

Morphological phylogeny of army ants and other dorylomorphs (Hymenoptera: Formicidae)

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Abstract. The dorylomorph group of ants comprises the three subfamilies of army ants (Aenictinae, Dorylinae, Ecitoninae) together with the subfamilies Aenictogitoninae, Cerapachyinae, and Leptanilloidinae. We describe new morphological characters and synthesize data from the literature in order to present the first hypothesis of phylogenetic relationships among all dorylomorph genera. These data include the first available character information from the newly discovered male caste of Leptanilloidinae. We used ant taxa from Leptanillinae, Myrmeciinae, and the poneromorph (Ponerinae *sensu lato*) subfamilies Amblyoponinae, Ectatomminae, and Paraponerinae as outgroups. We scored a total of 126 characters from twenty-two terminal taxa and used these data to conduct maximum parsimony and bootstrap analyses. The single most-parsimonious tree and bootstrap results support a single origin of army ants. The Old World army ant genus *Dorylus* forms a monophyletic group with the enigmatic genus *Aenictogiton*, which is currently known only from males; the second Old World army ant genus *Aenictus* is sister to this clade. This result generates the prediction that females of *Aenictogiton*, when discovered, will be observed to possess the army ant syndrome of behavioural and reproductive traits. The monophyly of the New World army ants (Ecitoninae) is supported very strongly, and within this group the genera *Eciton*, *Nomamyrmex*, and *Labidus* form a robust clade. The monophyly of Leptanilloidinae is also upheld. The subfamily Cerapachyinae appears paraphyletic, although this conclusion is not supported by strong bootstrap results. Relationships among genera of Cerapachyinae similarly are not resolved robustly, although parsimony results suggest clades consisting of (*Acanthostichus* + *Cylindromyrmex*) and (*Cerapachys* + *Sphinctomyrmex*). We tested for the effect of incompletely known taxa by conducting a secondary analysis in which the two genera containing ~50% missing character data (*Aenictogiton* and *Asphinctanilloides*) were removed. The strict consensus of the seventeen most-parsimonious trees from this secondary analysis is poorly resolved outside the army ants and contains no clades conflicting with the primary analysis. The position of *Leptanilla* shifts from forming the sister group to Leptanilloidinae (without high bootstrap support) in the primary analysis, to falling within a polytomy at the base of the root of the dorylomorphs when incompletely known taxa are removed. This instability suggests that the placement of *Leptanilla* within the dorylomorphs in our primary analysis may be spurious.

Introduction

The dorylomorph ants (formerly known as the doryline section; see Bolton, 1990b, 2003) comprise six subfamilies—Aenictogitoninae, Cerapachyinae, Leptanilloidinae, and the three army ant subfamilies Aenictinae, Dorylinae and

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Ecitoninae. Bolton (1990b) identified eight putative morphological synapomorphies shared by all six dorylomorph subfamilies: posteriorly shifted abdominal spiracles, presence of a metatibial gland (except in Leptanilloidinae), modification of the pygidium, specialization of the meta-pleural gland orifice, a strongly convex helcium sternite (i.e. the presternite of the third abdominal segment), absence of the furcula in the sting apparatus, absence of cerci in males, and a biaculeate subgenital plate in males.

Among dorylomorph ants, the three army ant subfamilies have received by far the most attention from biologists (e.g. Schneirla, 1971; Gotwald, 1995). Army ants predominantly occur in tropical and subtropical areas of Africa, the Americas, Asia, and Indo-Australia, although a few species range into more temperate regions. Ecitoninae contains five genera (Table 1), all restricted to the New World (Borgmeier, 1955; Watkins, 1976). The other two army ant subfamilies are monogeneric and are found only in the Old World. Dorylinae is primarily Afrotropical, with a few species occurring in the Oriental, Indo-Australian, and Palaearctic biogeographical regions. Most species of Aenictinae inhabit the Oriental and Indo-Australian regions, with a sizeable minority living in the Afrotropical region (Wilson, 1964; Bolton, 1995b).

All species within the three army ant subfamilies share a syndrome of behavioural and reproductive traits that includes obligate collective foraging, nomadism, and highly

modified queens called dichthadiigynes (Wilson, 1958a; Schneirla, 1971; Gotwald, 1995). Army ants never hunt or forage solitarily, as in most other ant species, but rather dispatch a mass of co-operative, leaderless foragers to locate and overwhelm prey simultaneously. Army ants also periodically emigrate to new foraging locations and do not construct permanent nests. Their permanently wingless queens have abdomens capable of pronounced expansion, which allows the production of up to millions of eggs per month in some species. Variation does occur in the expression of these traits, as seen for example in the configuration of their obligate collective foraging (column vs. swarm raiding) and in the relative rigidity of their nomadic cycles. Although a few other ant species display one or two components of this syndrome, army ants are the only ants known so far to possess all three components (see Brady, 2003).

Cerapachyinae is a cosmopolitan group containing five genera totalling approximately 200 described species (Brown, 1975; MacKay, 1996; de Andrade, 1998b). This group was removed from the subfamily Ponerinae and reinstated as a separate subfamily based on several morphological characters shared with other dorylomorph taxa (Bolton, 1990a, b). Several cerapachyine species display behaviours that in some respects resemble those of army ants (Wilson, 1958b; Brown, 1975; Hölldobler, 1982; Buschinger *et al.*, 1989; Fisher, 1997; Ravary & Jaisson, 2002). This similarity in morphology and behaviour has long motivated speculation that members of Cerapachyinae are closely related to army ants.

The Neotropical subfamily Leptanilloidinae has been associated variously with army ants, cerapachyines, and the nondorylomorph genus *Leptanilla* Emery (Mann, 1923; Borgmeier, 1955; Brown, 1975; Bolton, 1990a). Recent morphological work has placed this subfamily within the dorylomorphs (Bolton, 1990b, 2003), possibly as sister to the remainder of the group (Baroni Urbani *et al.*, 1992; Grimaldi *et al.*, 1997). Leptanilloidinae consists of two genera with a total of eight described species, all united by several proposed synapomorphies (Brandão *et al.*, 1999). These ants are very rarely encountered and with one exception are known only from workers. The exception is a recent collection of two males of the newly discovered *L. mckennae* (Longino, 2003), whose association with this genus has been substantiated with molecular data (Ward, 2005). Excepting *L. mckennae*, each described species from this subfamily is known only from its type locality, so the true diversity of this subfamily may not be fully realized. Brief observations of foraging trails and larval transport are reminiscent of army ants in some respects, but nothing else is known of leptanilloidine behaviour (Brandão *et al.*, 1999).

