

The internal phylogeny of ants (Hymenoptera: Formicidae)

CESARE BARONI URBANI, BARRY BOLTON* and

PHILIP S. WARD† Zoological Institute of the University, Rheinsprung 9, CH-4051 Basel, Switzerland,

*Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K., and

†Department of Entomology, University of California, Davis, California 95616, U.S.A.

Abstract. The higher phylogeny of the Formicidae was analysed using 68 characters and 19 taxa: the 14 currently recognized ant subfamilies plus 5 potentially critical infrasubfamilial taxa. The results justified the recognition of 3 additional subfamilies: Aenictogitoninae Ashmead (new status), Apomyrminae Dlussky & Fedoseeva (new status), and Leptanilloidinae Bolton (new subfamily). A second analysis on these better delimited 17 subfamilies resulted in 24 equally most parsimonious trees. All trees showed a basal division of extant Formicidae into two groups, the first containing (Myrmicinae, Pseudomyrmecinae, Nothomyrmecinae, Myrmecinae, Formicinae, Dolichoderinae, Aneuretinae) and the second the remaining subfamilies. Clades appearing within these groups included the Cerapachyinae plus ‘army ants’, the Nothomyrmecinae plus Myrmecinae, the ‘formicoid’ subfamilies (Aneuretinae + Dolichoderinae + Formicinae), and the Old World army ants (Aenictinae + Aenictogitoninae + Doryline), but relationships within the last two groups were not resolved, and the relative positions of the Apomyrminae, Leptanillinae and Ponerinae remained ambiguous. Moreover, a bootstrap analysis produced a consensus tree in which all branches were represented in proportions much lower than 95%. A reconstruction of the ground plan of the Formicidae indicated that the most specialized of all recent ants are the members of the subfamily Dorylinae and the least specialized ones are the monotypic Apomyrminae.

Introduction

Modern work on the higher phylogeny of ants dates from Brown's (1954) division of the Formicidae into two groups of subfamilies – the poneroid complex (containing Ponerinae, Cerapachyinae, Myrmicinae, Dorylinae and Leptanillinae) and the myrmecoid complex (comprising Myrmecinae, Pseudomyrmecinae, Dolichoderinae and Formicinae). A similar scheme was followed by Wilson *et al.* (1967) and by Wilson (1971). Taylor (1978) proposed an arrangement in which two members of the myrmecoid complex (Myrmecinae and Pseudomyrmecinae) were transferred to the poneroid complex, the latter being explicitly diagnosed by two derived features of abdominal morphology. Unfortunately no synapomorphy was identified for the remaining subfamilies, renamed the formicoid complex. A lack of apomorphic characters also characterizes

the ant phylogenies presented by Dlussky & Fedoseeva (1988) and Hölldobler & Wilson (1990).

Baroni Urbani (1989) carried out the first explicit cladistic analysis of the ant subfamilies, using a larger set of characters than in any previous study. He presented a fully resolved cladogram, and gave one or more synapomorphies for all branchings but one. However, his data set yielded a large number of other equally parsimonious trees, some differing considerably in topology (Baroni Urbani, 1990; Carpenter, 1990b; Ward, 1990). Bolton (1990c) offered a Hennigian-style phylogeny of the ant subfamilies, derived from his morphological studies of the army ants, cerapachyines and leptanillines. His results were partly congruent with those of Ward (1990), who focused on the position of the Pseudomyrmecinae in the poneroid complex, but there was disagreement on the placement of the genus *Nothomyrmecia*. Finally, relationships within the formicoid complex of subfamilies have been examined by Lutz (1986) and Shattuck (1992), with conflicting results.

Correspondence: Dr C. Baroni Urbani, Zoologisches Institut der Universität, Rheinsprung 9, CH-4051 Basel, Switzerland.

Thus there is continuing ambiguity over the relationships of the major ant clades, notwithstanding a considerable explosion of new character information. In this paper we attempt a cladistic analysis of the Formicidae by compiling and synthesizing information on a large suite of characters, including new data on abdominal morphology. These characters have been examined in a wide variety of species and castes. Although the analysis is basically at the level of subfamilies, it became clear to us that in order to prevent the inadvertent inclusion of non-monophyletic groups it was desirable to expand the set of terminal taxa to include certain genera and tribes.

Taxa included in the analysis

The 14 currently recognized subfamilies of the Formicidae have been considered in the present study. These are all those recognized by Baroni Urbani (1989) plus the Cerapachyinae, Aenictinae and Aneuretinae raised or reinstated to subfamily status later (Bolton, 1990a, c). In addition we have treated certain anomalous taxa, whose morphological features suggest that they may not be cladistic members of the subfamilies to which they are currently assigned, as independent terminal taxa, as noted in the list below.

The majority of the characters employed in this paper have already been mentioned in recent literature, e.g. Lutz (1986), Baroni Urbani (1989), Bolton (1990a, b, c), Ward (1990). Sources are indicated in the paragraph corresponding to each character description. Whenever possible the characters have been verified by ourselves, by examining material in the collections of the Department of Entomology, The Natural History Museum (London), the Department of Entomology, University of California, Davis, and the Santschi collection, Natural History Museum of Basel. Cryptic anatomical characters, like the condition of the metacoxal cavities, the configuration of the presclerites of abdominal segments III and IV, and tergosternal fusion of abdominal segments II–IV, have been checked by dissecting a sub-sample of specimens as listed below. These specimens, with the dissected sclerites either mounted in Euparal on microscope slides or glued to card points, have been deposited in the original collection from which the material was extracted. When not stated otherwise the specimens dissected were always workers.

FORMICIDAE

Aenictinae: *Aenictus aratus*, *Aenictus dentatus*, *Aenictus binghami*, *Aenictus eugenii*, *Aenictus fergusoni*, *Aenictus moebii* (male), *Aenictus* sp. (Bhutan, male), *Aenictus* sp. (Cameroon), *Aenictus* sp. (Sri Lanka, male), *Aenictus* sp. (Ghana, male), *Aenictus* sp. (Ghana, male), *Aenictus* sp. (Zambia, male).

Aenictogiton sp. (Angola, male), *Aenictogiton* sp. (Zambia, male), *Aenictogiton* sp. (Zambia, male). Known only from the male, this genus was described by Emery (1901c) as a member of the Dorylinae (s.l.), transferred to the Ponerinae by Brown (1954, 1975) and re-transferred

to the Dorylinae by Borgmeier (1955: 54). Recent progress in our understanding of ponerine morphology and sub-familial limits make attribution to the Ponerinae untenable. For this reason *Aenictogiton* has been treated as a separate taxon in the analysis.

Aneuretinae: *Aneuretus simoni*.

Anomalomyrmini: *Protanilla* sp. (Pakistan), *Protanilla* sp. (E. Malaysia), *Protanilla* sp. (Nepal). See note under Leptanillini.

Apomyrmini: *Apomyrma stygia* (worker, gyne). See note under Leptanillini.

Cerapachyinae: *Acanthostichus* sp. (Brasil), *Acanthostichus* sp. (Colombia), *Acanthostichus* sp. (male), *Cerapachys biroi*, *Cerapachys centurio*, *Cerapachys dumbletoni*, *Cerapachys edentatus*, *Cerapachys foreli* (worker, male), *Cerapachys fragosus*, *Cerapachys longitarsus* (male), *Cerapachys nitidulus*, *Cerapachys nkomoensis* (worker, male), *Cerapachys sulcinodis*, *Cerapachys turneri* (s.l.), *Cerapachys wroughtoni*, *Cerapachys* sp. (E. Malaysia), *Cerapachys* sp. (Sulawesi), *Cerapachys* sp. (Nigeria), *Cerapachys* sp. (Zaire), *Cerapachys* sp. (Cameroun), *Cerapachys* sp. (Madagascar, male), *Cerapachys* sp. (Mexico, male), *Simopone conciliatrix*, *Simopone grandis*, *Simopone marleyi*, *Simopone* sp. (Nigeria), *Simopone* sp. (Madagascar, male), *Sphinctomyrmex imbecilis*, *Sphinctomyrmex occidentalis*, *Sphinctomyrmex steinheili*, *Sphinctomyrmex rufiventris* (worker, male), *Sphinctomyrmex turneri*, *Sphinctomyrmex* sp. (Australia, male).

Dolichoderinae: *Azteca xanthochroa*, *Bothriomyrmex pubens*, *Dorymyrmex nigriventris*, *Dolichoderus attelaboides*, *Dolichoderus bispinosus*, *Dolichoderus cuspidatus*, *Dolichoderus doriae*, *Dolichoderus mariae* (male), *Dolichoderus taschenbergi*, *Forelius rufus*, *Iridomyrmex detectus* (male), *Leptomyrmex nigriventris*, *Leptomyrmex pallens*, *Liometopum microcephalum*, *Papyrius nitidus*, *Philidris cordatus*, *Tapinoma erraticum*, *Technomyrmex albipes*, *Technomyrmex taylori*.

Dorylinae: *Dorylus affinis*, *Dorylus fimbriatus* (worker, male), *Dorylus fulvus* (worker, male), *Dorylus gribodoi* (male), *Dorylus labiatus*, *Dorylus laevigatus* (worker, male), *Dorylus opacus*, *Dorylus nigricans* (worker, gyne, male), *Dorylus* sp. (Angola), *Dorylus* sp. (Cameroun), *Dorylus* sp. (South Africa), *Dorylus* sp. (Kenya, worker, male), *Dorylus* sp. (Nigeria), *Dorylus* sp. (Uganda, male), *Dorylus* sp. (Liberia, male), *Dorylus* spp. (Zambia, males).

Ecitoninae: *Cheliomyrmex andicola*, *Cheliomyrmex megalonyx* (male), *Cheliomyrmex morosus* (worker, male), *Eciton burchelli* (worker, male), *Eciton hamatum* (worker, male), *Labidus coecus* (male), *Labidus praedor*, *Neivamyrmex andrei* (male), *Neivamyrmex californicus*, *Neivamyrmex harrisii* (male), *Neivamyrmex nigrescens*, *Neivamyrmex opacithorax*, *Neivamyrmex pertyi* (male), *Neivamyrmex swainsoni* (male), *Nomamyrmex esenbecki*, *Nomamyrmex hartigi* (worker, male).

Formicinae: *Acropyga acutiventris*, *Anoplolepis fallax* (male), *Anoplolepis tenella*, *Bregmatomyrma cariosa* (gyne), *Camponotus herculeanus*, *Camponotus semi-testaceus*, *Camponotus sericeiventris*, *Camponotus* sp. (Thailand), *Cataglyphis nodus*, *Dendromyrmex* sp., *Formica*

dolosa, *Formica exsecta* (worker, male), *Formica pratensis* (worker, male), *Lasiophanes hoffmanni*, *Lasius brunneus* (worker, male), *Lasius niger* (worker, male), *Lepisiota bipartita*, *Lepisiota frauenfeldi*, *Melophorus* sp., *Myrmecocystus mexicanus*, *Myrmelachista gallicola*, *Myrmoteras* sp. (Sulawesi), *Oecophylla longinoda*, *Oecophylla smaragdina*, *Polyrhachis medusa*, *Polyrhachis militaris*, *Polyrhachis rheia*, *Polyrhachis schistacea* (worker, male), *Polyrhachis thrinax*, *Pseudolasius* sp. (S. India, male), *Stigmacros froggatti* (male).

Leptanillini: *Leptanilla japonica*, *Leptanilla revelierei*, *Leptanilla* sp. (Malaysia), *Leptanilla* sp. (Sabah). To prevent pre-judgement of their systematic relationships the three tribes currently constituting the subfamily Leptanillinae, namely Leptanillini, Anomalomyrmini and Apomyrmini (Bolton, 1990b), have been coded separately in the data matrix.

Leptanilloides sp. (Colombia). We felt unsatisfied with the current placement of this poorly known genus, originally described as an army ant (i.e. subfamily Dorylinae s.l.) by Mann (1923), transferred to the Cerapachyinae (as tribe) by Brown (1975) and maintained as such by Bolton (1990a). In our cladistic analysis the genus was treated as a separate terminal taxon. These ants appear to share several plesiomorphic characters with the Cerapachyinae but no unequivocal synapomorphies (see below).

Myrmeciini: *Myrmecia analis*, *Myrmecia chasei*, *Myrmecia desertorum*, *Myrmecia fulvipes* (worker, male), *Myrmecia gulosa*, *Myrmecia piliventris*, *Myrmecia pilosula*, *Myrmecia pyriformis*, *Myrmecia simillima* (worker, male), *Myrmecia swalei*.

Myrmicinae: *Acanthognathus brevis*, *Acanthomyrmex ferox*, *Aphaenogaster simonellii*, *Aphaenogaster swammerdami*, *Atta sexdens* (worker, male), *Carebara vidua* (worker, male), *Cataulacus erinaceus* (worker, male), *Crematogaster* sp. (Ivory Coast), *Dicroaspis laevidens*, *Harpagoxenus sublaevis*, *Huberia striata*, *Hypocryptocerus haemorrhoidalis*, *Leptocephalus versicolor*, *Liomyrmex* sp., *Megalomyrmex foreli*, *Melissotarsus emeryi*, *Messor andrei* (worker, male), *Messor meridionalis*, *Messor oertzeni*, *Messor structor*, *Monomorium abyssinicum*, *Monomorium kusnezowi* (worker, male), *Myrmecina* sp. (Sabah), *Myrmica alaskensis*, *Myrmica hamulata* (worker, male), *Myrmica jacobsoni* (worker, male), *Myrmica ruginodis*, *Myrmicaria natalensis*, *Myrmicaria opaciventris* (worker, male), *Ocymyrmex fortior*, *Pheidolegeton diversus* (worker, male), *Pogonomyrmex barbatus*, *Pogonomyrmex subdentatus* (worker, male), *Romblonella opaca*, *Serrastruma lujae* (worker, male), *Solenopsis* sp. (Sumba Island), *Stereomyrmex horni*, *Tatuidris* sp. (Costa Rica), *Tetramorium bellicosum*, *Tetramorium weitzzeckeri*.

Nothomyrmeciinae: *Nothomyrmecia macrops* (worker, male).

Ponerinae: *Acanthoponera minor*, *Acanthoponera mucronata*, *Amblyopone australis* (worker, male), *Amblyopone longidens*, *Amblyopone pallipes*, *Amblyopone reclinata*, *Amblyopone saundersi*, *Anochetus graeffei*, *Centromyrmex bequaerti*, *Centromyrmex feae*, *Concoctio concentra*, *Diacamma rugosum*, *Dinoponera australis*, *Discothyrea*

mixta, *Discothyrea oculata*, *Ectatomma opaciventre*, *Ectatomma ruidum* (worker, male), *Ectatomma tuberculatum* (worker, male), *Gnamptogenys ammophilala*, *Gnamptogenys concinna*, *Gnamptogenys menadensis*, *Harpegnathos saltator*, *Heteroponera brouni*, *Heteroponera dentinodis* (s.l.), *Heteroponera dolo*, *Heteroponera mayri*, *Hypoponera* sp. (Trinidad), *Leptogenys chinensis*, *Leptogenys* sp. (Sumatra, male), *Megaponera foetens*, *Myopopone castanea*, *Mystrium camillae*, *Mystrium* sp. (Madagascar, male), *Odontomachus rixosus*, *Odontoponera transversa*, *Onychomyrmex hedleyi*, *Ophthalmapone berthoudi*, *Pachycondyla crassinoda*, *Pachycondyla porcata*, *Pachycondyla striata*, *Pachycondyla* sp. (Brazil), *Paltothyreus tarsatus*, *Paraponera clavata* (worker, male), *Phrynoponera gabonensis*, *Platythyrea angusta*, *Platythyrea arnoldi*, *Platythyrea conradti*, *Platythyrea cibrinodis* (male), *Platythyrea lamellosa*, *Platythyrea modesta* (worker, male), *Platythyrea quadridentata*, *Platythyrea schultzei*, *Platythyrea turneri*, *Plectroctena mandibularis*, *Ponera coarctata*, *Prionopelta antillana*, *Prionopelta opaca* (male), *Probolomyrmex darwini*, *Probolomyrmex guineensis*, *Proceratium algircum*, *Proceratium boltoni*, *Proceratium croceum*, *Proceratium stictum*, *Psalidomyrmex procerus*, *Rhytidoponera araneoides*, *Rhytidoponera confusa* (worker, male), *Rhytidoponera purpurea*, *Rhytidoponera taurus*, *Simopelta* sp., *Typhlomyrmex rogenhoferi*.

Prionomyrmecini (currently placed in Myrmecinae). While Ogata's (1991) recent study provides a good definition of *Myrmecia*, and hence Myrmeciini, the position of the monotypic Baltic amber fossil genus *Prionomyrmex* remains problematic. Hence we retained the two tribes (Myrmeciini, Prionomyrmecini) as separate terminal taxa. Other fossil Myrmeciinae are even more poorly understood (see e.g. Brandão *et al.*, 1990) and have been excluded from the present study. For *Prionomyrmex* we assumed that the metapleural gland (character 11) and the sting (character 36) were present since they are found in related taxa.

Pseudomyrmecinae: *Myrcidris epicharis* (worker, gyne, male), *Pseudomyrmex concolor* (worker, male), *Pseudomyrmex euryblemma* (worker, male), *Pseudomyrmex filiformis*, *Pseudomyrmex gracilis* (worker, male), *Pseudomyrmex ita* (worker, male), *Pseudomyrmex ocularis*, *Pseudomyrmex perbisci*, *Pseudomyrmex salvini*, *Pseudomyrmex schuppi*, *Pseudomyrmex spinicola*, *Pseudomyrmex tenuissimus*, *Pseudomyrmex termitarius*, *Pseudomyrmex triplarinus* (worker, male), *Pseudomyrmex* sp. (Costa Rica), *Tetraponera aethiops*, *Tetraponera allaborans* (worker, male), *Tetraponera ambigua*, *Tetraponera grandis* (worker, male), *Tetraponera morondavensis* (worker, male), *Tetraponera natalensis*, *Tetraponera penzigi*, *Tetraponera punctulata* (worker, male), *Tetraponera rufonigra* (worker, male), *Tetraponera tessmanni*.

Outgroups

Relationships between the ants and other vespoid families have not been fully resolved (cf. Brothers, 1975;

Hermann, 1975; Carpenter, 1990a), so we followed the conservative course of choosing two outgroups: Vespidae and Bradynobaenidae. *A posteriori*, however, we noticed that both families are closely comparable with respect to our set of 68 characters (see below, Table 1). We have not made use of the fossil taxa Armaniinae or Sphecomyrminae as outgroups because many of the characters of interest in our data matrix cannot be assessed in these groups.

VESPIDAE

The characters of the Vespidae, when not stated otherwise, were essentially derived from Berland & Bernard (1951), Brothers (1975), and/or by examination of material in the collection at the Natural History Museum in Basel.

Euparagiinae: *Euparagia scutellaris*.

Polistinae: *Belonogaster eumenoides*, *Polistes dominulus* (worker, male), *Polistes gallicus* (worker, male), *Polistes marginalis* (male), *Polistes nimpha*, *Polybia ignobilis*, *Ropalidia fasciata*.

Stenogastrinae: *Liostenogaster flavolinaeata* (worker, male).

Vespinae: *Vespa crabro*, *Vespula germanica* (worker, male).

BRADYNABAENIDAE

Chyphotes sp. (female), *Chyphotes* sp. (male), *Typhocles pecularis* (female, male). In addition *Apterogyna* spp. were examined externally but not dissected.

In the present study essentially relaxed specimens were used for dissection (exceptions *Camponotus*, *Harpegnathos*, *Lasius*, *Messor*, *Paltothyreus*, *Rhytidoponera*). For all segments the tergum and sternum were considered fused when we were unable to separate them without causing irregular breakage. When the tergum and sternum separated cleanly along a line coincident with the tergosternal suture we considered them to be unfused even if considerable force was required to effect this separation. In many cases the presclerites were found to be fused even when they were followed by unfused sclerites. The results of these dissections are not mentioned in the following text unless they represent new data or conflict with published information.

Character coding, description, and distribution

All multistate characters from earlier cladistic analyses have been re-coded as binary. No *a priori* decisions about character polarity or ground plan character states within polymorphic terminal taxa were made. Character states were coded according to their observed occurrences, and a terminal taxon was considered polymorphic if two character states occurred within it (regardless of frequency). In effect, character polarity was determined *a posteriori* by outgroup-rooting of the tree. Characters which we considered to be restricted to the ant worker caste (characters 6, 10, 14 and 21 in the list below) were coded as absent in the outgroups.

We included, whenever possible, at least one clear autapomorphy for each terminal taxon. Quite often characters present in two or more taxa appeared as additional autapomorphies as a consequence of the phylogenetic reconstruction. The distribution of all characters among the 21 taxa included in the analysis is given in Table 1.

List of characters

1. Worker and gyne. Head hypognathous (0), or prognathous (1). At least a functional prognathus should be recognized for all worker ants. This is a potential synapomorphy of all Formicidae. Among other Hymenoptera marked prognathus of females is known only in Bethylidae.

2. Worker and gyne. Labrum with two rows of peg-like teeth (1) or without (0). Character state (1), already described by Brown *et al.* (1970), has been arbitrarily selected here as an autapomorphy of the Apomyrmini. The majority of Anomalomyrmini also show some peg-like teeth on the labrum, but they are never arranged in double rows.

3. Worker and gyne. Labium with a pair of cylindrical transparent pegs (?paraglossae) present (0) or absent (1). Coded according to Gotwald (1969). Absence in *Apomyrma* and *Aneuretus* according to Brown *et al.* (1970) and Gotwald (1970) respectively. One *Leptanilla japonica* specimen shows, distal to the labial palpi, a couple of thin, paired, finger-like structures that we interpret as homologous with the ant 'paraglossae'. This character has been coded as absent in the outgroup(s); true paraglossae occur in vespids and other Aculeata (Brothers, 1975) but these appear to be different from the structures described in ants by Bugnion (1927) and Gotwald (1969) and are probably not homologous with them.

4. Worker and gyne. Clypeus normally developed (0), or so extremely reduced as to be nearly invisible on the head in dorsal view (1). This character is coded after Bolton (1990c) who described it perfectly but did not use it in his cladogram. In addition to the taxa considered by Bolton, the clypeus is reduced in some ponerines as well (e.g. *Probolomyrmex*). The clypeus is reduced in female *Chyphotes* but still visible in full-face view.

5. Worker and gyne. Clypeus with flat medial surface separated by two steep angles from the sides (1) or, more or less rounded, of usual shape (0). Character state (1) is likely to represent the most reliable autapomorphy of the Anomalomyrmini. Their bizarre mandibular pilosity, though not exactly the same, is approached by at least one myrmicine genus: *Tatuidris*. A toothed, bicarinate and/or flat clypeus is found in a number of myrmecines as well (e.g. *Meranoplus*, *Vollenhovia*, members of the *Solenopsis* genus-group, etc.), but the remarkable trapezoidal plate present in all Anomalomyrmini (see e.g. fig. 4 in Bolton, 1990c) appears to be distinctive enough for the present purpose.

6. Worker. Eyes present (0), or absent (1). Absent in *Anillidris* among Dolichoderinae. Absent at least in

Table 1. Matrix with the presence or absence of characters among the 18 taxa considered. ? = unknown, p = polymorphic. Characters polymorphic for one or more taxa are shaded.

Probolomyrmex, *Typhlomyrmex*, *Centromyrmex* and *Concoctio* among Ponerinae. Among Ecitoninae, only *Cheliomyrmex* and some *Neivamyrmex* are regularly eyeless. Blind Myrmicinae include at least *Liomyrmex*, *Bondroitia* and *Anillomyrma*. The reduction of the eyes correlated with hypogaeic habits is morphoclinal e.g. in *Solenopsis*. All known Leptanillini, Anomalomyrmmini, Apomyrmmini, Aenictinae, Dorylinae and *Leptanilloides* are blind. This is character 35 in Bolton's (1990c) phylogeny.

7. Worker and gyne. Malar area so reduced that when the head is in full-face view, the mandibles appear to arise from the eyes (1), or malar area visible in dorsal view (0). This character, exhibited by a number of wasps, would further contribute to the separation between *Myrmecia* on the one hand and *Nothomyrmecia* and *Prionomyrmex* on the other. It appears, however, in another ant genus as well: *Harpegnathos* (Ponerinae). Blind ants are considered as having a normally developed malar area.

8. Worker, gyne and male. Antennal socket exposed (0), or not (1). This is a potential synapomorphy for all army ants, but is polymorphic among Ponerinae. The antennal socket, in addition, is exposed in some Myrmicinae (e.g. *Pristomyrmex*). Bolton (1990c: 1353) gives an exhaustive description of this character. The antennal socket is covered by an extension of the antennal sclerite (torulus) in *Chyphotes*.

9. Worker and gyne. Antennae with scape elongated (1) or short (0). Character state (1) is diagnostic of the Formicidae; coded after Dlussky (1983) and Baroni Urbani (1989).

10. Worker. Promesonotal suture fused (1) or mobile (0). Coded largely after Gregg (1953), Ward (1990) and Bolton (1990c: 1354). In workers unfused (mobile) in Formicinae, Dolichoderinae, Aneuretinae, Nothomyrmecinae, Myrmecinae, Pseudomyrmecinae, Leptanillinae, Leptanilloidinae. Fused (immobile) in Cerapachyinae, Dorylinae, Aenictinae, Ecitoninae, Myrmicinae. Polymorphic in Ponerinae (mostly unfused and mobile; fused only in *Probolomyrmex*, *Discothyrea*, *Proceratium*, *Rhytidoponera* and a few *Gnamptogenys*). The function of suture mobility in workers remains unknown. Ant gynes show a mesosoma differently organized both morphologically and mechanically. We therefore regard this as a strictly worker character and we coded it absent, i.e. lacking fusion, in outgroups.

11. Worker and gyne. Metapleural gland present (1) or absent (0). Coded after Hölldobler & Engel-Siegel (1984).

12. Worker and gyne. Opening of the metapleural gland covered from above by a cuticular flange (1), or not (0). This is character 16 of Bolton (1990c). The character is apparently absent among all Myrmicinae, Ponerinae, and Dolichoderinae we have seen. Quite a few Formicinae species (e.g. *Formica exsecta*, *Notoncus gilberti*, *Gigantiops destructor*, *Melophorus bagoti*, and many others but not all) also show the metapleural gland opening covered from above by a cuticular expansion but the structure of army ants as described and figured by Bolton appears profoundly different with its long border parallel to the major body axis. We can confirm the presence of this

structure in all the (many) army ants species we have been able to examine. Due to the small size the flange covering the metapleural gland cannot be seen under a normal microscope in *Leptanilla*, but a SEM inspection revealed this structure among Leptanillini as well (Fig. 1). What we regard as the same structure, however, appears to be absent in *Apomyrma* but present in the undescribed Nepalese *Protanilla* worker available for this study and in the gyne of another undescribed *Protanilla* species from Sri Lanka. In addition, a less developed but probably homologous carina is seen in *Nothomyrmecia*, *Myrmecia* and *Pseudomyrmecinae*.

13. Worker, gyne and male. Metacoxal cavities open or sutured (0), or closed (1). Closed in some Ponerinae according to Ward (1990, character 26) and Bolton (1990a, character 5). In fact, the metacoxal cavities are closed among the majority of ants. Open metacoxal cavities have been found in Nothomyrmecinae and all Myrmeciini examined (Ward, 1990). Among Ponerinae the sutured condition is the dominant one in the sample of specimens dissected for the present study.

The condition exhibited by *Aneuretus simoni* is not clear. The sole literature information available (Bolton, 1990c: 1361) states that this species shows the open condition. This statement was based on a dissection executed by D. Agosti and examined by Bolton. Baroni Urbani dissected one syntype worker from the Basel Museum collection and found the metacoxal cavities closed. S. Shattuck (personal communication) also dissected a specimen and found that the metacoxal cavities were open. Until these discrepancies are resolved we code the character as polymorphic in Aneuretinae. Because of this, we experimentally performed the cladistic analysis of our data matrix two more times, with this character coded as present and absent for Aneuretinae; the resulting cladograms were topologically identical (but different in length).

Among outgroups, the metacoxal cavities are polymorphic among wasps and within wasp subfamilies as well, though the open condition seems to be the dominant one. According to our sample, the metacoxal cavities are closed in *Vespa* and *Polistes* and open in all remaining species dissected. This character is equally polymorphic among Bradynobaenidae, i.e. the metacoxal cavities are closed in *Chyphotes* females and otherwise open.

14. Worker. 'Metatibial gland' present (1), or absent (0). The 'metatibial gland' was first described as present in army ants and polymorphic among Cerapachyinae by Borgmeier (1955: 16). The polymorphism of the gland among Cerapachyinae is coded after Bolton (1990c: 1346). Borgmeier (1955) described this structure as a yellow strip ('gelbe Streife') and Bolton is the first to interpret it as a gland and to mention an open glandular pit in some *Cerapachys* species. The morphology and the function of this gland are completely unknown. At least topographically it corresponds well to the tibial gland described in *Crematogaster* (Leuthold, 1968; Pasteels *et al.*, 1970). If the pit observed in Cerapachyinae corresponds to a glandular opening the two glands may be not homologous since the opening of the tibial gland in *Crematogaster* lies

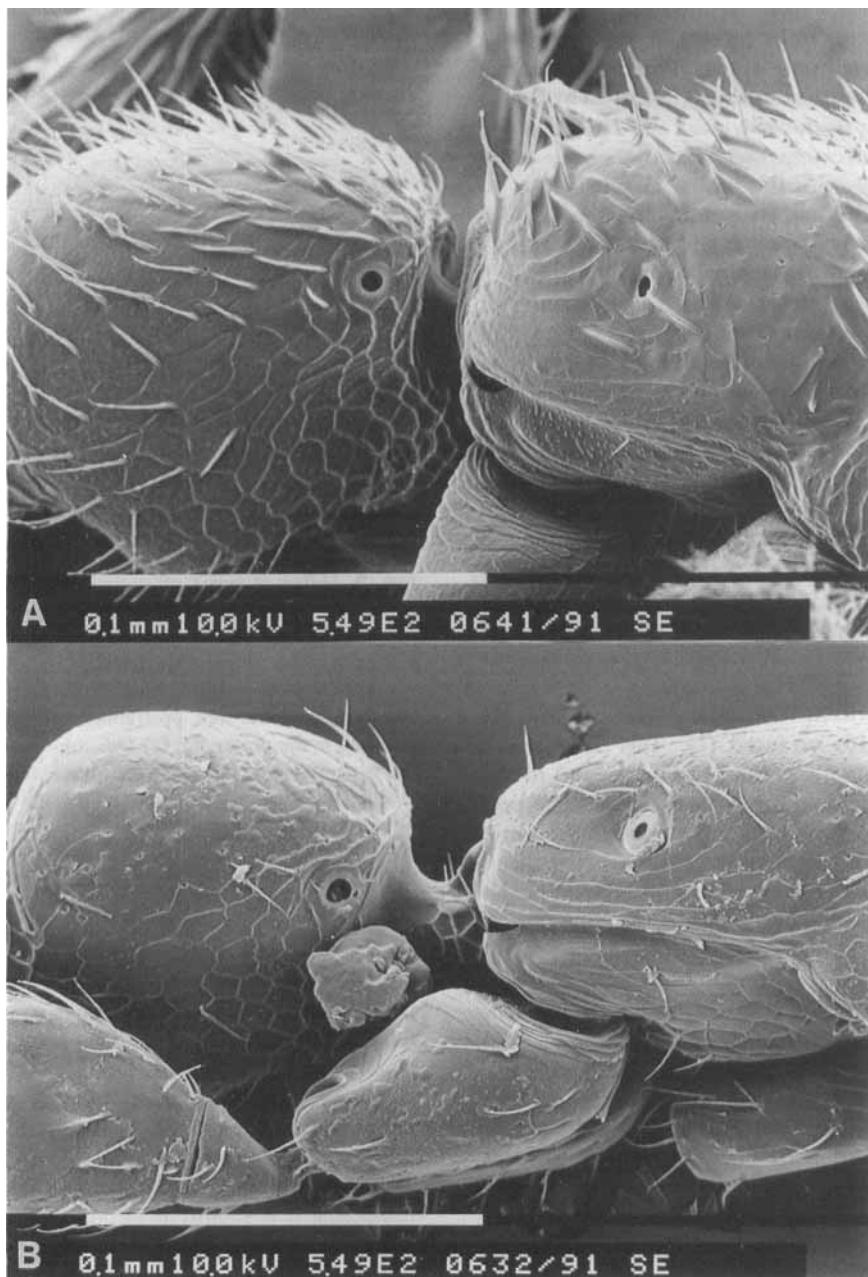


Fig. 1. Metapleural gland opening covered by a longitudinal cuticular flap in two *Leptanilla* species. (A) *L. japonica*. (B) *L. revelierei*.

close to the unguitractor plate on the last tarsomere. One should not forget that an exocrine gland with the opening close to the unguitractor of all six terminal tarsomeres is widespread in ants and probably in Hymenoptera (Billen, 1990b: 89). The gland observed in *Crematogaster* is more likely to be the result of hypertrophic development of the latter extending back up to the tibia. For this reason this character has been coded as absent instead of polymorphic among Myrmicinae. We have been unable to see traces of this structure in the available specimens of *Protanilla* (one of which is brown pigmented), and, again, not only the size, but the colour prevent detection of it in

Apomyrma and *Leptanilla*. At least in one *L. japonica* specimen a structure potentially corresponding to the glandular opening for shape and location has been revealed by SEM examination, but no equivalent structure could be detected in other *japonica* specimens or in *L. revelierei*. For these reasons, this character has been coded absent in Anomalomyrmini, in Apomyrmini and in Leptanillini, and in all outgroups.

15. Worker and gyne. Basitarsal sulcus on metatarsi present (1) or absent (0). This is character 23 of Ward (1990), briefly mentioned but not used by Bolton (1990c: 1346). The material available for the present study con-

firms what already resulted from these two papers. The basitarsal sulcus appears to be present in *Nothomyrmecia* and *Myrmecia*, polymorphic among Pseudomyrmecinae and Ponerinae. The basitarsal structures described by Bolton (1990c) in *Simopone* (Cerapachyinae) and Hölldobler & Palmer (1989) in *Onychomyrmex* (Ponerinae) are probably not homologous with the basitarsal sulcus, due to their different positions and structural appearances. This character is absent or unknown among all other taxa.

16. Worker and gyne. Abdominal segment II (petiole) with (1) or without (0) tergosternal fusion. This is character 9 of Bolton (1990c) and character 32 of Ward (1990). The petiole, in the present sample of species, was found to be regularly fused in *Leptanilla* and *Protanilla*, among all Formicinae and Dolichoderinae, in all Myrmicinae workers (but unfused in the male of *Pheidologeton diversus*, though in the worker it is regularly fused), and in Aneuretinae. This character, on the other hand, is polymorphic among Ponerinae. All other ants examined show the unfused condition. Among vespid wasps tergosternal fusion of abdominal segment II is polymorphic: unfused in *Vespa*, *Polistes* and *Euparagia*, and fused in all remaining species examined. Bradynobaenids also show a petiole at least anteriorly fused.

17. Worker. Presclerites of abdominal segment III (helcium), unfused (0) or fused (1). This corresponds to character 2 in Bolton's (1990c) phylogeny and to the first two states of Ward's (1990) character 34. The present study confirmed fusion among Cerapachyinae and Ponerinae, and lack of fusion among Pseudomyrmecinae. The presclerites appear to be fused in *Aneuretus* and in all Dolichoderinae except some *Dolichoderus*. The Myrmicinae appear to be equally polymorphic, showing unfused presclerites in most species dissected. Otherwise the presclerites are regularly fused in *Leptanilla*, *Protanilla*, *Apomyrma*, Dorylinae, Ecitoninae, Formicinae and Aenictinae (workers only). Fusion of abdominal presclerites III is polymorphic among wasps (presclerites fused at least in *Ropalidia* and *Belonogaster*, unfused in the other species examined). The presclerites are apparently unfused also in Bradynobaenidae.

18. Worker and gyne. Presternite of abdominal segment III (helcium sternite) protruding ventrally (0) or not (1). This character and the previous one correspond to the binary transformation of Ward's (1990) tri-state character 34. Notice that binary re-coding is not always additive for this character. It is equivalent to Bolton's (1990c) character 15 ('sternite of helcium convex and bulging ventrally'). The helcium sternite bulges ventrally (i.e. is visible from the sides) in all Dorylinae, Aenictinae, Ecitoninae, Cerapachyinae and *Leptanilloides* (see also figs 22 and 23 in Bolton, 1990a). It is invisible from the sides in all remaining taxa considered here, still invisible but elongated cranially in *Apomyrma*. Interpretation of this character may be sometimes difficult in some species due to the fact that most (not all) Ponerinae show a ventral protuberance on the anterior margin of abdominal segment III sternite (Fig. 2). This protuberance belongs to the sternum proper and not to the presternite. The

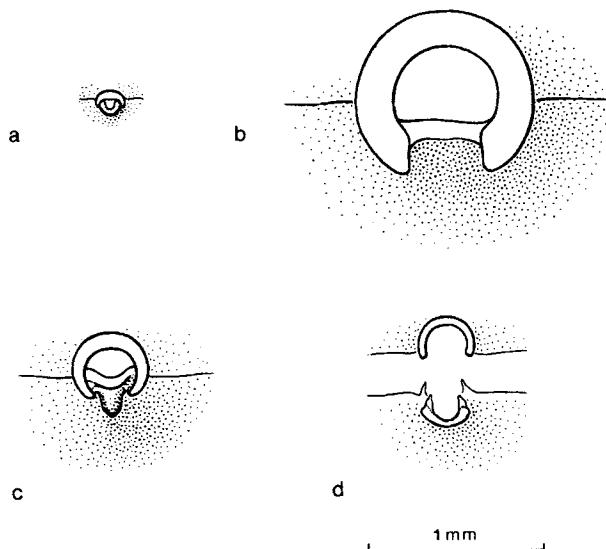


Fig. 2. Different types of organization of the presclerites of abdominal segment III (=helcium sclerites). (a) *Cerapachys fragosus*, showing pretergite and presternite fused, pretergite embracing the presternite laterally, and presternite bulging ventrally. (b) *Paraponera clavata* with fused pretergite and presternite, the latter not protruding ventrally but still laterally enclosed in the pretergite. (c) *Odontoponera transversa*, showing the same condition described for *Paraponera* but with a ventrally bulging protuberance originating from the sternum proper. (d) *Messor oertzeni* with pretergite and presternite unfused, presternite ventrally bulging but not embraced by the pretergite. The sternum and tergum and their relative presclerites have been artificially separated for clarity.

true presternite of all Ponerinae examined is very reduced, never visible from the side, and often entirely plane (Fig. 2b). This character and the following one are more difficult to assess among wasps, due to their much wider body diameter, but the presternite seems not to protrude at all at least in *Vespa* and *Polistes* and to be protruding among the other species dissected. In *Euparagia* it is slightly protruding but poorly developed. For these reasons we preferred to code it as unknown among Vespidae. The presternite is not protruding in Bradynobaenidae.

19. Worker and gyne. Presternite of abdominal segment III (helcium sternite) overlapped laterally by pretergite (0), or not (1). This is character 35 of Ward (1990). The presternite of abdominal segment III appears to be totally or partially enclosed by the corresponding pretergite in all ants and wasps examined except for the Myrmicinae.

20. Worker. Spiracle of abdominal segment III large and situated far forward, very close to or on anterior face of tergite (1), or situated more posteriorly (0). Character state (1) is a synapomorphy of the three leptanilline tribes in Bolton (1990b) and corresponds to character 8 in the phylogeny of Bolton (1990c). The character is present in all Anomalomyrmini and Apomyrmini we examined. On the other hand, we have some light and electron

microscopy evidence that in some *Leptanilla revelierei* and *L. japonica* workers the spiracle appears to be reduced in size or missing. Since a large spiracle is present in the great majority of the Leptanillini we examined, including workers from the same soil sample – and probably from the same nest – as those in which the spiracle was not visible, we interpret these specimens as abnormal and we coded the spiracle as present among Leptanillini too. On the other hand, a large spiracle situated forward on the postpetiole is well visible in *Ankylomyrma* (Myrmicinae). Thus this character has been coded as polymorphic for Myrmicinae.

21. Worker. Maximum diameter of abdominal segment III subequal to the minimum diameter of abdominal segment IV in the sagittal plane (0), or clearly smaller than abdominal segment IV (presclerites excluded) (1). This character is essentially the same as character 5 in Baroni Urbani (1989). Notice that coding of this character differs between males and females among Ponerinae and Nothomyrmecinae, and is equal in gynes and males but different in workers among army ants s.str. See also character 45.

22. Worker. Abdominal segment III without complete fusion of tergum and sternum (0) or with complete fusion (1). Coded after Gotwald (1969) and Ward (1990, character 33). It corresponds to character 3 of Bolton (1990c). Sternite and tergite of abdominal segment III are regularly fused in Ecitoninae, Aenictinae, Dorylinae, Cerapachyinae, Apomyrmini, Ponerinae, Anomalomyrmini, Leptanillini and *Leptanilloides*, and unfused in the other ants. Most wasps show unfused sclerites of abdominal segment III, though these sclerites are definitely fused in *Ropalidia fasciata* and fused only in the first half in *Belonogaster eumenoides*.

23. Worker. Dorsal stridulatory organ between abdominal segments III and IV present (1) or absent (0). Coded after Markl (1973). This is character 39 in Ward (1990) and is present in all Pseudomyrmecinae. Polymorphism of this character within Ponerinae and Myrmicinae has been documented by Markl (1973). The organ, in addition, is absent in all army ants s.l., and in *Protanilla*, *Apomyrma* and Vespidae (present study). Obviously non-homologous paired stridulitria are present on abdominal tergite V in Bradynobaenidae.

24. Worker. Ventral stridulatory organ between abdominal segments III and IV present (1) or absent (0). A ventral stridulatory organ is present in *Nothomyrmecia* (Taylor, 1978) and it has been recently noted in *Rhytidoponera* by Markl in Hölldobler & Wilson (1990) and by Ward (present study).

25. Worker and gyne. Abdominal segment IV without differentiated presclerites (0), or with differentiated presternite and pretergite (1). This character and the two following correspond to character 36 of Ward (1990) re-coded here in binary form. Notice that binary re-coding is not always additive for this character. Differentiated presclerites of abdominal segment IV are regularly missing in Formicinae, Dolichoderinae, in *Apomyrma*, and in *Nothomyrmecia*. *Aenictogiton* males lack differentiated

presclerites of abdominal segment IV but this character does not vary concordantly in workers and males: *Dorylus* and *Aenictus* workers exhibit the presclerites, while males do not. All other worker ants examined show character state (1). Among outgroups clearly differentiated presclerites on abdominal segment IV are generally lacking or poorly developed (*Polybia* and *Belonogaster*). *Liostenogaster* is equivocal, showing no true presclerites but a marked thickening of the anterior border of the sclerites. Differentiated abdominal presclerites IV are present in *Apterogyna* and hence the Bradynobaenidae have also been coded as polymorphic.

26. Worker and gyne. Abdominal segment IV with differentiated pretergite and presternite not fused (0), or fused (1). This character, together with characters 23 and 25, corresponds to character 36 of Ward (1990) re-coded here in additive binary form. The presclerites of abdominal segment IV are regularly fused in all Ponerinae, Myrmecini, *Leptanilla* and *Protanilla*. This character is polymorphic among Myrmicinae and Cerapachyinae. All other ants and wasps examined show the unfused condition. Even among the few wasps showing reduced presclerites, they are never fused.

27. Worker and gyne. Presclerites of abdominal segment IV longer than one half of A III and with the sides running parallel (1) or not (0). Character state (1), first discovered and described by Taylor (1978), recurs in all following ant phylogenies. It is character 19 in Baroni Urbani (1989), character 1 in Bolton (1990c) and it corresponds to character 36 state 2, and, in part, to characters 37 and 38 of Ward (1990). A tubular form of the abdominal IV presclerites (i.e. round shape coupled with a length at least subequal to the width, not simply ring-shaped as in, e.g., all Myrmicinae) is present only among all Myrmecini, Ponerinae and Cerapachyinae. In *Cerapachys fragosus* the presclerites are obviously fused and, at the same time, they form a characteristic tubular structure. *Cheliomyrmex* workers show longitudinally well developed presclerites on abdominal segment IV nearly as large as those of abdominal segment III but they differ from the condition described above by being conical and still much larger in diameter than in length (Fig. 3). The morphology of the abdominal IV presclerites of *Cheliomyrmex*, in addition, is approached by at least some Dorylinae and by the ponerine genus *Centromyrmex*.

28. Worker and gyne. Presternite of abdominal segment IV, when present, subequal to or longer than the pretergite (0), or notably shorter than the pretergite (1). This is character 38 of Ward (1990). The short presternite is present in Myrmicinae and Pseudomyrmecinae only. State 0 of this character for *Leptanilloides* is documented by figs 22 and 23 of Bolton (1990a).

29. Worker and gyne. Tergum and sternum of abdominal segment IV completely fused (1) or not (0). This appears to be the strongest autapomorphy of the Ponerinae. Coded after Gotwald (1969), Ward (1990) and Bolton (1990a, c).

30. Worker and gyne. Spiracles of abdominal segments 5–7 visible without dissection, (1) or not (0). Synapomorphy of the ‘doryline section’ according to Bolton (1990c). This

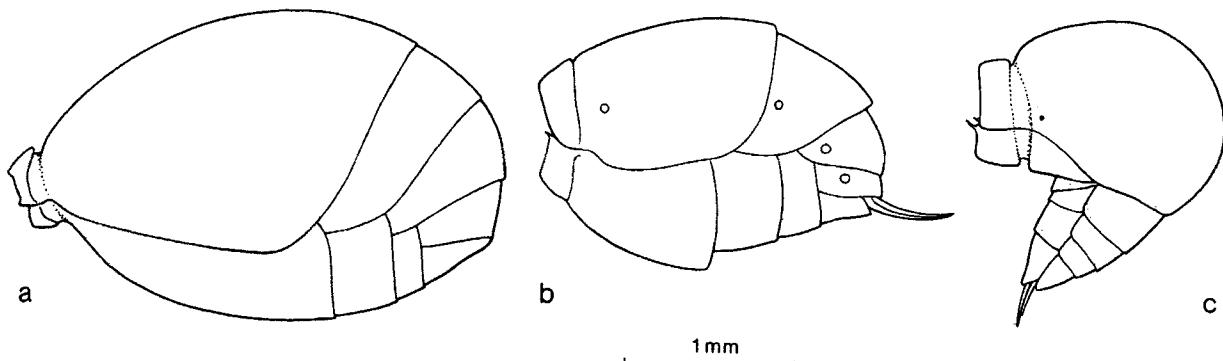


Fig. 3. Different morphologies of the presclerites of abdominal segment IV. (a) *Messor oertzeni*, with presclerites small, narrow and ring-shaped. (b) *Cheliomyrmex andicola*, with presclerites broad and conical. (c) *Proceratium algircum*, with presclerites broad and tubular.

is a very clear-cut character universally present in all the (many) species of Dorylinae and Aenictinae we examined. Excluding obvious cases of worker physogastry the spiracles are regularly visible in major workers of *Pheidologeton diversus* (replete?) but not in minors. For these reasons this character has been coded, as Bolton did, as present in Aenictinae, Cerapachyinae, Dorylinae, Ecitoninae, and absent in Myrmicinae.

31. Worker and gyne. Pygidium bidentate (1) or not (0). This character, universal among Dorylinae, is described by Emery (1910) and Bolton (1990a). Character 13 in the phylogeny of Bolton (1990c), treating all modifications of the worker pygidium as homologous, has not been used in this analysis. Here we regard the bidentate condition and the spinose condition as autapomorphies of the Dorylinae and Cerapachyinae respectively (see also discussion in Bolton (1990a: 65)). The third condition described by Bolton (1990c: 1348), in which the pygidium occurs as a 'U-shaped sclerite', is treated as a separate character (no. 33) in this paper.

32. Worker and gyne. Pygidium bordered apically by minute spines (1) or not (0). This appears to be one of the strongest potential autapomorphies of the Cerapachyinae as noticed first by Brown (1954). It is absent in *Leptanilloides*. The condition of this and the previous character among Ponerinae is much more variable: Bolton (1990a) already reported that *Pachycondyla crassinoda* exhibits a pair of strong pygidial teeth. *Pachycondyla impressa* shows denticles at the margins of the hypopygium. Several other ponerines have hypopygial denticles, e.g. some *Amblyopone*, *Paraponera*, and some *Dinoponera*. Also a couple of *Dinoponera* species (*D. australis*, *D. mutica*) have pygidial denticles, but here the pygidium is biconvex. Here we take a conservative course of action by coding this character as present among Cerapachyinae after exclusion of *Leptanilloides* and polymorphic among Ponerinae.

33. Worker and gyne. Pygidium reduced to a narrow U-shaped sclerite impressed or concave dorsally (1) or not (0). Coded after Bolton (1990c: 1348) as present in Aenictinae, Ecitoninae and *Leptanilloides*.

34. Worker. Pygidium dorsally covered by abdominal tergum VI (1) or not (0). This character, first described by

Brown (1975) represents the most striking autapomorphy of *Leptanilloides*. This has been treated as a worker and gyne character for the purpose of outgroup comparison.

35. Worker and gyne. Acidopore present (1) or absent (0). This is the principal autapomorphy of the Formicinae. Coded after Forel (1878).

36. Worker and gyne. Sting and lancets articulated (0), or disarticulated (1). Character state (1) is another important Formicinae autapomorphy (Forel, 1878). According to Kugler (personal communication) even in highly reduced apparatus the lancets fit into grooves in the sting – except in the Formicinae.

37. Worker and gyne. Furcula well developed (0), or extremely reduced to absent (1). Character state (1) given as a synapomorphy of Ecitoninae, Cerapachyinae, Aenictinae and Dorylinae by Bolton (1990c). The furcula, in addition, is missing (or fused with the sting base) among Formicinae (Hermann & Blum, 1968; Lutz, 1986), in two Ponerinae genera (Hermann & Blum, 1967), in the Dolichoderinae and in *Aneuretus* (Hermann & Blum, 1981). According to Kugler (1978) the furcula is generally present in Myrmicinae, though with various degrees of reduction up to at least one case of complete loss (*Atopomyrmex*). Presence in *Myrmecia* and *Nothomyrmecia* according to Kugler (1980). Presence of the furcula in *Leptanilla* and *Protanilla* has been confirmed by a personal communication of Charles Kugler. Presence of a well-developed furcula in *Typhoctes* and other Aculeata from Hermann (1975) and Hermann & Chao (1983).

38. Worker (gyne and male?). Proventriculus sclerotized (1) or flaccid (0). Coded according to Eisner (1957). This coding could be an oversimplification but Emery (1925b: 5) gives an interesting discussion on plausible similarities among the proventriculi of some Dolichoderinae and Formicinae. This character has been described essentially for workers but it is very likely to apply to gynes and males too. It is the same as character 25 in Baroni Urbani (1989).

39. Worker and gyne. Epithelium of the Dufour gland crenellate (1) or not (0). Character state (1) is a potential synapomorphy of Dorylinae and Aenictinae. Coded after Billen & Gotwald (1988) and Billen (1986). Absence of character state (1) among wasps according to Johan Billen

(personal communication). This character corresponds to character 30 in Bolton's (1990c) cladogram.

40. Worker and gyne. Pavan's gland present (1), absent (0). Pavan's gland is a synapomorphy of the Dolichoderinae and Aneuretiniae according to Billen (1987).

41. Worker and gyne. Sting bulb gland present (1) or absent (0). Character state (1) is cited as a synapomorphy of Nothomyrmecinae and Myrmeciini by Billen (1990a).

42. Worker-gyne dimorphism pronounced (1) or essentially limited to the wings and alar sclerites (0). This is character 22 in Baroni Urbani (1989) re-coded here as polymorphic among Ponerinae, Myrmicinae and Cerapachyinae. Character state (1) describes taxa in which the castes differ strongly in morphology and/or size. As such, it has been coded present among driver ants s.l. and Formicinae, and polymorphic among Cerapachyinae, Ponerinae, Myrmicinae and Dolichoderinae (see e.g. *Technomyrmex*).

43. Gyne dichthadiiform (1) or not (0). This is character 20 of Baroni Urbani (1989). There is some controversy in the ant literature over the application of this term, see for instance Wheeler (1910, 1916), Borgmeier (1950), Gotwald & Brown (1966) and Hölldobler & Wilson (1990). For the purposes of this survey we restrict the term to include only those monstrously modified gynes found in Dorylinae, Aenictinae, Ecitoninae and Leptanillini.

44. Gyne and male. 'Crowding' of wing venation present (1) or absent (0). Character state (1) is an autapomorphy of Formiciinae (Lutz, 1986).

45. Gyne. Abdominal segment III poorly differentiated from the following ones (0) or forming a differentiated postpetiole (1). Coded after Baroni Urbani (1989). This character has been coded '1' for the Anomalomyrmini in spite of the morphology exhibited by the previously sole gyne known (Bolton, 1990b). As Bolton (1990b) already suggested, this specimen is likely to be teratological. Another undoubted *Protanilla* queen, representing an undescribed species from Sri Lanka, shows a postpetiole completely comparable to the one known for workers. Character state (1) is also present among Myrmicinae, Pseudomyrmecinae, Myrmeciini and polymorphic among Ponerinae (see e.g. *Paraponera*).

46. Gyne. Bursa copulatrix exposed (1) or not (0). This character was given as a synapomorphy of Dorylinae (including Aenictinae) + Leptanillinae by Baroni Urbani (1989, character 11). It is not shown, however, by Aenictinae and was given as an autapomorphy of Dorylinae by Bolton (1990c, characters 48, and, in part, 50). The bursa copulatrix is, in fact, exposed among Leptanillini as well (see e.g. Emery, 1910).

47. Male. Antennal sockets at the anterior margin of the head, with the border of the socket often overlapping the mandibles (1), or at some distance behind, at least a trace of the clypeus visible between the socket and the anterior margin of the head (0). Character state (1) is present in all species of *Aenictogiton* (at least 7 species examined), all *Aenictus* (35 nominal taxa examined), Dorylinae (88 nominal taxa examined), and absent in Ecitoninae (62 nominal taxa examined). It is, however,

polymorphic among what are currently regarded as males of Leptanillini (e.g. present in *Leptanilla* and absent in *Yavnella*), Ponerinae (generally absent but present e.g. in *Probolomyrmex*) and Cerapachyinae (see e.g. figs 96–98 in Brown, 1975).

48. Male. Posterior margin of head with a deep and narrow incision (1), or without it (0). Character state (1) is an autapomorphy of *Aenictogiton* (Emery, 1901c; Santschi, 1919, 1924; Brown, 1975).

49. Male. Antennal scape shorter than the sum of the two following antennomeres (0), or longer (1). The short male scape appears to be characteristic of Vespidae, Apomyrmini, Myrmeciini, Nothomyrmecinae, Pseudomyrmecinae, and the fossils Formiciini and Prionomyrmecini. Otherwise the relative size of the scape is polymorphic among Ponerinae, Myrmicinae, and Dolichoderinae and longer than the two following joints in all other taxa from which the male is known.

50. Male. Forewings with (0), or without pterostigma (1). This is equivalent to character 7 in Baroni Urbani (1989). Absence of a pterostigma is characteristic of the Leptanillini (Bolton, 1990c, character 10). The pterostigma is also missing in at least some Attini (Emery, 1922). According to Lutz (1986), presence of the pterostigma should be polymorphic among Formiciinae. Among outgroups, the pterostigma is polymorphic in Bradynobaenidae (Brothers, 1975).

51. Male. Hindwings with basal hamuli (0) or without (1). Retention of the hamuli in *Nothomyrmecia* contrasts with the apparent derived absence of this character in all other ants (Taylor, 1978). In the present study, however, basal hamuli (hamuli along the anterior margin of the hindwing, proximal to the distal hamuli, i.e. proximal to the point where the radial vein reaches the wing margin) have been observed in alates (both sexes) of some *Myrmecia* and *Amblyopone* species, in addition to the male of *Nothomyrmecia*. Basal hamuli are also present in *Chyphotes* and *Typhoctes* but lost in some other bradynobaenids and apparently absent in Vespidae (Brothers, 1975).

52. Male. Jugal lobe of hindwings present (0) or absent (1). Character 6 in the phylogeny of Bolton (1990c). Presence of the lobe in Prionomyrmecini inferred from the statement of Wheeler (1915a: 26) that the male of *P.longiceps* is 'almost exactly like that of *Myrmecia* in both anterior and posterior wings'. Examination of the material available for the present study confirmed the absence of the lobe among Leptanillini and the genera of the doryline section. Winged males of *Apomyrma* and *Anomalomyrma*, of course, are not yet known. In addition, the jugal lobe is absent in *Aenictogiton* (4 species examined), in all Pseudomyrmecinae examined (many species in 3 genera), in all Dolichoderinae (17 species in 13 genera examined), in all Formicinae (19 species in 17 genera examined), and in all Myrmicinae (42 species in 40 genera examined). Male Myrmeciini available show a jugal lobe. The jugal lobe is present in *Nothomyrmecia*, but this character is highly polymorphic among Ponerinae from being clearly present e.g. in *Leptogenys* sp. and *Platythyrea crucheti*, weak in *Ectatomma quadridens*,

and clearly absent in *Paraponera clavata* and *Mystrum mysticum* among others. Among wasps this character is also polymorphic. It is absent in Vespini (species examined *Vespa rufa*, *V.adulterina* and *Vespa crabro*), present in *Euparagia*, Polistini + Polybiini (examined *Polistes biglumis*, *P.dominulus*, *P.gallicus*, *P.bischoffi*, *P.exclamans*, *Mischocyttarus mexicanus*, *Parapolybia indica*), and polymorphic among Stenogastrini (present in *Anischnogaster iridipennis*, *Stenogaster* sp., *S.adusta*, *Parischnogaster* sp., *P.gracilipes*, *Eustenogaster fraterna*, absent in *Metischognaster drewseni*). The jugal lobe is usually present in Bradynobaenidae but absent in *Typhoctes*.

