 136°52'	12 km SW of Olympic Dam	SA	19.i.84	GPB,ARD
486. *nigriceps*, *s.l.*	30°34' 136°52'	12 km SW of Olympic Dam	SA	19.i.84	GPB,ARD
487. *princeps*	30°34' 136°52'	12 km SW of Olympic Dam	SA	19.i.84	GPB,ARD
488. *princeps*	30°34' 136°52'	12 km SW of Olympic Dam	SA	19.i.84	GPB,ARD
489. *nigriceps*, *s.l.*	31°13' 136°40'	15 km NW of Pimba	SA	19.i.84	GPB,ARD
490. *fuscipes*	31°08' 136°23'	Lake Hart	SA	19.i.84	GPB,ARD
491. *fuscipes*	31°08' 136°23'	Lake Hart	SA	19.i.84	GPB,ARD
492. *varians*	37°14' 139°48'	Little Dip CP	SA	28.i.84	BRS
493. *sp.17*	37°40' 144°23'	6 km NE of Bacchus Marsh	Vic	4.ii.84	GPB,DJH
494. *sp.17*	37°40' 144°23'	6 km NE of Bacchus Marsh	Vic	4.ii.84	GPB,DJH
495. *pyriformis*	37°15' 142°54'	McDonald Park, 4 km NW of Ararat	Vic	4.ii.84	GPB,DJH
496. *nigriceps*, *s.l.*	35°20' 138°29'	Sellicks Hill	SA	24.iii.84	JG
497. *rufinodis*	35°59' 137°11'	Vivonne Bay	SA	10.iv.84	CS
498. *sp.9*	35°41' 136°58'	Western River CP	SA	10.iv.84	CS
499. *nigriscapa*	35°41' 136°58'	Western River CP	SA	10.iv.84	CS
500. *sp.9*	35°57' 136°44'	Flinders Chase NP	SA	10.iv.84	CS

APPENDIX 1 (cont.).

501. *pyriformis*	35°40' 137°35'	5 km NW of Kingscote	SA	10.iv.84	CS
502. *rufinodis*	35°40' 137°35'	5 km NW of Kingscote	SA	10.iv.84	CS
503. *pilosula*, *s.l.*	35°41' 136°58'	Western River CP	SA	10.iv.84	CS
504. *nigriceps*, *s.l.*	30°25' 139°05'	Gammon Ranges NP	SA	April '84	GJM
505. *nigriceps*, *s.l.*	34°55' 139°18'	Mannum	SA	22.iv.84	CS
506. *nigriceps*, *s.l.*	34°55' 139°18'	Mannum	SA	22.iv.84	CS
507. *nigriceps*, *s.l.*	27°20' 140°08'	Chillimookoo WH	SA	Sept. '83	MBT
508. *nigriceps*, *s.l.*	27°36' 139°54'	Cuttapirie Corner WH	SA	9.vi.84	JR
509. *simillima*	32°57' 149°54'	Fitzgerald's Mountain	NSW	10.v.82	BBL
510. *auriventris*	19°00' 146°04'	12 km W of Paluma	Qld	3.xi.80	BBL
511. *cephalotes*	31°56' 141°14'	Black Hill Creek	NSW	20.iv.69	RHM
512. *nigriceps*, *s.l.*	27°59' 119°18'	Sandstone	WA	29.iii.75	D&D
513. *nigrocincta*	19°00' 146°04'	12 km W of Paluma	Qld	3.xi.80	BBL
514. *brevinoda*, *s.l.*	19°00' 146°04'	12 km W of Paluma	Qld	3.xi.80	BBL
515. *rufinodis*	34°44' 135°52'	Proper Bay, Port Lincoln	SA	19.viii.81	cu
516. *nigriceps*, *s.l.*	34°25' 140°33'	Katarapko Island	SA	29.xii.80	JG
517. *nigriceps*, *s.l.*	33°21' 117°02'	Arthur River	WA	17.vi.62	AMD
518. *nigriceps*, *s.l.*	33°19' 117°20'	Wagin	WA	17.ii.62	AMD

APPENDIX 1 (cont.).

519.	nigriceps, s.l.	27°59' 118°55'	35 km W of Sandstone	WA	29.iii.75	AMD
520.	vindex	30°23' 115°31'	Hill River district	WA	9.iv.55	AMD
521.	ferruginea	30°21' 148°53'	Pilliga	NSW	8.ii.80	BBL
522.	nigriceps, s.l.	25°13' 132°31'	60 km W of Erldunda	NT	6.x.84	JG
523.	nigriceps, s.l.	30°04' 138°17'	Farina Creek	SA	21.x.84	JG
524.	princeps	30°02' 130°03'	Muckera WH	SA	9.ix.84	LJ
525.	fucosa	32°28' 122°32'	120 km W of Balladonia	WA	31.viii.84	BBL
526.	aberrans	33°59' 139°37'	7 km NW of Morgan	SA	17.xi.76	PJMG
527.	aberrans	35°14' 138°29'	Maslins Beach	SA	2.xii.84	PJMG
528.	auriventris	20°55' 148°30'	Eungella NP	Qld	8.i.85	RMD, KRMcD
529.	nigrocincta	20°55' 148°30'	Eungella NP	Qld	9.i.85	RMD KRMcD
530.	pyriformis	34°57' 138°45'	Uraidla	SA	8.iii.85	GPB, AW, JG
531.	pilosula, s.l.	34°57' 138°45'	Uraidla	SA	8.iii.85	GPB, AW, JG
532.	forficata, s.l.	37°40' 145°22'	Mt Dandenong	Vic	7.iii.85	DTB
533.	varians	34°11' 139°58'	Near Waikerie	SA	20.iii.85	MBT
534.	nigrocincta	25°49' 152°37'	Mannumburra Fauna Sanctuary Mt Bauple	Qld	Jan. '85	cu
535.	nigriscapa	35°09' 136°53'	Browns Beach	SA	6.iv.85	GPB

APPENDIX 1 (cont.).

536. *rufinodis*	35°10' 136°53'	2 km S of Browns Beach	SA	6.iv.85	GPB
537. *pyriformis*	35°36' 137°32'	3 km S of Emu Bay	SA	16.v.85	CS
538. *rufinodis*	35°36' 137°32'	3 km S of Emu Bay	SA	16.v.85	CS
539. *sp.9*	35°44' 136°44'	Cape Torrens CP	SA	16.v.85	CS
540. *fuscipes*	34°32' 136°16'	Reevesby Island	SA	1.ii.85	KLG
541. *fuscipes*	34°32' 136°16'	Reevesby Island	SA	Jan. '85	SAP
542. *pyriformis*	34°56' 138°36'	Wattle Park, Adelaide	SA	28.iv.85	DG
543. *simillima*	34°11' 150°59'	Helensburg	NSW	23.xii.84	MWJC
544. *forficata*, *s.l.*	42°54' 147°55'	10 km N of Eaglehawk Neck	Tas	7.ix.86	GPB

APPENDIX 2. Museum Acronyms.

ANIC	Australian National Insect Collection, C.S.I.R.O. Division of Entomology, Canberra, A.C.T., Australia
BMNH	British Museum (Natural History), London, England
GMNH	Muséum d'Histoire Naturelle, Geneva, Switzerland
MCSN	Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass., U.S.A.
MNHP	Muséum National d'Histoire Naturelle, Paris, France
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHMW	Naturhistorisches Museum, Vienna, Austria
NHRM	Naturhistoriska Riksmuseet, Stockholm, Sweden
NMV	National Museum of Victoria, Melbourne, Vic., Australia
OUM	University Museum, Oxford, England
QM	Queensland Museum, Brisbane, Qld, Australia
QVM	Queen Victoria Museum and Art Gallery, Launceston, Tas., Australia
RIB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
SAM	South Australian Museum, Adelaide, S.A., Australia
TM	Tasmanian Museum and Art Gallery, Hobart, Tas., Australia
WAM	Western Australian Museum, Perth, W.A., Australia
ZMB	Zoologisches Museum, Universität Humboldt, Berlin, German Democratic Republic
ZMH	Zoologisches Museum für Hamburg, Hamburg, Federal Republic of Germany

APPENDIX 3. Collector Acronyms.

AC	A. Currie
ACN	A.C. Nilson
ADB	A.D. Bishop
ADS	A.D. Selby
AEB	A.E. Baesjou
AF	A. Forel
AHE	A.H. Elston
AMD	A.M. Douglas
AML	A.M. Lea
AN	A. Nilson
ANB	A.N. Burns
AP	A. Page
APA	A.P. Andrews
APS	A.P. Spry
ARD	A.R. Davis
ASm	A. Smith
ASi	A. Simson
AW	A. Wells
AWF	A.W. Forbes
A&B	A.P. Andrews and H.D. Barker
B	Briggs
BBL	B.B. Lowery
BC	B. Connor
BCM	B.C. Mollison
BG	B. Gray
BRS	B.R. Schulz
BW	B. Wainwright
B,Bea	R. Barnett, H.D. Barker *et al.*
B&D	H.D. Barker and A.J. Dartnall
B&M	E.B. Britton and S. Misko
B&UB	E.B. Britton and F.H. Uther Baker
CBa	C. Barrett
CBo	C. Borch
CDK	C.D. King
CEC	C.E. Cole
CFD	C.F. Deuquet
CH	C. Hawkins
CHB	C.H. Borch
CHea	C. Howard *et al.*
CL	C. Lord
CM	C. Miller
CO	C. Oke
CPH	C.P. Haskins
CPL	C.P. Ledward
CS	C. Shanahan
CTM	C.T. Mercovich
cu	collector unknown
CVM	C.V. Morrisset
CW	C. Warner
C,I&W	R.H. Crozier, H.T. Imai and P.S. Ward
C&I	R.H. Crozier and H.T. Imai
C&U	I.F.B. Common and M.S. Upton

APPENDIX 3 (cont.)

DAD	D.A. Duckhouse
DC	D. Carter
DCP	D.C. Pearse
DDG	D.D. Giuliani
DG	D. Gardner
DGB	D.G. Browning
DHa	D. Havenstein
DHC	D.H. Colless
DHi	D. Hill
DJH	D.J. Hill
DLGW	D.L.G. Williams
DRBa	D.R. Barty
DRBr	D.R. Bridgland
Ds̲	P.J. Darlingtons̲
DS̄	D. Smith
DTB	D.T. Booth
D&D	A.M. and M.J. Douglas
EBB	E.B. Britton
ECl	E. Clark
ECy	E. Cymerman
ED	E. Damel
EFR	E.F. Riek
EGK	E.G. Kearney
EHB	E.H. Bourne
EJ	E. Jarvis
EJD	E.J. Dumigan
ELS	E.L. Smith
EM	E. Mjöberg
ESm	E. Smith
ESu	E. Sutton
ETG	E.T. Giles
EW	E. Warwick
EWFe	E.W. Ferguson
EWFi	E.W. Fischer
FAC	F.A. Cudmore
FDB	F. DuBoulay
FEW	F.E. Wilson
FHT	F.H. Taylor
FPD	F.P. Dodd
FWS	F.W. Shepherd
FXW	F.X. Williams
GAC	G.A. Currie
GBM	G.B. Monteith
GDN	G.D. Neville
GFG	G.F. Gross
GFH	G.F. Hill
GHL	G.H. Lowe
GJM	G.J. Mutze
GJT	G.J. Taylor
GPB	G.P. Browning
GT	G. Turner
GW	G. Wearne

APPENDIX 3 (cont.)

GWK	G.W. Kendrick
G&M	G.F. Gross and E.G. Matthews
HAP	H.A. Potter
HB	H. Bougier
HC	H. Clark
HDB	H.D. Barker
HEH	H.E. Hill
HF	H. Frahn
HH	H. Hacker
HJC	H.J. Carter
HMin	H. Mincham
HMit	H. Mitchell
HMH	H.M. Hale
HPS	H.P. Schrader
HR	H. Reynolds
HT	H. Thompson
HTI	H.T. Imai
HV	H. Van der Woude
HW	H. Womersley
HWD	H.W. Davey
H,G&G	J.A. Herridge, G.F. and M. Gross
H,Hea	C. Howard, L. Hill *et al.*
H&T	H.M. Hale and N.B. Tindale
IHC	I.H. Cole
IMD	I.M. Dixson
I,K&T	H.T. Imai, M. Kubota and R.W. Taylor
JAH	J.A. Hill
JAK	J.A. Kershaw
JCa	J. Calaby
JCC	J.C. Cardale
JCG	J.C. Goudie
JCl	J. Clark
JD	J. Dowse
JED	J.E. Dixon
JEF	J.E. Feehan
JFF	J.F. Field
JFG	J.F. Greenhill
JFo	J. Forse
JFr	J. Freeland
JFT	J.F. Thompson
JG	J. Gardner
JGOT	J.G.O. Tepper
JGR	J.G. Reuther
JHC	J.H. Calaby
JHe	J. Henry
JHi	J. Hickmer
JJP	J.J. Potter
JJW	J.J. Walker
JMacQ	J. MacQueen
JMcA	J. McAreavey
JP	J. Pedler
JR	J. Reid

APPENDIX 3 (cont.)

JSW	J.S. Whinray
JT	J. Thurmer
JWE	J.W. Evans
JWH	J.W. Haacke
JWM	J.W. Mellor
KC	K. Crosby
KDF	K.D. Fairey
KHLK	K.H.L. Key
KLG	K.L. Gowlett
KM	K. Millar
KP-J&p	K. Peake-Jones and party
KRMcD	K.R. McDonald
KRN	K.R. Norris
K,U&B	K.H.L. Key, M.S. Upton and J. Baulderson
K,W&p	K.H.L. Key, M.J.D. White and party
K&F	Keall and Farr
K&K	K.H.L. and M.A. Key
L	Leggett
LBT	L.B. Thorn
LHM	L.H. Mincham
LH*ea*	L. Hill *et al.*
LJ	L. Jansen
LJC	L.J. Chinnick
LJN	L.J. Newman
LMO'H	L.M. O'Halloran
LP	L. Peaoler
LPK	L.P. Kelsey
LR	L. Rodway
LW	L. Wetherell
L&W	J. Lawrence and T. Weir
MacG	MacGillivray
MAR	M.A. Robertson
MBT	M.B. Thompson
McI&D	R.S. McInnes and J. Dowse
MDB	M.D. Beard
MG	M. Geeves
MH	M. Hamilton
MJ	M. Joshua
MJB	M.J. Benson
MJDW	M.J.D. White
MJS	M.J. Smith
MK	M. Keck
MRF	M.R. Flynn
MSU	M.S. Upton
MS-S	M. Stafford-Smith
MW	M. Webster
MWJC	M.W.J. Crosland
M,H&H	E.G. Matthews, H. and A. Howden
NBT	N.B. Tindale
NG	N. Geary
PA	P. Aitken
PAM	P.A. Matthew

APPENDIX 3 (cont.)

PC	P. Christy
PD	P. Dyer
PGK	P.G. Kempster
PJD	P.J. Darlington
PJMG	P.J.M. Greenslade
PJW	P.J. Webb
PMer	P. Mercer
PMey	P. Meyer
PR	P. Ranford
PT	P. Turner
PWB	P.W. Boyer
RBa	R. Bates
RBl	R. Blackwood
RC	R. Chapple
RCC	R.C. Chandler
RD	R. Davies
RDR	R.D. Robinson
RH	R. Harvey
RHD	R.H. Dreghorn
RHG	R.H. Green
RHM	R.H. Mew
RJB	R.J. Bartell
RJKa	R.J. Kaires
RJKo	R.J. Kohout
RJM	R.J. Muir
RLR	R.L. Robert
RMacQ	R. MacQueen
RMD	R.M. Delaney
RPa	R. Patterson
RPe	R. Peakall
RR	R. Rocca
RS	R. Smith
RSMcI	R.S. McInnes
RVS	R.V. Southcott
RW	R. Wallace
RWT	R.W. Taylor
RYB	R.Y. Berg
SAP	S.A. Parker
SB	S. Barker
SC	S. Carter
SHP	S.H. Parlett
SJK	S.J. Knight
SS	State School
SW	S. Witting
TG	T. Greaves
TGC	T.G. Campbell
TH	T. Hume
THK	T.H. Kerkhof
TW	T. Wilson
T&B	R.W. Taylor and R.J. Bartell
UJ	U. John
U&B	M.S. Upton and Barret

APPENDIX 3 (cont.)

VS	V. Seliscak
VVH	V.V. Hickman
WBB	W.B. Barnard
WC	W. Crawshaw
WFH	W.F. Humphries
WH	W. Heron
WHM	W.H. Matthews
WJMV	W.J.M. Vestjens
WLB	W.L. Brown
WMM	W.M. Mann
WMW	W.M. Wheeler
WPC	W.P. Clements
WR	W. Rafferty
WWF	W.W. Froggatt
Z&Z	A. and F.R. Zeitz

APPENDIX 4. Comparison of various linear measurements (described in Chapter 2) in different Myrmecia species (taken from gold-coated specimens illustrated by SEM in Chapter 3).

Species	Measurements (mm)									
	TL	ML	HL	HW	SL	MeL	PW	PNH	PNL	PNW
forceps	c.22	4.02	3.54	3.63	4.23	6.13	2.11	1.08	2.13	1.11
pyriformis	c.21	3.35	3.21	3.21	3.28	6.03	2.09	1.18	1.98	1.13
sp.9	c.23	3.97	3.59	3.49	3.88	6.60	2.42	1.28	2.11	1.28
mjobergi	c.29	5.68	4.69	4.01	5.54	8.23	2.67	1.56	2.96	1.44
nigriscapa	c.20	3.58	3.28	3.23	3.85	5.91	2.13	1.26	1.90	1.17
tarsata	c.22	3.51	3.41	3.43	3.63	6.40	2.37	1.39	1.83	1.30
auriventris	c.19	3.16	3.18	3.21	2.99	5.48	2.14	1.10	1.75	1.09
flavicoma	c.20	3.16	3.10	3.12	3.48	5.93	1.99	1.14	1.83	1.12
gulosa	c.23	3.93	3.68	3.49	4.41	6.80	2.14	1.25	2.40	1.13
arnoldi	c.23	4.07	3.78	3.59	4.71	6.70	2.23	1.23	2.44	1.06
simillima	c.22	3.92	3.65	3.75	3.96	6.20	2.40	1.28	2.03	1.27
atrata [1]	c.23	4.43	3.98	3.92	4.42	7.32	2.46	1.31	2.79	1.14
atrata [2]	c.23	3.80	3.57	3.39	4.46	6.68	2.16	1.22	2.37	1.11
fulgida	c.25	4.25	4.23	4.08	4.97	7.68	2.71	1.42	2.60	1.44
fuscipes [3]	c.23	3.66	3.59	3.43	4.30	6.68	2.21	1.17	2.43	1.06
fuscipes [4]	c.20	3.26	3.12	2.93	3.84	5.60	1.88	1.00	1.99	0.96
fuscipes [5]	c.14	2.05	2.24	2.07	2.69	4.23	1.37	0.78	1.50	0.68
fuscipes [5]	c.21	3.31	3.23	3.01	4.01	5.93	2.01	1.10	2.15	1.05
sp.11	c.21	3.77	3.40	3.33	4.03	6.10	2.00	1.17	2.22	1.05
desertorum	c.24	3.97	3.68	3.49	4.53	6.70	2.22	1.22	2.49	1.33
princeps	c.27	4.68	4.20	3.99	5.15	7.65	2.49	1.38	2.92	1.41
vindex	c.23	3.84	3.65	3.51	4.37	6.65	2.24	1.41	2.53	1.28
sp.17	c.19	3.07	2.95	2.81	3.63	5.50	1.95	1.10	1.93	1.02
pulchra	c.18	2.84	3.04	3.25	3.08	5.40	2.16	1.20	1.63	1.18
nigrocincta	c.17	2.79	2.59	2.52	2.71	4.84	1.77	0.94	1.68	0.85
harderi	c.13	2.00	2.08	2.14	1.83	3.62	1.57	0.91	1.20	0.86
aberrans	c.14	2.00	2.62	2.76	1.81	4.04	1.80	1.06	1.17	0.89
cephalotes	c.15	2.28	2.13	2.45	2.17	4.01	1.72	0.94	1.28	0.93
pilosula, s.l.	c.13	2.25	2.14	2.27	1.95	3.73	1.62	0.96	1.16	0.91
swalei	c.13	2.16	2.10	2.16	1.67	3.57	1.71	1.05	1.05	0.94
tepperi	c.12	2.17	1.97	2.05	1.82	3.48	1.53	0.94	1.07	0.91

APPENDIX 4 (cont.).

Species	TL	ML	HL	HW	SL	MeL	PW	PNH	PNL	PNW
	Measurements (mm)									
piliventris, *s.s.*	c.15	2.22	2.37	2.59	1.97	4.26	1.94	1.08	1.36	1.17
sp.15	c.9	1.22	1.39	1.43	1.11	2.60	0.96	0.63	0.81	0.53
fucosa	c.12	1.89	1.98	1.93	1.55	3.31	1.30	0.90	1.26	0.84
urens	c.8	1.22	1.37	1.37	1.22	2.42	0.92	0.56	0.83	0.55

1 From Jerramungup, W.A.
2 From Ravensthorpe, W.A.
3 From 2 km S of Peak Charles, W.A.
4 From 4 km W of Nullarbor, S.A.
5 From Port Parham, S.A.