Aenictogitoninae is a monogeneric subfamily confined, as far as currently known, to central Africa (Brown, 1975). To date only males have been collected from this rarely encountered subfamily. These males possess several conspicuous traits unique to the subfamily, including a characteristic pattern of pilosity and a somewhat bizarre head shape. In

Table 1. Dorylomorph subfamilies and genera, with army ant taxa in bold. In parentheses is the number of extant described species in each genus, as tabulated from Bolton (1995a) with amendments based on subsequent work (Terayama & Kubota, 1993; Zhang, 1995; MacKay, 1996, 1998; de Andrade, 1998b; Brandão *et al.*, 1999; Yamane & Hashimoto, 1999; Xu, 2000; Zhou, 2001; Longino, 2003).

Aenictinae
<i>Aenictus</i> Shuckard (116 spp.)
Aenictogitoninae
<i>Aenictogiton</i> Emery (7 spp.)
Cerapachyinae
<i>Acanthostichus</i> Mayr (21 spp.)
<i>Cerapachys</i> F. Smith (140 spp.)
<i>Cylindromyrmex</i> Mayr (10 spp.)
<i>Simopone</i> Forel (16 spp.)
<i>Sphinctomyrmex</i> Mayr (22 spp.)
Dorylinae
<i>Dorylus</i> Fabricius (61 spp.)
Ecitoninae
<i>Cheliomyrmex</i> Mayr (4 spp.)
<i>Eciton</i> Latreille (12 spp.)
<i>Labidus</i> Jurine (8 spp.)
<i>Neivamyrmex</i> Borgmeier (121 spp.)
<i>Nomamyrmex</i> Borgmeier (2 spp.)
Leptanilloidinae
<i>Asphinctanilloides</i> Brandão, Diniz, Agosti & Delabie (3 spp.)
<i>Leptanilloides</i> Mann (5 spp.)

spite of these unique traits, it has long been recognized that these ants resemble male army ants in general habitus (Ashmead, 1905, 1906; Emery, 1910). This association was supported by the morphological phylogeny of ant subfamilies of Baroni Urbani *et al.* (1992), which placed Aenictogitoninae within a polytomy along with the two Old World army ant subfamilies. Because workers and queens of Aenictogitoninae have yet to be observed, it remains unknown to what degree they may possess the army ant syndrome of behavioural and reproductive adaptations.

In seeking to establish the monophyly of the dorylomorph ants, Bolton (1990b) produced a phylogeny that indicated that Cerapachyinae was nested within army ants in the following arrangement: (Ecitoninae + (Cerapachyinae + (Aenictinae + (Dorylinae))))). This conclusion of army ant polyphyly was based on an intuitive approach rather than a quantitative cladistic analysis, and the monophyly of (Cerapachyinae + (Aenictinae + (Dorylinae))) was supported by only one character. It should be noted that resolution of relationships within the dorylomorphs was not the principal goal of that paper. Its purpose instead was to establish the monophyly of the dorylomorphs, and in this respect it was very convincing: eight putative synapomorphies were identified that unite the group.

The first morphological phylogeny to include all extant ant subfamilies in a quantitative cladistic framework (Baroni Urbani *et al.*, 1992) conflicted with that of Bolton (1990b) by placing Cerapachyinae as sister to all army ants plus Aenictogitoninae (this subfamily was not included in the analysis by Bolton). Bootstrap support for this result was fairly low (53%). Grimaldi *et al.* (1997) performed analyses on a slightly modified version of the dataset used by Baroni Urbani *et al.* (1992). The 'preferred cladogram' of Grimaldi *et al.* (1997), based on a successive weighting analysis that excluded Aenictogitoninae, showed monophyletic army ants with a Bremer support of zero. This result was sensitive to the addition and deletion of taxa; most of their analyses that included Aenictogitoninae resulted in Cerapachyinae as a sister group to Ecitoninae (with a Bremer support of one), rendering army ants paraphyletic (Grimaldi *et al.*, 1997).

These studies used dorylomorph subfamilies as terminal taxa, implicitly assuming their monophyly. In some cases, especially with regard to Cerapachyinae, this assumption may not hold. This subfamily was established essentially on the grounds of a single autapomorphy, the presence of a dentate pygidium. All other characters defining this subfamily are arguably plesiomorphic (Bolton, 1990a). In the current study, only genera or species groups possessing putative autapomorphies were used as terminal taxa. We still necessarily relied on supraspecific taxa in this study, however, due to the high levels of incomplete caste representation among dorylomorph ants, as explained below.

The goal of the current study was to increase the contribution of morphological data towards resolving the phylogeny of the dorylomorph ants. In doing so, we present

the first hypothesis of phylogenetic relationships among all dorylomorph genera. We also explored the sensitivity of our results to incomplete data by conducting additional analyses that eliminated characters and taxa containing a large proportion of unknown information.

Materials and methods

Taxa

All terminal taxa used in this study were genera, with one exception. The use of species as terminal taxa was precluded by incomplete caste representation in many species. The majority of species within the dorylomorphs and *Leptanilla* are described from either isolated males or workers, which has resulted in largely parallel classification systems. For example, both the worker and male caste from the same species are known from only three of the 116 described species of *Aenictus* and four of the sixty-one described species of *Dorylus* (Bolton, 2003). A sampling strategy that relied on the selection of exemplar species would result either in an inadequate selection of species in most dorylomorph genera, or in a huge number of missing data entries.

The use of supraspecific taxa did not completely solve the problem of partial caste representation. Some castes or life stages remain entirely unknown for all species within certain genera: *Aenictogiton* Emery (workers, queens, and larvae unknown); *Asphinctanilloides* Brandão, Diniz, Agosti & Delabie (queens, males, and larvae unknown); *Cheliomyrmex* Mayr (queens unknown); and *Leptanilloides* Mann (queens unknown).

In the final data matrix, *Aenictogiton* and *Asphinctanilloides* contained missing data entries for approximately half of the characters in the matrix. Adding taxa with a large proportion of missing character data (i.e. 'incomplete taxa') has the potential to decrease the accuracy of phylogenetic inference among complete taxa (Huelsenbeck, 1991; Novacek, 1992; Wiens & Reeder, 1995; Nixon, 1996; Wiens, 1998b). Recent simulation studies, however, suggest that a substantial reduction in accuracy may not be the usual outcome (Wiens, 2003a, b). We thus conducted separate analyses with and without these two incomplete taxa to test their influence on inferred relationships among more completely known groups.

The lack of secure autapomorphies for *Cerapachys* Smith creates doubt that it is monophyletic. For the current study, this genus was divided into two previously established sections, the '*Cerapachys* lineage' and the '*Phyracaces* lineage' (Brown, 1975). Each of these two groups possesses a potential autapomorphy unique within the dorylomorphs. Ants in the '*Cerapachys* lineage' are characterized by an antennal club consisting of an enlarged and egg-shaped terminal segment (attenuated in a few species). In species belonging to the '*Phyracaces* lineage' the sides of the petiole meet the dorsal face at a sharp, well-defined dorsolateral margin, which often extends to the mesosoma and sometimes the head. It should be noted that a weak

dorsolateral border on the petiole also occurs in many *Simopone* species.

Other than this modification to *Cerapachys*, all existing genera within the dorylomorphs were included as the ingroup terminal taxa (Table 1 and Appendix). Particular attention was paid to the entire range of morphological diversity in larger dorylomorph genera by using previously defined subgenera or species groups as a guide, including the fourteen species groups established within *Neivamyrmex* Borgmeier (Borgmeier, 1955), the five species groups within *Aenictus* (Wilson, 1964), the nine species groups within the 'Cerapachys lineage' and the nine species groups within the 'Phyracaces lineage' (Brown, 1975), and the six subgenera of *Dorylus*.

Fossils of dorylomorph ants are limited to only a few specimens, which occur comparatively recently in the fossil record and preserve an incomplete assemblage of castes. The extinct species of dorylomorphs include: workers of *Acanthostichus hispaniolicus* de Andrade (Dominican amber; de Andrade, 1998a); workers, including ergatogynes, and males of *Cerapachys annosus* (Wheeler) (Baltic amber; Wheeler, 1915); a worker of *Cerapachys favosus* (Wheeler) (Baltic amber; Wheeler, 1915); workers of *Neivamyrmex ectopus* Wilson (Dominican amber; Wilson, 1985a, b); and queens of three species of *Cylindromyrmex* (Dominican amber; de Andrade, 1998b, 2001). Two extant army ant species, *Dorylus nigricans* Illiger and *Neivamyrmex iridescens* Borgmeier, have also been reported from copal of undetermined (but probably very recent) age (DuBois, 1998). All extinct species fit comfortably into established genera and are unlikely to represent transitional taxa between higher-level groups. Due to the extreme paucity of fossil dorylomorphs, information from them was only explicitly considered in a few cases (e.g. characters 11, 15, 20, 33).

Previous work (Bolton, 1990b) identified eight characters uniting the dorylomorphs, providing reasonable a priori definition of the ingroup. We combined the ingroup with six outgroup taxa in a simultaneous, unconstrained analysis of the data (Farris, 1972; Nixon & Carpenter, 1993). The subfamily Leptanillinae is a potential sister group to the dorylomorphs (Bolton, 1990b; Baroni Urbani *et al.*, 1992; Grimaldi *et al.*, 1997) and shares several characters with the dorylomorphs, including several originally proposed as dorylomorph synapomorphies. From this subfamily we selected the genus *Leptanilla* because it is by far the most well-known member of this group (Bolton, 1990c). Several other outgroup taxa were chosen from the poneromorph ants (formerly known as the subfamily Ponerinae; Bolton, 2003), another group frequently considered close relatives to the dorylomorphs. Because of the likely paraphyly of this group (Hashimoto, 1991b, 1996; Ward, 1994; Sullender & Johnson, 1998; Keller, 2000; Ward & Brady, 2003), we included representatives from three poneromorph subfamilies, i.e. Amblyoponinae (*Amblyopone* Erichson and *Onychomyrmex* Emery), Paraponerinae (*Paraponera* F. Smith) and Ectatomminae (*Rhytidoponera* Mayr). These genera are conventionally considered to retain many primi-

tive characteristics in each of their respective subfamilies, except for *Onychomyrmex*, which was included because of its apparent – although not well studied – army antlike behaviours (Wheeler, 1916; Wilson, 1958a; Brown, 1960; Hölldobler & Palmer, 1989; Miyata *et al.*, 2003). The final outgroup was the myrmeciine genus *Myrmecia* Fabricius, which has also been judged to possess many primitive ant characteristics (Wheeler, 1933; Clark, 1951; Wilson, 1971; Ogata, 1991; but see Ward & Brady, 2003). All trees were rooted using Amblyoponinae.

We studied specimens from the following museum collections, either in person or through loaned material: Australian National Insect Collection (ANIC), The Natural History Museum, London (BMNH), Cornell University Insect Collection (CUIC), Museum of Comparative Zoology, Harvard University (MCZC), Museu de Zoologia da Universidade de São Paulo (MZSP), National Museum of Natural History, Washington D.C. (USNM), P. S. Ward Collection, University of California at Davis (PSWC), Bohart Museum of Entomology, University of California at Davis (UCDC), W. H. Gotwald, Jr. Collection, Utica College (WHGC). The approximate numbers of species observed from each caste in each terminal taxon are listed below. Abbreviations: w, worker; m, male; q, queen (only army ant queens are indicated).

Dorylomorphs. Aenictinae – *Aenictus*: 27 w, 26 m, 6 q. Aenictogitoninae – *Aenictogiton*: 5 m. Cerapachyinae – *Acanthostichus*: 8 w, 9 m; *Cerapachys*: 52 w, 18 m; *Cylindromyrmex*: 7 w, 3 m; *Simopone*: 14 w, 2 m; *Sphinctomyrmex*: 18 w, 5 m. Dorylinae – *Dorylus*: 17 w, 18 m, 2 q. Ecitoninae – *Cheliomyrmex*: 2 w, 2 m; *Eciton*: 9 w, 6 m, 2q; *Labidus*: 3 w, 3 m; *Neivamyrmex*: 34 w, 34 m, 2q; *Nomamyrmex*: 2w, 2 m. Leptanilloidinae – *Asphinctanilloides*: 2 w; *Leptanilloides*: 4 w, 1 m.

Outgroups. Leptanillinae – *Leptanilla*: 13 w, 6 m. Myrmeciinae – *Myrmecia*: 45 w, 45 m. Amblyoponinae – *Amblyopone*: 14 w, 6 m; *Onychomyrmex*: 3 w, 1 m. Ectatomminae – *Rhytidoponera*: 10 w, 10 m. Paraponerinae – *Paraponera*: 1 w, 1 m.

Characters

In most cases, a particular character state occurred in all species observed within a given terminal taxon. When variation within a terminal taxon was observed, we adopted one of two solutions. If the groundplan for the taxon could be reasonably inferred to be a particular state based on taxonomic or phylogenetic information, then it was coded as monomorphic for that character state. This practice is defended by a growing body of literature that argues for the greater overall accuracy of phylogeny when using inferred ancestral state reconstruction compared with polymorphic coding of supraspecific taxa (Bininda-Emonds *et al.*, 1998; Wiens, 1998a; Kornet & Turner, 1999; Simmons, 2001). Cases where this was employed are explained in the character descriptions below. In situations where it was not

possible to infer the ancestral state, polymorphic coding was used instead.

Some characters in our study were completely new, whereas others were suggested or discovered by previous investigators. In these earlier studies the characters were often limited to a narrow range of taxa and were not discussed in a cladistic context. We have recognized this prior work by including appropriate citations even in cases where it provided only the original inspiration. We verified these characters (except for some involving internal morphology), added many more species to these observations, and in some cases redefined characters or character states.

In scoring several characters involving internal morphology (especially glandular features) we depended exclusively on literature sources, which typically did not provide information on all terminal taxa. Incomplete characters such as these were nonetheless included because they may provide information on relationships within a specific group (e.g. genera of Ecitoninae). Simulation studies show that including characters with amounts of missing data approaching 75% can still result in more accurate phylogenetic inference compared with excluding those characters, or at the very least usually does not result in a substantial loss of accuracy (Wiens, 1998b). Although the amount of missing data for any character in the present analysis was less than 75%, we conducted a separate analysis excluding all characters missing more than 50% data entries to verify that these incomplete characters were not biasing results. We also note that characters scored exclusively from the literature (e.g. internal morphology) or requiring special preparation (e.g. ventral dissection) could be verified for only a limited number of species per terminal taxon.

Some characters employed in this analysis show homoplasy when viewed across the entire diversity of ants. For example, reduction of segmented characters such as palps has undoubtedly occurred many times in various ant lineages. Studies have shown that characters showing considerable homoplasy at a larger scale still offer valuable information within lower levels, even though they also may add some overall noise to the analysis (Wiens, 1995, 1998c, 2000; Poe & Wiens, 2000). We thus used such characters when they displayed conservation within many terminal taxa, suggesting that their rates of evolution are still low enough to provide some valid phylogenetic signal.

We also included autapomorphies for each terminal taxon. Because terminal taxa in our analysis consist of multiple species, autapomorphies provide evidence supporting their monophyly (i.e. they act as synapomorphies at this level). Also, information concerning terminal branch lengths may be of future importance in documenting rates of morphological evolution and implementing maximum likelihood or Bayesian techniques for ancestral character state reconstruction (Cunningham *et al.*, 1998; Schultz & Churchill, 1999) or phylogenetic inference (Lewis, 2001).

Phylogenetic analyses

PAUP* 4.0b10 (Swofford, 2003) was used for all phylogenetic analyses. We obtained the most-parsimonious (MP) trees using the branch-and-bound algorithm with the following settings: no limit to MAXTREES; multiple states within a taxon treated as polymorphism; and branches collapsed if minimum length is zero (a potentially important consideration in this dataset given that missing character data may increase the number of zero-length branches due to ambiguous character optimizations; see Kearney & Clark, 2003). All characters included in each analysis received equal weight. Branch support was assessed with the nonparametric bootstrap (Felsenstein, 1985) by conducting 1000 branch-and-bound replicates with the same settings as above.

The primary phylogenetic analysis included the entire dataset. As discussed above, we conducted two additional analyses to explore the influence of incomplete taxa and characters, respectively, on the inferred phylogeny. In one analysis, the two taxa containing a large proportion of missing data (*Aenictogiton* and *Asphinctanilloides*) were excluded in order to gauge their effect on relationships inferred for the other taxa. In a separate analysis, we excluded all characters missing more than 50% data entries. These ancillary analyses used the same tree-searching conditions as the primary analysis.

We used MACCLADE 4 (Maddison & Maddison, 2000) to reconstruct ancestral character states under unambiguous, ACCTRAN, and DELTRAN modes.

Character descriptions

All multistate characters are unordered except characters 48 and 74; in defining states for these two characters we explicitly assumed an ordered model of transitions between states. The first sentence of each character description indicates the castes for which the character is defined in this study. Characters also included in Baroni Urbani *et al.* (1992) are so noted in the final sentence, but we modified these characters and/or state assignments in many cases. Reference made to *Cerapachys* encompasses both the '*Cerapachys* lineage' and the '*Phyracaces* lineage'. The data matrix can be found in the Appendix.

1. Worker and queen. *Genal teeth*: (0) absent; (1) present as lateral, blunt lobes that overhang the mandibles dorsally; (2) present as lateral, acute teeth that do not overhang the mandibles.

The presence of lateral blunt teeth on the genae has been proposed as a synapomorphy of Leptanilloidinae (*Asphinctanilloides* + *Leptanilloides*) (Brandão *et al.*, 1999). The teeth are very small to absent in *A. anae* and *L. mckennae* (Longino, 2003). Many species within Amblyoponinae, including most species of *Amblyopone* (Brown, 1960), possess acute

genal teeth that occur posterolateral to the mandibles and do not overhang them.

2. Worker and queen. *Clypeus*: (0) developed below antennal socket, as long or longer (anteroposteriorly) than the diameter of the antennal condylar bulb; (1) absent or reduced to an extremely thin strip.

The clypeus is absent in most army ant taxa, although it shows slight development in some Ecitoninae, especially *Neivamyrmex pseudops* (Forel) and most *Eciton* species. Still, in no army ant species is the clypeus (in the region below the antennal socket) as long as the diameter of the antennal condylar bulb. This character forms a morphocline within Cerapachyinae (Bolton, 1990b). Only *Cylindromyrmex*, however, possesses a clypeus developed to the degree defined above. *Amblyopone* has been coded polymorphic to reflect the extreme reduction found in some species (e.g. *A. mutica* (Santschi), *A. hackeri* Wheeler, *A. lucida* Clark). Note that on some occasions there may be a well-developed clypeal apron – a thin translucent lamella extending anteriorly from the clypeal margin – whereas the clypeus itself remains undeveloped. Modified from character 4 in Baroni Urbani *et al.* (1992).

3. Worker, queen, and male. *Specialized, stout setae on anterior margin of clypeus*: (0) absent; (1) present.

The presence of these specialized setae is a putative synapomorphy of Amblyoponinae (Ward, 1994), including *Amblyopone* and *Onychomyrmex*.

4. Worker and queen. *Malar area*: (0) easily visible in dorsal view; (1) reduced such that the compound eyes are placed in anterior position on the head.

A reduced malar area resulting from forward-positioned compound eyes is an autapomorphy of *Myrmecia* (Ward & Brady, 2003). Character 7 in Baroni Urbani *et al.* (1992).

5. Worker. *Torus of antennal socket*: (0) covered at least partially by frontal carinae; (1) completely exposed, such that the antennal socket including the entire circumference of the torulus is clearly visible in dorsal view.

Although in most cases the degree of covering is quite minimal in groups within Cerapachyinae, this condition still differs from that seen in army ants, *Leptanilla*, and Leptanilloidinae, where the entire socket including the torulus is completely exposed. *Sphinctomyrmex* and many *Cerapachys* (almost exclusively limited to the ‘*Cerapachys* lineage’) also show completely exposed sockets. Variation in the exposure of the antennal socket has been used in part to define species complexes within *Acanthostichus* (MacKay, 1996), but in no species is the torulus completely exposed in this genus. Modified from character 8 in Baroni Urbani *et al.* (1992).

6. Worker. *Antennal scape*: (0) not flattened along entire length; (1) flattened, forming an anterior ridge along its entire length.

In dorsal view, the scape in *Acanthostichus* and *Cylindromyrmex* is flattened with a ridge evident on the anterior edge. Although a few other taxa have a scape that looks flattened at its posterior end (e.g. *Nomamyrmex* and some *Simopone*), in these cases a ridge has not formed along the entire length of the scape.

7. Worker. *Relative length of second and third antennal segments, as expressed by the ratio (second segment/third segment)*: (0) > 0.5; (1) < 0.5.

The first funicular (second antennal) segment is less than half the length of the second funicular (third antennal) segment in *Eciton*. In all other taxa included in this analysis, the first funicular segment is much longer, and is usually subequal to or longer than the second funicular segment.

8. Worker. *Antennal club, in the form of an enlarged, egg-shaped terminal segment*: (0) absent; (1) present.

Almost all members of *Cerapachys* ‘*Cerapachys* lineage’ have a terminal antennal segment in the form of an egg-shaped club that is much thicker than the penultimate segment. Species of the *Cerapachys* ‘*Phyracaces* lineage’ instead have an apical segment approximately the same width as the penultimate segment (Brown, 1975), a trait shared with all other taxa included in this analysis. A few species of *Sphinctomyrmex* have the last two segments thickened, but in these cases the last segment is not much thicker than the penultimate one. Note that some other taxa outside the dorylomorphs also display strongly clavate antennae.

9. Worker and queen. *Antennal scrobes encircling the eye region*: (0) absent; (1) present.

The genus *Paraponera* is characterized by antennal scrobes that run posterodorsally above the eye, and then curve around the eye to run back down the head below the eye.

10. Worker and queen. *Longitudinal groove running posteriorly on malar area from mandibular articulation, ending at midlength of the head*: (0) absent; (1) present.

The presence of this character has been used to distinguish *Acanthostichus* from *Cylindromyrmex* (Bolton, 1994). However, *Cylindromyrmex* workers and queens also possess this longitudinal groove, but observation is difficult in some species due to the striations of the head (de Andrade, 1998b). This character is also present in some *Cerapachys* (Bolton, 2003).

11. Worker and queen. *Angular carina between antennal socket and lateral margin of head*: (0) absent; (1) present.

The presence of this character has been implied to be synapomorphic for (*Cerapachys* + *Leptanilloides* + *Simopone* + *Sphinctomyrmex*) (Brown, 1975), although it is quite weak in a few species belonging to this group (e.g. *L. mckennae*). The carina is also present in at least some *Asphinctanilloides* (Brandão *et al.*, 1999) and is also evident in extinct species of *Cerapachys* (Wheeler, 1915).

12. Worker and queen. *Numerous longitudinal striations on dorsum of head, of mesosoma, and of petiole*: (0) absent; (1) present.

Dorsal longitudinal striations are an autapomorphy of *Cylindromyrmex* (de Andrade, 1998b).

13. Worker. *Prementum*: (0) clearly visible with mouthparts fully closed, and flanked by the labrum anteriorly and by a maxilla on each side; (1) concealed behind labrum and mesially projecting outgrowths from the maxillae that meet along the midline.

Character state 1 occurs only in dorylomorph taxa. Coded after Bolton (2003).

14. Worker, queen, and male. *Distal margin of labrum*: (0) bilobed, with median portion concave or cleft; (1) smoothly curved, with median straight or slightly convex.

Most ant taxa have a labrum with a bilobed distal margin, which is sometimes medially cleft. In all known castes of *Aenictogiton* and *Dorylus*, however, the labrum is smoothly curved at its distal margin (Gotwald, 1969).

15. Worker. *Number of labial palp segments*: (0) four; (1) three; (2) two; (3) one.

The coding of this character assumes irreversible evolution from greater to fewer segments. Thus, taxa that contain some species with three segments and others with two segments have been coded with a groundplan of three segments: *Neivamyrmex* (Borgmeier, 1957; Gotwald, 1969); *Cerapachys* (Kusnezov, 1954; Brown, 1975); *Cylindromyrmex* (Gotwald, 1969; Brown, 1975); and *Amblyopone* (Brown, 1960; Gotwald, 1969). The two known fossil species of *Cerapachys* have four-segmented labial palps (Wheeler, 1915) and the extinct *Acanthostichus hispaniolicus* has three-segmented palps (de Andrade, 1998a); this is consistent with the assumption of irreversibility. Several *Simopone* species possess four segments (e.g. *S. grandis* Santschi and *S. marleyi*). Taxa in this study that only have two segments include *Aenictus* and *Dorylus* (Gotwald, 1969), Leptanilloidinae (Brandão *et al.*, 1999), *Rhytidoponera* (Brown, 1958), and *Onychomyrmex* (Wheeler, 1916). All known species of *Myrmecia* are four-segmented (Ogata, 1991) whereas those of *Leptanilla* are one-segmented (Kutter, 1948; Bolton, 1990c).

16. Worker. *Eyes*: (0) present; (1) absent.

Although eye loss has certainly occurred many times during the history of ant evolution, its consistency within many genera in this study argues for its phylogenetic usefulness. Taxa that completely lack eyes in all known species include *Aenictus*, *Asphinctanilloides*, *Cheliomyrmex*, *Dorylus*, *Leptanilla*, and *Leptanilloides*. A few species of *Amblyopone*, *Cerapachys*, *Neivamyrmex*, and *Sphinctomyrmex* are also eyeless, but these taxa have been coded with the groundplan of eyes present.

17. Worker. *Ommatidia*: (0) unmodified or absent; (1) unitary and greatly enlarged.

Many members of Ecitoninae possess distinctly enlarged single-faceted eyes (some *Neivamyrmex*; all *Eciton*, *Labidus*, and *Nomamyrmex*). The only other known case of this phenomenon in ants occurs in at least two insular species of the poneromorph genus *Proceratium* (Brown, 1974, 1980).

18. Worker. *Blunt tubercles on dorsal surface of pronotum*: (0) absent; (1) present.

Among included taxa, only *Paraponera* possesses large, raised tubercles on the dorsum of the pronotum.

19. Worker, queen, and male. *Anteroventral pronotal angle*: (0) without a distinct tooth in front of the fore coxa; (1) with a distinct tooth in front of the fore coxa.

A distinct, usually acute, anteroventral pronotal tooth is an autapomorphy of *Rhytidoponera* (Brown, 1958) and occurs in all adult castes.

20. Worker. *Pronotal connection*: (0) mobile; (1) immobile, with incomplete fusion dorsally and laterally; (2) immobile, with incomplete fusion laterally and complete fusion dorsally; (3) immobile, with complete fusion dorsally and laterally.

This character refers to the degree of fusion between the pronotum and the mesonotum (dorsal) or mesopleuron (lateral). In the mobile state, the pronotum is attached to the mesonotum and mesopleuron via a movable membrane. Incomplete fusion occurs when the two somites join together to form a prominent sulcus or groove. In complete fusion, very little or no trace of a suture remains.

The taxonomic and phylogenetic utility of the dorsal suture between the pronotum and the mesonotum ('promesonotal suture') has been recognized for some time (Gregg, 1953; Bolton, 1990b; Baroni Urbani *et al.*, 1992). These studies, however, considered a binary form of the character (mobile vs. fused). The systematic patterns of the lateral suture between the pronotum and the mesopleuron ('promesopleural suture') have only recently received detailed examination (Perrault, 1999). Recognizing that the dorylomorphs are variable regarding this character, Perrault established two broad categories. His first group contained Ecitoninae, *Aenictus*, and *Sphinctomyrmex* on the basis of complete or near-complete fusion of the pronotum and mesopleuron. His second group collected the remaining Cerapachyinae along with *Dorylus* on the basis of fusion with a sulcus ('fusion noto-pleurale avec gouttière ou fissure'). Our own observations largely support this categorization. The mobile connection found in Leptanilloidinae (Brandão *et al.*, 1999) is unique among doryline section taxa, but quite prevalent in the outgroup taxa.

The '*Cerapachys* lineage' has been coded polymorphic for three states (1, 2, and 3) for the following reasons. No *Cerapachys* possesses a mobile pronotal connection. One extant *Cerapachys* species, *C. wroughtoni* of the '*Cerapachys* lineage', possesses an incompletely fused promesonotal suture; all other *Cerapachys* show complete fusion (Brown, 1975; Bolton, 1994). Brown (1975) reported that the two extinct *Cerapachys* species have a well-defined promesonotal suture, but the formal description of these fossils clearly states that the thorax is 'without promesonotal or mesoepinotal sutures or depressions' (Wheeler, 1915: 28). (Brown apparently mistook the presence of a promesonotal ridge in one of the ergatogyne specimens for a suture. Such ridges are common in ergatogynes even when the corresponding workers lack a suture; this can be readily observed in extant *Cerapachys* species.) Furthermore, incomplete promesopleural fusion is not uncommon in extant *Cerapachys* of both lineages.

21. Worker. *Promesopleural lobe in ventral view*: (0) forming a relatively broad strip that curves at its posterior end and extends almost to the midline of the body; (1) forming a relatively broad strip that curves at its posterior end but terminates far short of the midline of the body; (2) forming a relatively narrow strip that does not curve at its posterior end, but remains laterally orientated.

The promesopleural lobe was recently studied by Perrault (1999) and after augmentation and redefinition of character states appears to be a somewhat useful character for the dorylomorphs. The promesopleural lobe is fully visible only in ventral view after the removal of the legs and coxa. A broad promesopleural lobe curves and extends to near the midline of the body in all outgroup taxa and *Leptanilloides*. In *Cerapachys*, *Cylindromyrmex*, and *Sphinctomyrmex* it instead terminates far short of the midline. In *Simopone*, *Acanthostichus*, and all army ant taxa it is much narrower and terminates without curving towards the midline. Some cerapachyines showed morphologies somewhat intermediate between the last two states, and the requirement of ventrally dissected specimens limited available material for observation. This character has potential for future refinement after additional study, and may also prove useful in other ant groups.

22. Worker. *Position of propodeal spiracle*: (0) low on the side and posterior, such that it is at or behind the midlength in lateral view; (1) high and far forward, such that it is anterior to the midlength in lateral view.

A propodeal spiracle that is shifted low and posteriorly has been proposed on separate occasions to be apomorphic for Cerapachyinae (Bolton, 1990a, b), Leptanilloidinae (Brandão *et al.*, 1999), and Leptanillinae (including *Leptanilla*; Bolton, 1990c). However, this position also occurs in many poneromorphs, including the four genera included in this study, and other taxa. In some cases it is difficult to assess the height of the spiracle due to dorsal depression of the propodeum, but its position relative to the midlength provides unambiguous definition.

23. Worker. *Propodeal spiracle*: (0) slit-shaped; (1) round to elliptical.

Slit-shaped is defined here to mean that the aperture of the spiracle is very elongate (length four or more times the width) and with parallel sides. The propodeal spiracle is slit-shaped in *Paraponera*, *Myrmecia*, and most members of Ecitoninae (exceptions are *Cheliomyrmex* and some *Neivamyrmex*). Note that the distribution of states in workers is considerably different from that in the male caste (character 97).

24. Worker, queen, and male. *Metacoxal cavities*: (0) open; (1) closed.

The metacoxal cavities are visible only in ventral view after removal of the legs and coxa. In the closed state, the metacoxal cavities are surrounded by fused sclerites. Dorylomorphs and Leptanillinae (including *Leptanilla*) have closed metacoxal cavities (Bolton, 1990b). The metacoxal cavities are closed in *Onychomyrmex* but open with sclerites overlapping one another in *Amblyopone* (Ward, 1994). Character 13 in Baroni Urbani *et al.* (1992).

25. Worker. *Metapleural gland opening*: (0) not flanked above by carinalike flange that is directed anterodorsally; (1) with such a flange.

A dorsal cuticular flange covers the metapleural gland in dorylomorphs, *Leptanilla*, *Myrmecia*, and several other taxa not included in this study. Character 12 in Baroni Urbani *et al.* (1992).

26. Worker. *Metapleural gland*: (0) directed laterally and not visible as a crescentic slit-shaped cavity in posterior view; (1) directed posterodorsally and visible as a crescentic slit-shaped cavity in posterior view.

Character state 1 is a putative synapomorphy for Amblyoponinae (Ward, 1994), including *Amblyopone* and *Onychomyrmex*.

27. Worker. *Longitudinal impression subtending propodeal spiracle*: (0) absent; (1) present.

The presence of this character is an autapomorphy for *Dorylus* (Bolton, 1990b).

28. Worker. *Endophragmal pit*: (0) absent; (1) present.

The endophragmal pit, which is located anterior or anteroventral to the propodeal spiracle, is a character that was studied in a comparative context quite some time ago (Reid, 1941), yet has never been used in a cladistic analysis. Our observations confirm Reid's assessment of its presence exclusively within *Dorylus* and Ecitoninae among dorylomorphs, although it is extremely reduced in some *Neivamyrmex* species.

29. Worker and queen. *Horns or teeth on posterodorsal corner of propodeum*: (0) absent; (1) present.

Among taxa included in this study, only *Eciton* displays horns (in queens) or teeth (in workers) on the posterodorsal margin of the propodeum. In a few *Eciton* species, these teeth are completely fused together to form a lamellar keel.

30. Worker. *Propodeal lobes*: (0) present; (1) absent.

This character, commonly (and inaccurately) referred to as 'metapleural' lobes, occurs on the posteroventral corner of the propodeum in lateral view. The absence of propodeal lobes has been considered a separate apomorphy for both *Dorylus* (Bolton, 1990b) and Leptanilloidinae (Brandão *et al.*, 1999). Such lobes are also absent from many other ant taxa, including (in this study) *Leptanilla*.

31. Worker, queen, and male. *Foretibial spur (calcar) with conspicuous velum*: (0) present; (1) absent.

The base of the foretibial spur has a distinct translucent lamella (velum), unobstructed by cuticular teeth, in *Myrmecia* (Schönitzer & Lawitzky, 1987), *Amblyopone*, and *Onychomyrmex*. A distinct velum also occurs in a few other taxa not included in the present study – *Nothomyrmecia* Clark and some Ponerini (Ward & Brady, 2003). In *Paraponera* males the foretibial spur has an apparent velum (i.e. a transparent lamella) most readily discerned with backlighting, but it is overgrown by fine cuticular teeth except at the distal extremity. In *Paraponera* workers and queens the entire structure is obscured by cuticula. To reflect this ambiguity, *Paraponera* is coded as unknown. A distinct velum is clearly absent in all other taxa.

32. Worker and queen. *Flaring, crescent-shaped comb on foretibial spur*: (0) absent; (1) present.

The presence of a foretibial comb is a putative synapomorphy for Formicidae, although a similar feature is also found in the taphid genus *Methocha* (Schönitzer & Lawitzky, 1987). In ant taxa with a full comb on the foretibial spur, the comb usually remains approximately the same width or tapers towards the spur base. In both *Aenictus* and Ecitoninae, however, the comb is

crescent-shaped in that it narrows medially and then flares out at the spur base to end in a sharply defined border. Some species within *Dorylus* and *Acanthostichus* approach this morphology, but still do not produce this characteristic shape.

33. Worker and male. *Number of apical middle tibial spurs*: (0) two; (1) one; (2) none.

All known species of *Cylindromyrmex*, including two extinct species, possess two robust, pectinate middle tibial spurs (de Andrade, 1998b). *Simopone* has no spur at all (Wheeler, 1916; Bolton, 1994). Based on our observations, other dorylomorphs generally have one spur (but see Bolton, 2003). In some taxa (e.g. some *Aenictus*), the spur is much reduced. Species within *Onychomyrmex* have either one or no spur, and this genus has been coded polymorphic for states 1 and 2. *Leptanilla* is coded as possessing one spur after López *et al.* (1994) and Ogata *et al.* (1995).

34. Worker. *Submedial stout spine(s) on dorsum of mesotarsus*: (0) absent; (1) present.

The presence of one or more such spines is an autapomorphy for *Acanthostichus* (see also Brown, 1975).

35. Worker and queen. *Metabasitarsal sulcus*: (0) absent; (1) present on anterior surface; (2) present on ventral surface.

Among the taxa in the current study, an anterior metabasitarsal sulcus is found only in *Myrmecia* and *Paraponera*. It is also present, however, in *Nothomyrmecia*, *Prionomyrmex* Mayr, and some *Pseudomyrmecinae* (Ward, 1990; Ward & Brady, 2003). A ventral metabasitarsal sulcus appears to be autapomorphic for *Simopone*. Modified from character 15 in Baroni Urbani *et al.* (1992).

36. Worker. *Metatibial gland*: (0) externally absent; (1) externally visible.

The metatibial gland, which is located on the ventral surface of the hind tibia, has been proposed as a synapomorphy for the dorylomorphs (Bolton, 1990b). Bolton (1990b) indicated that all *Simopone*, some *Cerapachys* and *Acanthostichus*, and a few species in Ectoninae lack a visible gland. Because the gland is prominently visible in all *Acanthostichus* species observed, and is listed as present in the recent revision of this genus (MacKay, 1996), it has been coded as present for this genus. Although this character is present in most observed species of the '*Phyracaces* lineage', it is absent from many of the '*Cerapachys* lineage' and thus has been coded as polymorphic in this latter taxon. Within Ectoninae it has been coded as present in most genera on the strength of its occurrence in virtually all species. *Nomamyrmex* is the main exception, where it appears to be secondarily occluded by thickened cuticle; this genus has been coded as externally absent. It is also reported absent from all species of Leptanilloidinae (Brandão *et al.*, 1999).

The histology of this gland indicates possible internal differences between Cerapachyinae and the army ant genera (Hölldobler *et al.*, 1996; Billen, 1997). Unfortunately, very few species have been investigated, and major groups from the dorylomorphs have not yet been examined. Histological information has thus not been incorporated into the present analysis, although this appears to hold future promise. Character 14 in Baroni Urbani *et al.* (1992).

37. Worker. *Number of apical hind tibial spurs*: (0) two; (1) one; (2) none, or reduced to a minute setiform vestige.

Many species of *Aenictus* and *Onychomyrmex* show size reductions in their single spur, or a complete absence. These two genera have been coded as polymorphic for states 1 and 2. *Leptanilla* has been previously considered polymorphic, varying between one and two spurs (Bolton, 1990c), but careful scrutiny of these minute ants often reveals the presence of two spurs (López *et al.*, 1994). This genus has hence been coded with a groundplan of two spurs. Only one species of *Cerapachys* (*C. crawleyi* of the '*Cerapachys* lineage') has two spurs, a situation unique within the dorylomorph outside of *Cylindromyrmex* (see also Brown, 1975). This character has thus been coded as polymorphic for states 0 and 1 in the '*Cerapachys* lineage'. Note that some species in various taxa possess thickened setae that resemble a second spur, but nonetheless are morphologically distinct from a true spur.

38. Worker. *Hind tibial spur*: (0) straight or slightly curved, with maximum width of comb approximately subequal to or narrower than maximum width of spur; (1) straight or slightly curved, with maximum width of comb much greater than maximum width of spur (discounting the base); (2) stout and bent inwards, with comb approximately subequal to width of spur; (3) crescent-shaped, with a row of fingerlike teeth.

If two spurs occur, this character refers to the larger of the two. Among taxa included in this study, a broadly pectinate spur (state 1) is shared by all genera of Leptanilloidinae (Brandão *et al.*, 1999) and Cerapachyinae; this morphology contrasts with the much narrower comb seen in army ants and most other taxa. Hashimoto (1991a) suggested that a stout, bent spur may define Amblyoponinae, and indeed this state is present in those *Onychomyrmex* with a spur, albeit in highly reduced form. The crescent-shaped spur of *Leptanilla* is coded after Hashimoto (1991a). The coding scheme used in the present study otherwise differs substantially from that paper.

39. Worker. *Tarsal claws*: (0) bifurcate, with submedian tooth in addition to apical tooth; (1) simple (lacking submedian tooth).

Within army ants, a worker submedian tooth on the tarsus is present only within Ectoninae (except *Neivamyrmex*). It is interesting to note that for *Neivamyrmex* this character is variable among males (a substantial number of species have a small yet clearly defined submedian tooth) but not among workers, where it is always absent. Within Cerapachyinae workers, the submedian tarsal tooth occurs only in *Simopone* and in some members of the '*Cerapachys* lineage' (Bolton, 2003). Among outgroup taxa, it is absent from *Amblyopone* and *Onychomyrmex*.

40. Worker. *Petiolar node*: (0) not dorsolaterally marginate; (1) dorsolaterally marginate.

The sides of the petiole meet the dorsal face at a sharp, well-defined dorsolateral margin in the '*Phyracaces* lineage' (Brown, 1975). This margin often extends to the mesosoma and sometimes the head. Such margination is

absent from other taxa, including the 'Cerapachys lineage', although a weak dorsolateral border occurs in some *Simopone* species.

41. Worker and male. *Tergosternal fusion of abdominal segment II (petiole)*: (0) absent; (1) present.

The petiole is fused in Leptanilloidinae, *Leptanilla*, and many poneromorphs, including (in this analysis) *Paraponera* and Amblyoponinae (anterior portion only). It is also fused in many other ant taxa not included in this analysis. Coded after Bolton (2003).

42. Worker. *Sternite of abdominal segment II*: (0) not shortened posteriorly relative to tergite; (1) shortened posteriorly.

State 1 is an autapomorphy for *Dorylus* (Bolton, 1990b).

43. Worker, queen, and male. *Helcial sternite*: (0) not protruding ventrally; (1) convex and protruding ventrally.

The helcium refers to the often highly modified presclerites of abdominal segment III (Bolton, 1990a). The presence of a convex, protruding helcial sternite was discovered and proposed as a synapomorphy for the dorylomorphs by Bolton (1990b). