

## Ants of the genus *Myrmecia* Fabricius: a review of the species groups and their phylogenetic relationships (Hymenoptera: Formicidae: Myrmeciinae)

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**Abstract.** *Myrmecia* Fabricius is revised at species-group level. Nine groups are recognized: those of *M.aberrans*, *M.cephalotes*, *M.gulosa*, *M.mandibularis*, *M.nigrocincta*, *M.picta*, *M.pilosula*, *M.tepperi* and *M.urens*. A key to the species groups is provided, and worker diagnoses, illustrations and species lists are given for each. Eight groups are constituted much as in the previous classification of John Clark, but defined using new characters. Phylogenetic relationships are investigated, with six cladograms derived from four sets of data, each with a different outgroup. The most plausible cladograms suggest that: (1) the *aberrans* group is the sister group to the others; (2) the *pilosula*, *tepperi* and *mandibularis* groups constitute a monophyletic assemblage, though monophyly of the first two is not confirmed; (3) the *gulosa*, *nigrocincta*, *urens* and *picta* groups constitute a monophyletic assemblage, though monophyly of the *picta* group is not confirmed; (4) the phylogenetic position of the *cephalotes* group is unclear.

### Introduction

Australian ants of the genus *Myrmecia*, known colloquially as 'bulldog ants', have attracted much attention from many myrmecologists and other biologists. Some species are very large in size (more than 30 mm in total length), and others relatively small (less than 8 mm long). Most species nest in soil, and some construct large mounds, sometimes with diameter exceeding 1 m. Some species, known commonly as 'Jack jumpers', are able to hop. Most species are highly aggressive, and several are known to cause painful, sometimes seriously allergic, even lethal, reactions in stung humans (Clarke, 1986). Scientific interest has, however, centred mainly on the widely accepted view that these

ants are among the most 'primitive' living today. *Myrmecia* retains many characters considered to be primitive in the family Formicidae. For example: the workers possess ocelli; the prothorax is well separated from, and freely movable against, the mesothorax; the mesonotum is distinctly defined; a lateral lobe is situated on each side of the mesosoma between the posterolateral corner of the mesonotum and the propodeum, and these lobes are connected transversely by a narrow mid-dorsal section of the metanotum; a pair of more-or-less long apical spurs is present on the middle and hind tibiae; and the sting is fully functional.

The biology of *Myrmecia* has been studied by many authors, including Wheeler (1933), Haskins & Haskins (1950), Freeland (1958), Gray (1971a, b, 1974a, b), Sisson (1974), Crossland, Crozier & Jefferson (1988) and Taylor (1989). Aspects of *Myrmecia* behaviour considered to be primitive were summarized by Wilson (1971).

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*Myrmecia* is the only extant representative of the subfamily Myrmeciinae, which also includes two genera represented only by fossils of Oligocene age: *Prionomyrmex* Mayr (see Wheeler, 1914) from the European Baltic amber and *Ameghinoa* Viana & Haedo Rossi (1957) from Argentina (Brown & Taylor, 1970).

*Myrmecia* is very diverse, and endemic to the Australian region. Ninety species have been reported from the Australian mainland and Tasmania, and one from New Caledonia. One Australian species has been introduced into New Zealand (Brown, 1958; Taylor, 1987).

In spite of its general myrmecological, evolutionary, biological and medical importance, and rather compact distributional range, the taxonomy of the genus has been confused. *Myrmecia* was acknowledged to be taxonomically difficult by Brown (1953b), who stated that '...many of its species are very variable in size, color and sculpture, while at the same time the specific differences are often based on characters that appear relatively trivial until their constancy is appreciated through the examination of large series from all parts of their ranges.'

Recent karyological studies suggest the occurrence of sibling species (Imai *et al.*, 1977; Crosland, Crozier & Imai, 1988; Imai & Taylor, 1986, 1989) and in such cases even relatively trivial morphological characters are known to indicate species differences. For example, in some groups of related forms specific differences in coloration clearly diagnose different taxa, while in other complexes similar levels of variability are merely infraspecific.

The primary aim of this paper is to revise the taxonomy of *Myrmecia* at species-group level. It is operationally desirable to sub-divide a genus of this size into species groups if such entities can be distinguished clearly and practically. Furthermore, the establishment of species groups is useful for consideration of the evolutionary history of *Myrmecia*, provided, of course, that they are reasonably considered to be monophyletic. Recognition of appropriate species groups is thus an important step toward a sound classification.

After reviewing the history of *Myrmecia* taxonomy, I will propose the recognition of nine species groups, partly derived from the classification of Clark (1951), and will define or redefine them based on the morphological

characters of workers. The phylogenetic relationships of the species groups will be assessed using cladistic methodology. A key to the species groups is given. Further work on the species-level taxonomy of the genus, including synonymies and descriptions of new species, will be presented elsewhere.

### Historical review

*Myrmecia* was established by Fabricius (1804) to include seven species which he had previously described in the genus *Formica* Linnaeus, and four new species. Although most of them were later transferred to other genera of the subfamilies Ponerinae, Ecitoninae or Myrmicinae, three of these species are still valid and correctly placed: *M. gulosa* (Fabricius), *M. forficata* (Fabricius) and *M. esuriens* Fabricius. Shuckard (in Swainson & Shuckard, 1840: 173) designated *M. gulosa* as type species of the genus.

In his comprehensive classification of ants, Emery (1911) recognized three subgenera: *Myrmecia* (*Myrmecia*), comprising thirty-eight forms grouped into seven species groups, *M. (Pristomyrmecia)* Emery, comprising six forms, and *M. (Promyrmecia)* Emery, comprising two forms (Table 1). Emery's classification was based mainly on the shape of the mandibles. Wheeler (1922) modified Emery's system, adding *M. (Halmamyrmecia)* Wheeler as a subgenus characterized by its jumping behaviour. It included the species of Emery's subgenus (*Pristomyrmecia*) and some members of his *pilosula* group of subgenus (*Myrmecia*). In later notes on the biology and taxonomy of myrmeciines, Wheeler (1933) did not refer again to his subgenus (*Halmamyrmecia*), and the taxon was eventually synonymized under *Promyrmecia* by Clark (1943). At the same time Clark raised *Promyrmecia* to full generic rank, extended its conception, and divided it into seven species groups. His *Promyrmecia* included Emery's subgenus (*Pristomyrmecia*) and the *pilosula* group, along with the species of Emery's original subgenus (*Promyrmecia*). Later Clark (1951) revised the whole subfamily Myrmeciinae, treating 118 species and subspecies. He then recognized eight species groups in *Promyrmecia* (adding the newly distinguished *M. urens* group), and five species groups in

*Myrmecia* (Table 1). His genus *Myrmecia* corresponded to Emery's subgenus (*Myrmecia*), except for transfer of the *pilosula* group to *Promyrmecia*.

Brown (1953a) rejected the segregation of *Promyrmecia* from *Myrmecia* on the basis of the lack of an appropriate morphological gap separating the two. He returned the *Promyrmecia* species to *Myrmecia*, and did not recognize subgenera within the newly reconstituted genus. No comprehensive alternative classification at species-group level was proposed. Brown later (1953b) commented on the nomenclature and other details of a number of species, described one as new, and proposed thirty-four new synonyms. His work, which did not treat all of the then known species and was basically a critical review of Clark (1951), is the most recent extensive taxonomic study on *Myrmecia*.

Subsequently there has been only one taxonomic change to the genus — the description of an additional species by Douglas & Brown (1959). The recent checklists of Taylor & Brown (1985) and Taylor (1987) outlined bibliographic information and the first gave summary distributions of each species. Both lists recognized ninety-one valid species, with 150 available names, including junior synonyms.

### *Myrmecia* Fabricius

*Myrmecia* Fabricius, 1804: 423. Type species: *Formica gulosa* Fabricius 1775, by subsequent designation of Shuckard, in Swainson & Shuckard, 1840: 173.

*Promyrmecia* Emery, 1911: 19 (as subgenus of *Myrmecia*). Type species: *Myrmecia aberrans* Forel, 1900: 54; by original designation. (Synonymy by Brown, 1953a: 1.)

*Promyrmecia* Emery; Clark, 1943: 84 (raised to genus).

*Pristomyrmecia* Emery, 1911: 21 (as subgenus of *Myrmecia*). Type species: *Myrmecia mandibularis* F. Smith, 1858: 145; by original designation. (Synonymized with *Promyrmecia* by Clark, 1943: 84.)

*Halmanyrmecia* Wheeler, 1922: 195 (as subgenus of *Myrmecia*). Type species: *Myrmecia pilosula* F. Smith, 1858: 146; by original designation. (Synonymized with *Promyrmecia* by Clark, 1943: 84.)

Workers of *Myrmecia* are easily distinguished morphologically, as follows (asterisks indicate apomorphic character states):

- (1) Ocelli present.
- \* (2) Eyes placed anteriorly on the head capsule.
- \* (3) Third antennal segment elongate.
- (4) Median portion of clypeus produced anteriorly with a median depressed area.
- \* (5) Clypeo-labral junction exposed.
- \* (6) Dorsal area of labrum produced.
- \* (7) Mandibles more or less elongate.
- (8) Maxillary palpus 6-segmented, labial palpus 4-segmented.
- (9) Pronotum separated from mesothorax by a movable connection.
- (10) Mesonotum distinctly defined.
- (11) Lateral lobes present dorsolaterally on metanotum.
- (12) Metanotum more or less distinctly defined.
- (13) Coxal cavities of hind legs open.
- (14) Mid and hind legs each with 2 tibial spurs.
- (15) Basitarsi of mid and hind legs bearing longitudinal sulci.
- (16) Tarsal claws of all legs each with a supplementary preapical tooth on its inner curve.
- \* (17) Abdominal segment III forming a distinct postpetiole.
- \* (18) Abdominal segment IV tubulate; with pretergite and presternite inserted into the postpetiolar exoskeleton.
- (19) Sting well developed.

### Definition of the groups, and their species composition

This study recognizes nine species groups in *Myrmecia*. They are listed in Table 1, in comparison with the arrangements of previous classifications. Brown (1953a, b) indicated that the definition of species groups by Clark (1951) was unclear and inconsistent. For example, *M. rogeri* Emery and *M. tricolor* Mayr, both of which were assigned to the *tricolor* group by Clark, have proved to be synonyms of *M. simillima* F. Smith, a member of Clark's *vindex* group. In spite of his failure to specify reasonable diagnostic characters, Clark's eight species groups are still perceptible in the classification presented here, but they are defined

Table 1. The species groups of myrmecine ants as proposed here, compared with those of previous authors.

| Emery (1911)                       | Clark (1951)                       | Present study                |
|------------------------------------|------------------------------------|------------------------------|
| Genus <i>Myrmecia</i>              | Genus <i>Promyrmecia</i>           | Genus <i>Myrmecia</i>        |
| Subgenus <i>Promyrmecia</i> [1]    | <i>aberrans</i> group [1]          | 1. <i>aberrans</i> group     |
|                                    | <i>picta</i> group [6]             | 2. <i>cephalotes</i> group   |
| Subgenus <i>Myrmecia</i>           | <i>cephalotes</i> group [2]        | 3. <i>gulososa</i> group     |
| <i>gulososa</i> group [3]          | <i>mandibularis</i> group [4]      | 4. <i>mandibularis</i> group |
| <i>vindex</i> group [3]            | <i>tepperi</i> group [8]           | 5. <i>nigrocincta</i> group  |
| <i>forficata</i> group [3]         | <i>varians</i> group [7]           | 6. <i>picta</i> group        |
| <i>tarsata</i> group [3]           | <i>urens</i> group [9]             | 7. <i>pilosula</i> group     |
| <i>nigrocincta</i> group [5, 7]    | <i>pilosula</i> group [7]          | 8. <i>tepperi</i> group      |
| <i>esuriens</i> group [3]          |                                    | 9. <i>urens</i> group        |
| <i>pilosula</i> group [6, 7, 9]    | Genus <i>Myrmecia</i>              |                              |
|                                    | <i>forceps</i> group [3]           |                              |
| Subgenus <i>Pristomyrmecia</i> [4] | <i>tricolor</i> group [3]          |                              |
|                                    | <i>vindex</i> group [3]            |                              |
|                                    | <i>gigas</i> group [3]             |                              |
|                                    | <i>nigrocincta</i> group [3, 5, 7] |                              |

The numbers in square brackets in the Emery and Clark classifications correspond to the group numbers listed for the present study.

using new and different character sets:

In the following discussion the composition of each group is given by listing valid, available species names. The lists are provisional and are likely still to include prospective junior synonyms. As well, I am aware of several undescribed species, but their attributes do not compromise the present species-group arrangement. For full synonymy of each species listed see Taylor & Brown (1985) or Taylor (1987).

Characters referred to in the species-group diagnoses are included in the lists comprising Tables 5 and 6; they are discussed in detail below, and most are illustrated in the accompanying figures. Species are listed using senior synonyms. In some cases types or type-compared voucher specimens of junior synonyms were studied. They are indicated in the appendix.

### The *aberrans* group (Figs 1–2)

#### Diagnosis of worker

- (1) Occipital carina absent (Fig. 19).
- (2) Clypeus overhung by paired projections of its anterior margin (Fig. 27).
- (3) Mandibles relatively broad and subtriangular (Fig. 30).

(4) Mandibular teeth arranged in a single row, without a supplementary ventral subapical tooth (as in Fig. 32).

(5) Basalmost dentition of mandible consisting of a single tooth (Fig. 30).

(6) Eyes less convex than in other species groups, with a truncate anterior portion (Fig. 22).

(7) Antennal scapes short: Scape Index ( $SI = \text{scape length/head width} \times 100$ ) < 75.

(8) Mid-dorsal area of metanotum forming a furrow, delimited anteriorly by the straight posterior margin of the mesonotum, posteriorly by the straight anterior margin of the propodeum (Fig. 39).

(9) Anterior peduncle of petiole not differentiated (Fig. 47).

(10) Postpetiole large and elliptical, about two-thirds or more as broad as gaster.

#### Species composition

*aberrans* Forel, *eupoecila* (Clark), *excavata* (Clark), *froggatti* Forel, *greavesi* (Clark), *maura* Wheeler, *maura formosa* Wheeler, *nobilis* (Clark).

Workers of the *aberrans* group are medium to large in size, with a robust body, short scapes, and short legs. The group is very distinctive

within *Myrmecia*. Unlike others, it has short, broad mandibles, and the clypeo-labral junction is partly concealed in frontal view by a pair of prominent clypeal projections. The group is distributed in southern and eastern areas of Australia; the species are rare, their colonies small and specimens seldom collected. The group corresponds to subgenus (*Promyrmecia*) of Emery (1911) and to the *aberrans* group of the genus *Promyrmecia* of Clark (1943). Although seven species are listed here the status of several has been questioned (Brown, 1953b).

**The *cephalotes* group (Figs 3-4)**

*Diagnosis of worker*

- (1) Occipital carina absent (as in Fig. 19).

- (2) Mandibular shaft without a sub-basal broadened area (as in Fig. 31).

- (3) Mandibular teeth a single row, without a supplementary ventral subapical tooth (as in Fig. 32).

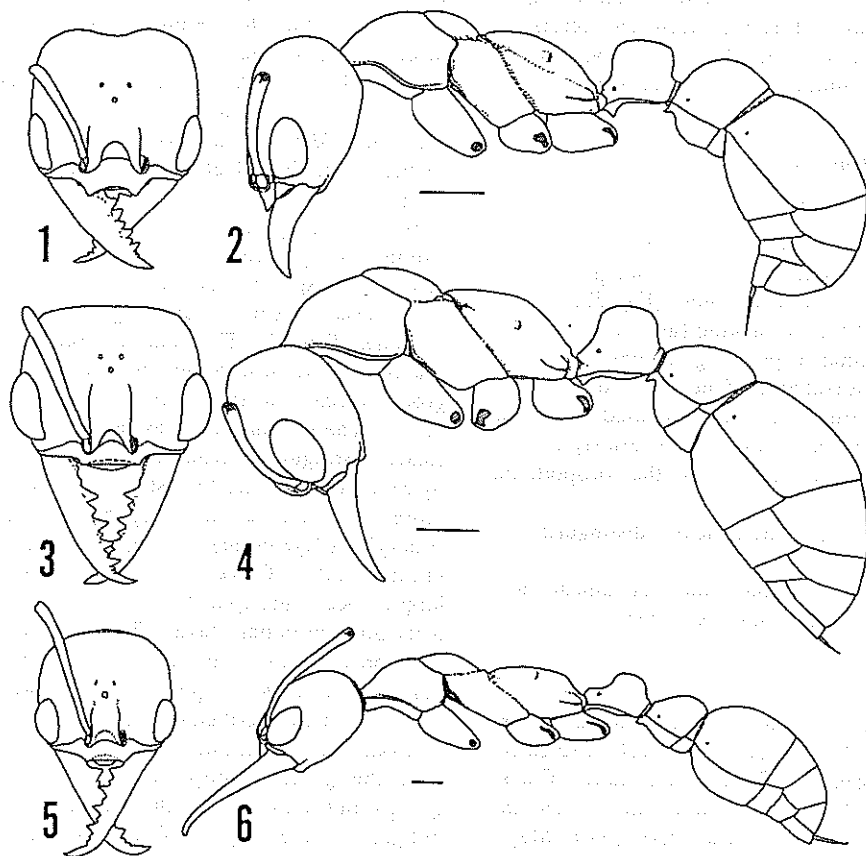
- (4) Dorsal surface of mandibles with a row of extremely long erect hairs, averaging about twice as long as the mandibular width or longer, and forming a psammophore (Fig. 37).

- (5) Antennal scapes short (SI < 100).

- (6) Mid-dorsal metanotal area narrow, but not forming a furrow: delimited anteriorly by the almost straight posterior margin of the mesonotum, and posteriorly by the rounded anterior margin of the propodeum.

- (7) Anterior peduncle of petiole not differentiated (as in Fig. 47).

- (8) Postpetiole large and elliptical, about



Figs 1-6. *Myrmecia* workers [scale line = 1 mm]. 1-2, *M. aberrans* Forel (*aberrans* group): 1, head; 2, profile; 3-4, *M. cephalotes* (Clark) (*cephalotes* group): 3, head; 4, profile; 5-6, *M. gulosa* (Fabricius) (*gulosa* group): 5, head; 6, profile.

two-thirds as broad as gaster.

(9) Posterior hind tibial spur spinose, not pectinate (Fig. 46).

#### Species composition

*callima* (Clark), *cephalotes* (Clark), *hilli* (Clark).

The ants of this group are brightly coloured, with light orange-brown trunk and legs, and sharply contrasting black heads. The size is medium for the genus, and the stature robust. The *cephalotes* group is distributed across eastern and western inland Australia. All species are relatively rare.

Species composition of the *cephalotes* group is here the same as in Clark (1943). Clark characterized these ants by the shape of the mandibles, the mandibular dentition and general coloration. More significant characters include those numbered (4) and (9) above, both of which are unique to the *cephalotes* group.

#### The *gulosa* group (Figs 5–6)

##### Diagnosis of worker

- (1) Occipital carina present (Fig. 20).
- (2) Supplementary ventral tooth present on subapical portion of mandible (Fig. 33).
- (3) Genal furrow lacking (as in Fig. 22).
- (4) Antennal scapes long;  $SI > 90$ .
- (5) Mid-dorsal area of metanotal dorsum delimited anteriorly by the rounded posterior margin of the mesonotum, posteriorly by the convex anterior margin of the propodeum (Fig. 41).
- (6) Petiolar peduncle clearly distinguishable (Fig. 48).
- (7) Postpetiole small and subconical, less than two-thirds as broad as gaster.

#### Species composition

*analis* Mayr,  *arnoldi* Clark,  *atrata* Clark,  *auriventris* Mayr,  *brevinoda* Forel,  *cardigaster* Brown,  *comata* Clark,  *decipians* Clark,  *desertorum* Wheeler,  *dimidiata* Clark,  *esuriens* Fabricius,  *fasciata* Clark,  *ferruginea* Mayr,  *flavicoma* Roger,  *flavicoma minuscula* Forel,  *forceps* Roger,  *forficata* (Fabricius),  *fulgida* Clark,  *gratiosa* Clark,  *gulosa* (Fabricius),  *hirsuta* Clark,  *inquilina* Douglas & Brown,

*longinodis* Clark,  *midas* Clark,  *mjobergi* Forel,  *nigriceps* Mayr,  *nigriscapa* Roger,  *pavida* Clark,  *piciceps* Clark,  *pulchra* Clark,  *pyriformis* F. Smith,  *regularis* Crawley,  *rowlandi* Forel,  *rubripes* Clark,  *rufinodis* F. Smith,  *simillima* F. Smith,  *subfasciata* Viehmeyer,  *suttoni* Clark,  *tarsata* F. Smith,  *vindex* F. Smith,  *vindex basirufa* Forel.

The ants of this group are generally slender and large in size, with long legs. They are the typical, large 'bulldog ants' of Australian idiom. Worker size may vary substantially, even within a single colony. The shape of the mandibles is variable: the outer marginal profile ranges interspecifically from concave to convex; the sub-basal portion from broadened to simply narrow and straight; and the number of larger teeth on the jaws from 3 to 6 or more. The length of the anterior peduncle of the petiole also varies, but the peduncle itself is always more-or-less distinct. The *gulosa* group ranges over much of the Australian mainland (except for the north-western coastal area) and Tasmania. *M. brevinoda* has been introduced on to the North Island of New Zealand (Brown, 1958).

When compared to previous classifications, the present conception of the *gulosa* group corresponds roughly to the subgenus (*Myrmecia*) of Emery, or the genus *Myrmecia* of Clark (Table 1). The main difference here is that both these authors included the *nigrocincta*-group species in their conceptions of '*Myrmecia*'. The *gulosa* group, as redefined here, is clearly distinguished from the *nigrocincta* group by characters (2) and (3) listed above. Furthermore, it embraces most species groups of Emery's (*Myrmecia*) (except the *pilosula* group), and of Clark's *Myrmecia*. This is the largest species group in *Myrmecia*, and includes forty-one nominal taxa. The species-level taxonomy at this point is by no means well resolved. More synonyms doubtless await detection, and undescribed species are represented in available collections. Future studies might split the *gulosa* group into smaller species groups, but, nonetheless, the previous constituent groups of Emery and Clark are here abandoned, because they were poorly conceived and obscurely defined.

*Myrmecia cardigaster* is transferred here from the *nigrocincta* group of Clark. This putative

species is considered to be closely related to the sympatric *M. rowlandi*. It has a similarly shaped petiole, and parallel frontal carinae. Within the *gulosa* group *M. esuriens* is unique in having short antennal scapes (SI < 110), short mandibles (MI 86–91), a straight anterior margin to the petiolar node in dorsal view, and a relatively large postpetiole (PsI > 60). These are all considered to be primitive characters in *Myrmecia* (see later section). These character states occur also in various smaller-sized species, such as those of the *urens* and *pilosula* groups (see below). Brown (1953b) has suggested that *M. esuriens* was probably an early offshoot of this group.

### The *mandibularis* group (Figs 7–8)

#### Diagnosis of worker

- (1) Occipital carina absent (as in Fig. 19).
- (2) Hairs on clypeus elongate, reaching anteriorly to the mid-length of the mandibles (Fig. 28).
- (3) Apical blade of mandibular teeth short and strongly curved (Fig. 36).
- (4) Ventral supplementary tooth present on subapical portion of mandible (as in Fig. 33).
- (5) Sub-basal teeth on mandible very low, vestigial or almost absent (Fig. 36).
- (6) Antennal scapes short (SI < 90).
- (7) Mid-dorsal area of metanotum forming a deep furrow, delimited anteriorly by the straight posterior margin of the mesonotum, posteriorly by the straight anterior margin of the propodeum (as in Fig. 40).
- (8) Anterior peduncle of petiole not differentiated (as in Fig. 47).
- (9) Postpetiole large and elliptical, more than two-thirds as broad as gaster.

#### Species composition

*fulviculis* Forel, *fulvipes* Roger, *gilberti* Forel, *luteiforceps* Clark, *mandibularis* F. Smith, *piliventris* F. Smith, *potteri* (Clark).

The species of this group are medium in size. The *mandibularis* group is characterized by the peculiar shape of the mandibles, the reduction in stature of their sub-basal teeth, and the elongate hairs on the clypeus. Similar reduction of the sub-basal mandibular teeth occurs also in

the *tepperi* group. The body colour is black, but the appendages are interspecifically variable in colour, and often brightly coloured. There is often conspicuously coloured pubescence on the gaster. The *mandibularis* group ranges from the east, through southern coastal to south western Australia, and Tasmania. As conceived here the group conforms with Emery's subgenus *Pristomyrmecia*, and with the *mandibularis* group of Clark. Although seven species are included, classification of the group remains somewhat confused, and a number of apparently undescribed species are represented in available collections. Three morphologically sibling species of the *M. piliventris* complex are known to vary greatly in karyotype (Imai & Taylor, 1986; Imai *et al.*, 1988), and this could foreshadow the existence of other such species in the *mandibularis* group.

### The *nigrocincta* group (Figs 9–10)

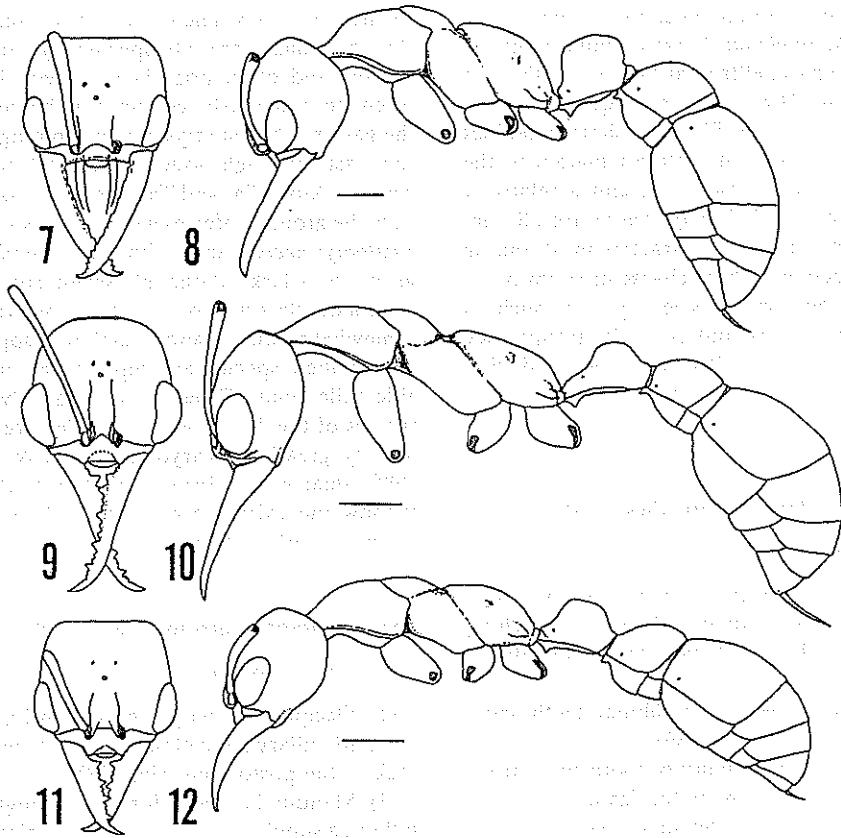
#### Diagnosis of worker

- (1) Occipital carina present (as in Fig. 20).
- (2) Maxillary palpi elongate, reaching almost back to the postocciput (Fig. 38).
- (3) Mandibular teeth forming a single row, without a supplementary ventral preapical tooth (as in Fig. 32).
- (4) Genal furrow present on each side of head, between clypeus and eye (Fig. 21).
- (5) Antennal scape long (SI > 100).
- (6) Mid-dorsal area of metanotum delimited anteriorly by the rounded posterior margin of the mesonotum, posteriorly by the convex anterior margin of the propodeum (as in Fig. 41).
- (7) Petiolar peduncle clearly distinguishable (as in Fig. 48).
- (8) Postpetiole small and subconical, less than two-thirds as broad as gaster.

#### Species composition

*flammicollis* Brown, *nigrocincta* F. Smith, *petiolata* Emery.

The members of this group have medium-sized slender bodies and long scapes and legs. Their distribution is restricted to the eastern region of Australia. The *nigrocincta*-group species resemble those of the *gulosa* group, but they are distinguished by characters (2), (3) and



Figs 7-12. *Myrmecia* workers [scale line = 1 mm]. 7-8, *M. mandibularis* F. Smith (*mandibularis* group): 7, head; 8, profile. 9-10, *M. nigrocincta* F. Smith (*nigrocincta* group); 9, head; 10, profile. 11-12, *M. picta* (F. Smith) (*picta* group): 11, head; 12, profile.

(4) listed above. Clark (1951) distinguished this group on its possession of concave outer mandibular margins, mandibular shafts broadened at the basal fourth or fifth to form an angular inner border, and an obsoletely sculptured mesothorax. This was not a satisfactory characterization. Similar mandibles occur in several species of the *gulosa* group, and the mesothoracic sculpturation varies intraspecifically in these and other species.

When Emery (1911) established the *nigrocincta* group it included three species: *apicalis* Emery, *nigrocincta* and *petiolata* (the former known only from New Caledonia, the others Australian). Subsequently, Clark (1951) added the new Australian species, *M. cordata*, but its name was later replaced, as a junior homonym, by *M. cardigaster* Brown (1953b).

*M. cardigaster* and *M. apicalis* are here transferred respectively to the *gulosa* and *pilosula* groups. Brown (1953b) described *flammicollis* and assigned it to the '*apicalis* group'. The definition and species composition of this '*apicalis* group' were not volunteered, but it is clear to me that *flammicollis* should be placed in the *nigrocincta* group, and that neither it nor *nigrocincta* are particularly close to *apicalis*.

#### The *picta* group (Figs 11-12)

##### Diagnosis of worker

- (1) Occipital carina absent (as in Fig. 19).
- (2) Mandibular teeth forming a single row, without a supplementary subapical tooth (as in Fig. 32).



(3) Head bicolourous; its anterior half yellow, the posterior portion black.

(4) Antennal scapes short (SI<90).

(5) Mid-dorsal metanotal area narrow, not forming a transverse furrow, delimited anteriorly by the rounded posterior margin of the mesonotum, posteriorly by the rounded anterior margin of the propodeum.

(6) Anterior peduncle of petiole not differentiated (as in Fig. 47).

(7) Postpetiole large, about two-thirds as broad as gaster.

(8) Anterior hind tibial spur at least half as long as its posterior partner, or longer (as in Fig. 44).

#### *Species composition*

*fucosa* Clark, *picta* F. Smith.

*M.fucosa* and *M.picta* are relatively small-sized *Myrmecia* species. The shape of the mandibles differs interspecifically: *M.fucosa* has a rather less broad sub-basal portion than *M.picta*. Although the coloration of trunk and gaster vary, the black and yellowish bicoloured head pattern is consistent. The *picta* group appears similar to the *urens* group, but is distinguished by the lack of an occipital carina, and the relative length of the anterior tibial spurs of the hind legs. The species composition is the same as that of Clark (1951), but his definition of the group was poorly expressed. The group is distributed across southern Australia.

#### The *pilosula* group (Figs 13–14)

##### *Diagnosis of worker*

(1) Occipital carina absent (as in Fig. 19).

(2) Apical blade of mandible relatively long (Fig. 34).

(3) Ventral tooth present on subapical portion of mandible (as in Fig. 33).

(4) Sub-basal portion of mandibles fully toothed (Fig. 34).

(5) Mid-dorsal metanotal area forming a transverse furrow, delimited anteriorly by a straight posterior margin to the mesonotum, posteriorly by a straight anterior margin to the propodeum (as in Fig. 40).

(6) Anterior peduncle of petiole short or indistinct (as in Fig. 47).

(7) Postpetiole large and elliptical, usually

about two-thirds or more as broad as the gaster.

#### *Species composition*

*apicalis* Emery, *celaena* (Clark), *chasei* Forel, *chasei ludlowi* Crawley, *chrysogaster* (Clark), *cydista* (Clark), *dispar* (Clark), *elegans* (Clark), *harderi* Forel, *michaelseni* Forel, *michaelseni queenslandica* Forel, *occidentalis* (Clark), *opaca* (Clark), *pilosula* F. Smith, *rugosa* Wheeler, *varians* Mayr.

Most of the species of the *pilosula* group are relatively small in size. The petiolar peduncle is usually undifferentiated, but several species have short peduncles (cf. *apicalis*, *pilosula*). The mandibles are either weakly broadened sub-basally (*dispar*, *apicalis*, etc.) or almost straight (*elegans*, *pilosula*, etc.). Coloration varies, often within a species. The group is distributed over much of the Australian mainland (but not in central and north-western areas) and Tasmania, and the New Caledonian *M.apicalis* is the only *Myrmecia* species endemic to a land area other than Australia or Tasmania. The *pilosula* group of Emery (1911) was heterogeneous. Clark (1943) removed several species and established the *picta*, *tepperi* and *varians* groups for them. The species of Clark's *varians* group were all later synonymized under *varians* by Brown (1953b). *M.varians* is here returned to the *pilosula* group.

As stated earlier, *M.apicalis* is transferred here from the *nigrocincta* group of previous authors. In the *pilosula* group *apicalis* is unique, not only because of its New Caledonian provenance, but also on account of its unusual body proportions. Unlike other members of the group it has elongate antennal scapes and a relatively small postpetiole.

The group includes sixteen nominate forms, but recent collaborative cytogenetic work by Imai and several Australian associates (Crosland, Crozier & Imai, 1988; Imai *et al.*, 1988; Imai & Taylor, 1989) indicates that several sibling species are included in the present '*M.pilosula*'.

#### The *tepperi* group (Figs 15–16)

##### *Diagnosis of worker*

(1) Occipital carina absent (as in Fig. 19).

(2) Hairs on the clypeus short, not reaching

beyond the basal quarter of the mandibles (cf. Fig. 28).

(3) Apical blade of mandibular teeth long and gently curved (Fig. 35).

(4) Ventral tooth present on subapical portion of mandible (as in Fig. 33).

(5) Sub-basal teeth on mandible very low, vestigial or almost lacking (Fig. 35).

(6) Antennal scapes short (SI < 95).

(7) Metanotal area forming a transverse furrow, delimited anteriorly by a straight posterior margin to the mesonotum, and posteriorly by a straight anterior margin to the propodeum (Fig. 40).

(8) Anterior peduncle of the petiole not differentiated (as in Fig. 47).

(9) Postpetiole large and elliptical, more than two-thirds as broad as gaster.

#### Species composition

*clarki* Crawley, *dixonii* (Clark), *swalei* Crawley, *tepperi* Emery, *testaceipes* (Clark).

The species of this group are small-sized. The *tepperi* group resembles the *pilosula* group in body size and proportions, and some species display colour patterns similar to others of the *pilosula* group. *M. tepperi* and its relatives can, however, be distinguished readily from members of the *pilosula* group by character (5) cited above. The *tepperi*-group species are also similar to those of the *mandibularis* group; like them they have the sub-basal portion of the mandibles armed with relatively reduced teeth. The *tepperi* group is recognizable because the apical blade of the mandible is more acute than in the *mandibularis* group; the mandibular shaft more slender, with its outer border slightly concave; and the hairs on the clypeus relatively short. The group ranges from south-western to south-eastern areas of continental Australia.

The *tepperi* group was established by Clark (1943) as an excision from the *pilosula* group of Emery (1911). The species composition here is the same as that of Clark (1943).

#### The *urens* group (Figs 17–18)

##### Diagnosis of worker

(1) Occipital carina present (as in Fig. 20).

(2) Antennal scape short (SI usually < 80).

(3) Metanotal area more or less open, delimited anteriorly by a rounded posterior margin to the mesonotum, and posteriorly by a convex anterior margin to the propodeum (as in Fig. 41).

(4) Anterior margin of propodeum widely rounded, not distinctly transverse.

(5) Anterior peduncle of petiole not differentiated (as in Fig. 47).

(6) Postpetiole large and elliptical, about two-thirds as broad as gaster, or nearly so.

(7) Anterior hind tibial spur short, less than half as long as posterior one (Fig. 45).

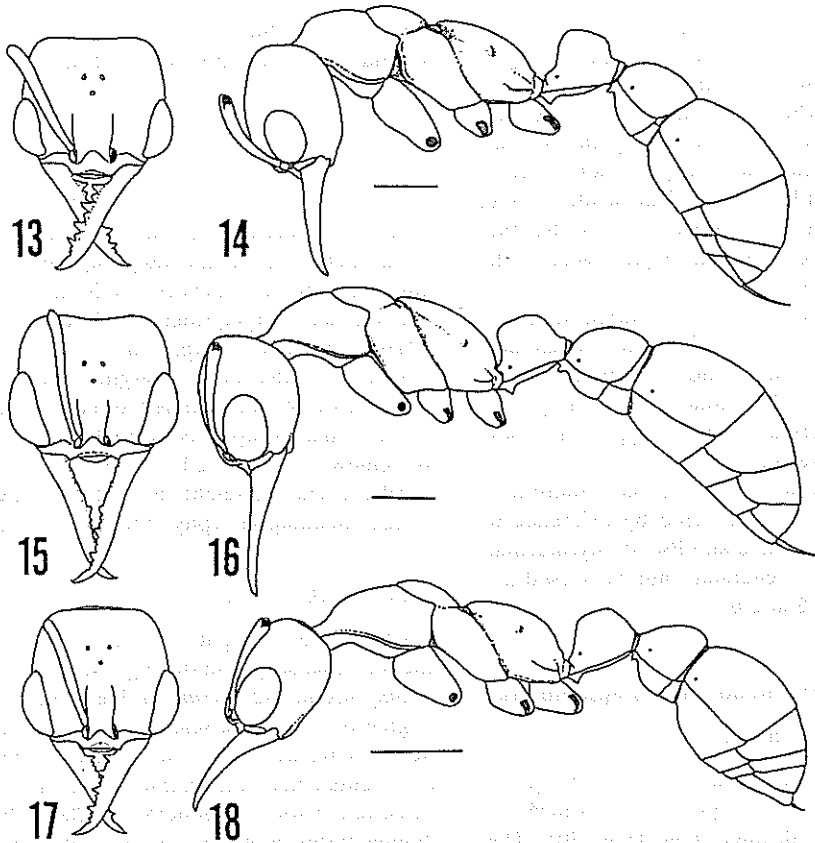
#### Species composition

*dichospila* Clark, *exigua* (Clark), *infima* Forel, *nigra* Forel, *rubicunda* (Clark), *urens* Lowne.

All of the *urens*-group species are small in size. They demonstrate wide-ranging intra-specific colour variation, even within single colonies. Their collective distribution is from south-eastern, through southern coastal, to south-western Australia. These species resemble those of the *picta* group. In fact, Emery (1911) considered *urens* to be a junior synonym of *picta*, and believed that *infima* and *nigra* were infraspecific forms of *picta*, which he assigned to his *pilosula* species group. When Clark (1943) established the *picta* group it still contained the species of the *urens* group, though he recognized the relevant taxa as separate species. Later, however, he separated the *urens* group from the *picta* group (Clark, 1951). His definition of the *urens* group, which invoked as distinguished characters aspects of pronotal sculpturation and mandibular dentition, was, however, obscure. This group in fact is unique in *Myrmecia* in having extremely short anterior spurs on the hind tibiae.

#### Character analysis

When considering phylogenetic relationships using cladistic methods the choice of an out-group is important. Apart from the related extinct Oligocene genera *Prionomyrmex* and *Ameghinoa* (see above), *Myrmecia* is the sole genus of subfamily Myrmeciinae. Thus, the out-group must be selected from another, putatively related, subfamily. The sister group most ap-



Figs 13–18. *Myrmecia* workers [scale line = 1 mm]. 13–14, *M. pilosula* F. Smith (*pilosula* group): 13, head; 14, profile. 15–16, *M. tepperi* Emery (*tepperi* group): 15, head; 16, profile. 17–18, *M. urens* Lowne (*urens* group): 17, head; 18 profile.

appropriate to the Myrmeciinae is not clearly recognizable. Several relevant hypotheses regarding the relationships of *Myrmecia* and the Myrmeciinae have been proposed, as follows:

(1) *Nothomyrmecia* is the sister group of *Myrmecia*. It has been often stated that the genus *Nothomyrmecia* Clark is closely related to *Myrmecia*. Brown (1954) assigned these genera to separate tribes of subfamily Myrmeciinae — the Myrmeciini and the Nothomyrmeciini; taxa which had been previously recognized as subfamilies by Clark (1934, 1951). This view was supported by Wheeler & Wheeler (1985), based on larval similarities. Taylor (1978), in the first comprehensive study of *Nothomyrmecia* following its

rediscovery in 1977, reinstated the subfamily Nothomyrmeciinae, but pointed out that there were many shared features linking *Nothomyrmecia* and *Myrmecia*, some of them unique among ants, despite the cladistically important separation between them based on tubulation of abdominal segment IV. The two subfamilies, and thus their contained genera, were recognized as sister taxa. Under these hypotheses *Nothomyrmecia* would clearly be the appropriate outgroup for cladistic analysis of the species groups of *Myrmecia*.

(2) Subfamily Pseudomyrmecinae is the sister group of subfamily Myrmeciinae. Brown (1954) has suggested that the ants of subfamily Pseudomyrmecinae share many features with

the Myrmeciinae (in which he included both *Myrmecia* and *Nothomyrmecia*). In his Fig. 1 Pseudomyrmecinae was drawn as a branch from (*Myrmecia* + *Prionomyrmex*), while the subfamily Dolichoderinae (including the Aneur-etinae of some classifications) was derived from *Nothomyrmecia*-like stock. The cladogram of Hölldobler & Wilson (1990) implies also that the sister group of subfamily Myrmeciinae is the Pseudomyrmecinae.

(3) Myrmeciinae is one of three trichotomous branches comprising (Myrmeciinae), (Pseudomyrmecinae) and (Myrmicinae + Cerapachyinae + Dorylinae (s.l.) + Leptanillinae + Ponerinae). This hypothesis was presented by Ward (1990).

In the following discussion, therefore, character states are polarized by reference to the Nothomyrmeciinae and Pseudomyrmecinae as outgroups. The character numbers used are those of Tables 5 and 6.

### Characters of the head and its appendages

#### *Occipital carina* (Character 1)

The *gulosa*-, *nigrocincta*- and *urens*-group species each have an occipital carina, which is a low but usually distinct ridge (Fig. 20). The other six groups have no such carinae (Fig. 19). This structure occurs in *Nothomyrmecia*, but only very weakly, and on the dorsal portion of the occiput. Subfamily Pseudomyrmecinae has no such structure. The occipital carina is considered here to be apomorphic, but analogous carinae have probably evolved several times in other ant subfamilies, such as Ponerinae, Myrmicinae and Cerapachyinae, as exoskeletal reinforcing structures.

#### *Genae* (Characters 2, 3)

The gena, which is the area of the head on each side between the anterior end of the eye and the mandibular insertion, is shortened in the *mandibularis* and *tepperi* groups, and in many species of the *gulosa* group, where the gena is shorter than the scape width. This character state results from the extreme anterior placement of the eye in these species, and is considered to be an apomorphy.

A peculiar short groove is found in the genal region of the *nigrocincta*-group species

(Fig. 21). Its function is not known, and it is considered an autapomorphy of the *nigrocincta* group.

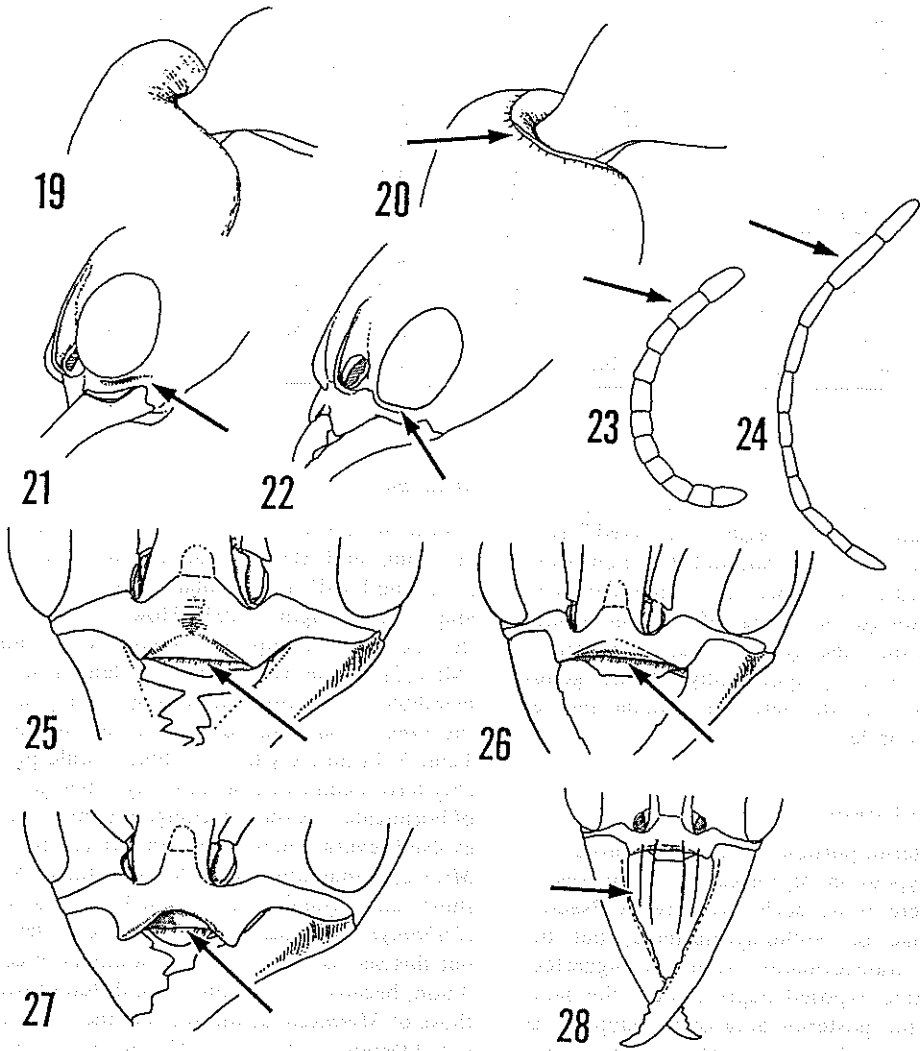
#### *Eyes* (Characters 4–6)

The strongly convex eyes of *Myrmecia* are considered here to be apomorphic. This feature occurs in most of the species groups. Primitively, the eyes are less convex, as in the *aberrans* group and Pseudomyrmecinae. Usually, in most *Myrmecia* species groups and the other relevant subfamilies, the outer margin of the eye is almost oval, with a rounded anterior border. In the *aberrans* group, however, the anterior part is somewhat truncated, so that the anterior border is nearly straight (Fig. 22). This peculiar state is an autapomorphy of the *aberrans* group.

#### *Antennae* (Characters 7–9)

Clark (1951) weighted the relative length of the antennal scapes in distinguishing his genera *Promyrmecia* and *Myrmecia*. He focused on the degree by which the scape extends beyond the degree by which the scape extends beyond the occipital border of the head. Brown (1953b) commented that this character was not in fact consistent with the 'genera' of Clark. Fig. 29 demonstrates, however, that the relative length of the scapes (scape length/head width) in the *gulosa* and *nigrocincta* groups is consistently greater than in other groups. Judging from the state in Nothomyrmeciinae and Pseudomyrmecinae shorter scapes are plesiomorphic. This condition is, however, variable, even within a single species group (Table 2), and elongation of the scape could have evolved many times in *Myrmecia*. Furthermore, it is often difficult to set up the boundary conditions in this kind of quantitative transformation series. I here tentatively treat the scapes of the *gulosa* and *nigrocincta* groups as 'long', based on the statistics of Fig. 29 (in measured specimens  $SL > 1/2 \times HW + 1.2$ ).

In the Pseudomyrmecinae the third antennal segment is shorter than the second, and almost as long as the fourth. In *Nothomyrmecia* the third antennal segment is longer than the second, and almost as long as the fourth. In *Myrmecia*, however, the third segment is as long as or longer than the second, but consistently longer than the fourth. Thus, the relative length of these three segments in each subfamily



Figs 19–28. 19–20, Occipital region, dorsolateral view; 19, *M. aberrans* (*aberrans* group); 20, *M. gulosa*, (*gulosa* group), showing occipital carina (arrow). 21–22, anterior region of head: 21, *M. nigrocincta* (*nigrocincta* group), lateral view, showing genal furrow (arrow); 22, *M. aberrans* (*aberrans* group), dorsolateral view, showing truncate anterior margin of eye (arrow). 23–24, left antennal funiculus: 23, *M. aberrans* (*aberrans* group), showing short third antennal segment (arrow); 24, *M. gulosa* (*gulosa* group), showing elongate third antennal segment (arrow). 25–27, clypeus, dorsolateral view, showing anterior depressed areas (arrows): 25, *M. gulosa* (*gulosa* group); 26, *M. mandibularis* (*mandibularis* group); 27, *M. aberrans* (*aberrans* group). 28, *M. mandibularis* (*mandibularis* group), showing elongate clypeal hairs (arrow).

is: Pseudomyrmecinae: second > third = fourth. The extreme state, seen in the *gulosa* group, has the third segment almost twice as long as the second. Most other groups have the third segment generally longer than the second (Fig. 24), but in the *aberrans* group it is only

Table 2. Scape index (SI = scape length/head width  $\times$  100) statistics for the species groups of *Myrmecia*.

|                           | Range   | Mean | SD   | n (individuals/species) |
|---------------------------|---------|------|------|-------------------------|
| <i>gulos</i> a group      | 91–136  | 113  | 13.8 | 98/37                   |
| <i>nigrocincta</i> group  | 111–120 | 117  | 3.73 | 8/3                     |
| <i>urens</i> group        | 66–95   | 77   | 6.83 | 19/5                    |
| <i>aberrans</i> group     | 62–73   | 66   | 3.04 | 14/6                    |
| <i>picta</i> group        | 80–87   | 83   | 2.73 | 6/2                     |
| <i>cephalotes</i> group   | 81–95   | 88   | 4.35 | 9/3                     |
| <i>mandibularis</i> group | 75–84   | 79   | 2.92 | 16/7                    |
| <i>tepperi</i> group      | 73–92   | 70   | 6.11 | 17/5                    |
| <i>pilosula</i> group     | 72–103  | 87   | 6.77 | 39/15                   |

about as long (Fig. 23). I suggest that elongation of the second and third segments evolved first in the ancestor of *Myrmecia*, and that elongation of the third segment occurred subsequently in the ancestor (or ancestors) of relevant species groups within the genus. Thus, the former condition is a synapomorphy of the genus *Myrmecia*, and the latter an apomorphy at species-group level.

#### Clypeus (Characters 10–13)

The anterior portion of the median projection of the clypeus in *Myrmecia* has a depressed area. There is no such structure in Pseudomyrmecinae or Nothomyrmecinae, but the following transformation series is suggested: (1) a simple exposed depression in the same plane as the posterior area of the clypeus, as seen in the *gulos*a group (Fig. 25); (2) the anterior margin of the clypeus raised, so that the depression is situated somewhat vertically, as in the *mandibularis* group (Fig. 26) and in *M. testaceipes* of the *tepperi* group; (3) the marginal ridge of the depression developed so as to overhang its anterior basin, as in the *aberrans* group (Fig. 27). In the *mandibularis* group the clypeus carries 1 or 2 pairs of extremely long setae. Although long hairs also occur on the clypeus in several species of the *urens* and *pilosula* groups, their length does not exceed the basal quarter of the mandibles. Those of the *mandibularis*-group species are relatively long, reaching, or even exceeding, the basal third of the mandibles (Fig. 28). This is an autapomorphy of the *mandibularis* group.

#### Mandibles (Characters 14–19)

In many species of *Myrmecia* the mandibles are long and slender, often exceeding the head length (MI: mandibular index = mandible length/head length  $\times$  100). However, those of the *aberrans* group are consistently short (MI < 85) (Table 3). The relative length of the mandibles in *Myrmecia* may range widely, as in the *urens* group, and elsewhere, as shown in Table 3. Primitively the mandibles would probably have been short, as in many other genera of Formicidae. Although elongation might have evolved several times, I here empirically regard *Myrmecia* mandibles with MI less than 85 as short, and primitive. It should be noted that *Nothomyrmecia* also has elongate mandibles, but this seems to represent a homoplastic condition, because its mandibles are different from those of *Myrmecia* as follows: (1) the teeth are not differentiated in size; (2) the masticatory margin is differentiated from the basal arm; (3) the mandibles do not cross when closed in dead specimens.

The sub-basal portion of the inner mandibular shaft varies from a broadened, angulate, convex corner, to a simple shaft, approximately equal in width to the basal insertion. Jaws of the former type can close tightly, with both inner margins and the anterior margin of the clypeus in contact. Sub-basally broadened mandibles occur in most species groups of *Myrmecia*, except the *cephalotes*, *mandibularis* and *tepperi* groups. This state, seen also in *Nothomyrmecia*, is considered to represent a vestigial triangular mandible, and is considered to be plesiomorphic. Evolution from the broad to the

Table 3. Mandibular index (MI = mandible length/head length  $\times$  100) statistics for the species groups of *Myrmecia*.

|                           | Range   | Mean | SD   | n (individuals/species) |
|---------------------------|---------|------|------|-------------------------|
| <i>gulosa</i> group       | 86–138  | 107  | 8.46 | 110/37                  |
| <i>nigrocincta</i> group  | 102–119 | 107  | 2.62 | 9/3                     |
| <i>urens</i> group        | 79–104  | 88   | 6.21 | 20/5                    |
| <i>aberrans</i> group     | 73–84   | 78   | 2.93 | 14/6                    |
| <i>picta</i> group        | 89–96   | 92   | 2.81 | 6/2                     |
| <i>cephalotes</i> group   | 102–116 | 108  | 4.70 | 8/3                     |
| <i>mandibularis</i> group | 96–120  | 107  | 7.38 | 17/7                    |
| <i>tepperi</i> group      | 100–115 | 107  | 4.81 | 17/5                    |
| <i>pilosula</i> group     | 88–115  | 101  | 6.15 | 39/16                   |

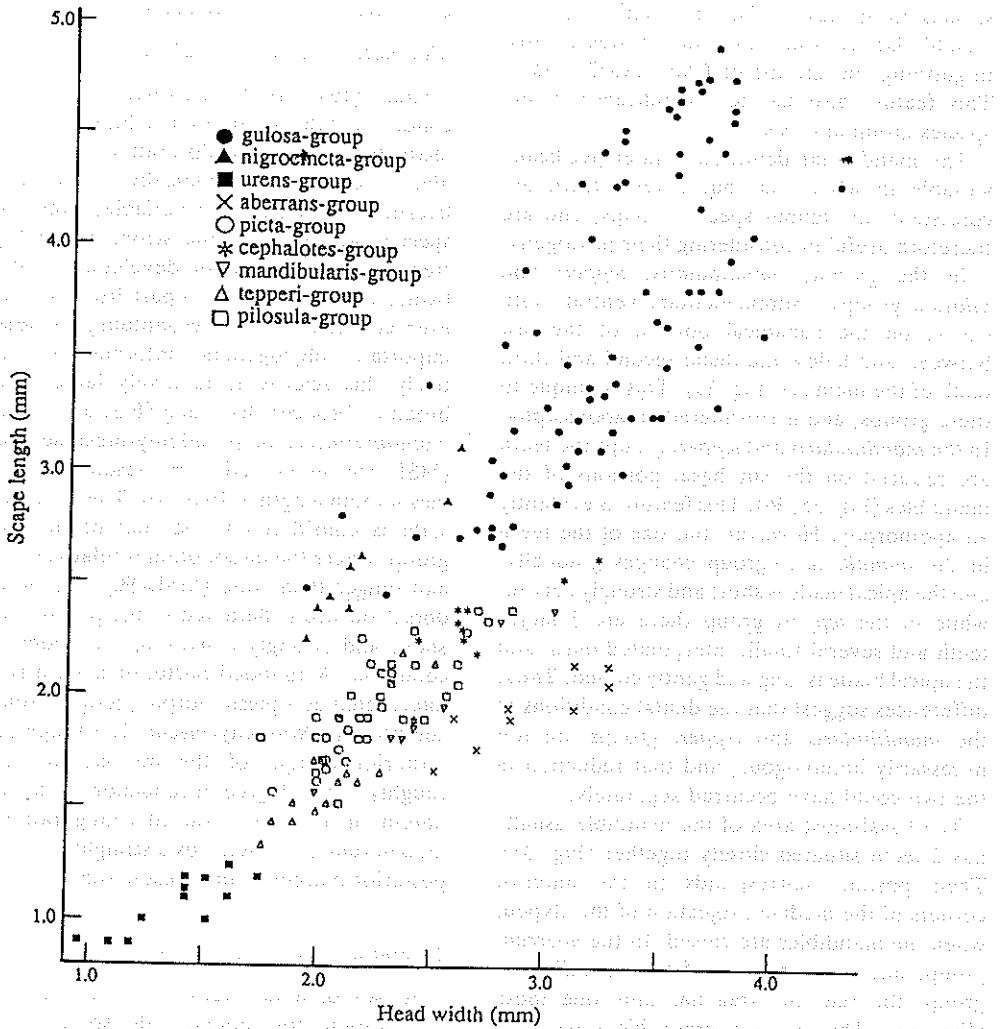


Fig. 29. Relative length of antennal scape in representative *Myrmecia* species classified by species group (each symbol represents a single specimen; total 171 measured).

slender condition, however, must have occurred several times, because the *gulosa*, *urens*, *picta* and *pilosula* groups demonstrate both conditions, and include intermediate species.

Clark (1943, 1951) often used the outline of the mandible as a discriminating character in his species group classification. He distinguished the states 'concave', 'straight' and 'convex'. I have not emphasized this set of character states in my analyses because (1) it is variable within several groups (e.g. those of *gulosa* and *pilosula*); (2) the differences are often quite subtle and obscure; (3) determination of polarity is difficult because of the frequent changes of shape which seem to have occurred, at least at species-group level. The inclination of the mandibular teeth also provided characters distinguishing the groups of Clark (1943, 1951). This feature also has less significance in my species-group analysis.

The mandibular dentition is interspecifically variable in *Myrmecia*, but several teeth are consistent throughout species groups, and are therefore useful in considering their phylogeny.

In the *gulosa*, *mandibularis*, *tepperi* and *pilosula* groups a supplementary ventral tooth occurs on the subapical portion of the jaw between and below the distal second and third teeth of the main set (Fig. 33). This is unique to these groups, and is considered an apomorphy. In the *mandibularis* and *tepperi* groups the teeth are reduced on the sub-basal portions of the mandibles (Figs 35, 36). This feature is evidently an apomorphy. However, the size of the teeth in the *mandibularis* group changes gradually, and the apical blade is short and strongly curved, while in the *tepperi* group there are 3 larger teeth and several small, interpolated ones, and the apical blade is long and gently curved. These differences suggest that the dental conditions of the *mandibularis* and *tepperi* groups are not necessarily homologous, and that reduction in the two could have occurred separately.

The basal-most area of the mandible usually has 2 teeth situated closely together (Fig. 31). Their position corresponds to the anterior corners of the median projection of the clypeus when the mandibles are closed. In the *aberrans* group, and some species of the *mandibularis* group, the relevant area has only one tooth (Fig. 30). This is an apomorphic state. The dorsal surfaces of the mandibles in the *cephalotes* group have a row of long, thick standing

hairs, which apparently constitute a psammophore (Fig. 37). This state is an autapomorphy of the *cephalotes* group.

#### *Maxillary palpi* (Character 20)

A 6-segmented maxillary palpus is considered primitive in the family Formicidae. This is the consistent condition in *Myrmecia*. Palpal elongation occurs in the *nigrocincta* group, where these appendages almost reach the post-occipital area (Fig. 38). This unique state is an autapomorphy of the *nigrocincta* group.

#### Characters of the mesosoma and legs

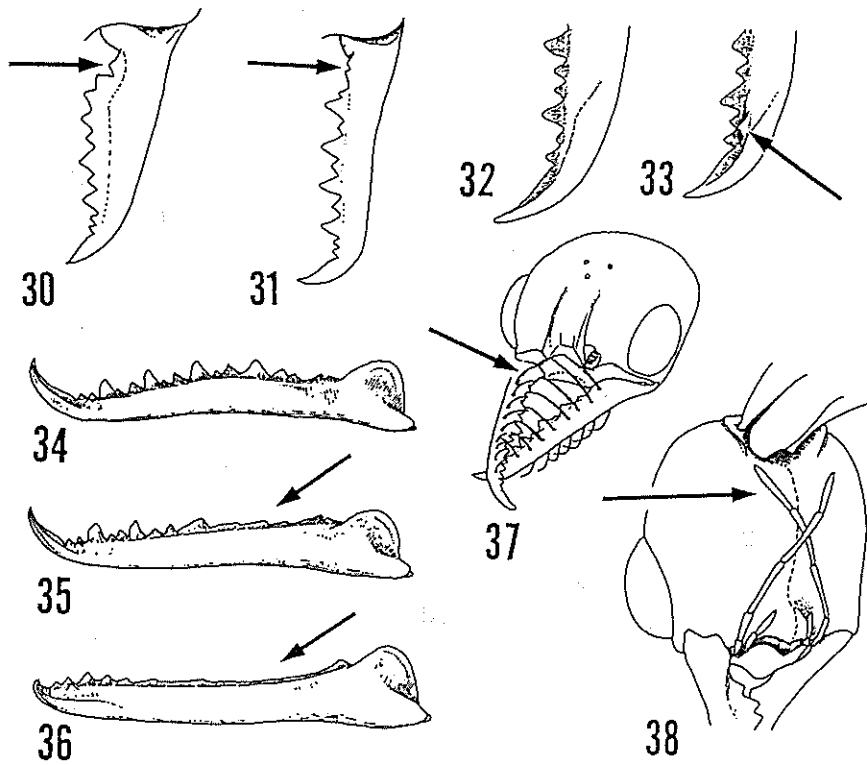
##### *Mesonotum* (Characters 21–23)

Clark (1943, 1951) often used the sculptural condition of the mesonotum in his species-group characterizations. Sculpturation is in fact almost useless taxonomically in *Myrmecia*, because it can be quite variable, even within species, and there is the strong possibility of frequent parallel loss or development of particular character states. Apart from this, however, characters of the mesonotum provide some important phylogenetic information. Primitively this sclerite is relatively large, and as broad or broader than long (Figs 39, 40), as in *Nothomyrmecia* or pseudomyrmecinae species (MSI: mesonotal index = mesonotum width/mesonotum length  $\times 100 < 90$ ). The apomorphic state is considered to be that of the *gulosa* group, where the mesonotum is relatively small, and longer than wide (MSI  $> 90$ ) (Fig. 41). Its dorsal surface is flattened in the plesiomorphic state, and strongly convex in the apomorphic condition. A rounded posterior margin is here interpreted as a plesiomorphy, judged from the condition in *Nothomyrmecia*. The shape of the posterior margin of the mesonotum relates roughly to the degree of reduction of the metanotum; in its most reduced configuration the metanotum is restricted by a straight, transverse posterior margin to the mesonotum.

##### *Lateral lobes* (Character 24)

A pair of dorsolateral lobes situated above the mesopleuron represent the spiracles of the mesothorax, and are present in all myrmeciines. Their relative position is variable: in the *gulosa*





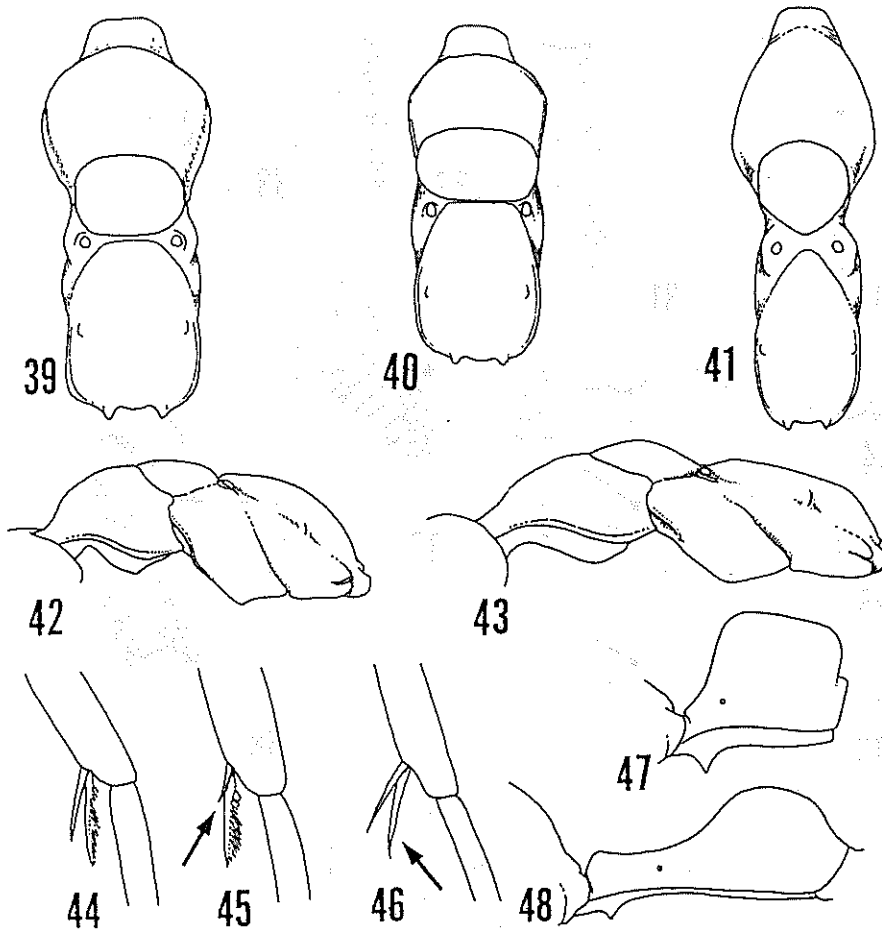
Figs 30–38. 30–35, mandibles. 30–31, left mandible, dorsal view, showing basal teeth (arrows): 30, *M. aberrans* (*aberrans* group); 31, *M. gulosa* (*gulosa* group). 32–33, apical portion of right mandible, ventral view: 32, *M. nigrocincta* (*nigrocincta* group); 33, *M. gulosa* (*gulosa* group), showing ventral tooth (arrow). 34–36, right mandible, ventral view, showing reduction of sub-basal teeth (arrows): 34, *M. pilosula* (*pilosula* group); 35, *M. tepperi* (*tepperi* group); 36, *M. mandibularis* (*mandibularis* group). 37, head of *M. hilli* (*cephalotes* group), dorsolateral view, showing dorsal psammophore on mandibles (arrow). 38, head of *M. nigrocincta* (*nigrocincta* group), ventrolateral view, showing elongate maxillary palpi (arrow).

group and others, the lobes are situated almost at the mid point between the mesonotum and the propodeum (Figs 39, 41); in the *tepperi*-, *mandibularis*- and *cephalotes*-group species (except for *M. callima*), and most members of the *pilosula* group (except *M. cydista* and *M. harderi* situated more posteriorly, almost at the same level as, or somewhat behind, the anterior margin of the propodeum (Fig. 40)). Judging from the configuration in *Nothomyrmecia* and the Pseudomyrmecinae, the former state is plesiomorphic.

#### *Metanotum* (Character 25)

The distinctness of the metanotum was used

by Clark (1951) as a character distinguishing *Myrmecia* from his *Promyrmecia*. His meaning of 'distinctness' is obscure, and several species of '*Promyrmecia*' have a distinctly represented metanotum, as demonstrated by Brown (1953a). The metanotum is here defined as a concave area between the mesonotum and the propodeum, laterally demarcated by lobes. The reduced metanotum is evidently an apomorphy, but there is gradation from a broad, transverse concavity, as in the *gulosa* group (Fig. 41), to a narrow furrow, as in the *tepperi* group (Fig. 40). Reduction of the metanotum is evidently correlated with transformation of the shape of the posterior margin of the mesonotum and the anterior margin of the propodeum, and the



Figs 39–48. 39–41, mesosoma, dorsal view: 39, *M. aberrans* (*aberrans* group); 40, *M. tepperi* (*tepperi* group); 41, *M. pyriformis* (*gulosa* group). 42–43, mesosoma, profile: 42, *M. tepperi* (*tepperi* group); 43, *M. forficata* (*gulosa* group). 44–46, left hind tibial spurs, anterior view: 44, *M. chasei* (*pilosula* group); 45, *M. urens* (*urens* group), showing short anterior spur (arrow); 46, *M. cephalotes* (*cephalotes* group), showing spinose posterior spur (arrow). 47–48, petiole, profile: 47, *M. aberrans* (*aberrans* group); 48, *M. desertorum* (*gulosa* group).

configuration and position of the lateral lobes.

#### *Propodeum* (Characters 26–27)

Primitively the dorsal outline of the *Myrmecia* trunk in profile is simple, and a single arch (Fig. 42), as in *Nothomyrmecia*, or among the pseudomyrmecines. Depression of the propodeal profile, or elevation of the pro- and mesonota (Fig. 43) is considered to be an apomorphy.

The anterior margin of the propodeum is raised and clearly distinguished from the mesonotum. In dorsal view it varies in outline, from a converging margin with a rather acutely angled median portion, as in the *gulosa* group (Fig. 41), to a straight, transverse margin, as in the *tepperi* group (Fig. 40). As stated above, this transformation is related to progressive reduction of the metanotum: the converging or convex anterior margin occurs where the metanotum is extensive medially, and the straight

margin occurs where metanotum is reduced in area. Thus, the transverse, straight margin is apomorphic.

#### Legs (Characters 28–29)

The hind tibiae in *Myrmecia* each have 2 spurs. The anterior one is usually poorly pectinate and the posterior one finely and relatively strongly pectinate. Primitively both spines are equal in length, or at most the anterior spur is a little shorter (Fig. 44). In the apomorphic state the anterior spur is much shorter, less than two-thirds the length of its pectinate partner, as in the *urens* group (Fig. 45).

In the *cephalotes* group the posterior spur is spinose, like the anterior spur (Fig. 46). This unique feature is the autapomorphy of that group.

#### Metasomal characters

##### Petiole (Character 30)

There is gradation in structure of the anterior portion of the petiole from a condition where the peduncle is weakly set-off or 'undifferentiated', as in the *aberrans* group (Fig. 47), to one where a long, slender peduncle is present (Fig. 48). The anterior portion of the petiole is pedunculate in *Nothomyrmecia* and the pseudomyrmecines. It is reasonable to suppose, however, that the non-pedunculate state is more primitive, judging from the condition represented in other formicid subfamilies, such

as the Ponerinae, Formicinae, Dolichoderinae, etc.

Although peduncular length is interspecifically variable, the *gulosa*- and *nigrocincta*-group species have distinct anterior peduncles. In the *pilosula* group differentiation of a peduncle is variable, ranging from indistinct in most species, to relatively clear in others, such as *M. pilosula* and *M. apicalis* (though the peduncle in these is relatively short).

##### Postpetiole (Character 31)

The postpetiole (abdominal segment III) of *Myrmecia* is clearly distinguished from the following segment (abdominal IV), in having a helcium (Bolton, 1990), consisting of a large tergite and small sternite which are not fused. As shown in Fig. 49 and Table 4, the *gulosa* and *nigrocincta* groups have the postpetiole relatively small, compared to the gaster. Abdominal segment III in ants is primitively a part of the gaster and not differentiated as a postpetiole, as in *Nothomyrmecia*. The pseudomyrmecines have a well-differentiated postpetiole, which is relatively small compared to the usual condition in *Myrmecia*. Reduction in postpetiolar size has probably occurred separately in relevant ant subfamilies, as has the evolution of a strongly posteriorly constricted postpetiole in the Ponerinae and Myrmicinae (Taylor, 1978). The shape of the postpetiole is also variable in *Myrmecia*: in the *aberrans*, *cephalotes*, *picta*, *mandibularis*, *tepperi* and *pilosula* groups the segment is hemispherical, with rounded anterior

Table 4. Postpetiole index (PSI = postpetiole width/gaster width  $\times$  100) statistics for the species groups of *Myrmecia*.

|                           | Range | Mean | SD   | n (individuals/species) |
|---------------------------|-------|------|------|-------------------------|
| <i>gulosa</i> group       | 40–63 | 51   | 4.07 | 111/37                  |
| <i>nigrocincta</i> group  | 51–62 | 56   | 3.68 | 9/3                     |
| <i>urens</i> group        | 60–76 | 69   | 3.64 | 19/5                    |
| <i>aberrans</i> group     | 66–73 | 69   | 2.03 | 14/6                    |
| <i>picta</i> group        | 60–68 | 64   | 2.82 | 6/2                     |
| <i>cephalotes</i> group   | 64–71 | 68   | 2.80 | 8/3                     |
| <i>mandibularis</i> group | 70–83 | 75   | 2.91 | 17/7                    |
| <i>tepperi</i> group      | 66–73 | 70   | 2.07 | 18/5                    |
| <i>pilosula</i> group     | 56–76 | 68   | 4.05 | 40/15                   |

margin; in the *gulosa* and *nigrocincta* groups it is subconical, with a somewhat convergent anterior outline. In terms of differentiation of the postpetiolar segment, the smaller, subconical condition is considered apomorphic.

### Phylogenetic considerations

The species of *Myrmecia* constitute a monophyletic group, marked by possession of the following synapomorphies: (1) the anteriorly placed eyes; (2) the elongate third antennal segment; (3) the frontally exposed clypeo-labral junction; (4) the dorsal extension of the labrum; (5) the well-constricted abdominal segment III, which forms a postpetiole, (6) the tubulate structure of abdominal segment IV.

The possible phylogenetic relationships of the species groups defined above have been investigated with PAUP version 2.4 (developed by D. L. Swofford). Following the considerations discussed in the previous section, the characters and their states were provisionally determined, and coded, as in Table 6. Since the phylogenetic relationship of the Myrmeciinae to other relevant ant subfamilies is not clear, as

discussed above, I processed four sets of data, and calculated the parsimonious trees separately for each, using PAUP. Each data set utilized a different outgroup, as follows: Case 1: a hypothetical ancestor, with all the characters of this analysis scored in the plesiomorphous state; Case 2: a pseudomyrmecine (*Tetraponera* + *Pseudomyrmex*); Case 3: a nothomyrmecine (*Nothomyrmecia*); Case 4: the Pseudomyrmecinae and Nothomyrmeciinae.

Nine trees were obtained from these data sets. The first set (Case 1) produced three equally parsimonious trees (Fig. 50). The second set (Case 2) produced three trees (Fig. 51), two of which showed the same phylogenetic patterns respectively as two of the first set, though synapomorphies were different. The third set (Case 3) produced two trees (Fig. 52), and the fourth set (Case 4) produced one tree (Fig. 53) which represents the same phylogenetic pattern as one of those in the third set. Thus, six essentially different phylogenetic patterns were derived.

The following conclusions are consistent for all four cases: (1) the *gulosa* and *nigrocincta* groups constitute a monophyletic assemblage; (2) the *mandibularis* and *tepperi* groups consti-

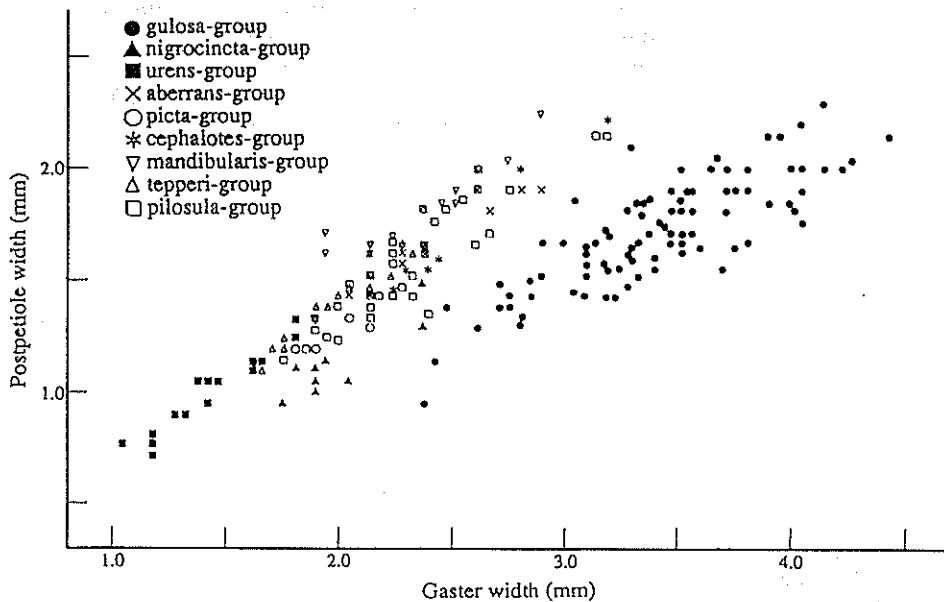


Fig. 49. Relative width of postpetiole in representative *Myrmecia* species classified by species group (each symbol represents a single specimen; total 189 measured).

Table 5. Characters and their transformations.

1. Occipital carina: absent (0) → present (1)
2. Gena: long (0) → short (1)
3. Genal furrow: absent (0) → present (1)
4. Eye (position): midlength on side (0) → anteriorly (1)
5. Eye (surface): less convex (0) → convex (1)
6. Eye (anterior margin): rounded (0) → truncate (1)
7. Antennal scape: short (0) → long (1)
8. Third antennal segment (compared with fourth): same length (0) → longer (1)
9. Third antennal segment (compared with second): same length (0) → longer (1)
10. Clypeus (anterior margin): horizontal (0) → raised (1)
11. Clypeal depression: exposed (0) → overhung (1)
12. Clypeal setae: short (0) → elongate (1)
13. Clypeo-labral connection: concealed (0) → exposed (1)
14. Mandible (length): short (0) → long (1)
15. Mandible (sub-basal area): broadened (0) → less broadened (1)
16. Ventral tooth of mandible at subapical region: absent (0) → present (1)
17. Sub-basal teeth of mandible: developed (0) → reduced (1)
18. Basal dentition of mandible: two teeth (0) → one tooth (1)
19. Psammophore on mandible: absent (0) → present (1)
20. Maxillary palpus: short (0) → long (1)
21. Mesonotum (length): broad (MSI < 90) → long (MSI > 90) (1)
22. Mesonotum (dorsal surface): flattened (0) → convex (1)
23. Mesonotum (posterior margin): rounded (0) → straight with rounded corners (1)
24. Lateral lobes (position): anterior or midlength (0) → posterior (1)
25. Metanotal region: spaced or not forming furrow (0) → furrow (1)
26. Propodeum (dorsal surface): raised (0) → depressed (1)
27. Propodeum (anterior dorsal margin): rounded/converging (0) → transversely straight (1)
28. Anterior hind tibial spur: long ( $\geq 2/3 \times$  posterior spur) (0) → short ( $\leq 1/2 \times$  posterior spur)
29. Posterior hind tibial spur: pectinate (0) → spinose (1)
30. Petiole: non-pedunculate (0) → pedunculate (1)
31. Postpetiole: large (0) → small (1)

0, plesiomorphic; 1, apomorphic.

tute a monophyletic assemblage (and this has sister-group relationship to the *pilosula* group, except in Tree 3 of Case 2); (3) the *picta*, *pilosula* and *tepperi* groups are not demonstrated each to be monophyletic.

The *picta*, *pilosula* and *tepperi* groups may reasonably be held to constitute separate species groups for three reasons: first, the present analysis does not imply that they are paraphyletic; secondly, the characters used in this analysis are limited to those of worker morphology, and the possibility remains that these groups will be shown to be monophyletic when new information is available; thirdly, in practical terms these groups are clearly and separately distinguishable within *Myrmecia*.

The differences between the various trees

result from the interpretation of character polarities. The program derives these polarities from character states present in the relevant outgroup, and assesses the distribution of character states in terms of parsimony. In particular, the cladograms of Cases 1 (Fig. 50) and 2 (Fig. 51), which involved the hypothetical and the pseudomyrmecine outgroups respectively, are quite different from those of Cases 3 and 4, which had *Nothomyrmecia* either as the outgroup, or as part of the outgroup. It should be noted that, if *Nothomyrmecia* were the sister group of *Myrmecia* (or Nothomyrmeciinae the sister group of Myrmeciinae), as in Cases 3 (Fig. 52) and 4 (Fig. 53), Clark's *Promyrmecia* (comprising the *aberrans* + *picta* + *cephalotes* + *mandibularis* + *tepperi* + *pilosula* groups)

Table 6. Character state matrix for the species groups of *Myrmecia*.

|  | <i>Myrmecia</i> |     |     |     |     |     |     |     |     | Not | Tet | Pse |
|--|-----------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
|  | gul             | nig | ure | abe | cep | pic | man | tep | pil |     |     |     |
| 1. Occipital carina                    | 1               | 1   | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 1   | 0   | 0   |
| 2. Gena                                | 1/0             | 0   | 1   | 0   | 0   | 0   | 1   | 1   | 0   | 0   | 0   | 0   |
| 3. Genal furrow                        | 0               | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   |
| 4. Eye (position)                      | 1               | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 0   | 0   | 0   |
| 5. Eye (surface)                       | 1               | 1   | 1   | 0   | 1   | 1   | 1   | 1   | 1   | 1   | 0   | 0   |
| 6. Eye (anterior margin)               | 0               | 0   | 0   | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   |
| 7. Antennal scape                      | 1               | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   |
| 8. Third ant. seg. (comp. with fourth) | 1               | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 0   | 0   | 0   |
| 9. Third ant. seg. (comp. with second) | 1               | 1   | 1   | 0   | 1   | 1   | 1   | 1   | 1   | *   | 1   | 1   |
| 10. Clypeus (anterior margin)          | 0               | 0   | 0   | 1   | 1   | 0   | 1   | 1/0 | 0   | *   | *   | *   |
| 11. Clypeal depression                 | 0               | 0   | 0   | 1   | 0   | 0   | 0   | 0   | 0   | *   | *   | *   |
| 12. Clypeal setae                      | 0               | 0   | 0   | 0   | 0   | 0   | 1   | 0   | 0   | 0   | 0   | 0   |
| 13. Clypeo-labral connection           | 1               | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 0   | 0   | 0   |
| 14. Mandible (length)                  | 1               | 1   | 1/0 | 0   | 1   | 1   | 1   | 1   | 1   | 1   | 0   | 0   |
| 15. Mandible (sub-basal area)          | 1/0             | 0   | 1/0 | 0   | 1   | 1/0 | 1   | 1   | 1/0 | 0   | *   | *   |
| 16. Ventral tooth                      | 1               | 0   | 0   | 0   | 0   | 0   | 1   | 1   | 1   | *   | *   | *   |
| 17. Sub-basal teeth                    | 0               | 0   | 0   | 0   | 0   | 0   | 1   | 1   | 0   | *   | *   | *   |
| 18. Basal dentition                    | 0               | 0   | 0   | 1   | 0   | 0   | 1/0 | 0   | 0   | *   | *   | *   |
| 19. Dorsal psammophore on mandibles    | 0               | 0   | 0   | 0   | 1   | 0   | 0   | 0   | 0   | *   | *   | *   |
| 20. Maxillary palpus                   | 0               | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | *   | *   |
| 21. Mesonotum (length)                 | 1               | 1   | 1   | 0   | 0   | 1   | 0   | 0   | 0   | 0   | 0   | 0   |
| 22. Mesonotum (dorsal surface)         | 1               | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   |
| 23. Mesonotum (posterior margin)       | 0               | 0   | 0   | 1   | 0   | 0   | 1   | 1   | 1   | 0   | 0   | 1   |
| 24. Lateral lobes                      | 0               | 0   | 0   | 0   | 1/0 | 0   | 1   | 1   | 1/0 | 0   | 0   | 1   |
| 25. Metanotum                          | 0               | 0   | 0   | 0   | 0   | 0   | 1/0 | 1   | 1   | 0   | 1   | 1   |
| 26. Propodeum (dorsal surface)         | 1               | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   |
| 27. Propodeum (anterior dorsal margin) | 0               | 0   | 0   | 1   | 0   | 0   | 1/0 | 1   | 1   | 0   | 0   | 0   |
| 28. Anterior hind tibial spur          | 0               | 0   | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 1   | 1   | 1   |
| 29. Posterior hind tibial spur         | 0               | 0   | 0   | 0   | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   |
| 30. Petiole                            | 1               | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 1/0 | 1   | 1   | 1   |
| 31. Postpetiole                        | 1               | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | *   | 1   | 1   |

Abbreviations: *abe*, *aberrans* group; *cep*, *cephalotes* group; *gul*, *gulosa* group; *man*, *mandibularis* group; *nig*, *nigrocincta* group; *pic*, *picta* group; *pil*, *pilosula* group; *tep*, *tepperi* group; *ure*, *urens* group; *Not*, *Nothomyrmecia* (Nothomyrmecinae); *Pse*, *Pseudomyrmex* (Pseudomyrmecinae); *Tet*, *Tetraoponera* (Pseudomyrmecinae); \*, not applicable.

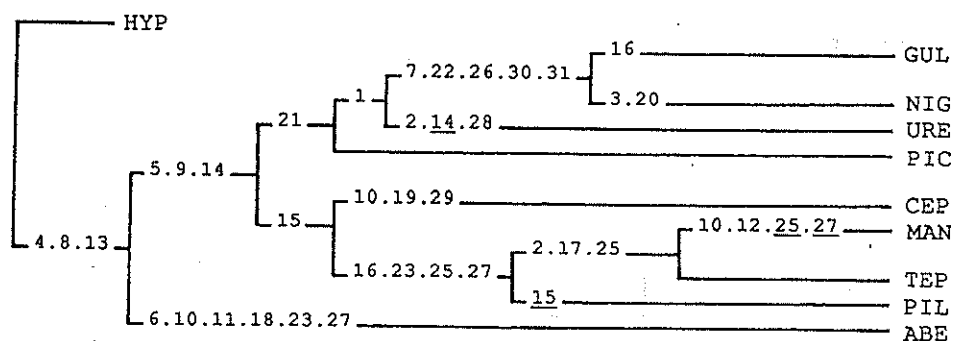
would be supported as a monophyletic taxon (refer Tree 1 of Case 3, and Case 4). Cases 3 and 4, however, involved many reversed character transformations (in ten or more series). In particular '*Promyrmecia*' in these cases possesses several less-probable synapomorphies (Characters 30 and 31). These characters have their polarities reinterpreted. That is, the large, less-differentiated postpetiole is derived from the small, well-differentiated one (Character 30), and the non-pedunculate petiole is derived from the pedunculate one (Character 31). On

the other hand, Cases 1 (Fig. 50) and 2 (Fig. 51) both show consistently that the '*Promyrmecia*' collective of species groups is paraphyletic, and that the *aberrans* group constitutes the earliest branch of the myrmecine cladogram. Even in these cases several reversals of character polarities are inevitable when parsimony is prioritized.

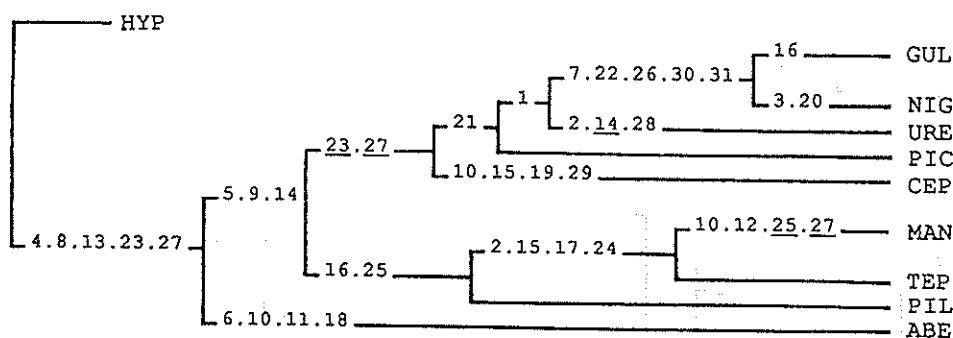
Tree 3 of Case 2 is distinctive in having the *pilosula* group (the sister group of (GUL + NIG + URE + PIC); these codes as in Table 6) and the *cephalotes* group (the sister group of

Case 1: Outgroup = hypothetical ancestor (HYP)  
(Length = 43; Consistency index = 0.744)

Tree 1



Tree 2



Tree 3

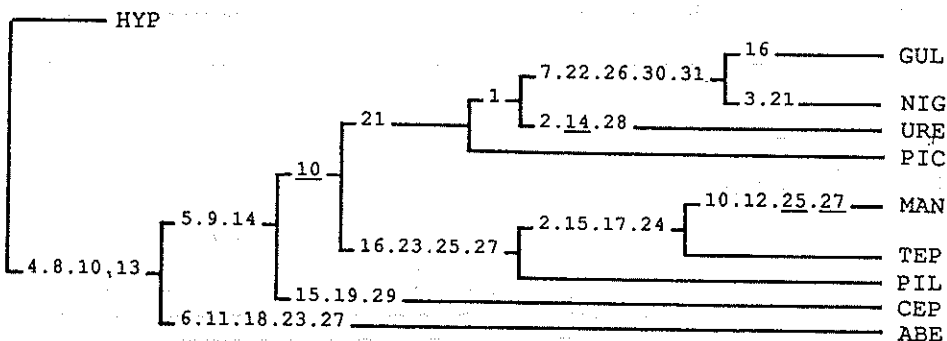


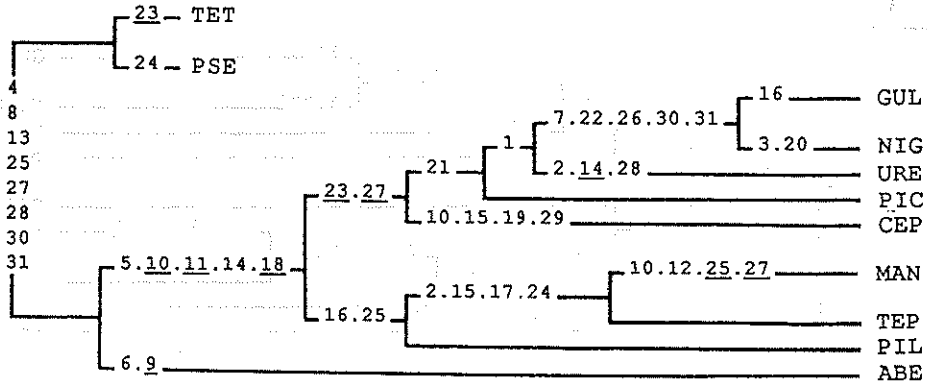
Fig. 50. Equally parsimonious cladograms of the species groups of *Myrmecia*, using a hypothetical ancestor plesiomorphic for all relevant characters as outgroup. Numbers indicate synapomorphies (see Table 5); those underlined are reversal interpretations of polarities compared to Table 5 (characters on the node between *Myrmecia* and the outgroup cannot be polarized). Abbreviations as in Table 6.

(MAN + TEP) uniquely positioned (Fig. 51). It weights Character 15 (sub-basal shape of mandibular shaft) as the only synapomorphy of (CEP + MAN + TEP), rather than Characters 16 (ventral tooth on subapical portion of mandible) and 25 (metanotum) as synapo-

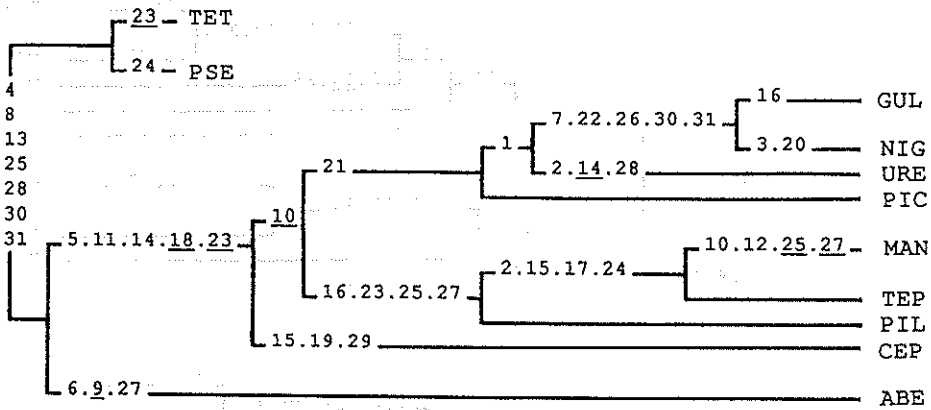
morphies of (MAN + TEP + PIL). As demonstrated above in the character analysis, the sub-basal shape of the mandibles is variable within the *gulos*, *urens*, *picta* and *pilosula* groups, so that repeated parallel evolution of the mandibular shaft from a sub-basally broadened

Case 2; Outgroup = Pseudomyrmecinae (*Tetraponera* + *Pseudomyrmex*)  
 (Length = 48; Consistency index = 0.677)

Tree 1



Tree 2



Tree 3

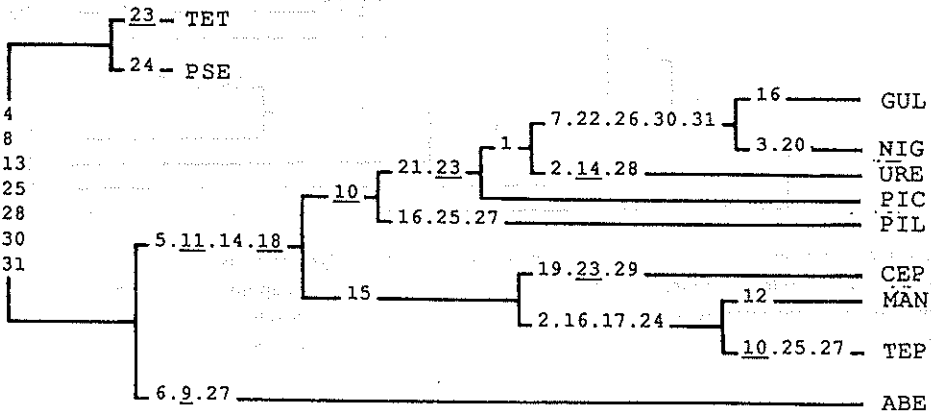
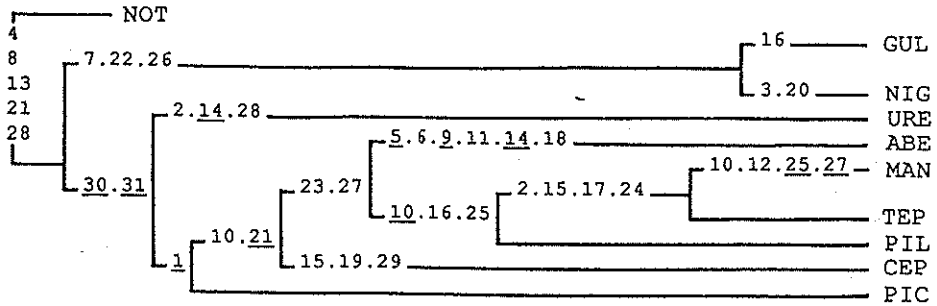


Fig. 51. Equally parsimonious cladograms of the species groups of *Myrmecia*, using the subfamily Pseudomyrmecinae as outgroup. Numbers indicate synapomorphies (see Table 5); those underlined are reversal interpretations of polarities compared to Table 5 (characters on the node between *Myrmecia* and the outgroup cannot be polarized). Abbreviations as in Table 6.



Case 3: Outgroup = Nothomyrmecinae  
(Length = 43; Consistency index = 0.744)  
Tree 1



Tree 2

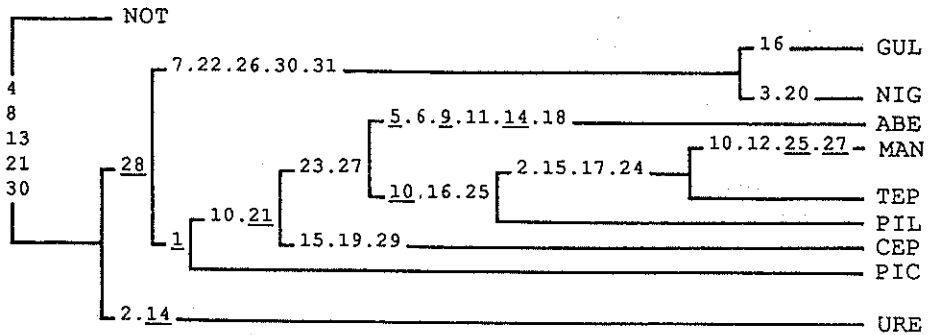


Fig. 52. Equally parsimonious cladograms of the species groups of *Myrmecia*, using the subfamily Nothomyrmecinae as outgroup. Numbers indicate synapomorphies (see Table 5); those underlined are reversal interpretations of polarities compared to Table 5 (characters on the node between *Myrmecia* and the outgroup cannot be polarized). Abbreviations as in Table 6.

Case 4: Outgroup = Nothomyrmecinae + Pseudomyrmecinae  
(Length = 49; Consistency index = 0.653)

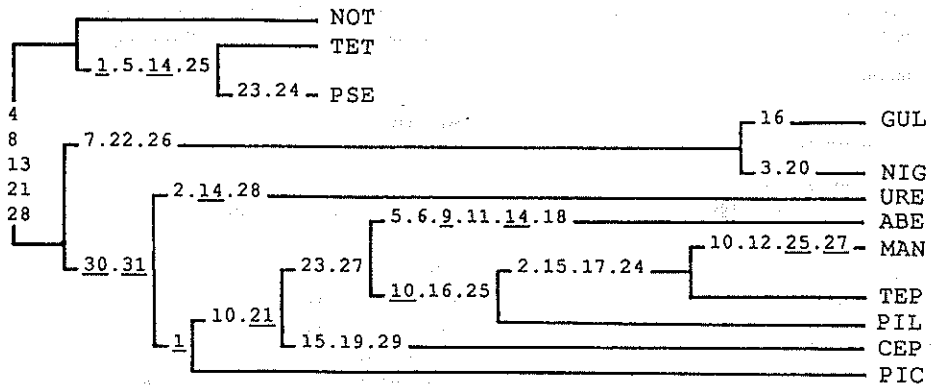


Fig. 53. A cladogram of the species groups of *Myrmecia*, using Nothomyrmecinae and Pseudomyrmecinae collectively as outgroup. Numbers indicate synapomorphies (see Table 5); those underlined are reversal interpretations of polarities compared to Table 5 (characters on the node between *Myrmecia* and the outgroup cannot be polarized). Abbreviations as in Table 6.

condition to a straight one is not improbable. Character 15 thus cannot carry much weight, and this cladogram is for that reason less plausible than the others presented here.

Thus, Trees 1–3 of Case 1 (Fig. 50) and Trees 1 and 2 of Case 2 (Fig. 51) are the more plausible, and some levels of phylogenetic certainty or uncertainty are reasonably clear, as follows: (1) the *mandibularis*, *tepperi* and *pilosula* groups constitute a monophyletic assemblage, even though the *tepperi* and *pilosula* groups might be paraphyletic; (2) the *gulosa*, *nigrocincla*, *urens* and *picta* groups constitute another monophyletic assemblage; even though the *picta* group might be paraphyletic; (3) the *aberrans* group is the sister group of the remaining eight groups together; (4) the position of the *cephalotes* group is uncertain, but it seems at least to be the sister group of one of the following monophyletic assemblages ((MAN + TEP) + PIL), (((GUL + NIG) + URE) + PIC), or (((((GUL + NIG) + URE) + PIC) + (MAN + TEP) + PIL)).

#### Key to the species groups of *Myrmecia*

- 1 Occipital carina present (Fig. 20) ..... 2
  - Occipital carina absent (Fig. 19) ..... 4
- 2(1). Subapical portion of mandible with a supplementary ventral tooth below the main series (Fig. 33) ..... *gulosa* group
  - Subapical portion of mandible with a single row of teeth (Fig. 32) ..... 3
- 3(2). Genal furrow present (Fig. 21) .....
  - ..... *nigrocincla* group
  - Genal furrow absent ..... *urens* group
- 4(1). Anterior margin of clypeus overhung by a bilateral pair of large, forwardly-directed projections (Fig. 27) ..... *aberrans* group
  - Anterior margin of clypeus not overhung by such projections ..... 5
- 5(4). Posterior hind tibial spur essentially spinose (Fig. 46) ..... *cephalotes* group
  - Posterior hind tibial spur finely, but distinctly pectinate (Fig. 44) ..... 6
- 6(5). Subapical portion of mandible with a single row of teeth ..... *picta* group

- Subapical portion of mandible with a supplementary ventral tooth below the main series ..... 7
- 7(6). Sub-basal teeth of mandible fully developed (Fig. 34) ..... *pilosula* group
  - Sub-basal teeth of mandible reduced in size, low and reduced (Figs 35, 36) ..... 8
- 8(7). Clypeus with elongate hairs which reach or exceed 1/3 the length of the mandibles (Fig. 28) ..... *mandibularis* group
  - Clypeus without such elongate hairs .....
    - ..... *tepperi* group

#### Acknowledgments

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#### Appendix

##### *Specimens examined*

All specimens examined for this study were from the Australian National Insect Collection, Canberra, or on loan from one of the other institutions indicated below. Nominal species studied are listed below, with specimen and institutional codes. The former indicate that relevant types or type-compared voucher specimens were examined. Nominal species which have been assigned to junior synonymy by previous authors are listed here alphabetically, and their names are also indicated in brackets

after their senior synonyms. Subspecific names still extant are listed as trinomens following the binominal name of their nominotypical subspecies. Specimen codes: T = holotype, paratypes or syntypes examined; C = Voucher specimen(s) examined, which had been previously compared with type material by Dr R. W. Taylor. Institutional codes: ANIC = Australian National Insect Collection, Canberra, Australia; BMNH = The Natural History Museum, London, U.K.; MVMA = Museum of Victoria, Melbourne, Australia.

#### List of species examined

Myrmeciinae: *M.aberrans* Forel [ANIC]; *M.analis* Mayr (C) [ANIC]; *M.apicalis* Emery (T) [ANIC]; *M.arnoldi* Clark (T) [ANIC]; *M.athertonensis* Forel (T) [ANIC]; *M.atrata* Clark (T) [ANIC]; *M.auriventris* Mayr (C) [ANIC] (= *athertonensis*); *M.brevinoda* Forel (T) [ANIC]; *M.callima* (Clark) (T) [ANIC, MVMA]; *M.cardigaster* Brown (T) [ANIC]; *M.celaena* (Clark) (T) [MVMA]; *M.cephalotes* (Clark) (T) [MVMA]; *M.chasei* Forel (C) [ANIC]; *M.chasei ludlowi* Crawley (T) [MVMA]; *M.chrysogaster* (Clark) (T) [MVMA]; *M.clarki* Crawley (T) [MVMA]; *M.coelatinoda* Wheeler [ANIC]; *M.comata* Clark (T) [ANIC]; *M.crassinoda* Clark (T) [MVMA]; *M.cydista* (Clark) (T) [MVMA]; *M.decipans* Clark (T) [ANIC]; *M.desertorum* Wheeler [ANIC] (= *lutea*, = *princeps*); *M.dichospila* Clark (T) [MVMA]; *M.dimidiata* Clark (T) [ANIC]; *M.dispar* (Clark) (T) [ANIC]; *M.dixonii* (Clark) (T) [MVMA]; *M.elegans* (Clark) (T) [ANIC, MVMA]; *M.esuriens* Fabricius (C) [ANIC]; *M.eupoecila* (Clark) (T) [MVMA]; *M.excavata* (Clark) (T) [MVMA]; *M.exigua* (Clark) (T) [MVMA]; *M.fallax* Clark (T) [ANIC]; *M.fasciata* Clark (T) [ANIC]; *M.flammicollis* Brown [ANIC]; *M.flavicomma* Roger [ANIC]; *M.flavicomma minuscula* Forel (T) [ANIC]; *M.forceps* Roger (C) [ANIC] (= *singularis*); *M.forficata* (Fabricius) [ANIC]; *M.froggatti* Forel (T) [MVMA]; *M.fucosa* Clark (T) [MVMA]; *M.fulgida* Clark (T) [ANIC]; *M.fulviculis* Forel [ANIC]; *M.fulvipes* Roger [ANIC]; *M.fuscipes* Clark (T) [ANIC]; *M.gilberti* Forel (T) [ANIC]; *M.gratiosa* Clark (T) [ANIC]; *M.greavesi*

(Clark) (T) [MVMA]; *M.gulosa* (Fabricius) (C) [ANIC]; *M.harderi* Forel (T) [ANIC, MVMA] (= *maloni*); *M.hematosticta* Wheeler (T) [ANIC]; *M.hilli* (Clark) (T) [MVMA]; *M.hirsuta* Clark (T) [ANIC]; *M.infima* Forel [ANIC]; *M.inquilina* Douglas & Brown [ANIC]; *M.longinodis* Clark (T) [ANIC]; *M.lutea* Crawley (T) [ANIC]; *M.luteiforceps* Wheeler (T) [ANIC, MVMA]; *M.maloni* (Clark) (T) [MVMA]; *M.mandibularis* F. Smith [ANIC] (= *coelatinoda*); *M.marmorata* (Clark) (T) [MVMA]; *M.maura* Wheeler (T) [ANIC, MVMA] (= *hematosticta*); *M.maura formosa* Wheeler (T) [ANIC, MVMA]; *M.michaelseni* Forel (T) [ANIC]; *M.michaelseni queenslandica* Forel [ANIC]; *M.midas* Clark (T) [ANIC]; *M.mjobergi* Forel (T) [ANIC]; *M.murina* Clark (T) [ANIC]; *M.nigra* Forel [ANIC]; *M.nigriceps* Mayr (C) [ANIC]; *M.nigriscapa* Roger (C) [ANIC]; *M.nigrocincta* F. Smith (C) [ANIC]; *M.nobilis* (Clark) (T) [MVMA]; *M.occidentalis* (Clark) (T) [MVMA]; *M.opaca* (Clark) (T) [MVMA]; *M.pavida* Clark (T) [ANIC]; *M.petiolata* Emery (C) [ANIC]; *M.picta* F. Smith (T) [BMNH], (C) [ANIC]; *M.picticeps* Clark (T) [ANIC]; *M.piliventris* F. Smith (T) [BMNH]; *M.pilosula* F. Smith (T) [BMNH]; *M.potteri* (Clark) (T) [ANIC]; *M.princeps* Clark (T) [ANIC]; *M.pulchra* Clark (T) [ANIC, MVMA] (= *crassinoda*, = *fallax*, = *murina*); *M.pyriformis* F. Smith (T) [BMNH]; *M.regularis* Crawley (T) [MVMA]; *M.rowlandi* Forel (T) [ANIC]; *M.rubicunda* (Clark) (T) [ANIC]; *M.rubripes* Clark (T) [ANIC]; *M.rufinodis* F. Smith (C) [ANIC]; *M.rugosa* Wheeler (T) [ANIC]; *M.scabra* (Clark) (T) [MVMA]; *M.shepherdi* (Clark) (T) [MVMA]; *M.simillima* F. Smith (T) [BMNH]; *M.singularis* Clark (T) [ANIC]; *M.suttoni* Clark (T) [ANIC]; *M.swalei* Crawley [ANIC]; *M.tarsata* F. Smith (T) [BMNH]; *M.tepperi* Emery [ANIC]; *M.testaceipes* (Clark) (T) [MVMA]; *M.urens* Lowne [ANIC]; *M.varians* Mayr [ANIC] (= *marmorata*, = *shepherdi*, = *wilsoni*); *M.vindex* F. Smith (C) [ANIC]; *M.vindex basirufa* Forel (T) [ANIC]; *M.wilsoni* (Clark) [MVMA].

Nothomyrmeciinae: *Nothomyrmecia macrops* Clark [ANIC].

Pseudomyrmecinae: *Pseudomyrmex apache* Creighton; *P.mexicanus* Roger; *Tetraponera allaborans* Walker; *T.attenuata* F. Smith; *T.nigra* Jerdon; *T.rufonigra* Jerdon [all ANIC].

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