53. Male. Propodeal spiracle slit-shaped (0), or round to elliptical (1). This character is inspired by character 32 of Bolton (1990c) but differently defined, since transitions from round to oval and to elliptical are difficult to define. The present study confirms presence of a clearly slit-shaped spiracle among all Dorylinae and Ecitoninae. The spiracle is slit-shaped in *Nothomyrmecia* too. It appears to be regularly round in Dolichoderinae, Cerapachyinae, *Aenictogiton* and Leptanillini. The propodeal spiracle, for the purpose of the present analysis, has been coded as slit-shaped among Formicinae (cf. Lutz, 1986). The propodeal spiracle is strongly slit-shaped in all male vespid wasps and bradynobaenids examined.

54. Male. With tergosternal fusion of abdominal segment III (1) or not (0). Character 27 of Bolton (1990c). Character state (1) is present in Aenictinae, Cerapachyinae, Ponerinae, Leptanillini, *Aenictogiton* and Dorylinae and absent in all other taxa examined and from which the male is known. Abdominal segment III is unfused in males of all outgroups we examined.

55. Male. Abdominal segment IV without differentiated presclerites (0), or with differentiated presclerites (1). Presclerites of abdominal segment IV are present in all males of Ponerinae, Cerapachyinae, Ecitoninae, Myrmeciinae, Pseudomyrmecinae and Myrmicinae examined. Abdominal segment IV presclerites are absent in *Aenictogiton*. Notice that this character is distributed quite differently than the equivalent character (25) for workers and gynes. The Bradynobaenidae have been coded polymorphic for this character because of the condition in *Apterogyna*.

56. Male. Abdominal tergite VII mostly desclerotized and largely concealed by the hypertrophied tergite VI (1), or tergites VI and VII equally sclerotized and telescopically arranged like the other gastral segments (0). Character state (1) is an autapomorphy of the Aenictinae, absent from the potentially related genus *Aenictogiton*.

57. Male. Abdominal sternite VIII with (1) or without (0) long anterior apodemes. Putative synapomorphy of Aenictinae + Dorylinae of Bolton (1990c, character 33). This structure is present in *Aenictogiton* as well.

58. Male. Cerci present (1) or absent (0). This character, coupled with the retractility of genitalia, is used by Bolton (1990c: 1351) as a synapomorphy of his 'doryline section'. Here, the two characters will be treated separately as they are in Bolton's own phylogeny (page 1352). Cerci, among the Ponerinae, are missing at least in *Amblyopone australis* (Fritsch, 1987), *Probolomyrmex* (Taylor, 1965) and

Mystrum spp. (Emery, 1911; Fritsch, 1987). For these reasons, this character has been coded as polymorphic among the Ponerinae. Among Formicinae, the presence of cerci is equally polymorphic, since they are missing at least in *Pseudolasius*, *Paratrechina*, and in the tribe Plagiolepidini (Emery, 1925b). In addition, cerci are absent among a few degenerate (ergatoid) males of *Anergates* and *Cardiocondyla* (in the latter they may coexist with normal males) among the Myrmicinae. Cerci are absent among Vespidae and polymorphic in Bradynobaenidae (Brothers, 1975).

59. Male. Subgenital plate (= sternite of abdominal segment IX) biaculeate (1) or not (0). This is character 19 in Bolton (1990c). It is universally present among army ants but it shows a high degree of polymorphism among other taxa. Ponerinae showing moderate to strong biaculeate conditions range from *Paraponera clavata* (Emery, 1901a) to *Amblyopone santschii*, *Platythyrea lamellosa* and *Anochetus graeffei* (Fritsch, 1987). In addition, a bifurcate *lamina subgenitalis* has been described at least for *Leptanilla minuscula* and *L.tenuis* (Santschi, 1907) and in *Nothomyrmecia* (Taylor, 1978). Among most known leptanilline species this part is very reduced and covered by the eighth abdominal sternite which prevents examination. Hence, it has been not described. In addition, the subgenital plate is deeply incised at least in *Myrmicaria opaciventris* (Myrmicinae) and *Iridomyrmex detectus* (both present study), among different palaearctic *Tapinoma* species (Emery, 1925a) and in *Tapinoma sessile* (Krafcik, 1959) (Dolichoderinae) but it is not among other known Dolichoderinae. Among Formicinae, the subgenital plate is incised at least in *Myrmelachista gallicola* (present study), though it seems to be not so in the majority of the species described by Clausen (1938) and is trifurcate in at least some *Cataglyphis* species (see e.g. Tinaut, 1990). One may be tempted not to homologize the dolichoderine and formicine condition to that of the army ants which, as a matter of fact, nearly universally show a much more pronounced condition with sharp spines directed backwards. Nonetheless even the 'typical' army ant morphology is far from being unequivocal. At least a few *Cerapachys* species show in fact extreme reduction of these spines and of the infraspinal incision in a way which is entirely comparable to that of the Dolichoderinae and of the Formicinae just mentioned, see e.g. the published figures of an unidentified Malaysian *Cerapachys* and of *C.clarki* by Brown (1975: 107, figs 116, 122). For these reasons, this character has been coded as absent in Myrmeciini (Fritsch, 1987) and Vespidae (present study), polymorphic among Ponerinae, Myrmicinae, Formicinae and Dolichoderinae, and present in Leptanillini, Nothomyrmecinae, *Aenictogiton* and army ants s.l. Some (not all) bradynobaenid males have a triaculeate subgenital plate; hence the character has been coded as polymorphic for Bradynobaenidae.

60. Male. Genitalia with normally thin 'lamina annularis' (= basal ring) (0) or with very large lamina annularis, almost egg-shaped (1). Character state (1) is an autapomorphy of the Ecitoninae according to Borgmeier (1955). This corresponds to character 27 in Baroni Urbani (1989) and character 26 in Bolton (1990c).

61. Male. Genitalia retractile (0) or not (1). This character is here coded after Emery (1895). Character state (0) is given as a synapomorphy of Ecitoninae, Cerapachyinae, Aenictinae and Dorylinae by Bolton (1990c, character 17). However, the male genitalia are retractile among all wasps and, in ants, in *Mystrium* (Emery, 1911) and *Platythyrea* (Brown, 1975) among Ponerinae, and in some Myrmicinae as well (e.g. *Carebara*, according to Emery, 1895). They appear to be retractile in *Aenictogiton* too.

62. Male. Genitalia much larger than the rest of the gaster (1) or of normal size (0). Coded after Baroni Urbani (1989) where it is given as an autapomorphy of the Leptanillini (s.str.).

63. Larva with a haemolymph feeding organ on abdominal segment III (1) or without (0). This is character 8 in Baroni Urbani (1989). Character state (1) is an autapomorphy of the Leptanillini (Wheeler & Wheeler, 1965; Masuko, 1990); absence in *Apomyrma* according to Wheeler & Wheeler (1970).

64. Larva. Mandibles with outer (1) or inner (0) masticatory margin. Character 9 in Baroni Urbani (1989). Character state (1) is an autapomorphy of the Leptanillini according to Wheeler & Wheeler (1965); absence in *Apomyrma* according to Wheeler & Wheeler (1970).

65. Larva with (1) or without (0) conspicuous food pocket (trophothylax). Character state (1) is an autapomorphy of the Pseudomyrmecinae according to Wheeler & Wheeler (1976).

66. Pupae naked (1) or with cocoon (0). Character 18 in Baroni Urbani (1989) and character 31 in Bolton (1990c). Coded after Wheeler (1915b), Wheeler & Wheeler (1976) and Gotwald (1982). Among the Formicinae pupae are naked in nest weaving species, and sporadically in some *Lasius* and *Formica*. Pupae of the genera *Prenolepis* and *Paratrechina* appear to be regularly naked (Trager, 1984). Hence the Formicinae must be coded as polymorphic for this character. Members of the subfamily Ponerinae usually have the pupae enclosed in a cocoon but there are some exceptions, involving the genera *Amblyopone* (Mann, 1919), *Discothyrea* (Emery, 1910), *Probolomyrmex* (Taylor, 1965), *Hypoponera* (Taylor, 1967) and *Ponera* (Ward, unpubl.). The pupae of *Apomyrma* are enclosed in a cocoon according to Brown *et al.* (1970). Absence of cocoons in Leptanillini according to Masuko (1990). Among wasps, the presence of an operculum produced by the labial glands of the larvae (e.g. Polistini) has been considered as homologous with the cocoon. When the operculum is made by workers with mud or other materials (e.g. *Stenogaster*), it cannot be considered homologous to the cocoon. The Vespidae are, hence, polymorphic for this character.

67. Stereotyped adult carrying behaviour with the carried individual under the head (1) or not (0). This and the following character correspond to character 16 in Baroni Urbani (1989) re-coded here in binary form and modified according to the following literature sources: Möglich & Hölldobler (1974), Duelli (1977), Hölldobler & Wilson (1990), Masuko (1990).

68. Stereotyped adult carrying behaviour with the carried individual over the head (1) or not (0). This and

the previous character correspond to character 16 in Baroni Urbani (1989) re-coded here in binary form and modified according to the following literature sources: Möglich & Hölldobler (1974), Duelli (1977), Hölldobler & Wilson (1990), Masuko (1990). Presence of character state (1) in *Aneuretus simoni* according to a personal communication of James Traniello.

Characters included in previous phylogenies and excluded from the present analysis

A broad array of characters was used in our analysis, but certain traits were excluded because of excessive variability, difficulty of definition or interpretation, inadequate knowledge, or because they appeared in the literature too recently to be considered. Excluded characters include the following:

Worker and gyne. Mandibles long and linear with one apical and several irregular preapical teeth on the whole internal border, as opposed to present on the masticatory border only. This was given as an autapomorphy for the Myrmeciinae by Baroni Urbani (1989, character 6).

Worker. Proprioceptor zone on abdominal sternite II reduced (as opposed to conspicuously present). This is character 36 of Bolton (1990c) where it is given as a synapomorphy of Aenictinae and Dorylinae. The zone, however, may be very reduced in a few *Cerapachys* species, such as *C.flavoclavata* (present study) and *C.centurio* (Brown, 1975: 98, fig. 69). On the other hand it is well developed in some Dorylinae such as *Dorylus spininodis* (see Emery, 1901b, pl. I, fig. 21) and the major workers of *D.molestus* (present study). This character is, hence, too variable to be phylogenetically informative.

Worker. Petiole with a long anterior peduncle. Given as an apomorphy of the Aneuretinae in Bolton (1990c) and Shattuck (1992), and contrasted with a sessile or subsessile petiole in Dolichoderinae. A glance at the published figures of the Baltic amber species *Protaneuretus succineus* and *Paraneuretus tornquisti* (Wheeler, 1915a), and at *Dolichoderus dibolia* (Wilson, 1985) shows the opposite conditions, with the petiole of *D.dibolia* much more pedunculate than that of the known Aneuretinae. Another, still undescribed, Dominican amber *Dolichoderus* with comparably pedunculate petiole is preserved in the collection of the Natural History Museum in Stuttgart (No. Do 61-K-1). The petiole also has a long anterior peduncle in *Oecophylla* (Formicinae). This character, hence, is polymorphic in the three subfamilies most greatly affected by its coding.

Worker. Helcium (= pretergite and presternite of abdominal segment III) fused in posterior foramen of abdominal segment II (as compared to very mobile in Dolichoderinae). This is listed as an apomorphy of Aneuretinae in Bolton (1990c) but can be explained as an artefact resulting from fixation of the specimens examined. Other specimens show normal articulation between petiole and gaster.

Worker. Sclerites of abdominal segment III reduced (as opposed to large among Dolichoderinae). This is also

an apomorphy of Aneuretinae in Bolton (1990c), but a consideration of additional material including fossil taxa (e.g. Wheeler, 1915a) suggests that the distinction will not hold up.

Worker. Shape of the gaster. This corresponds to character 24 in the phylogeny of Baroni Urbani (1989). The parallel sides of the gaster were interpreted as an autapomorphy for the Ponerinae (including Cerapachyinae), but it is evident that different degrees of incursion of the gastral sides render difficult an objective use of this character.

Worker, gyne and male. Abdominal pretergite III anteriorly notched or more or less deeply emarginate. Most Formicinae and Dolichoderinae (but not *Aneuretus*) exhibit this condition, but it is polymorphic in Formicinae (absent in a group of African *Polyrhachis*).

Other characters not here considered are the sensillar structures on the antennae and labial palpi recently described by Hashimoto (1991a), morphology of the hind tibial spur (Hashimoto, 1991b), and some of the larval characters employed by Shattuck (1992). There is no doubt that some of these could be profitably incorporated into future multi-character analyses of formicid relationships, if their variability at lower taxonomic levels is not too great.

Methods of cladistic analysis

The cladistic analysis was performed by PAUP 3.0b (Swofford, 1989). Search for the shortest tree(s) was made by the exact branch-and-bound algorithm which is guaranteed to find all optimal trees. The same data set was also analysed by Hennig86, Version 1.5 (Farris, 1988), with identical results. We also carried out the following two additional analyses:

1. The degree of cladistic covariation of our data was assessed using the procedure of Faith & Cranston (1991). The permutation tail probability (PTP) of our original data matrix was estimated by generating 99 simulated matrices containing the same number of present, absent, polymorphic or unknown states per character as our actual data matrix (outgroups excluded) but randomly distributed among the taxa. Randomization of character states and generation of matrices was performed by the Pascal program César written by Véronique Perrot. Calculation of tree length for each simulated matrix was performed by Hennig86, because of its much greater speed compared to PAUP.

2. We conducted a bootstrap analysis (Felsenstein, 1985) of our data, using the procedure available in PAUP. This was carried out using the mathematically approximate, but much faster, default option of heuristic search. One hundred bootstrap replicates were performed and no limits to the maximum number of trees to be retained in memory were imposed.

We also tested specific phylogenetic hypotheses with PAUP, by re-running the analysis of the data matrix after loading an additional CONSTRAINTS statement. We

used MacClade 2.1 (Maddison & Maddison, 1987) for graphic display of the number of synapomorphies on different branches of the cladogram and for tracing of selected characters.

In our analyses the two outgroups (Bradynobaenidae, Vespidae) appeared on adjacent branches. Our formicid trees were rooted at the point where these two outgroups joined the rest of the tree. We make no assumption that the two outgroups are sister groups although they have been arbitrarily drawn that way on most of the cladograms.

Tree length

The lengths of our trees can be calculated in two ways, depending on the accounting system used for polymorphic characters. Given that our terminal taxa are supraspecific (subfamilies, tribes) it seems reasonable to suppose that the ancestral species of each was monomorphic with respect to the characters considered here. One could then code polymorphic characters as 'unknown' and, for the purposes of calculating the minimum number of steps, ignore the additional evolutionary change *within* the terminal taxa which is implied by the polymorphism. Alternatively such change could be taken into account by counting one additional step per polymorphic character per taxon. Since our data matrix contains 84 occurrences of polymorphic characters, computing the length of the tree by the second method results in a tree 84 steps longer. (For the modified data matrix analysed in the second part of this paper the discrepancy is 87 steps. Obviously these are just minimum estimates of the number of secondary gains or losses within the terminal taxa.) The method of computing tree length strongly affects the value of the consistency index, i.e. the ratio of (the cumulative minimum range of steps for the characters considered)/(the number of steps actually implied by the phylogeny in question). In the discussion below we give tree lengths and consistency indices calculated both ways.

Results of the first cladistic analysis

Cladistic analysis of our data matrix yielded 72 equally most parsimonious trees, of length 110 and consistency index 0.618 (0.553 excluding 'uninformative', i.e. autapomorphic, characters). Taking into account the polymorphism of terminal taxa, tree length is 194 and consistency index 0.351 (0.292 excluding 'uninformative' characters).

Applying Faith & Cranston's (1991) test for cladistic covariation we found significant cladistic structure in our data set. In fact the 99 randomized trees we derived from our data set had a minimum length of 142 and a maximum length of 150 (without taking into account polymorphism of terminal taxa). The expected tree length corresponding to the 5% level ($L_{0.05}$) is 143, and our actual trees (length 110) have a permutation tail probability (PTP) of ≤ 0.01 .

Fig. 4 shows the strict consensus of all 72 trees. The Formicinae are positioned basally, and after that there is a division into two groups of taxa: the poneroid group

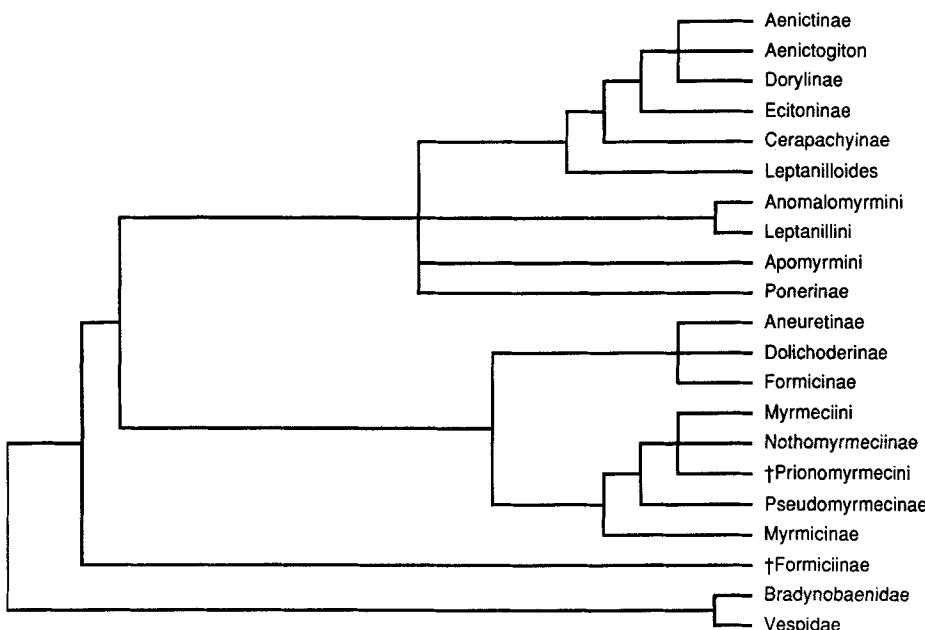


Fig. 4. Strict consensus tree calculated from the 72 equally most parsimonious trees resulting from the cladistic analysis.

(*sensu* Bolton, 1990c) and all others. The poneroid group has a basal polytomy involving Apomyrmini, Ponerinae, (Anomalomyrmini + Leptanillini), and (Leptanilloides + Cerapachyinae + army ants). In a majority (75%) of the 72 trees the two leptanilline tribes are part of a clade containing the 6 taxa at the top of the cladogram. Notice that *Leptanilloides* consistently appears as a sister group of (Cerapachyinae + army ants). The position of Apomyrmini is uncertain.

The three remaining equivocally resolved clades are as follows:

1. Clade Aenictinae + *Aenictogiton* + Dorylinae. Several synapomorphies support this clade, but there are no unequivocally shared apomorphies among any two of the constituent taxa. All three possible reconstructions are equally probable and are represented in equal numbers in our 72 trees. Thus *Aenictogiton*, known only from the male caste, cannot be confidently placed in either subfamily.

2. Clade Formicinae + Dolichoderinae + Aneuretinae. There are two resolutions, represented with equal frequency in our 72 trees: (Formicinae + (Aneuretinae + Dolichoderinae)) and (Aneuretinae + (Dolichoderinae + Formicinae)).

3. Clade Myrmeciini + Nothomyrmecinae + Prionomyrmecini. These three taxa consistently cluster together, but all three possible resolutions appear with equal frequency (24 trees each).

Fig. 5 illustrates one of the 72 trees and shows the number of characters which change unambiguously on each branch.

Taxonomic consequences of the analysis

In the following we discuss the terminal taxa included in

our primary data set, and propose some taxonomic changes based on the results of the first phase of cladistic analysis.

Subfamily AENICTINAE Emery

This taxon is characterized by the largely desclerotized abdominal tergite VII in the male, and by other apomorphies listed in Bolton (1990c). We maintain its subfamily status.

Subfamily AENICTOGITONINAE Ashmead, new status

Tribe *Aenictogitonini* Ashmead, 1905: 381.

The genus *Aenictogiton* is characterized by two apomorphic characters: deeply and narrowly incised posterior border of the male head, and male propodeal spiracle round (contrasting with the slit-shaped condition in Ecitoninae, Dorylinae and Aenictinae). Other characteristic features, not included in our data matrix, are the elongate and laterally compressed mesosoma, the absence of notaularia, and the unique, dorsally depressed shape of the petiole. Although the affinities of *Aenictogiton* clearly lie with Aenictinae and Dorylinae, it cannot be unambiguously assigned to, or placed as a sister group of, either one of them. Such a decision must probably await the discovery of workers and queens. If we maintain subfamily status for both Aenictinae and Dorylinae as recently proposed by Bolton (1990c) we are forced to raise *Aenictogitonini* to subfamily rank in order to avoid the risk of defining a paraphyletic taxon.

Subfamily ANEURETINAE Emery

Here we take the conservative course of maintaining subfamily status for the Aneuretinae, in accordance with contemporary usage (recently, a different view has been expressed only by Baroni Urbani, 1989). In our analysis the Aneuretinae are characterized by the fol-

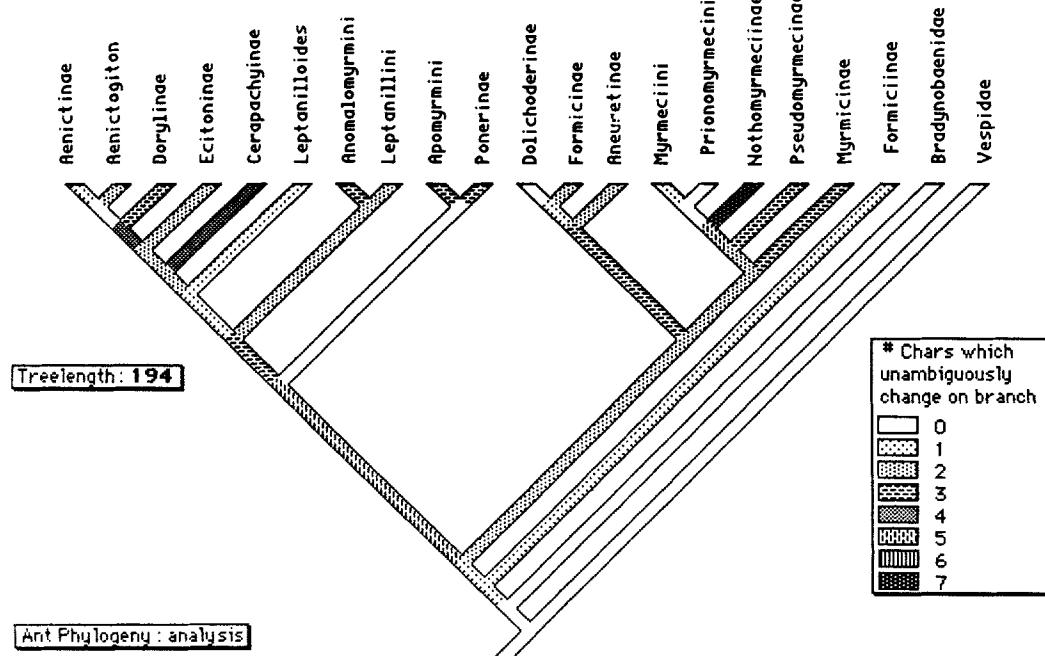


Fig. 5. One of the most equally parsimonious trees, showing the number of character apomorphies unambiguously arising on each branch.

lowing apomorphy: stereotyped adult carrying behaviour with the individual carried over the head (character 68). (Presence of a pupal cocoon also maps as an apomorphy of Aneuretinae on our cladograms but it is almost certainly a plesiomorphy.) The sole living representative of these ants (*Aneuretus*) shows numerous individual differences from extant dolichoderines, but it is difficult to establish unequivocal synapomorphies for Aneuretinae especially when taking into account fossil taxa (cf. Shattuck, 1992; and see previous discussion under 'Excluded characters').

Tribe ANOMALOMYRMINI Taylor

The Anomalomyrmini are the sister group of the Leptanillini in our cladistic analysis. The two taxa appear to be linked by only one synapomorphy: spiracle of the postpetiole large and moved forward (character 20). However among the putative Leptanillini autapomorphies included in our data matrix, i.e. characters 61–64 concerning size and retractility of male genitalia, larval mandibles, and larval LHF organ, some may well prove to be shared with Anomalomyrmini. We prefer the conservative course of leaving the Anomalomyrmini as a tribe within Leptanillinae, while awaiting the discovery of anomalomyrmine males and larvae.

Subfamily APOMYRMINAE Dlussky & Fedoseeva, new status

Aromyrmini (misspelling) Dlussky & Fedoseeva, 1988: 78.

This monotypic taxon appears to be characterized by the following apomorphies: toothed labrum (character 2), spiracles of abdominal segment III forwards (character 20), and secondary loss of the presclerites of abdominal segment IV (character 25). There are no unequivocal

synapomorphies placing it as a sister group of the Ponerinae or any other terminal taxon. Equally parsimonious reconstructions include the Apomyrmini as a sister group of the 8 taxa at the top of the cladogram in Fig. 4, and as a sister group of the same taxa plus Ponerinae. (In the latter reconstruction lack of abdominal IV presclerites is plesiomorphic.)

Subfamily CERAPACHYINAE Forel

Cerapachyinae are characterized by the following characters: long abdominal IV presclerites (character 27) and spinose pygidium (character 32). On our cladograms the following also map as apomorphies but they are almost certainly plesiomorphies: worker eyes (character 6) and pupal cocoon (character 66).

Subfamily DOLICHOCHODERINAE Forel

Our analysis did not reveal apomorphic characters for this subfamily, but one likely dolichoderine apomorphy is the apparently universal capacity to synthesize cyclopentanoid monoterpenes (Blum & Hermann, 1978; Attigalle & Morgan, 1984). According to Wilson *et al.* (1956) and Billen (personal communication) *Aneuretus simoni* lacks the typical '*Tapinoma odor*'. Shattuck (1992) proposed additional potential apomorphies including loss of pupal cocoon and several larval characters derived from Wheeler & Wheeler (1976).

Subfamily DORYLINAЕ Leach

The Dorylinae are distinguished by the following apomorphies: bidentate pygidium (character 31) and exposed bursa copulatrix (character 46). Absence of a differentiated postpetiole (character 21) also appears as an apo-

morphy, i.e. as a secondary loss, but this is an artefact of character optimization which obscures an almost certain primary absence.

Subfamily ECITONINAE Forel

The Ecitoninae are characterized by the hypertrophied basal ring of the male genitalia and by an apparent secondary loss of the tergosternal fusion of abdominal segment III in males. Other apomorphic characters, not included in our matrix, are listed by Bolton (1990c). In our analysis Ecitoninae consistently appear as an outgroup to the other army ants.

Subfamily FORMICINAE Lepeletier

Defined by the presence of an acidopore, the Formicinae are part of an unresolved trichotomy with Aneuretinae and Dolichoderinae. Other autapomorphies of Formicinae were given by Shattuck (1992), who also presented additional putative apomorphies suggesting a sister group relationship between Formicinae and Dolichoderinae.

Subfamily FORMICIINAE Lutz

The 'crowding' of wing venation (character 44) is an apomorphy of this subfamily. For additional characterization see Lutz (1986). The relationship of this fossil taxon to other formicid groups remains somewhat uncertain because of the large number of characters whose states are unknown in Formiciinae.

Subfamily LEPTANILLINAE Emery

This subfamily, here considered to comprise the two tribes Leptanillini and Anomalomyrmini (q.v.), is characterized by the apomorphic condition of character 20 (spiracles of abdominal segment III large and placed forward). In our results the Leptanillinae appear as part of an unresolved basal cluster of poneroid taxa.

Subfamily LEPTANILLOIDINAE Bolton, new subfamily

Type genus *Leptanilloides* Mann, 1923.

The sole unequivocal apomorphy of this taxon is character 34 (pygidium covered dorsally by abdominal tergum VI). In our analysis *Leptanilloides* appears as a sister group to (Cerapachyinae + (Ecitoninae + (Dorylinae + Aenictinae + Aenictogiton))). It does not exhibit the two apomorphies of Cerapachyinae (q.v.), the subfamily in which it had been previously placed. To avoid making the latter subfamily paraphyletic, we consider it advisable to recognize *Leptanilloides* as a member of its own subfamily. Knowledge of the male caste of this taxon is highly desirable.

Subfamily MYRMECIINAE Emery

The sole apomorphy for the tribe Myrmecini in our data set is character 7 (reduced malar area). Although the Myrmecini and Prionomyrmecini do not share any unequivocal synapomorphies, the presence of a postpetiole is one possible shared derived feature. On our cladograms this appears as a symplesiomorphy between these two, with a secondary loss in Nothomyrmecinae. This character reconstruction seems unlikely, however,

since the absence of a postpetiole in *Nothomyrmecia* is undoubtedly primary. Given that additional information on *Prionomyrmex* is unlikely to appear in the near future, we take the conservative position of retaining Prionomyrmecini as a tribe within the subfamily Myrmecinae.

Subfamily MYRMICINAE Lepeletier

The following features of this subfamily appear as apomorphic: absence of 'paraglossae' (character 3), promesonotal suture fused (character 10), and abdominal pre sternite III not overlapped by pretergite (character 19). Our results, which place Myrmicinae basally within a clade containing Pseudomyrmecinae, Myrmecini, Prionomyrmecini and Nothomyrmecinae, are due in part to common sharing of derived states of characters 21 and 45 (worker and gyne postpetiole). As noted above, we do not find credible the secondary losses which this implies in *Nothomyrmecia*.

Subfamily NOTHOMYRMECIINAE Clark

The following characters appear as apomorphies: ventral stridulitrum (character 24) and biaculeate subgenital plate (character 59). Retention of the basal hamuli (character 51) and absence of postpetiole, while mapping as apomorphies, are better interpreted as plesiomorphies.

Subfamily PONERINAE Lepeletier

This subfamily is characterized by the tergosternal fusion of abdominal segment IV (character 29), and long abdominal IV presclerites (character 27), although the latter are apparently convergently developed in Cerapachyinae and Myrmecinae. Members of the Ponerinae exhibit by far the highest number of polymorphic characters in our data matrix (25 out of 68).

Tribe PRIONOMYRMECINI Brown

No unequivocal apomorphies emerge for this tribe and we maintain it in the subfamily Myrmecinae (q.v.).

Subfamily PSEUDOMYRMECINAE Emery

This subfamily is characterized by the larval trophothylax (character 65). Additional putative apomorphies, not included in our data matrix, are given by Ward (1990).

The subfamily phylogeny of ants

We attempted at this point a reanalysis of the internal phylogeny of ants at the subfamily level, using a modified data matrix containing the two outgroups as before and the 17 ant subfamilies recognized above. Merging the Anomalomyrmini into the Leptanillinae and the Prionomyrmecini into the Myrmecinae, required re-coding a few characters as polymorphic for these two subfamilies. The nature of these few changes can be easily deduced by a glance at the data matrix of Table 1. When a character was unknown in one of the merged taxa and known in the other we coded the composite taxon as having the known state. A cladistic analysis of the new matrix generated 24

equally parsimonious trees, of which the strict consensus tree (Fig. 6) shows 3 polytomies corresponding to 4 unresolved dichotomies.

The common description of all 24 trees is as follows: tree length 104, consistency index 0.635 (0.573 excluding 'uninformative' characters). Taking into account the polymorphism of terminal taxa, tree length is 193, consistency index 0.352 (0.294 excluding 'uninformative' characters).

In order to assess the robustness of our results, we conducted a bootstrap analysis as described in the methods section, using the subfamilies data matrix (17 ingroup taxa). The results are summarized in Fig. 7 which depicts the 50% majority rule consensus tree of the 100 bootstrap trees *plus* compatible minority groupings. In subsequent discussion we refer to this as the 'bootstrap tree', although it should be borne in mind that support for most branches of the tree is not strong (see below). The 'bootstrap tree' has a tree length of 105 and consistency index of 0.629 (0.567 excluding 'uninformative' characters). Taking into account the polymorphism of terminal taxa, tree length is 194, consistency index 0.351 (0.292 excluding 'uninformative' characters). The 'bootstrap tree' is similar to the set of 24 most parsimonious trees but it is one step longer on account of a minority grouping (Myrmicinae + Pseudomyrmecinae).

None of the clades in the 'bootstrap tree' appears with a frequency $\geq 95\%$ and most are represented in fewer than 50% of the 100 bootstrap replicates. This suggests that the branches of our cladogram are determined by only a few characters and/or that the majority of the characters contain more noise than signal about the higher relationships of the ants. Table 2 provides diagnostics of each

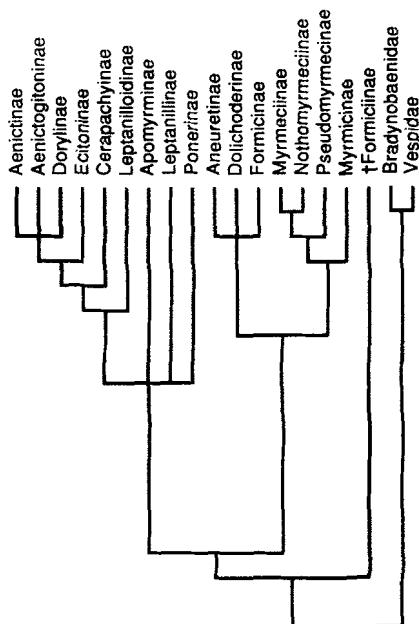


Fig. 6. Strict consensus tree resulting from the cladistic analysis of the 17 ant subfamilies recognized in the present paper. The polytomies indicate equivocally resolved branchings.

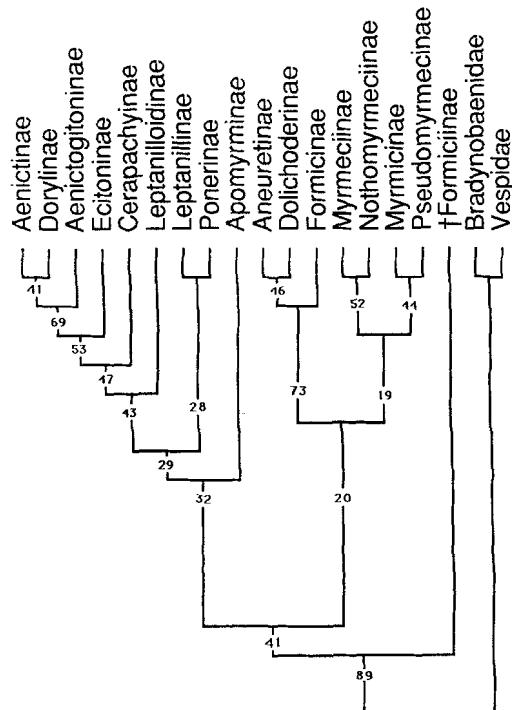


Fig. 7. A fully resolved ant phylogeny derived from the bootstrap analysis. This is the majority-rule consensus of all bootstrapped trees together with compatible minority groupings. The figures on the different branches indicate the percentage of 100 bootstrap trees with that branch.

character in terms of its consistency index and retention index on the 'bootstrap tree'.

Fig. 8 shows the number of characters which unambiguously change on each branch of the 'bootstrap tree'. Notice that some clades are not supported by any character change at all. These include the clade comprising the Aenictinae + Dorylinae, the reasons for which reside in the uncertain affinities of the Aenictogitoninae (but the three subfamilies together share at least three synapomorphies), and the clade containing the Myrmecinae, Nothomyrmecinae, Pseudomyrmecinae and Myrmicinae. Most other branches are defined by one or two apomorphies. The one exception to this is the 'poneroid group' on the left side of Fig. 8 which, although appearing in only 32% of the bootstrap trees, is defined by changes in characters 4, 6, 17 and 22 (but we believe that the first two of these – reduced clypeus and absence of eyes – are unlikely to have evolved in the manner dictated by character optimization).

Evolution of the formicid ground plan

One of the questions arising from our analysis is how much of the sharing of character states by any possible pair of ant subfamilies is explainable by common ancestry as opposed to convergent evolution. Table 3 gives the number of homoplastically shared character states under one possible (arbitrary) reconstruction of character state

Table 2. Diagnostics of the contribution of the different characters to the bootstrap tree. Uninformative characters omitted.