APPENDIX 5. Comparison of various indices (described in Chapter 2) in different *Myrmecia* species (calculated from linear measurements in Appendix 4).

Species			Indices				
	CI	MI	MI2	SI	PNI	PNI2	MeI
forceps	103	114	111	119	52	51	34
pyriformis	100	104	104	102	57	60	35
sp.9	97	111	114	108	61	61	37
mjobergi	86	121	142	118	49	53	32
nigriscapa	98	109	111	117	62	66	36
tarsata	101	103	102	106	71	76	37
auriventris	101	99	98	94	62	63	39
flavicoma	101	102	101	112	61	62	34
gulosa	95	107	113	120	47	52	31
arnoldi	95	108	113	125	43	50	33
simillima	103	107	105	108	63	63	39
atrata [1]	98	111	113	111	41	47	34
atrata [2]	95	106	112	125	47	51	32
fulgida	96	100	104	117	55	55	35
fuscipes [3]	96	102	107	120	44	48	33
fuscipes [4]	94	104	111	123	48	50	34
fuscipes [5]	92	92	99	120	45	52	32
fuscipes [5]	93	102	110	124	49	51	34
sp.11	98	111	113	119	47	53	33
desertorum	95	108	114	123	53	49	33
princeps	95	111	117	123	48	47	33
vindex	96	105	109	120	51	56	34
sp.17	95	104	109	123	53	57	35
pulchra	107	93	87	101	72	74	40
nigrocincta	97	108	111	105	51	56	37
harderi	103	96	97	88	72	76	43
aberrans	105	76	72	69	76	91	45
cephalotes	115	107	93	102	73	73	43
pilosula, *s.l.*	106	105	99	91	78	83	43
swalei	103	103	100	80	90	100	48
tepperi	104	110	106	92	85	88	44

APPENDIX 5 (cont.).

Species	Indices CI	MI	MI2	SI	PNI	PNI2	MeI
piliventris, s.s.	109	94	86	83	86	79	46
sp.15	103	88	85	80	65	78	37
fucosa	97	95	98	78	67	71	39
urens	100	89	89	82	66	67	38

1 From Jerramungup, W.A.
2 From Ravensthorpe, W.A.
3 From 2 km S of Peak Charles, W.A.
4 From 4 km W of Nullarbor, S.A.
5 From Port Parham, S.A.

APPENDIX 6. Comparison of various indices (described in Chapter 2) in different *Myrmecia* species (calculated from linear measurements in Clark's (1951) figures of workers).

Species (name used by Clark)	Indices						
	CI	MI	MI2	SI	PNI	PNI2	MeI
forceps							
(*forceps*)	99	121	122	122	48	53	37
(*singularis*)	103	111	107	113	50	51	34
brevinoda, *s.l.*							
(*decipiens*)	105	121	115	105	68	65	33
(*gigas*)	94	96	102	94	44	56	33
(*gigas*)	102	115	113	105	51	49	36
(*gigas*)	100	111	111	100	55	55	36
(*gigas*)	102	115	113	103	48	50	36
(*gigas*)	109	122	112	100	59	56	37
(*gigas*)	115	109	95	105	66	60	36
(*gigas*)	111	115	104	102	64	61	40
(*longinodis*)	101	112	111	99	48	55	38
forficata, *s.l.*							
(*brevinoda*)	100	108	108	103	73	66	39
(*forficata*)	101	102	102	95	59	67	39
(*rubra*)	99	101	101	99	77	73	42
hirsuta	98	116	119	115	64	54	33
pyriformis							
(*pyriformis*)	104	107	103	109	66	57	42
(*simillima*)	100	116	116	109	55	56	38
regularis	96	103	107	108	65	71	36
mjobergi	80	121	152	121	50	54	33
nigriscapa							
(*analis*)	104	109	105	117	58	63	38
(*nigriscapa*)	103	105	102	112	61	65	38
tarsata	99	105	107	107	62	69	42
auriventris	108	99	91	98	70	82	41
flavicoma							
(*comata*)	103	106	103	96	73	62	38
(*flavicoma*)	102	100	99	98	65	57	38
gulosa	107	110	103	118	63	59	38

APPENDIX 6 (cont.)

Species			Indices				
(name used by Clark)	CI	MI	MI2	SI	PNI	PNI2	MeI
arnoldi							
(*arnoldi*)	99	114	114	121	46	53	35
(*rubripes*)	95	109	115	119	44	45	34
rufinodis							
(*crudelis*)	100	98	98	102	54	52	38
(*gracilis*)	98	102	104	129	47	54	39
(*rufinodis*)	98	105	107	109	46	55	42
simillima							
(*rogeri*)	101	102	101	104	61	60	39
(*tricolor*)	106	101	96	101	56	57	40
(*tricolor nigriventris*)	101	104	102	94	61	58	42
atrata							
(*atrata*)	100	108	108	123	44	43	35
(*pavida*)	100	115	115	120	45	53	34
ferruginea							
(*dimidiata*)	97	114	117	127	48	47	34
(*fasciata*)	96	112	116	123	52	48	36
(*suttoni*)	95	101	106	113	47	60	36
fulgida	101	109	107	121	50	57	36
fuscipes	95	108	114	123	45	52	35
nigriceps, *s.l.*							
(*desertorum*)	102	105	103	112	56	61	36
(*lutea*)	99	109	110	124	44	45	35
(*nigriceps*)	93	114	123	119	50	50	37
princeps	94	120	128	120	41	42	34
rowlandi	92	113	123	85	52	53	43
vindex							
(*gratiosa*)	91	106	116	118	43	48	35
(*vindex*)	99	106	107	116	52	53	36
esuriens	108	96	89	87	74	75	43
midas	97	108	111	96	74	80	35
pulchra							
(*fallax*)	101	94	93	105	72	81	40
(*murina*)	106	95	90	97	92	97	42
(*picticeps*)	106	95	90	95	57	63	40
(*pulchra*)	112	96	86	106	79	78	43
apicalis	101	108	106	101	52	49	47
cordata	93	108	116	91	49	48	38
nigrocincta	104	115	111	101	49	55	42
petiolata	105	107	102	99	45	46	39

APPENDIX 6 (cont.)

Species			Indices				
(name used by Clark)	CI	MI	MI2	SI	PNI	PNI2	MeI
harderi							
(*celaena*)	109	99	91	73	82	85	46
(*harderi*)	107	100	93	79	74	68	45
(*maloni*)	117	102	88	79	79	72	46
(*scabra*)	106	110	104	81	88	81	46
aberrans							
(*aberrans*)	104	80	77	69	91	94	48
(*eupoecila*)	109	88	81	71	74	88	50
(*excavata*)	121	90	74	71	87	91	46
(*formosa*)	116	93	81	77	76	74	50
(*froggatti*)	111	76	68	69	82	94	52
(*greavesi*)	108	80	74	70	98	107	50
(*haematosticta*)	110	90	82	75	89	85	59
(*maura*)	115	82	71	68	99	100	51
(*nobilis*)	107	76	71	69	75	91	49
cephalotes							
(*callima*)	121	111	92	94	72	73	47
(*cephalotes*)	119	105	88	91	106	86	49
(*hilli*)	107	107	100	91	72	75	41
chasei	109	110	101	86	103	100	49
chasei	118	106	91	81	88	84	48
chasei	106	107	101	83	74	78	46
chrysogaster	108	101	94	69	81	75	50
clarki	106	113	107	93	84	83	43
dispar	114	106	93	83	82	76	46
michaelseni	109	110	101	84	80	78	48
pilosula, *s.l.*							
(*pilosula*)	109	99	91	87	75	71	52
queenslandica							
(*cydista*)	108	100	92	67	79	79	44
rugosa							
(*ruginodis*)	107	106	99	80	87	74	48
swalei							
(*dixoni*)	112	112	100	70	78	72	48
(*swalei*)	104	99	95	69	86	81	47
(*testaceipes*)	115	105	91	70	92	89	51
tepperi	107	108	101	86	84	77	48
varians							
(*elegans*)	102	114	112	79	90	87	48
(*goudiei*)	106	106	100	84	69	66	49
(*marmorata*)	106	114	108	70	78	70	43
(*occidentalis*)	109	101	93	86	63	64	45
(*opaca*)	106	99	94	89	75	78	45
(*shepherdi*)	99	101	101	81	77	74	45
(*varians*)	100	114	114	86	71	65	43
(*wilsoni*)	102	108	106	83	87	79	47

APPENDIX 6 (cont.)

Species		Indices					
(name used by Clark)	CI	MI	MI2	SI	PNI	PNI2	MeI
fulviculis	104	101	97	83	75	77	45
fulvipes, *s.l.*							
(*fulvipes*)	107	95	89	80	86	98	47
luteiforceps	103	111	107	76	81	84	44
mandibularis							
(*laevinodis*)	106	107	101	85	82	81	47
(*mandibularis*)	110	116	105	81	81	78	45
piliventris, *s.l.*							
(*gilberti*)	101	94	93	75	78	78	51
(*piliventris*)	106	109	103	83	79	88	47
(*potteri*)	113	99	88	69	84	72	50
(*rectidens*)	105	102	97	80	76	75	50
picta	101	87	87	71	74	78	42
fucosa	96	95	99	73	63	68	39
urens							
(*dichospila*)	102	88	87	63	79	74	44
(*exigua*)	96	102	106	75	59	61	41
(*infima*)	99	93	94	64	77	76	40
(*nigra*)	99	91	92	66	60	67	37
(*rubicunda*)	104	102	98	59	60	60	44
(*urens*)	98	96	98	61	76	77	40

APPENDIX 7. Chromosome numbers of Formicidae from sources published after 1932. Whelden & Haskin's (1953) results have been omitted (see Smith & Peacock, 1957). [*Note* - Numbers preceding the species or genus names denote footnotes which are given at the end of the table.]

Taxon	Haploid number (n)	Source
Myrmeciinae		
Myrmecia		
arnoldi	7	Present study
#1,8 *atrata*	38,39	Present study
#3 *brevinoda*, *s.s.*	42	Imai et al. (1977); A.D.Bishop (pers. comm.)
cephalotes	33	Imai et al. (1977)
desertorum	32	Present study
#1 *decipiens*	43,44	A.D.Bishop (pers. comm.)
#3 *forceps*	31	Present study
#1 *forficata*, *s.s.*	25,26	Imai et al. (1977); A.D.Bishop (pers.comm.)
fulgida	20	Present study
fulvipes, *s.l.*		
(Leumeah, N.S.W.)	6	Imai et al. (1977)
(Picadilly Circus, A.C.T.)	30	Imai et al. (1977)
#1 *fuscipes*	37,38	Present study
gulosa	19	Imai et al. (1977)
michaelseni	32	Present study
#3 *nigriceps*, *s.s.*	35-37,39	Present study
nigrocincta	11	Imai et al. (1977)
piliventris, *s.l.*		
(Black Mountain, A.C.T.)	2	Imai & Taylor (1986)
(A.C.T. & N.S.W.)	34	Imai & Taylor (1986)
pilosula, *s.l.*		
(Tidbinbilla, A.C.T.)	1	Crosland & Crozier (1986)
#2,3,4,8 (Leumeah, N.S.W.)	4,5	Imai et al. (1977)
#2,4 (Western River, S.A.)	8	Present study
#2,4 (Flinders Chase, S.A.)	12	Present study
#3,8 (Victoria & Picadilly Circus, A.C.T.)	15,16	Crozier (1966); Imai et al. (1977)
princeps	15,20	Present study
#1,3 *pyriformis*	40,41	Imai et al. (1977); A.D.Bishop (pers. comm.); present study
regularis	20	A.D.Bishop (pers. comm.)
rufinodis	5	Present study
swalei	26	Present study
tepperi	35	Present study
#1 *vindex*	23,24,26,29	Present study
sp.7 (ANIC)	33	Present study
sp.11 (ANIC)	18	Present study
sp.12 (ANIC)	37	Present study
#1 *sp.13* (ANIC)	20,21	Present study
#1 *sp.14* (ANIC)	28,31	Present study

APPENDIX 7 (cont.).

#1 *sp.16* (ANIC)	33,34	Present study
sp.17 (ANIC)	17	Present study
Ponerinae		
Amblyopone		
cf. *fortis*	22	Imai et al. (1977)
#2,3 *australis*	24	Imai et al. (1977)
Anochetus		
graeffei	15	Imai et al. (1984)
madaraszi	14	Imai et al. (1984)
yerburyi	15	Imai et al. (1984)
sp.1	12	Goni et al. (1982)
sp.2	19	Goni et al. (1982)
sp.4	15	Imai et al. (1984)
sp.5	17	Imai et al. (1984)
Bothroponera		
rubiginosa	38	Imai et al. (1984)
rufipes	24	Imai et al. (1984)
sp.2 (ANIC)	30	Imai et al. (1977)
sp.1 (nr *tesserinoda*)	24	Imai et al. (1984)
#3 *sp.2* (nr *tesserinoda*)	26	Imai et al. (1984)
*1 *Brachyponera*		
lutea	8	Imai et al. (1977)
sinensis (=*luteipes*)	11	Imai & Kubota (1972)
#4 *sp.*	11	Goni et al. (1982)
Centromyrmex		
feae	22	Imai et al. (1984)
Cerapachys		
biroi	14	Imai et al. (1984)
brevis	23	Imai et al. (1977)
sp.	25	Goni et al. (1982)
Cryptopone		
sauteri	14	Imai & Kubota (1972)
?rotundiceps	6	Imai et al. (1977)
Diacamma		
vagans	7	Imai et al. (1984)
sp.2	15	Imai et al. (1984)
sp.	33	H.T.Imai (pers.comm.)
sp.	18	Goni et al. (1982)
Ectomomyrmex		
sp.	19	Imai et al. (1984)
Gnamptogenys		
sp.1	21	Goni et al. (1982)
sp.2	18	Goni et al. (1982)
Heteroponera		
relicta	11	Imai et al. (1977)
Hypoponera		
sp.1 (ANIC)	19	Imai et al. (1977)
sp.2 (ANIC)	19	Imai et al. (1977)
sp.	19	Goni et al. (1982)

APPENDIX 7 (cont.).

Leptogenys		
diminuta (var. *leviceps*)	19	Imai et al. (1984)
hysterica	13	Imai et al. (1984)
minchini	26	Imai et al. (1984)
ocellifera	23	Imai et al. (1984)
sp.1	19	Goni et al. (1982)
sp.2	24	Goni et al. (1982)
sp.5 (nr *peuqueti*)	15	Imai et al. (1984)
Mesoponera		
sp.1	14	Goni et al. (1982)
sp.2	11	Goni et al. (1982)
sp.3	18	Goni et al. (1982)
Odontomachus		
#3 *sp.1* (ANIC)	22	Imai et al. (1977)
sp.1	22	Goni et al. (1982)
#6 *sp.2*	15	Goni et al. (1982)
sp.3	22	Goni et al. (1982)
Odontoponera		
transversa	23	Imai et al. (1984)
*2 *Pachycondyla*		
obscurans	11	Imai et al. (1984)
#6 *sp.*	11	Goni et al. (1982)
Ponera		
pennsylvanica	6	Hauschteck-Jungen & Jungen (1983)
scabra	3,4	Imai & Kubota (1972)
sp.	6	Imai (1969)
Probolomyrmex		
sp.	14	Goni et al. (1982)
sp.	46	H.T.Imai (pers.comm.)
Proceratium		
silaceum	18	Crozier (1970a)
Rhytidoponera		
aciculata	26	Imai et al. (1977)
chalybea	21	Imai et al. (1977)
impressa	21	Imai et al. (1977)
#1 *maniae*	19,20, 22-24	Imai et al. (1977)
mayri	25	Imai et al. (1977)
'metallica'		
#2,4,8 (Western form)	10-12	Crozier (1969a); Imai et al. (1977); Crozier (1980)
#1 (Eastern form)	17-23	Crozier (1969a); Imai et al. (1977); Crozier (1980)
purpurea	19	Imai et al. (1977)
tasmaniensis	23	Crozier (1969a)
victoriae	21	Crozier (1969a); Imai et al. (1977)
Sphinctomyrmex		
#1 *steinheili*	22,23	Imai et al. (1977)

APPENDIX 7 (cont.).

Dorylinae		
Aenictus		
brevicornis	12	Imai et al. (1984)
sp. nr *camposi*	15	Hung et al. (1972)
Pseudomyrmecinae		
Tetraponera		
allaborans	16	Hung et al. (1972)
sp.	22	Goni et al. (1982)
Myrmicinae		
Acanthomyrmex		
sp.1	11	Goni et al. (1982)
sp.2	11	Goni et al. (1982)
Acromyrmex		
ambiguus	19	Goni et al. (1983)
hispidus	19	Goni et al. (1983)
heyeri	19	Goni et al. (1983)
Aphaenogaster		
beccarii	23	Imai et al. (1984)
depilis	17	Hauschteck-Jungen & Jungen (1983)
famelica	17	Imai (1971)
fulva	18	Crozier (1977b)
gibbosa	11	Hauschteck-Jungen & Jungen (1983)
lamellidens	19	Crozier (1977b)
#1 *longiceps*	22,23	Imai et al. (1977)
osimensis	16	Imai (1971)
#7 '*rudis*'		
(lighter upper New York State form)	16-18	Crozier (1969b)
(darker upper New York State form)	18	Crozier (1969b)
('*miamiana*')	18	Crozier (1977b)
(18-chromosome Montane form)	18	Crozier (1977b)
(Coastal Plains form)	20,21	Crozier (1969b,1977b)
(22-chromosome Montane form)	22	Crozier (1977b)
(Alachua County form)	22	Crozier (1977b)
sardoa	17	Hauschteck-Jungen & Jungen (1983)
smythiesi	11	Imai (1971)
	17	Imai et al. (1984)
subterranea	11	Hauschteck (1962); Hauschteck-Jungen & Jungen (1983)
testaceopilosa	17	Hauschteck-Jungen & Jungen (1983)
tipuna	17	Hung et al. (1972)

APPENDIX 7 (cont.).

Aphaenogaster (cont.)		
treatae	21	Crozier (1977)
sp.	15	Goni et al. (1982)
Cardiocondyla		
nuda	14	Imai et al. (1984)
sp.	20	Goni et al. (1982)
Chelaner		
#4 *rothsteini*	11	Imai et al. (1977)
whitei	12	Imai et al. (1977)
#4 *sp.1* (ANIC)	16	Imai et al. (1977)
sp.2 (ANIC)	11	Imai et al. (1977)
Colobostruma		
alinodis	11	Crozier (1968c)
sp.1 (ANIC)	11	Imai et al. (1977)
Crematogaster		
biroi	12	Imai et al. (1984)
brunnea (var. *rabula*)	18	Imai et al. (1984)
laboriosa	13	Imai (1969)
rothneyi	25	Imai et al. (1984)
#3 *subnuda*	18	Imai et al. (1984)
#4 *sp.1* (ANIC)	12	Imai et al. (1977)
sp.2 (ANIC)	13	Imai et al. (1977)
sp.1	13	Goni et al. (1982)
sp.2	18	Goni et al. (1982)
sp.3	18	Goni et al. (1982)
sp.4	12	Goni et al. (1982)
sp.	20	Imai (1969)
Epopostruma		
sp.	10	Crozier (1968c)
Formicoxenus		
nitidulus	15	Buschinger & Francoeur (1983)
Harpagoxenus		
sublaevis	20	Hauschteck-Jungen & Jungen (1983)
Leptothorax		
acervorum	13	Hauschteck-Jungen & Jungen (1983)
congruus	9	Imai & Kubota (1972)
corticalis	9	E.Hauschteck-Jungen in Crozier (1975)
interruptus	12	Hauschteck-Jungen & Jungen (1983)
longispinosus	12	Crozier (1970a)
nylanderi	11	Hauschteck-Jungen & Jungen (1983)
provancheri	11	Buschinger & Francoeur (1983)
schaumi	9	Hauschteck-Jungen & Jungen (1983)
#6 *spinosior*	12	Imai (1969)
tuberum	9	Hauschteck (1961); Hauschteck-Jungen & Jungen (1983)

APPENDIX 7 (cont.).

Leptothorax (cont.)		
unifasciatus	9	Hauschteck-Jungen & Jungen (1983)
sp.	16	Imai (1969)
Lophomyrmex		
bedoti	19	Imai et al. (1984)
Manica		
rubida	22	Hauschteck-Jungen & Jungen (1983)
Mayriella		
abstinens	9	Imai et al. (1977)
Meranoplus		
#2 *bicolor*	8	Imai et al. (1984)
minor	11	Imai et al. (1977)
sp. (*hirsutus* gp)	11	Crozier (1970)
sp. (*oceanicus* gp)	10	Crozier (1966)
sp.4 (ANIC)	11	Imai et al. (1977)
sp.5 (ANIC)	11	Imai et al. (1977)
Messor		
aciculatum	22	Imai (1969)
barbarus	21	E.Hauschteck-Jungen in Crozier (1975)
#1 *sp.*	20,21	Imai et al. (1984)
Monomorium		
dichroum	8	Imai et al. (1984)
glabrum	19	Imai et al. (1984)
#4 *indicum*	10,11	Imai et al. (1984)
latinode	35	Imai et al. (1984)
minimum	11	Crozier (1970a)
orientale	10	Imai et al. (1984)
pharaonis	11	Smith & Peacock (1957); Imai (1969)
scabriceps	19	Imai et al. (1984)
subopacum	17	E.Hauschteck-Jungen in Crozier (1975)
viridum	11	Crozier (1970a)
sp.1 (ANIC)	11	Imai et al. (1977)
#2,3 *sp.2* (ANIC)	21	Imai et al. (1977)
sp.1	11	Goni et al. (1982)
sp.2	11	Goni et al. (1982)
sp.5	17	Imai et al. (1984)
sp.6 (nr *glabrum*)	19	Imai et al. (1984)
sp. (nr *orientale*)	11	E.Hauschteck-Jungen in Crozier (1975)
Myrmecina		
americana	14	E.Hauschteck-Jungen in Crozier (1975)
gramminicola	14	E.Hauschteck-Jungen in Crozier (1975)
sp.	33	H.T.Imai (pers.comm.)
sp.	34	H.T.Imai (pers.comm.)

APPENDIX 7 (cont.).

Myrmica		
laevinodis	24	Hauschteck (1965); Hauschteck-Jungen & Jungen (1983)
lobicornis	24	Hauschteck-Jungen & Jungen (1983)
rubra	23	Imai (1969)
ruginodis	24	Hauschteck-Jungen & Jungen (1983)
sabuletti	23	Hauschteck-Jungen & Jungen (1983)
schencki	23	Hauschteck-Jungen & Jungen (1983)
sulcinodis	24	Hauschteck-Jungen & Jungen (1983)
	28	Hauschteck (1965)
Myrmicaria		
brunnea	22	Imai et al. (1984)
sp.1	22	Goni et al. (1982)
sp.2	22	Goni et al. (1982)
sp.3	22	Goni et al. (1982)
Oligomyrmex		
asinus	22	Imai et al. (1984)
sauteri	18	Hung et al. (1972)
sp.6 (ANIC)	19	Imai et al. (1977)
sp.1	18	Goni et al. (1982)
sp.2	22	Imai et al. (1984)
sp.4	16	Imai et al. (1984)
sp.5	13	Imai et al. (1984)
Orectognathus		
clarki	15	Crozier (1968c)
darlingtoni	11	Imai et al. (1977)
versicolor	11	Imai et al. (1977)
Pheidole		
cornutula	10	Goni et al. (1983)
dentata	10	Crozier (1970)
dentigula	10	Crozier (1970)
fallax	10	Goni et al. (1983)
fervida	10	Imai (1966)
indica	10	Imai et al. (1984)
latinoda	21	Imai et al. (1984)
mus	6	Imai et al. (1984)
#1 nodus	17-20	Imai & Kubota (1975)
pallidula	10	Hauschteck-Jungen & Jungen (1983)
	12	Hauschteck (1961)
rotschana	10	Imai et al. (1984)
spinninodis	10	Goni et al. (1983)
strobeli	10	Goni et al. (1983)
woodmasoni	9	Imai et al. (1984)
sp.20 (ANIC)	10	Imai et al. (1977)
sp.21 (ANIC)	10	Imai et al. (1977)
sp.22 (ANIC)	10	Imai et al. (1977)

APPENDIX 7 (cont.).

Pheidole (cont.)		
sp.23 (ANIC)	10	Imai et al. (1977)
sp.24 (ANIC)	9	Imai et al. (1977)
sp.25 (ANIC)	10	Imai et al. (1977)
sp.26 (ANIC)	10	Imai et al. (1977)
sp.27 (ANIC)	10	Imai et al. (1977)
sp.28 (ANIC)	10	Imai et al. (1977)
#4 *sp.29* (ANIC)	10	Imai et al. (1977)
#4 *sp.30* (ANIC)	10	Imai et al. (1977)
sp.31 (ANIC)	10	Imai et al. (1977)
sp.32 (ANIC)	10	Imai et al. (1977)
sp.1	10	Goni et al. (1982)
sp.2	10	Goni et al. (1982)
sp.3	10	Goni et al. (1982)
sp.4	10	Goni et al. (1982)
#1 *sp.5*	16,17	Goni et al. (1982)
sp.6	10	Goni et al. (1982)
sp.7	8	Goni et al. (1982)
sp.8	19	Goni et al. (1982)
sp.9	9	Goni et al. (1982)
sp.10	10	Goni et al. (1982)
sp.1 (nr *grayi*)	21	Imai et al. (1984)
sp.3	10	Imai et al. (1984)
sp.4	10	Imai et al. (1984)
sp.5	15	Imai et al. (1984)
sp.8	10	Imai et al. (1984)
sp.9 (nr *fossulata*)	10	Imai et al. (1984)
sp.11	10	Imai et al. (1984)
sp.13 (nr *watsoni*)	14	Imai et al. (1984)
sp.14	9	Imai et al. (1984)
sp. (*concentrica* gp)	9	Crozier (1966)
sp.	10	Imai (1969)
Pheidologeton		
diversus	21	Imai et al. (1984)
Podomyrma		
#7 *adelaidae*	22	Imai et al. (1977)
Pristomyrmex		
pungens	12	Imai (1969); Itow et al. (1984)
sp.	11	Goni et al. (1982)
Proatta		
sp.	16	Goni et al. (1982)
Smithistruma		
sp.	13	W.L.Brown in Crozier (1975)
sp.	8	Goni et al. (1982)
Solenopsis (= *Diplorhoptrum*)		
aurea	16	Crozier (1970a)
fugax	11	Hauschteck (1961); Imai (1969)
#3 *geminata*	16	Crozier (1970a); Imai et al. (1984)
invicta	16	Glancey et al. (1976)
molesta	11	Crozier (1970a)
richteri	16	Glancey et al. (1976)

APPENDIX 7 (cont.).

Solenopsis (= *Diplorhoptrum*) (cont.)		
saevissima	16	Goni et al. (1983)
sp.	11	Crozier (1966)
sp.	19	Goni et al. (1982)
Stenamma		
brevicorne	4	Hauschteck (1962)
westwoodi	20	E.Hauschteck-Jungen in Crozier (1975)
Strongylognathus		
huberi	14	Hauschteck (1962)
Strumigenys		
friedae	12	Imai et al. (1977)
Symmyrmica		
chamberlini	14	Buschinger & Francoeur (1983)
*3 *Tetramorium* (= *Xiphomyrmex*)		
caespitum	14	Hauschteck (1961); Imai (1969)
guineense	11	Imai (1969)
semilaeve	14	E.Hauschteck-Jungen in Crozier (1975)
simillimum	7	Imai et al. (1984)
smithi	13	Imai et al. (1984)
sp.2 (ANIC)	9	Imai et al. (1977)
sp.3 (ANIC)	10	Imai et al. (1977)
sp.4 (ANIC)	9	Imai et al. (1977)
sp.1	11	Goni et al. (1982)
sp.3	13	Goni et al. (1982)
sp.4	7	Goni et al. (1982)
#1 *sp.3*	17,18	Imai et al. (1984)
sp.	10	Hung et al. (1972)
Triglyphothrix		
lanuginosa	7	Imai et al. (1984)
walshi	7	Imai et al. (1984)
sp.1	10	Goni et al. (1982)
sp.2	9	Goni et al. (1982)
Trigonogaster		
sp.	12	Imai et al. (1984)
Vollenhovia		
emeryi	18	Imai (1969)
sp.	11	W.L.Brown in Crozier (1975)
#3 *sp.3* (ANIC)	20	Imai et al. (1977)
Nothomyrmeciinae		
Nothomyrmecia		
macrops	46	A.D.Bishop & R.H.Crozier in Taylor (1978b)
Dolichoderinae		
Bothriomyrmex		
gibbus	11	Hauschteck-Jungen & Jungen (1983)
sp.	11	Hauschteck (1963)

APPENDIX 7 (cont.).

Conomyrma		
flava	13	Cokendolpher & Francke (1984)
pyramica	19	Goni et al. (1983)
Dolichoderus		
quadripunctatus	14	Imai (1969)
#3 *scabridus*	14	Crozier (1966); Imai et al. (1977)
sp.	9	Goni et al. (1982)
Dorymyrmex		
bicolor	13	Crozier (1970a)
?pulchellus	9	Crozier (1968a,1970a)
?thoracicus	9	Crozier (1970a)
Forelius		
foetidus	16	Crozier (1970a)
Iridomyrmex (Old World)		
anceps	9	Imai et al. (1984)
glaber	14	Crozier (1968b)
#2 *gracilis*		
(Race A)	9	Crozier (1968b)
(Race B)	9	Crozier (1968b)
itoi	14	Imai & Yosida (1964)
itinerans	8	Crozier (1968b)
mattiroloi	9	Crozier (1968b)
nitidus	8	Crozier (1968b); Imai et al. (1977)
'*purpureus*'		
(blue form)	9	Crozier (1968a,1968b); Imai et al. (1977); Halliday (1978)
(red form)	9	Crozier (1968a,1968b); Halliday (1978)
(small purple form)	9	Halliday (1978)
(yellow form)	9	Halliday (1978)
(black form)	9	Imai et al. (1977); Halliday (1978)
(*sanguineus*)	9	Halliday (1978)
(dark yellow form)	9	Halliday (1978)
?*sp.7* (ANIC) (?=*Bothriomyrmex pusillus*)	11	Imai et al. (1977)
sp.8 (ANIC) (*darwinianus* gp)	7	Imai et al. (1977)
sp.9 (ANIC) (*darwinianus* gp)	6	Imai et al. (1977)
sp.10 (ANIC) (*itinerans* gp)	8	Imai et al. (1977)
sp.13 (ANIC) (*gracilis* gp)	9	Imai et al. (1977)
sp.14 (ANIC) (*gracilis* gp)	9	Imai et al. (1977)
#4 *sp*.15 (ANIC) (*gracilis* gp)	9	Imai et al. (1977)

APPENDIX 7 (cont.).

Iridomyrmex (Old World) (cont.)		
sp.16 (ANIC) (*gracilis* gp)	9	Imai et al. (1977)
sp.17 (ANIC) (*gracilis* gp)	9	Imai et al. (1977)
sp.	7	Crozier (1968b)
sp.	9	Goni et al. (1982)
3 spp	9	Crozier (1968b)
Iridomyrmex (New World)		
humilis	8	Crozier (1968b)
pilifer	9	Crozier (1970a)
sp. nr *pilifer*	9	Crozier (1970a)
Leptomyrmex		
erythrocephalus	12	Imai et al. (1977)
Tapinoma		
erraticum	8	Hauschteck-Jungen & Jungen (1983)
indicum	5	Imai et al. (1984)
	7	H.T.Imai in Crozier (1975)
melanocephalum	5	Crozier (1970b); Imai et al. (1984)
nigerrimum	9	Hauschteck-Jungen & Jungen (1983)
sp.	5	Goni et al. (1982)
#2 *sessile*	8	Crozier (1970b)
simrothi	9	Hauschteck-Jungen & Jungen (1983)
Technomyrmex		
albipes	8	Imai et al. (1977); Imai et al. (1984)
	9	Crozier (1968b)
sp.2 (*bicolor* gp)	14	Imai et al. (1984)
sp.	15	Goni et al. (1982)
Formicinae		
Acantholepis		
capensis	9	Imai et al. (1984)
lunaris	9	Imai et al. (1984)
sp.1 (nr *sericea*)	9	Imai et al. (1984)
sp.2 (nr *fergusoni*)	9	Imai et al. (1984)
Acropyga		
sp.	15	Goni et al. (1982)
Anoplolepis		
longipes	17	Imai et al. (1984)
sp.	17	Goni et al. (1982)
Brachymyrmex		
sp.	9	Crozier (1970a)
Calomyrmex		
sp.1 (ANIC)	14	Imai et al. (1977)

APPENDIX 7 (cont.).

Camponotus		
aethiops	21	Hauschteck-Jungen & Jungen (1983)
alii	21	Hauschteck-Jungen & Jungen (1983)
bonariensis	20	B.Goni in Hauschteck-Jungen & Jungen (1983); Goni et al. (1983)
caryae	9	Imai (1969)
compressus (India)	10	Kumbkarni (1965b)
compressus (Tunisia)	20	Hauschteck-Jungen & Jungen (1983)
consobrinus	23	Imai et al. (1977)
#1 *crassisquamis*	19,20	Imai et al. (1984)
cruentatus	18	Hauschteck-Jungen & Jungen (1983)
dolendus	10	Imai et al. (1984)
foreli	17	Hauschteck-Jungen & Jungen (1983)
japonicus	14	Imai (1969)
kiusiuensis	14	Imai (1969)
lateralis	14	Hauschteck (1962)
ligniperda	14	Hauschteck (1961); Hauschteck-Jungen & Jungen (1983)
mitis	10	Imai et al. (1984)
mus	13	Goni et al. (1983)
obscuripes	14	Imai (1969)
paria	20	Imai et al. (1984)
pilicornis	25	Hauschteck-Jungen & Jungen (1983)
punctulatus	20	Goni et al. (1983)
rufipes	20	B.Goni in Hauschteck-Jungen & Jungen (1983); Goni et al. (1983)
rufoglaucus	18	Hauschteck-Jungen & Jungen (1983)
sericeus	22	Imai et al. (1984)
sylvaticus	20	Hauschteck-Jungen & Jungen (1983)
taylori	12	Imai et al. (1984)
thraso	20	Imai et al. (1984)
tokioensis	9	Imai & Kubota (1972)
vagus	14	Hauschteck (1962)
#3 *variegatus*	13	Imai et al. (1984)
sp. (*impressus* gp)	26	Crozier (1970a)
sp.1 (ANIC) (?*perthianus*)	23	Imai et al. (1977)
sp.2 (ANIC) (?*nigriceps*)	23	Imai et al. (1977)
sp.3 (ANIC)	24	Imai et al. (1977)
sp.5 (ANIC)	16	Imai et al. (1977)
sp.8 (ANIC)	16	Imai et al. (1977)
sp.9 (ANIC)	19	Imai et al. (1977)
sp.10 (ANIC)	23	Imai et al. (1977)

APPENDIX 7 (cont.).

Camponotus (cont.)		
sp.11 (ANIC)	16	Imai et al. (1977)
sp.12 (ANIC)	19	Imai et al. (1977)
sp.13 (ANIC)	10	Imai et al. (1977)
sp.14 (ANIC)	19	Imai et al. (1977)
sp.1	9	Imai & Kubota (1972)
sp.1	19	Goni et al. (1982)
sp.2	20	Goni et al. (1982)
sp.3	19	Goni et al. (1982)
sp.4	18	Goni et al. (1982)
sp.5	20	Goni et al. (1982)
sp.6	22	Goni et al. (1982)
sp.7 (nr variegatus)	16	Imai et al. (1984)
#5 sp.9 (nr variegatus)	17,18	Imai et al. (1984)
sp.10 (nr infuscus)	10	Imai et al. (1984)
sp.12 (nr variegatus)	17	Imai et al. (1984)
sp. (nr variegatus)	10	Hung et al. (1972)
sp.	13	Imai (1969)
Cataglyphis		
albicans	26	Hauschteck-Jungen & Jungen (1983)
bicolor	26	Hauschteck-Jungen & Jungen (1983)
setipes	27	Imai et al. (1984)
Formica		
aquilonia	26	Rosengren et al. (1980)
cinerea	27	Hauschteck-Jungen & Jungen (1976)
cunicularia	27	Hauschteck-Jungen & Jungen (1976)
dakotensis	26	A.C.F.Hung in Crozier (1975)
exsecta	26	Hauschteck-Jungen & Jungen (1976)
fusca	27	Imai (1969); Hauschteck-Jungen & Jungen (1976)
gagates	27	Hauschteck-Jungen & Jungen (1976)
japonica	27	Imai (1969)
lemani	27	Hauschteck-Jungen & Jungen (1976)
lugubris	26	Hauschteck-Jungen & Jungen (1976); Rosengren et al. (1980)
montana	27	Hung (1969)
'nylanderi'	26	Rosengren et al. (1980)
obscuripes	26	Hung (1969)
pergandei	26	A.C.F.Hung in Crozier (1975)
picea	26	Imai (1969); Hauschteck-Jungen & Jungen (1976)
polyctena	26	Hauschteck-Jungen & Jungen (1976); Rosengren et al. (1980)

APPENDIX 7 (cont.).

Formica (cont.)		
pratensis	26	Hauschteck-Jungen & Jungen (1976); Rosengren et al. (1980)
pressilabris	26	Rosengren et al. (1980)
reflexa	26	A.C.F.Hung in Crozier (1975)
rufa	26	Hauschteck-Jungen & Jungen (1976)
rufibarbis	27	Hauschteck-Jungen & Jungen (1976);Rosengren et al. (1980)
sanguinea	26	Imai (1969); Hauschteck-Jungen & Jungen (1976)
subintegra	26	Hung (1969)
transkaucasica	26	Imai (1969); Rosengren et al. (1980)
truncorum	26	Imai (1969); Hauschteck-Jungen & Jungen (1976)
	26-28	Rosengren et al. (1980)
ulkei	26	Hung (1969)
uralensis	26	Rosengren et al. (1980)
yessensis	26	Imai (1969)
4 spp	26	A.C.F.Hung in Crozier (1975)
3 spp (*fusca* gp)	27	A.C.F.Hung in Crozier (1975)
Lasius		
alienus	14	Hauschteck (1962)
	15	Pearson (1982); Hauschteck-Jungen & Jungen (1983)
emarginatus	15	Hauschteck (1962)
flavus	15	Imai (1966); Hauschteck-Jungen & Jungen (1983)
fuliginosus	14	Hauschteck (1962); Hauschteck-Jungen & Jungen (1983)
nearcticus	15	Crozier (1970)
niger	15	Hauschteck (1962); Imai (1969); Pearson (1982)
pallitarsis	14	Hauschteck (1962)
talpa	15	Imai (1969)
umbratus	15	Hauschteck (1962)
Notoncus		
?ectatomoides	22	Imai et al. (1977)
*4 *Oecophylla*		
smaragdina	8	Crozier (1970a); Imai et al. (1984)
Opisthopsis		
rufithorax	25	Imai et al. (1977)

APPENDIX 7 (cont.).

Paratrechina		
indica	15	Imai et al. (1984)
longicornis	8	Hung et al. (1972); Imai et al. (1984)
parvula	15	E.Hauschteck-Jungen in Crozier (1975)
sp.1 (ANIC)	15	Imai et al. (1977)
sp.1	8	Goni et al. (1982)
sp.2	13	Goni et al. (1982)
sp.3	14	Goni et al. (1982)
sp.4	8	Goni et al. (1982)
sp.5	14	Goni et al. (1982)
sp.3	15	Imai et al. (1984)
Plagiolepis		
barbara	9	Hauschteck-Jungen & Jungen (1983)
pygmaea	9	Hauschteck-Jungen & Jungen (1983)
sp.	9	E.Hauschteck-Jungen in Crozier (1975)
Polyergus		
samurai	27	Imai (1969)
Polyrhachis		
ammon	21	Imai et al. (1977)
dives	21	Hung et al. (1972)
hippomanes	20	Imai (1969)
lamellidens	21	Imai (1969)
rastellata	21	Crozier (1970a)
simplex	21	Imai et al. (1984)
sp.1 (ANIC)	21	Imai et al. (1977)
sp.1	21	Goni et al. (1982)
sp.2	21	Goni et al. (1982)
#2 sp.3	20	Goni et al. (1982)
Prenolepis		
imparis	8	Hauschteck (1962)
#1 sp.	17,18	Goni et al. (1982)
Prolasius		
sp.1 (ANIC)	9	Imai et al. (1977)
sp.2 (ANIC)	9	Imai et al. (1977)
Pseudolasius		
sp. nr emeryi	14	Hung et al. (1972)
Stigmacros		
sp.1 (ANIC)	19	Imai et al. (1977)
sp.3 (ANIC)	10	Imai et al. (1977)

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*1 Snelling (1981) synonymizes Brachyponera and Pachycondyla but in view of the disparate chromosome numbers Brown's (1973) nomenclature has been preferred

*2 Nomenclature followed is that of Brown (1973).

*3 Nomenclature followed is that of Bolton (1976,1977).

*4 Ledoux's (1954) count of n=?12 for _Oecophylla longinoda_ has been omitted (see Smith and Peacock, 1957).

#1 Robertsonian polymorphism
#2 Pericentric inversion polymorphism
#3 C-band polymorphism in short arms
#4 Translocation polymorphism
#5 Fission inversion polymorphism
#6 B-chromosome polymorphism
#7 Possible B-chromosome polymorphism
#8 Chromosome deletion

APPENDIX 8. Chromosome numbers of Symphyta from sources published after 1932. Benson's (1950) review does not give sources for the numbers he cites and has been omitted. [*Note* - Numbers preceding species names denote footnotes which are given at the end of the table.]

Taxon	Haploid number	Source
SIRICOIDEA		
Siricidae		
Sirex		
cyaneus	8	Sanderson (1970)
juvencus	8	Sanderson (1970)
noctilio	8	Sanderson (1970)
Urocerus		
augus	18	Sanderson (1970)
gigas	13	Sanderson (1970)
TENTHREDINOIDEA		
Tenthredinidae		
Aglaostigma		
albicincta	15	Nogusa (1965)
amoorensis	16	Naito (1982)
nebulosa	10	Nogusa (1965)
occipitosa	17	Naito (1982)
sapporonis	9	Naito (1982)
sp.	22	Naito (1982)
Allantus		
luctifer	8	Naito (1982)
meridionalis	9	Nogusa (1965)
nakabusensis	10	Naito (1982)
sp.	8	Naito (1982)
Alphostromboceros		
konowi	7	Naito (1982)
Ametastegia		
geranii	9	Nogusa (1965)
pallipes	6	Sanderson (1970)
Aneugmenus		
japonicus	7	Naito (1982)
kiotonis	7	Naito (1982)
Asiemphytus		
albilabris	15	Naito (1982)
Athalia		
japonica	8	Naito (1982)
lugens infumata	8	Naito (1982)
rosae japonensis	8	Naito (1982)
Birka		
carinifrons	7	Naito (1982)
Corymbus		
fujisana	10	Naito (1982)
nipponica	10	Naito (1982)

APPENDIX 8 (cont.).

Croesus		
japonicus	8	Nogusa (1965)
Dolerus		
ephyppiatus	8	Naito (1982)
gessneri	8	Naito (1982)
japonicus	9	Naito (1982)
*1 lewisii	14	Naito (1982)
subfasciatus	9	Naito (1982)
yokohamensis	8	Naito (1982)
Empria		
sp.	15	Naito (1982)
Empronus		
obsoletus	10	Naito (1982)
Eriocampa		
mitsukurii	9	Naito (1982)
Eutomostethus		
juncivorus	6	Nogusa (1965)
Hemibeleses		
nigriceps	16	Nogusa (1965)
Hemitaxonus		
athyrii	6	Naito (1971)
japonicus	6	Naito (1971)
melanogyne	6	Naito (1982)
minomensis	7	Naito (1982)
paucipunctatus	6	Naito (1971)
sasayamensis	6	Nogusa (1965); Naito (1971)
struthiopteridis	6	Nogusa (1965); Naito (1971)
tokunagai	7	Naito (1971)
Heptamelus		
ochroleucus	10	Naito (1982)
Lagidina		
irritans	18	Naito (1982)
platycerus	18	Naito (1982)
Loderus		
genucinctus insulicola	11	Naito (1982)
*1 eversmanni obscurus	14	Naito (1982)
Macrophya		
annulitibia	10	Naito (1978b)
apicalis	8	Naito (1978b)
carbonaria	10	Naito (1978b)
coxalis	10	Naito (1978b)
exilis	8	Naito (1978b)
falsifica	10	Naito (1978b)
fascipennis	12	Naito (1978b)
imitator	8	Naito (1978b)
infumata	9	Naito (1978b)
malaisei	10	Naito (1978b)
rohweri	10	Naito (1978b)
timida	10	Naito (1978b)
sp.	10	Naito (1982)
Nematinus		
alni	9	Naito (1982)

APPENDIX 8 (cont.).

Nematus		
leucotrochus	9	Sanderson (1970)
olfaciens	9	Sanderson (1970)
ribesii	9	Sanderson (1970)
sp.	9	Naito (1982)
Neostromboceros		
itoi	6	Naito (1982)
nipponicus	7	Naito (1982)
okinawaensis	7	Naito (1982)
sinanensis	7	Naito (1982)
Nesoselandria		
morio	6	Naito (1982)
Pachyprotasis		
albicoxis	11	Naito (1982)
asteris	10	Naito (1982)
erratica	10	Naito (1982)
fukii	10	Naito (1982)
hayasuensis	10	Naito (1982)
hiensis	10	Naito (1982)
hiyodorii	10	Naito (1982)
iwatai	10	Naito (1982)
longicornis	10	Naito (1982)
malaisei	11	Naito (1982)
nigronotata	10	Naito (1982)
nogusai	10	Naito (1982)
okutanii	10	Naito (1982)
pallidiventris	10	Naito (1982)
rapae	10	Naito (1982)
sasabensis	10	Naito (1982)
sawadai	10	Naito (1982)
sengaminensis	10	Naito (1982)
serii	10	Naito (1982)
tanakai	10	Naito (1982)
volatilis	10	Nogusa (1965)
yamahakkai	10	Naito (1982)
zukaensis	10	Naito (1982)
sp.1	10	Naito (1982)
sp.2	10	Naito (1982)
sp.3	10	Naito (1982)
sp.4	10	Naito (1982)
sp.5	10	Naito (1982)
sp.6	10	Naito (1982)
sp.7	10	Naito (1982)
sp.8	10	Naito (1982)
sp.9	10	Naito (1982)
sp.10	11	Naito (1982)
Parachractus		
leucopodus	10	Naito (1982)

APPENDIX 8 (cont.).

Perineura		
esakii	17	Naito (1982)
japonica	17	Naito (1982)
okutanii	17	Naito (1982)
pictipennis	17	Naito (1982)
sp.	17	Naito (1982)
Phyllocolpa		
sp.	9	Naito (1982)
Pontania		
sp.	9	Naito (1982)
Priophorus		
morio	6	Comrie (1938)
sp.	6	Naito (1982)
Pristophora		
erichsoni	7	Smith (1941)
rufipes	8	Comrie (1938)
sp.1	7	Naito (1982)
sp.2	8	Naito (1982)
sp.3	8	Naito (1982)
Propodea		
fentoni	10	Naito (1982)
Pseudohemitaxonus		
dryopteris	5	Naito (1982)
Pseudoheptamelus		
runari	7	Naito (1982)
Rocalia		
longipennis	10	Naito (1982)
sp.	8	Naito (1982)
Siobla		
ferox	9	Naito (1982)
metallica	9	Naito (1982)
sturmii	9	Naito (1982)
ruficornis	9	Naito (1982)
venusta apicalis	9	Naito (1982)
Strombocerina		
koebelei	7	Naito (1982)
Strongylogaster		
blechni	9	Naito (1982)
filicis	8	Naito (1982)
lineata	8	Nogusa (1965)
macula	7	Sanderson (1970)
mixta	9	Naito (1982)
moiwana	9	Naito (1982)
onocleae	8	Nogusa (1965)
osmundae	7	Naito (1982)
ruber	9	Naito (1982)
secunda	9	Naito (1982)
tambensis	7	Naito (1982)
Taxonus		
minomensis	9	Naito (1982)
japonicus	11	Naito (1982)

APPENDIX 8 (cont.).

Tenthredo		
abdominalis	10	Naito (1982)
*2 acerrima	18-21	Sanderson (1970)
arcuata	15	Sanderson (1970)
basizonata	9	Naito (1982)
colon nigriventris	10	Naito (1982)
contusa	10	Naito (1982)
convagenata	10	Naito (1978a)
cylindrica	10	Naito (1982)
dentina	10	Naito (1982)
fagi	13	Naito (1982)
ferruginea	12	Naito (1982)
finschi seguro	10	Naito (1982)
flavida	12	Naito (1982)
fukaii	10	Naito (1982)
flavomandibulata	10	Naito (1982)
fulva adusta	10	Naito (1982)
fuscoferminata	11	Naito (1982)
gifui	12	Naito (1982)
goliath	10	Naito (1982)
hokkaidonis	10	Naito (1982)
hylaris	9	Nogusa (1965)
japonica	10	Naito (1982)
jozana	9	Naito (1982)
limbata	10	Naito (1982)
marginella	11	Sanderson (1970)
matsumurai	19	Naito (1982)
melanogaster	10	Naito (1982)
mortivaga	10	Naito (1982)
nigropicta	10	Naito (1982)
nitidiceps	10	Naito (1978a)
olivacea	10	Naito (1978a)
opaciceps	10	Naito (1978a)
ornatula	10	Naito (1982)
perkinsi	18	Sanderson (1970)
picticornis	10	Naito (1982)
procincta	10	Naito (1982)
providens	10	Naito (1982)
pseudolivacea omega	10	Naito (1978a)
rubrocaudata	10	Naito (1982)
subolivacea	10	Naito (1978a)
takeuchii	10	Naito (1978a)
ussuriensis	10	Naito (1982)
versuta	10	Naito (1982)
viridatrix	10	Naito (1982)
sp.1	10	Naito (1982)
sp.2	10	Naito (1982)
sp.3	10	Naito (1982)
sp.4	10	Naito (1982)
sp.5	10	Naito (1982)
sp.6	10	Naito (1982)

APPENDIX 8 (cont.).

Tenthredopsis		
carinatus	8	Naito (1982)
litterata	9	Sanderson (1970)
nassata	9	Sanderson (1970)
_sp.1_	8	Naito (1982)
_sp.2_	8	Naito (1982)
_sp.3_	8	Naito (1982)
Rhogogaster		
_sp.1_	10	Naito (1982)
_sp.2_	10	Naito (1982)
_sp.3_	10	Naito (1982)
Argidae		
Arge		
nigrinodosa	8	Naito (1982)
Diprionidae		
Diprion		
abeiticolor	7	Smith (1941)
frutetorum	7	Maxwell (1958)
*3 _hercyniae_	7	Smith (1941); Maxwell (1958)
nemorum	7	Smith (1941)
pini	7	Maxwell (1958)
*3 _polytomum_	6	Smith (1941)
*4 _similis_	14	Smith (1941,1960)
Monoctenus		
juniperinus	7	Maxwell (1958)
Neodiprion		
abeitis	8	Maxwell (1958)
compar	7	Maxwell (1958)
lecontei	7	Maxwell (1958)
maurus	7	Maxwell (1958)
nanulus nanulus	7	Maxwell (1958)
pinetum	7	Maxwell (1958)
pratti banksianae	7	Maxwell (1958)
sertifer	7	Smith (1941)
swainei	8	Maxwell (1958)
taedae taedae	7	Maxwell (1958)
tsugae	7	Maxwell (1958)
virginiana	7	Maxwell (1958)
_sp._	8	Maxwell (1958)
5 spp	7	Maxwell (1958)

APPENDIX 8 (cont.).

CEPHOIDEA		
Cephidae		
Cephus		
cinctus	9	Mackay (1955)
Janus		
*2 integer	22-26	Crozier & Taschenberg (1972)

*1 Tetraploid species (Naito, 1982)
*2 Chromosome number polymorphism
*3 Smith (1941) found Diprion polytomum to have n = 6 in Europe but n = 7 in Canada. Knerer and Atwood (1973) later resurrected the name hercyniae for the n = 7 form.
*4 Some authors believed this species to be polyploid (Smith, 1941; Crozier, 1975; Naito, 1982) but this has been refuted by the describer of the karyotype (S.G.Smith in Crozier, 1977).

APPENDIX 9. Chromosome numbers of Apocrita (excluding Formicidae) from sources published after 1932. [*Note* - Numbers preceding species and genus names denote footnotes which are given at the end of the table.]

Taxon number	Haploid	Source
ICHNEUMONOIDEA		
Braconidae		
Bracon		
brevicornis	10	Speicher & Speicher (1940)
hebetor	10	Torvik-Greb (1935)
Phaenocarpa		
persimilis	17	G.Prince & H.Stace in Crozier (1977a)
Ichneumonidae		
Agrothereutes		
extrematus	10	Koonz (1939)
Mastrus		
smithii	10	Koonz (1936)
Venturia		
canescens	11	Speicher (1937)
PROCTOTRUPOIDEA		
Scelionidae		
Telenomus		
fariai	10	Dreyfus & Breuer (1944a,1944b)
CYNIPOIDEA		
Cynipidae		
Andricus		
collaris	10	Dodds (1938)
fecundatrix	10	Dodds (1938)
Aulacidea		
hieracii	10	Dodds (1938)
Biorrhiza		
pallida	10	Dodds (1938)
Callirhytis		
palmiformis	10	Goodpasture (1974a,1975b)
Diplolepis		
roseae	9	Stille & Davring (1980)
Neuroterus		
baccarum	10	Dodds (1938)
numismalis	10	Dodds (1938)
Pseudeucoila		
bochei	10	H.Jungen in Crozier (1975)
Trigonaspis		
megaptera	10	Dodds (1938)
Xestophanes		
potentillae	10	Dodds (1938)

APPENDIX 9 (cont.).

CHALCIDOIDEA		
Trichogrammatidae		
Trichogramma		
chilonis	5	Hung (1982)
evanescens	5	Hung (1982)
nubilale	5	Hung (1982)
pretiosum	5	Hung (1982)
spp	5	Fukada & Takemura (1943)
Eulophidae		
Melittobia		
chalybii	5	Schmieder (1938)
Tetrastichus		
gigas	6	Goodpasture (1974b)
megachilidis	6	Goodpasture (1974b)
Chalcididae		
Brachymeria		
intermedia	3	Hung (1986)
lasus	5	Hung (1986)
ovata	5	Hung (1986)
Leucospis		
affinis	6	Goodpasture (1974b)
Eurytomidae		
Eurytoma		
californica	10	Goodpasture (1974b)
Torymidae		
Monodontomerus		
clementi	6	Goodpasture (1975a)
montivagus	6	Goodpasture (1975a)
obscurus	4	Goodpasture (1975a)
saltuosus	5	Goodpasture (1975a)
Torymus		
baccharidis	6	Goodpasture & Grissell (1975)
californicus	6	Goodpasture & Grissell (1975)
capillaceous	6	Goodpasture & Grissell (1975)
koebelei	5	Goodpasture & Grissell (1975)
occidentalis	6	Goodpasture & Grissell (1975)
tubicola	6	Goodpasture & Grissell (1975)
umbilicatus	5	Goodpasture & Grissell (1975)
vesiculi	6	Goodpasture & Grissell (1975)
warreni	6	Goodpasture & Grissell (1975)
Pteromalidae		
Dibrachys		
sp.	5	Goodpasture (1974b)
Muscidifurax		
zaraptor	5	Goodpasture (1974b)

APPENDIX 9 (cont.).

Nasonia		
vitripennis	5	Pennypacker (1958); Whiting (1968)
	6	Goodpasture (1974b)
Pteromalus		
puparum	5	Guhl & Dozorceva (1934)
Encyrtidae		
Copidosoma		
truncatellum	10	Hunter & Bartlett (1975)
Aphelinidae		
Aphytis		
mytilaspidus	5	Rössler & DeBach (1973)

SPHECOIDEA		
(Apiformes group)		
Colletidae		
Colletes		
fulgidus longiplumosis	13	Goodpasture (1974b)
Hylaeus		
ellipticus	11	Goodpasture (1974b)
stevensi	14	Goodpasture (1974b)
Andrenidae		
Andrena		
duboisi	3	Goodpasture (1974b)
sp.	10	Goodpasture (1974b)
Halictidae		
Agapostemon		
virescens	17	Ramberg et al. (1984)
Augochlorella		
michaelis	16	Kerr (1972)
Augochloropsis		
sparsilis	8	Kerr (1972)
Dialictus		
lineatulus	12	Ramberg et al. (1984)
rhytidophorus	6	Kerr (1972)
zephyrus	13	Ramberg et al. (1984)
Nomia		
nevadensis angelesia	21	Goodpasture (1974b)
Pseudaugochloropsis		
graminea	8	Kerr (1972)
Megachilidae		
Anthidium		
mormonum	16	Goodpasture (1974b)
Ashmeadiella		
sp.	16	Goodpasture (1974b)
Coelioxys		
sp.	16	Goodpasture (1974b)
Dianthidium		
heterulkei heterulkei	15	Goodpasture (1974b)
Hoplitis		
robusta	16	Goodpasture (1974b)

APPENDIX 9 (cont.).

Megachile		
pacifica	16	Goodpasture (1974b)
relativa	16	Goodpasture (1974b)
rotundata	16	Klostermeyer & Soo Hoo (1968)
Osmia		
glauca	16	Goodpasture (1974b)
nigrifrons	16	Goodpasture (1974b)
pentstemonis	16	Goodpasture (1974b)
Stelis		
chlorocyanea	17	Goodpasture (1974b)
Trachusa		
gummifera	16	Goodpasture (1974b)
Anthophoridae		
Anthophora		
bomboides	18	Goodpasture (1974b)
californica	19	Goodpasture (1974b)
Ceratina		
acantha	17	Goodpasture (1974b)
Diadasia		
enavata	15	Goodpasture (1974b)
Exomalopsis		
aureopilosa	9	Kerr (1972)
sp.	8	Goodpasture (1974b)
Isepeolus		
viperinus	16	Kerr (1972)
Ptilothrix		
bombiformis	6	Goodpasture (1974b)
Svastra		
obliqua expurgata	21	Goodpasture (1974b)
Xylocopa		
fenesterata	16	Kumbkarni (1965a)
Apidae		
Apis		
cerana	16	Deodikar et al. (1959); Sharma et al. (1961); Fahrenhorst (1977)
*1 *dorsata*	16	Kumbkarni (1964); Fahrenhorst (1977)
*2 *florea*	16	Fahrenhorst (1977)
mellifera	16	Sanderson & Hall (1948); Kerr (1969); Fahrenhorst (1977)
*3 *Bombus*		
affinis	18	Owen (1983)
atratus	20	Kerr & Silveira (1972)
bimaculatus	18	Owen (1983)
edwardsii	18	Goodpasture (1974b)
ephippiatus	18	Owen (1983)
griseocollis	19	Owen (1983)
impatiens	18	Owen (1983)
melanopygus	18	Owen (1983)
mixtus	18	Owen (1983)

APPENDIX 9 (cont.).

Bombus (cont.)		
morio	20	Kerr & Silveira (1972)
perplexus	18	Owen (1983)
rufocinctus	19	Owen (1983)
sitkensis	18	Owen (1983)
ternarius	18	Owen (1983)
terricola	18	Owen (1983)
vagans	18	Owen (1983)
vosnesenskii	18	Owen (1983)
Lestrimelitta		
cubiceps	18	Kerr & Araujo (1957)
Melipona		
compressipes	9	Kerr (1972)
interrupta	9	Kerr (1952)
marginata	9	Kerr (1948)
nigra	9	Kerr (1952)
quadrifasciata	9	Kerr (1972)
*4 quinqefasciata	18	Kerr (1972)
rufiventris	9	Kerr (1952)
subnitida	9	Kerr & Silveira (1972)
Meliponula		
bocandei	18	Kerr & Araujo (1957)
Psithyrus		
ashtoni	25	Owen (1983)
Trigona		
angustula	17	Kerr & Silveira (1972)
beccarii	17	Kerr (1972)
braunsi	14	Kerr (1972)
clavipes	17	Kerr & Silveira (1972)
cupira	17	Kerr & Silveira (1972)
denoiti	18	Kerr (1972)
depilis	17	Kerr & Silveira (1972)
doederleini	15	Kerr & Silveira (1972)
*5 droryana	18	Kerr & Silveira (1972)
emerina	18	Kerr (1972)
ferruginea	18	Kerr & Araujo (1957)
fuscipennis	17	Kerr & Silveira (1972)
ghilianii	15	Kerr (1972)
gribodoi	14	Kerr & Silveira (1972)
longicornis	15	Kerr & Silveira (1972)
muelleri	8	Kerr & Silveira (1972)
postica	17	Kerr & Silveira (1972)
remota	18	Kerr (1972)
schrottkyi	18	Kerr & Silveira (1972)
spinipes	17	Kerr & Silveira (1972)
staudingeri	17	Kerr (1972)
subnuda	18	Kerr (1972)
subterranea	17	Kerr & Silveira (1972)
tataira	17	Kerr (1972)
testaceicornis	17	Kerr & Silveira (1972)
varia	15	Kerr & Silveira (1972)

APPENDIX 9 (cont.).

VESPOIDEA		
(Vespiformes group)		
Sapygidae		
*6 *Sapyga*		
pumila	25,26	Goodpasture (1974b)
Eumenidae		
Ancistrocerus		
adiabatus	6	Goodpasture (1974a)
spilogaster	6	Goodpasture (1974a)
simulator	7	Goodpasture (1974a)
tuberculiceps	10	Goodpasture (1974a)
Euodynerus		
foraminatus	8	Goodpasture (1974a)
Vespidae		
Polistes		
*7 *apachus*	22 or 25	Hung et al. (1981)
canadensis	16	Kerr (1952)
carolina	19	Hung et al. (1981)
exclamans	33	Hung et al. (1981)
fuscatus fuscatus	26	Goodpasture (1974b)
gallicus	21	Pardi (1947)
hebraues	9	Misra (1972)
jadwigae	9	Machida (1934)
jokohamae	6	Machida (1934)
metricus	26	Hung et al. (1981)
omissus	14	Pardi (1947)
simillimus	28	Pompolo & Takahashi (1986)
snelleni	13	Machida (1934)
versicolor versicolor	31	Pompolo & Takahashi (1986)
(Formiciformes group)		
Formicidae	see Appendix 7	

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*1 Deodikar & Thakar's (1966) count of n = 8 has been omitted.
*2 Thakar & Deodikar's (1966) count of n = 8 has been omitted.
*3 Whelden's (1954) count for *Bombus fervidus* has been omitted.
*4 Tetraploid species (Kerr, 1972).
*5 Kerr's (1952) count of n = 9 has been omitted.
*6 Chromosome number polymorphism.
*7 Discrepancy probably due to poor spread of chromosomes or presence of sibling species in sample (Hung et al., 1981).

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8. INDEX

This index contains all Myrmecia species and infraspecific names used in the text, including those which are unpublished. Unpublished names are preceded by '#', while synonyms are preceded by '*'. The chief reference is underlined, followed by the range of pages which use the name.