Character	Considering polymorphic characters as uncertainty					Accounting for polymorphism of terminal taxa				
	Min. steps	Actual steps	Max. steps	Consistency index	Retention index	Min. steps	Actual steps	Max. steps	Consistency index	Retention index
1	1	1	2	1	1	1	1	2	1	1
3	1	2	2	0.5	0	1	4	4	0.25	0
4	1	1	6	1	1	1	3	8	0.333	0.714
6	1	2	5	0.5	0.75	1	6	9	0.167	0.375
7	0	0	0	0/0	0/0	1	3	3	0.333	0
8	1	1	6	1	1	1	4	9	0.25	0.625
9	1	1	2	1	1	1	1	2	1	1
10	1	2	4	0.5	0.667	1	5	7	0.2	0.333
11	1	1	2	1	1	1	2	3	0.5	0.5
12	1	4	8	0.25	0.571	1	4	8	0.25	0.571
13	1	1	2	1	1	1	5	6	0.2	0.2
14	1	1	3	1	1	1	2	4	0.5	0.667
15	1	1	2	1	1	1	3	4	0.333	0.333
16	1	4	6	0.25	0.4	1	6	8	0.167	0.286
17	1	2	5	0.5	0.75	1	5	8	0.2	0.429
18	1	1	5	1	1	1	2	6	0.5	0.8
20	1	2	2	0.5	0	1	3	3	0.333	0
21	1	4	6	0.25	0.4	1	7	9	0.143	0.25
22	1	1	7	1	1	1	1	8	1	1
23	1	1	1	1	0/0	1	3	3	0.333	0
24	1	1	1	1	0/0	1	2	2	0.5	0
25	1	3	5	0.333	0.5	1	5	7	0.2	0.333
26	1	2	3	0.5	0.5	1	4	5	0.25	0.25
27	1	3	3	0.333	0	1	3	3	0.333	0
28	1	1	2	1	1	1	1	2	1	1
30	1	1	4	1	1	1	1	4	1	1
32	1	1	1	1	0/0	1	2	2	0.5	0
33	1	3	3	0.333	0	1	3	3	0.333	0
37	1	2	7	0.5	0.833	1	3	8	0.333	0.714
38	1	1	3	1	1	1	1	3	1	1
39	1	1	2	1	1	1	1	2	1	1
40	1	1	2	1	1	1	1	2	1	1
41	1	1	2	1	1	1	1	2	1	1
42	1	2	5	0.5	0.75	1	6	9	0.167	0.375
43	1	1	3	1	1	1	2	4	0.5	0.667
45	1	2	3	0.5	0.5	1	4	5	0.25	0.25
46	1	2	2	0.5	0	1	2	2	0.5	0
47	1	1	3	1	1	1	4	6	0.25	0.4
49	1	2	7	0.5	0.833	1	5	10	0.2	0.556
50	1	1	1	1	0/0	1	4	4	0.25	0
51	1	1	1	1	0/0	1	4	4	0.2	0
52	1	1	2	1	1	1	4	5	0.2	0.25
53	1	4	8	0.25	0.571	1	4	8	0.25	0.571
54	1	2	6	0.5	0.8	1	2	6	0.5	0.8
55	1	4	6	0.25	0.4	1	5	7	0.2	0.333
57	1	1	3	1	1	1	1	3	1	1
58	1	1	5	1	1	1	5	9	0.2	0.5
59	1	2	4	0.5	0.667	1	7	9	0.143	0.25
61	1	2	7	0.5	0.833	1	4	9	0.25	0.625
66	1	4	5	0.25	0.25	1	8	9	0.125	0.125
67	1	2	2	0.5	0	1	3	3	0.333	0
68	1	2	2	0.5	0	1	4	4	0.25	0

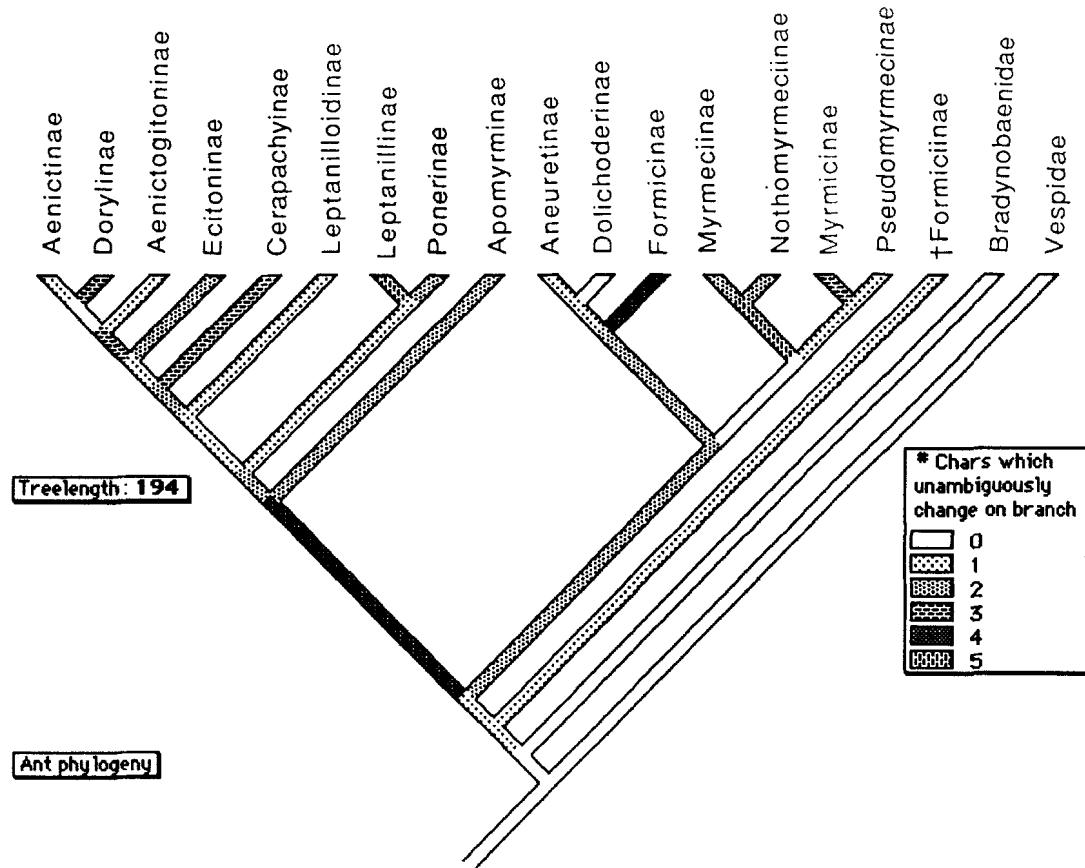


Fig. 8. Same bootstrap consensus tree as in Fig. 7 showing the number of character changes which occur unambiguously on each branch.

Table 3. Pairwise homoplasy matrix for the 19 taxa considered in the bootstrap tree for one possible reconstruction of character states (accelerated transformation).

evolution on the 'bootstrap tree' (Fig. 7). This particular reconstruction follows the accelerated transformation (ACCTRAN) option in PAUP, which maximizes the ratio of reversals to parallelisms. Note that other equally parsimonious reconstructions of character state evolution are possible which would alter these values somewhat. One can see that – in our reconstruction – homoplastic similarity is common between pairs of taxa. The number of shared homoplasies decreases, predictably, among closely related taxa, e.g. there are no homoplasies indicated between Myrmeciinae and Nothomyrmecinae, but the latter share 25 homoplasies with the Ponerinae (by far the most polymorphic ant subfamily). Homoplasy appears to be particularly frequent for the Myrmicinae; and even related taxa like Formicinae and Dolichoderinae share three homoplastic characters under this particular character state reconstruction.

Which of the known ants is the least specialized? One way to approach this question is to measure the patristic distances between all pairs of taxa including the outgroup(s). Such patristic distances are given in Table 4, again for one possible reconstruction of character state evolution on the 'bootstrap tree'. From the table it can be seen that both outgroups (*Vespidae* and *Bradyponaenidae*) share exactly the same patristic distances with the ant subfamilies included in the analysis. Considering as less specialized the ant subfamilies at smaller distances from the outgroup(s), allows us to propose the following series of increasing specialization.

1 Formicinae, 2 Apomyrminae, 3 Dolichoderinae, 4 Aneuretinae, 5 Formicinae, 6 Pseudomyrmecinae, 7 Leptanilloidinae + Myrmeciinae, 8 Myrmicinae, 9 Ponerinae, 10 Nothomyrmecinae, 11 Leptanillinae, 12 Ecitoninae.

13 Cerapachyinae, 14 Aenictinae, 15 Aenictogitoninae,
16 Dorylinae.

Thus, with respect to the 68 characters utilized in our analyses, the Apomyrmicinae are the least specialized living ants, while the Nothomyrmecinae and army ants (Ecitonina, Aenictinae, Dorylinae), in spite of being known for their 'wasp-like' males, show a much greater degree of divergence from presumptive ancestral conditions. The Formiciinae appear as the least specialized subfamily in absolute terms. This is credible also in view of their showing other characters that we regard as probably plesiomorphic, such as the large spiracles and the wing venation. We need nonetheless to be cautious about their position in the cladogram because of the considerable number of phylogenetically relevant characters which are unknown in this group.

Caution must also be applied because the preceding results are based on only one of many equally parsimonious reconstructions of character state evolution for our reference tree (Fig. 7). We suspect that most of these other reconstructions would not substantially alter the estimates of specialization, but the ambiguity in sharing of homoplastic characters remains. In view of this ambiguity, and taking into account the limited resolution of the bootstrap tree (few groupings occurring with a frequency of 50% or more), we feel that any discussion of the evolution of the formicid ground plan must remain circumspect. In what follows we make some inferences about the ground plan for the family Formicidae as a whole, i.e. for the clade comprising all formicid taxa including Formicinae.

Using the ‘xs h’ command of Hennig86 to diagnose characters on the ‘bootstrap tree’ (Fig. 7) we obtain the following character state resolutions for the ancestral

Table 4. Patristic distance triangular matrix for the 19 taxa considered in the bootstrap tree for one possible reconstruction of character states (accelerated transformation).

formicid node ('B' indicates that both '0' and '1' states are possible, under different reconstructions):

Character	1	2	3	4	5	6	7	8	9	10
State(s)	B	0	0	0	0	0	0	0	1	0
Character	11	12	13	14	15	16	17	18	19	20
State(s)	B	0	1	0	0	B	0	1	0	0
Character	21	22	23	24	25	26	27	28	29	30
State(s)	0	0	0	0	B	0	0	0	0	0
Character	31	32	33	34	35	36	37	38	39	40
State(s)	0	0	0	0	0	0	0	0	0	0
Character	41	42	43	44	45	46	47	48	49	50
State(s)	0	B	0	0	0	0	0	0	0	0
Character	51	52	53	54	55	56	57	58	59	60
State(s)	0	1	0	0	B	0	0	0	0	0
Character	61	62	63	64	65	66	67	68		
State(s)	0	0	0	0	0	B	0	0		

With respect to the characters of interest this suggests that the ancestral worker ant had well-developed eyes, a normally developed (not reduced) clypeus, exposed antennal sockets, elongated antennal scape, mobile pro-

mesonotal suture, closed metacoxal cavities, unfused abdominal segments III and IV (including the presclerites), no dorsal stridulatory organ, simple pygidium, and well-developed sting. The queen is indicated as being winged and without a postpetiole, the male as having a short scape, slit-shaped propodeal spiracle, *no cerci*, forewing with pterostigma and hindwing with basal hamuli *but without jugal lobe*. The optimization is ambiguous with respect to characters 1 (prognathia of head), 11 (metapleural gland), 16 (tergosternal fusion of petiole in worker), 25 (differentiated presclerites on worker abdominal segment IV), 42 (worker-gyne dimorphism), 55 (differentiated presclerites on male abdominal segment IV) and 66 (pupal cocoon). Some of these ambiguities result from the unknown condition in the Formicinae, and are 'resolved' at the next node which suggests that the ancestor of extant ants had a prognathous head and metapleural gland, but differed from the older hypothetical ancestor (of all ants) in that the male had a round to elliptical propodeal spiracle.

Most of these inferences are in line with traditional views on ant and aculeate evolution, or provide additional insight without contradicting these views. However, the three conditions italicized above are inconsistent with our expectations. We find it quite improbable that closed metacoxal cavities and, in males, absence of cerci and a jugal lobe, are part of the ground plan of the Formicidae.

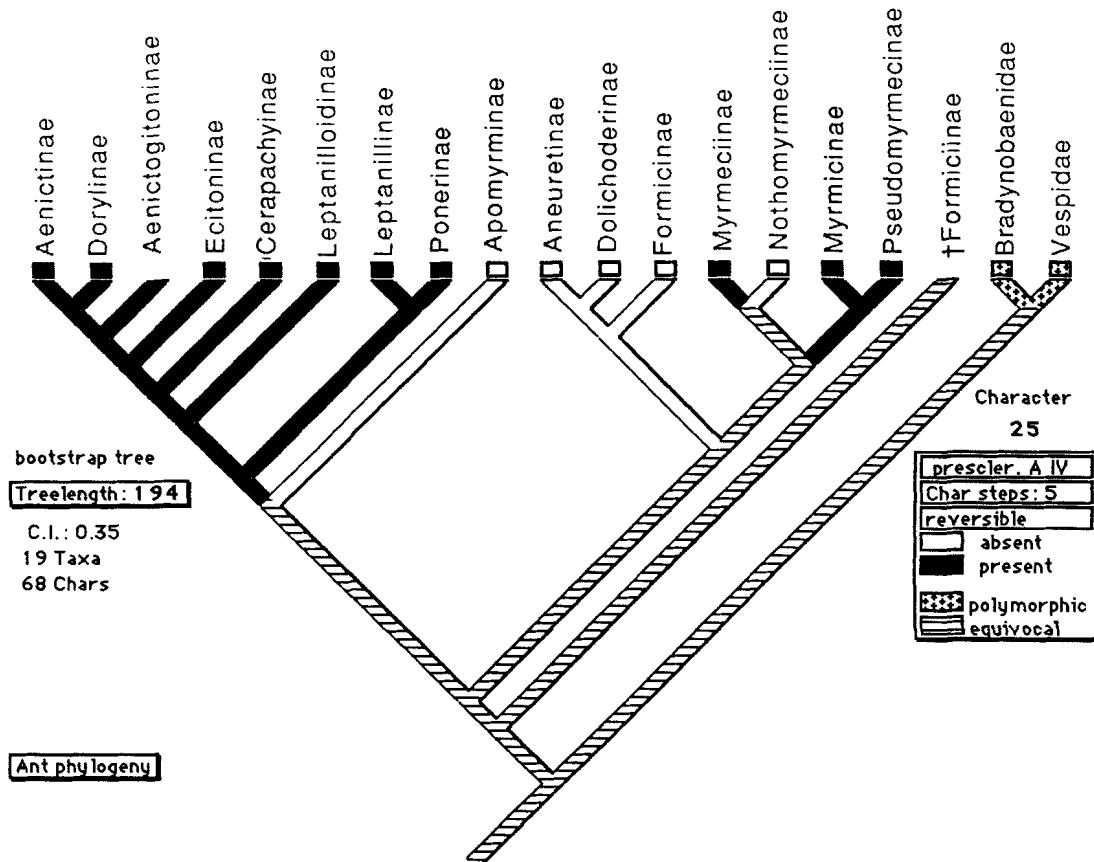


Fig. 9. Most parsimonious reconstruction of the evolution of the worker ant presclerites of abdominal segment IV on the 'bootstrap tree' of Fig. 7.

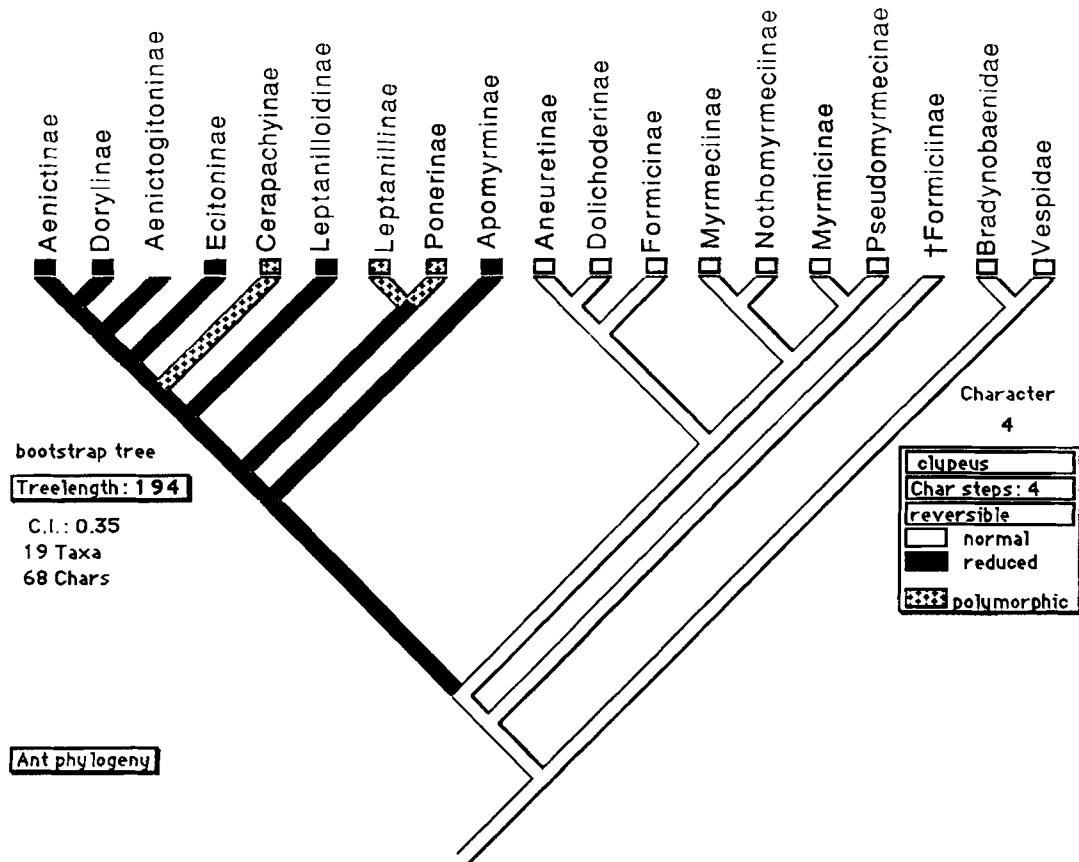


Fig. 10. Most parsimonious reconstruction of the evolution of the worker ant clypeus on the 'bootstrap tree'

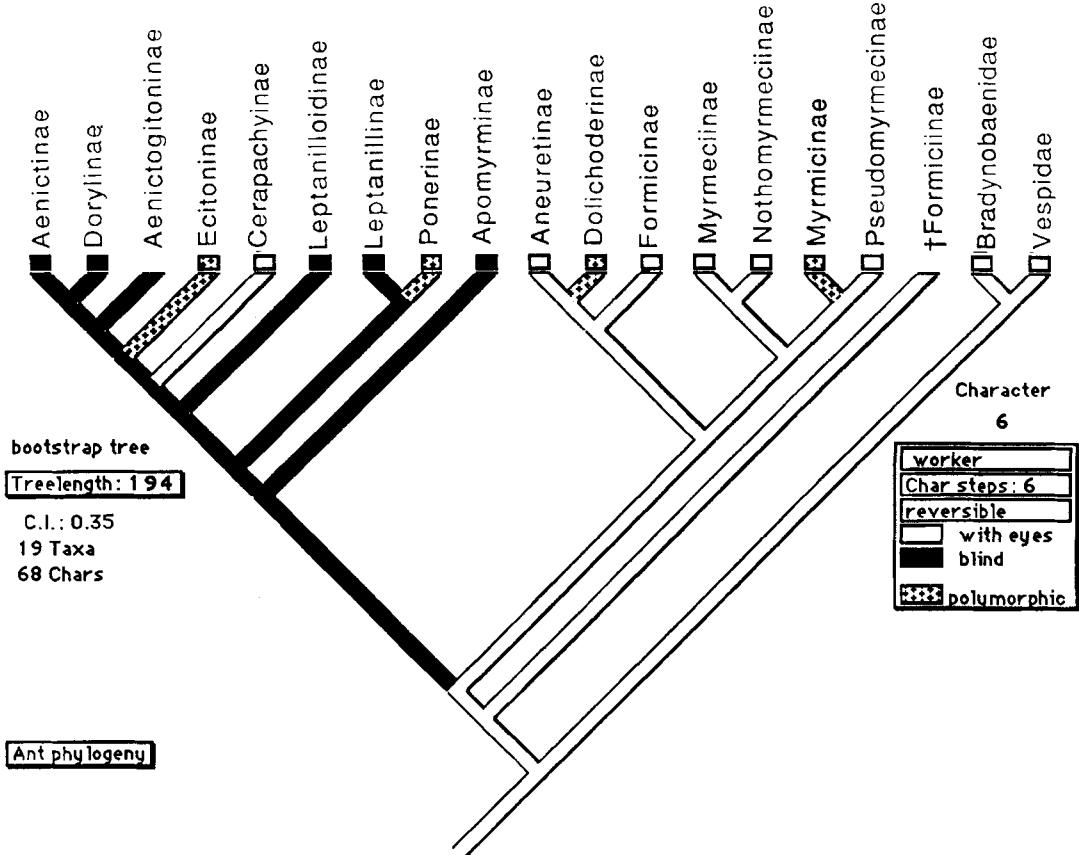


Fig. 11. Most parsimonious reconstruction of the evolution of eye loss among worker ants on the 'bootstrap tree'.

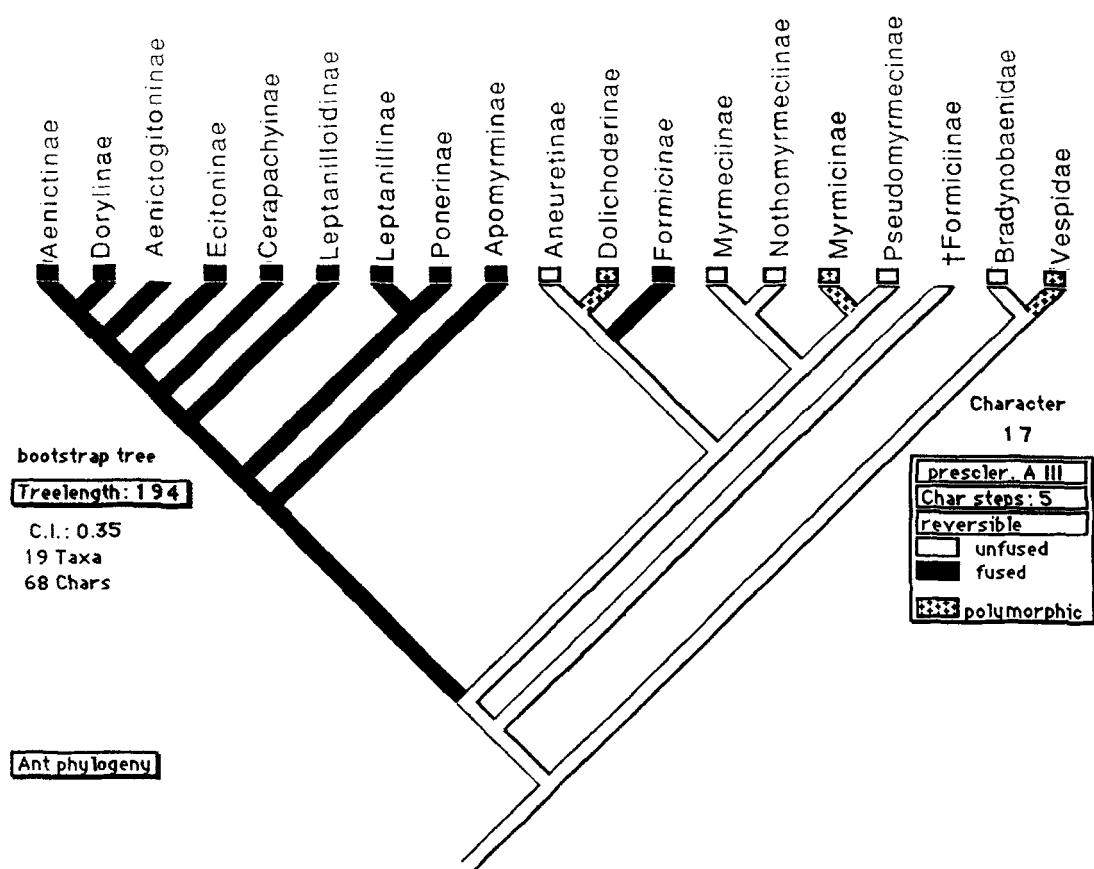


Fig. 12. Most parsimonious reconstruction of the evolution of worker ant presclerites of abdominal segment III on the 'bootstrap tree'

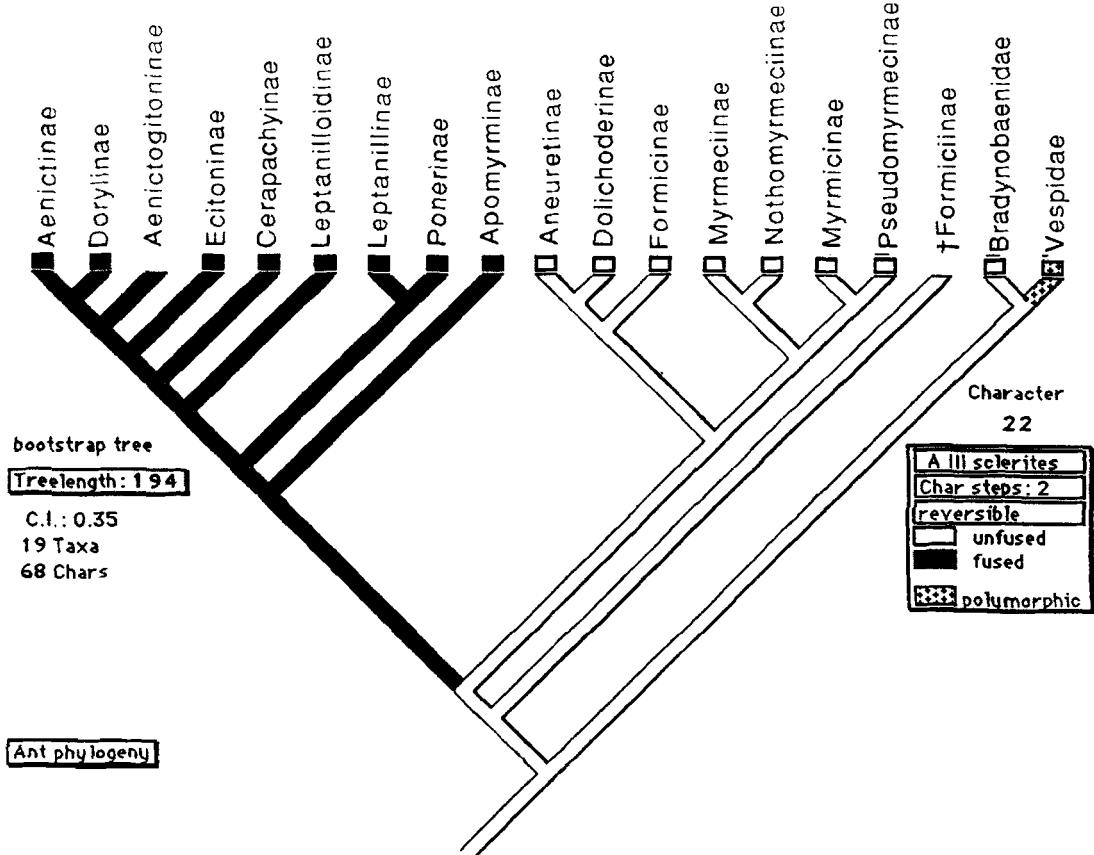


Fig. 13. Most parsimonious reconstruction of the evolution of worker ant sclerites of abdominal segment III on the 'bootstrap tree'

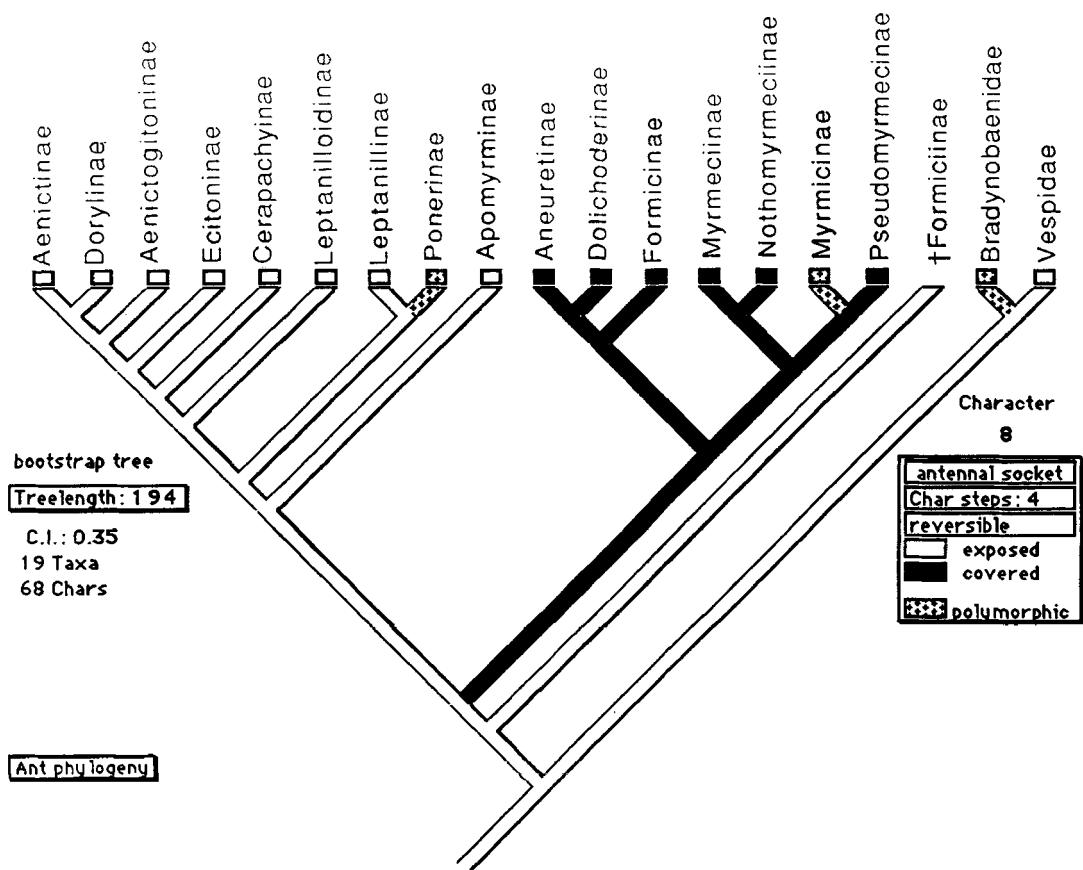


Fig. 14. Most parsimonious reconstruction of the evolution of the worker ant antennal socket on the 'bootstrap tree'

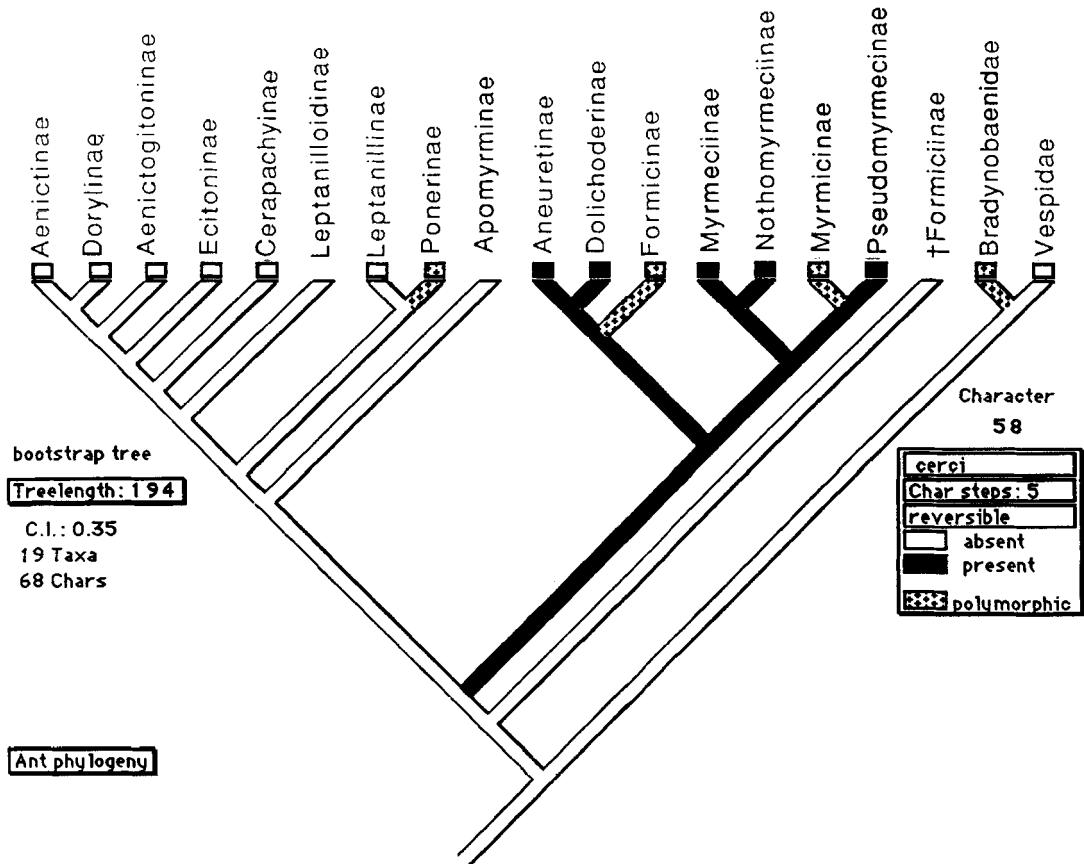


Fig. 15. Most parsimonious reconstruction of the evolution of male ant cerci on the 'bootstrap tree'

Loss of cerci and the jugal lobe, and closure of the metacoxal cavities, appear to have evolved repeatedly, both in ants and in other vespoids. Optimization of such highly homoplastic characters on our cladogram leads to spurious results.

Figs 9–15 illustrate character state resolutions over the entire reference tree, for particular characters of interest. These further demonstrate the need for caution when using parsimony to infer character evolution. For example, the *de novo* origin of eyes from a blind ancestor in Ponerinae workers, implied by Fig. 11, seems quite untenable; instead loss of eyes has almost certainly occurred multiple times within the ‘poneroid group’ of ants (i.e. the clade composed of Apomyrminae and taxa to the left). We feel confident in this assertion because most ponerine workers have well-developed eyes, the eyeless species being confined to a few specialized taxa within the subfamily. This information was not incorporated into the data matrix, however, where the subfamily was simply coded as ‘polymorphic’. While such agnosticism may be appropriate for initial phylogenetic and character state reconstructions, the results may need reinterpretation in the light of more detailed information about character state distributions within terminal taxa.

Final considerations

Given the large number of characters employed, one could expect to have higher confidence in the ant phylogeny given in this paper than in previously published schemes. Nonetheless, we have no doubt that the addition of new characters, including those derived from molecular data, will lead to further changes and improved resolution. We emphasize that considerable uncertainty remains in the phylogenetic results given here.

We consider it interesting to explore, in terms of the present data matrix, some of the alternative ant phylogenies appearing in the literature. We assess these phylogenies by considering the number of additional steps which they imply for our set of characters (beyond the 104 steps implied in our set of 24 equally shortest trees).

(a) The position of the extinct Formiciinae

In our analysis the Formiciinae appear as the sister group of all remaining ants, but this is not a very robust result. However, constraining the Formiciinae to be the sister group of the Formicinae, which was Lutz’s (1986) original hypothesis, increases tree length by three steps.

(b) The position of the Leptanillinae

In our cladograms the Leptanillinae appear to share an uncertain position at the root of the clade containing Ponerinae, Apomyrminae, Cerapachyinae, Leptanilloidinae and army ants. They occurred as the sister group of the Ponerinae in 28% of the bootstrap replicates (Fig. 7). Earlier ant phylogenies depicted the Leptanillinae as the sister group of the Dorylinae and this hypothesis was upheld by Baroni Urbani (1989). Maintaining the

Leptanillinae, after inclusion of the Anomalomyrmini, as a sister group of Dorylinae implies seven additional evolutionary steps.

(c) Is *Nothomyrmecia* the least specialized living ant?

This is a widely accepted idea in ant phylogeny and it is frequently cited in papers dealing with behaviour, physiology, biochemistry, etc. This idea also received some support in the phylogenies proposed by Baroni Urbani (1989) and Bolton (1990c). It is not supported, however, by the patristic distances given in Table 4 which suggest that *Nothomyrmecia* has undergone a considerable amount of evolutionary change compared with the formicid ground plan. Nonetheless some of these changes, e.g. loss of postpetiole, are probably spurious artefacts of character optimization. Forcing the Nothomyrmecinae to be the sister group of all remaining living ants requires three additional steps in our cladograms.

(d) The placement of the Myrmicinae and Pseudomyrmecinae

Most older, subjective, phylogenies of the Formicidae depicted the Myrmicinae and the Pseudomyrmecinae as sister groups. These subfamilies also appear as sister taxa in the cladistic analyses by Baroni Urbani (1989) and Ward (1990). This clade appears in our ‘bootstrap tree’ as a compatible minority clade, present in 44% of the replicates (this produces trees one step longer than the set of most parsimonious trees). Carpenter’s (1990b) reanalysis of Baroni Urbani’s (1989) data using *a posteriori* weighting resulted in the Myrmicinae being a sister group of (Pseudomyrmecinae + (Ponerinae + Myrmecinae)). Forcing such a clade to appear with our data implies six additional steps.

(e) The ‘complexes’

The idea of having the Formicidae divided into two monophyletic groups has been an attractive one. Brown (1954) recognized a ‘myrmecoid complex’ including the subfamilies Formicinae, Dolichoderinae, Myrmecinae and Pseudomyrmecinae, and a ‘poneroid complex’ comprising all the remaining ant subfamilies. Taylor (1978) proposed a ‘formicoid complex’ including Nothomyrmecinae (removed from Myrmecinae), Aneuretinae, Dolichoderinae and Formicinae, and he expanded Brown’s poneroid complex to include Myrmecinae and Pseudomyrmecinae. To test the credibility of these clades within the present state of knowledge we added subfamilies not yet recognized at the time. They were placed in the complexes at positions suggested by contemporary knowledge of their sister group relationships. A tree containing Brown’s (1954) poneroid and myrmecoid complexes requires only three additional evolutionary steps. It is substantially similar to our present results except for the attribution of the Myrmicinae to the poneroid complex. Taylor’s (1978) division of the ants according to the presence/absence of abdominal IV presclerites appears to need more *ad hoc* hypotheses about the evolution of the remaining characters in our data matrix. We have some evidence, now, that the abdominal IV presclerites may

have been acquired (probably as an adaptation to a more efficient stinging posture) more than once (Fig. 9). Splitting the subfamilies Nothomyrmecinae and Myrmecinae into two different complexes needs five additional steps.

The results of the present study also provide some support for a basal dichotomy of the extant Formicidae (the fossil Formiciinae, as we have seen, are not likely to belong to either of these branches). One of our branches includes the subfamilies Aenictinae, Dorylinae, Aenictogitoninae, Ecitoninae, Cerapachyinae, Leptanilloidinae, Leptanillinae, Ponerinae and Apomyrminae, and the other is composed of Aneuretinae, Dolichoderinae, Formicinae, Myrmecinae, Nothomyrmecinae, Myrmicinae and Pseudomyrmecinae. The first of these, which corresponds to Bolton's (1990c) ' poneroid group', is characterized in our cladograms by changes in characters 4 (reduced clypeus, Fig. 10), 6 (loss of the eyes, Fig. 11), 17 (fusion of abdominal III presclerites, Fig. 12), and 22 (fusion of abdominal III sclerites, Fig. 13). Eye loss (blind workers) is almost certainly not a synapomorphy of this group, but rather shows convergence across several included taxa. The second branching is supported in our cladograms by changes in characters 8 (covered antennal socket, Fig. 14) and 58 (presence of male cerci, Fig. 15). Not a great deal of confidence can be placed in this clade, however, since the first character changes elsewhere on the tree, and the second character (male cerci) is probably a symplesiomorphy whose optimization on the tree (Fig. 15) produces a misleading history of changes. It is clear that additional characters and character analysis are needed, including a better understanding of the characters here coded as polymorphic within subfamilies.

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References

- Ashmead, W.H. (1905) A skeleton of a new arrangement of the families, subfamilies, tribes and genera of the ants, or the superfamily Formicoidea. *Canadian Entomologist*, **37**, 381–384.
- Attygalle, A.B. & Morgan, E.D. (1984) Chemicals from the glands of ants. *Chemical Society Reviews*, **13**, 245–278.
- Baroni Urbani, C. (1989) Phylogeny and behavioural evolution in ants, with a discussion of the role of behaviour in evolutionary processes. *Ethology Ecology & Evolution*, **1**, 137–168.
- Baroni Urbani, C. (1990) Comparing different hypotheses about the origins and patterns of ant diversity. *Proceeding of the 11th International Congress International Union for the Study of Social Insects*, India, pp. 309–310.
- Berland, L. & Bernard, F. (1951) Super-ordre des Hyménoptéroïdes. Ordre des Hyménoptères. Hymenoptera Linné, 1758. In: *Traité de zoologie anatomie—systématique biologie*. Tome X. *Insectes supérieurs et Hémiptéroïdes*. Fascicule I. *Névroptéroïdes—Mécoptéroïdes Hyménopteroïdes (Symphytes et Térébrantes)*, pp. 1–975. Fascicule II. *Hyménoptéroïdes (Aculatés) Psocoptéroïdes. Hémiptéroïdes Thysanoptéroïdes* (ed. by P.-P. Grassé), pp. 976–1948. Masson et Cie Edit., Paris.
- Billen, J.P.J. (1986) Comparative morphology and ultrastructure of the Dufour gland in ants (Hymenoptera: Formicidae). *Entomologia Generalis*, **11**, 165–181.
- Billen, J.P.J. (1987) Morphology and ultrastructure of the exocrine glands in social Hymenoptera. *Proceedings of the 10th International Congress of the International Union for the Study of Social Insects*, Munich, pp. 81–84.
- Billen, J.P.J. (1990a) The sting bulb gland in *Myrmecia* and *Nothomyrmecia* (Hymenoptera: Formicidae): a new exocrine gland in ants. *International Journal of Insect Morphology and Embryology*, **19**, 133–139.
- Billen, J.P.J. (1990b) A survey of the glandular system of fire ants. *Applied Myrmecology* (ed. by R. K. Vander Meer, K. Jaffe and A. Cedeno), pp. 85–94. Westview Press, Boulder.
- Billen, J.P.J. & Gotwald, W.H., Jr (1988) The crenellate lining of the Dufour gland in the genus *Aenictus*: a new character for interpreting the phylogeny of Old World army ants (Hymenoptera, Formicidae). *Zoologica Scripta*, **17**, 293–295.
- Blum, M.S. & Hermann, H.R., Jr (1978) Venoms and venom apparatuses of the Formicidae: Dolichoderinae and Aneuretinae. *Handbuch der Experimentellen Pharmakologie*. Vol. 48. *Arthropod Venoms* (ed. by S. Bettini), pp. 871–894. Springer Verlag.
- Bolton, B. (1990a) Abdominal characters and status of cerapachyne ants. *Journal of Natural History*, **24**, 53–68.
- Bolton, B. (1990b) The higher classification of the ant subfamily Leptanillinae (Hymenoptera: Formicidae). *Systematic Entomology*, **15**, 267–282.
- Bolton, B. (1990c) Army ants reassessed: the phylogeny and classification of the doryline section (Hymenoptera, Formicidae). *Journal of Natural History*, **24**, 1339–1364.
- Borgmeier, T. (1950) A fêmea dichtadiiforme e os estádios evolutivos de *Simopelta pergandei* (Forel), e a descrição de *S. bicolor* n.sp. (Hym. Formicidae). *Revista de Entomologia*, **21**, 369–380.
- Borgmeier, T. (1955) Die Wanderameisen der neotropischen Region (Hym. Formicidae). *Studia Entomologica*, **3**, 1–718, 87 pl.
- Brandão, C.R.F., Martins-Neto, R.G. & Vulcano, M.A. (1990) The earliest known fossil ant (first southern hemisphere mesozoic record) (Hymenoptera: Formicidae: Myrmecinae). *Psyche*, **96**, 195–208.

- Brothers, D.J. (1975) Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutilidae. *University of Kansas Science Bulletin*, **50**, 483–648.
- Brown, W.L., Jr (1954) Remarks on the internal phylogeny and subfamily classification of the family Formicidae. *Insectes Sociaux*, **1**, 21–37.
- Brown, W.L., Jr (1975) Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platthyreini, Cerapachyini, Cylindromyrmeceini, Acanthostichini, and Aenictogitini. *Search: Agriculture (Cornell University)*, **5**, 1–115.
- Brown, W.L., Jr, Gotwald, W.H. & Léveillé, J. (1970) A new genus of ponerine ants from West Africa with ecological notes. *Psyche*, **77**, 259–275.
- Brown, W.L., Jr & Nutting, W.L. (1950) Wing venation and the phylogeny of the Formicidae. *Transactions of the American Entomological Society*, **75**, 113–132, 2 pl.
- Bugnion, E. (1927) Les pièces buccales, le sac infrabuccal et le pharynx des fourmis. *Folia Myrmecologica et Termitologica*, **1**, No. 1, 1–12, No. 6, 59–88, No. 8/9, 43–91.
- Carpenter, J.M. (1990a) On Brother's aculeate phylogeny. *Sphecos*, **19**, 9–10.
- Carpenter, J.M. (1990b) On Baroni Urbani's ant phylogeny. *Notes from Underground*, **3**, 6–8.
- Clausen, R. (1938) Untersuchungen über den männlichen Copulationsapparat der Ameisen, speziell der Formicinae. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **6**, 233–346.
- Dlussky, G.M. (1975) Formicoidea, Formicidae, Sphecomyrminae. *The Higher Hymenoptera of the Mesozoic* (ed. by A. P. Rasnitsyn), pp. 114–122. Transactions of the Paleontological Institute of the Academy of the Sciences of the USSR 147 [Russian].
- Dlussky, G.M. (1983) A new family of Upper Cretaceous Hymenoptera: an 'intermediate link' between the ants and the scolioids. *Paleontological Zhurnal*, **3**, 65–78 [Russian].
- Dlussky, G.M. & Fedoseeva, E.B. (1988) Origin and early evolution of the ants. *Cretaceous Biocenotic Crisis and Insect Evolution* (ed. by A. G. Ponomarenko), pp. 70–144. 'Nauka', Moscow [Russian].
- Duelli, P. (1977) Das soziale Tragverhalten bei neotropischen Ameisen der Gattung *Pseudomyrmex* (Hym. Formicidae): eine Verhaltensnorm als Hinweis für Phylogenie und Taxonomie? *Insectes Sociaux*, **24**, 359–365.
- Eisner, T. (1957) A comparative morphological study of the proventriculus of ants (Hymenoptera, Formicidae). *Bulletin of the Museum of Comparative Zoology at Harvard College*, **116**, 439–492, 25 pls.
- Emery, C. (1895) Die Gattung *Dorylus* Fab. und die systematische Eintheilung der Formiciden. *Zoologisches Jahrbücher, Abtheilung für Systematik*, **8**, 685–778, pl. 14–17.
- Emery, C. (1901a) A propos de la classification des Formicides. *Annales de la Société Entomologique de Belgique*, **45**, 197–198.
- Emery, C. (1901b) Studi sul polimorfismo e la metamorfosi nel genere 'Dorylus'. *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna*, Ser. V, **9**, 415–433, 2 pl.
- Emery, C. (1901c) Note sulle Doriline. *Bullettino della Società Entomologica Italiana*, **33**, 43–56.
- Emery, C. (1910) Hymenoptera Fam. Formicidae Subfam. Dorylinae. In: *Genera Insectorum* (ed. by P. Wytsman), Fasc. 102, 34 pp., 1 pl. L. Desmet-Verteneuil Impr., Bruxelles.
- Emery, C. (1911) Hymenoptera Fam. Formicidae Subfam. Ponerinae. In: *Genera Insectorum* (ed. by P. Wytsman), Fasc. 112, 125 pp., 3 pl. L. Desmet-Verteneuil Impr., Bruxelles.
- Emery, C. (1920) La distribuzione geografica attuale delle formiche – tentativo di spiegarne la genesi col soccorso di ipotesi filogenetiche e paleogeografiche. *Memorie della Reale Accademia dei Lincei (Anno 317), Classe di Scienze Fisiche, Matematiche e Naturali*, Ser. 5, **13**, 357–450.
- Emery, C. (1922) Hymenoptera Fam. Formicidae Subfam. Myrmicinae. *Genera Insectorum* (ed. by P. Wytsman), Fasc. 174^c, pp. 207–397. L. Desmet-Verteneuil Impr., Bruxelles.
- Emery, C. (1925a) Revision des espèces paléarctiques du genre *Tapinoma*. *Revue Suisse de Zoologie*, **32**, 45–64.
- Emery, C. (1925b) Hymenoptera Fam. Formicidae Subfam. Formicinae. *Genera Insectorum* (ed. by P. Wytsman), Fasc. 183, 302 pp., 4 pl. L. Desmet-Verteneuil Impr., Bruxelles.
- Faith, D.P. & Cranston, P.S. (1991) Could a cladogram this short have arisen by chance alone?: On permutation tests for cladistic structure. *Cladistics*, **7**, 1–28.
- Farris, J.S. (1988) *Hennig86, Reference Manual*, 18 pp.
- Felsenstein, J. (1978) The number of evolutionary trees. *Systematic Zoology*, **27**, 27–33.
- Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 379–404.
- Forel, A. (1878) Der Giftapparat und die Analdrüsen der Ameisen. *Zeitschrift für wissenschaftliche Zoologie*, **30** (Suppl.), 28–68, 2 pl.
- Fritsch, A. (1987) Untersuchungen am männlichen Kopulationsapparat der Ponerinae und Cerapachyinae (Formicidae, Hym.). Ph.D. thesis, University of Basle.
- Gotwald, W.H., Jr (1969) Comparative morphological studies of the ants, with particular reference to the mouthparts. *Ithaca (New York): Cornell University, Agricultural Experimental Station, Memoir*, **408**, 150 pp.
- Gotwald, W.H., Jr (1970) Mouthpart morphology of the ant *Aneuretus simoni*. *Annals of the Entomological Society of America*, **63**, 950–952.
- Gotwald, W.H., Jr (1982) Army ants. *Social Insects* (ed. by H. R. Hermann), Vol. IV, pp. 157–254. Academic Press, New York.
- Gotwald, W.H., Jr & Brown, W.L., Jr (1966) The ant genus *Simopelta* (Hymenoptera: Formicidae). *Psyche*, **73**, 261–277.
- Gregg, R.E. (1953) Morphological considerations affecting the taxonomy of certain genera of ants (Hymenoptera, Formicidae). *Proceedings of the Entomological Society of Washington*, **55**, 324–330.
- Hashimoto, Y. (1991a) Phylogenetic study of the family Formicidae based on the sensillum structures on the antennae and labial palpi (Hymenoptera, Aculeata). *Japanese Journal of Entomology*, **59**, 125–140.
- Hashimoto, Y. (1991b) Phylogenetic implications of the spur structures of the hind tibia in the Formicidae (Hymenoptera). *Japanese Journal of Entomology*, **59**, 289–294.
- Hermann, H.R. (1975) The ant-like venom apparatus of *Typhoctes peculiaris*, a primitive mutilid wasp. *Annals of the Entomological Society of America*, **68**, 882–884.
- Hermann, H.R. & Blum, M.S. (1967) The hymenopterous poison apparatus. III. *Eciton hamatum* (Formicidae). *Annals of the Entomological Society of America*, **60**, 1282–1291.
- Hermann, H.R. & Blum, M.S. (1968) The hymenopterous poison apparatus. VI. *Camponotus pennsylvanicus* (Hymenoptera: Formicidae). *Psyche*, **75**, 216–227.
- Hermann, H.R. & Blum, M.S. (1981) Defensive mechanisms in the social Hymenoptera. *Social Insects* (ed. by H. R. Hermann), Vol. II, pp. 76–197. Academic Press, New York.
- Hermann, H.R. & Chao, J.-T. (1983) Furcula, a major component of the hymenopterous venom apparatus. *International Journal of Insect Morphology and Embryology*, **12**, 321–337.
- Hölldobler, B. & Engel-Siegel, H. (1984) On the metapleural gland of ants. *Psyche*, **91**, 201–224.
- Hölldobler, B. & Palmer, J.M. (1989) A new tarsal gland in ants and the possible role in chemical communication. *Naturwissenschaften*, **76**, 271–274.

- senschaften, **76**, 385–386.
- Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Mass.
- Krafchick, B. (1959) A comparative study of the male genitalia of North American ants (Formicidae) with emphasis on generic differences. Ph.D. thesis, University of Maryland.
- Kugler, C. (1978) A comparative study of the myrmicine sting apparatus (Hymenoptera, Formicidae). *Studia Entomologica*, **20**, 413–548.
- Kugler, C. (1980) The sting apparatus in the primitive ants *Nothomyrmecia* and *Myrmecia*. *Journal of the Australian Entomological Society*, **19**, 263–267.
- Leuthold, R.H. (1968) A tibial gland scent-trail and trail-laying behavior in the ant *Crematogaster ashmeadi* Mayr. *Psyche*, **75**, 233–248.
- Lutz, H. (1986) Fossilfundstelle Messel, Nr. 50: eine neue Unterfamilie der Formicidae (Insecta: Hymenoptera) aus dem mittteleozänen Ölschiefer der 'Grube Messel' bei Darmstadt (Deutschland, S-Hessen). *Senckenbergiana lethaea*, **67**, 177–218.
- Maddison, W.P. & Maddison, D.R. (1987) *MacClade*, version 2.1. Cambridge, Massachusetts. A computer program distributed by the authors.
- Mann, W.M. (1919) The ants of the British Solomon Islands. *Bulletin of the Museum of Comparative Zoology at Harvard College*, **63**, 273–391.
- Mann, W.M. (1923) Two new ants from Bolivia. *Psyche*, **30**, 13–18.
- Markl, H. (1973) The evolution of stridulatory communication in ants. *Proceedings of the VIIth International Congress of the International Union for the Study of Social Insects, London*, pp. 258–265.
- Masuko, K. (1990) Behavior and ecology of the enigmatic ant *Leptanilla japonica* Baroni Urbani (Hymenoptera: Formicidae: Leptanillinae). *Insects Sociaux*, **37**, 31–57.
- Mayr, G.L. (1868) *Die Ameisen des baltischen Bernsteins*. Königsberg, Beiträge zur Naturkunde Preussens 1 (herausgegeben von der Königlichen physikalisch-ökonomischen Gesellschaft), iv + 102 pp., 5 pl.
- Möglich, M. & Hölldobler, B. (1974) Social carrying behaviour and division of labor during nest moving in ants. *Psyche*, **81**, 219–236.
- Ogata, K. (1991) Ants of the genus *Myrmecia* Fabricius. A review of the species groups and their phylogenetic relationships (Hymenoptera, Formicidae, Myrmeciinae). *Systematic Entomology*, **16**, 353–381.
- Pasteels, J.M., Crewe, R.M. & Blum, M.S. (1970) Etude histologique et examen au microscope électronique à Balayage de la glande sécrétant la phéromone de piste chez deux *Crematogaster* nord-américains (Formicidae, Myrmicinae). *Comptes Rendus de l'Académie des Sciences, Paris*, Série D, 271, 835–838, 2 pl.
- Santschi, F. (1907) Fourmis de Tunisie capturées en 1906. *Revue Suisse de Zoologie*, **15**, 305–334.
- Santschi, F. (1919) Fourmis nouvelles du Congo. *Revue Zoologique Africaine*, **6**, 243–250.
- Santschi, F. (1924) Descriptions de nouveaux Formicides africains et notes diverses. II. *Revue Zoologique Africaine*, **12**, 195–224.
- Shattuck, S.O. (1992) Higher classification of the ant subfamilies Aneuretinae, Dolichoderinae and Formicinae (Hymenoptera: Formicidae). *Systematic Entomology*, **17**, 199–206.
- Swofford, D.L. (1989) *PAUP, Phylogenetic Analysis Using Parsimony*, version 3.0b. Champagne, Illinois. A computer program distributed by the Center for Biodiversity, Illinois Natural History Survey.
- Taylor, R.W. (1965) A monographic revision of the rare tropopolitan ant genus *Probolomyrmex* Mayr (Hymenoptera: Formicidae). *Transactions of the Royal Entomological Society of London*, **117**, 345–365.
- Taylor, R.W. (1967) A monographic revision of the ant genus *Ponera* Latreille (Hymenoptera: Formicidae). *Pacific Insects Monograph*, **13**, 112 pp.
- Taylor, R.W. (1978) *Nothomyrmecia macrops*: a living-fossil ant rediscovered. *Science*, **201**, 979–985.
- Tinaut, A. (1990) Taxonomic situation of the genus *Cataglyphis* Förster, 1850 in the Iberian Peninsula. II. New position for *C. viatica* (Fabricius, 1787) and redescription of *C. velox* Santschi, 1929 stat.n. (Hymenoptera, Formicidae). *Eos*, **66**, 49–59.
- Trager, J.C. (1984) A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the continental United States. *Sociobiology*, **9**, 51–162.
- Walker, A.K., Kitching, I.J. & Austin, A.D. (1990) A reassessment of the phylogenetic relationships within the Microgastrinae (Hymenoptera: Braconidae). *Cladistics*, **6**, 291–306.
- Ward, P.S. (1990) The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): generic revision and relationship to other formicids. *Systematic Entomology*, **15**, 449–489.
- Wheeler, G.C. & Wheeler, J. (1965) The ant larvae of the subfamily Leptanillinae (Hymenoptera, Formicidae). *Psyche*, **72**, 24–34.
- Wheeler, G.C. & Wheeler, J. (1970) The larval of *Apomyrma* (Hymenoptera: Formicidae). *Psyche*, **77**, 276–279.
- Wheeler, G.C. & Wheeler, J. (1976) Ant larvae: review and synthesis. *Memoirs of the Entomological Society of Washington*, **7**, v + 108 pp.
- Wheeler, W.M. (1902) An American *Cerapachys*, with remarks on the affinities of the Cerapachyinae. *Biological Bulletin*, **3**, 181–191.
- Wheeler, W.M. (1910) *Ants*. Columbia Biological Series 9. Columbia University Press, New York.
- Wheeler, W.M. (1915a) The ants of the Baltic amber. *Schriften der physikalisch-ökonomischen Gesellschaft zu Königsberg in Pr.*, **55** (1914), 1–142.
- Wheeler, W.M. (1915b) On the presence and absence of cocoons among ants, the nest spinning habits of the larvae and the significance of the black cocoons among certain Australian species. *Annals of the Entomological Society of America*, **8**, 323–342.
- Wheeler, W.M. (1916) The Australian ants of the genus *Onychomyrmex*. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, **60**, 45–54, 2 pl.
- Wheeler, W.M. (1920) The subfamilies of Formicidae, and other taxonomic notes. *Psyche*, **27**, 46–55.
- Wheeler, W.M. (1928) *The Social Insects*. Harcourt, Brace and Company, New York.
- Wilson, E.O. (1971) *The Insects Societies*. The Belknap Press of Harvard University Press, Cambridge, Mass.
- Wilson, E.O. (1985) Ants of the Dominican amber (Hymenoptera: Formicidae). 3. The subfamily Dolichoderinae. *Psyche*, **92**, 17–37.
- Wilson, E.O., Carpenter, F.M. & Brown, W.L., Jr (1967) The first mesozoic ants, with the description of a new subfamily. *Psyche*, **74**, 1–19.
- Wilson, E.O., Eisner, T., Wheeler, G.C. & Wheeler, J. (1956) *Aneuretus simoni* Emery, a major link in ant evolution. *Bulletin of the Museum of Comparative Zoology*, **115**, 81–99, 3 pl.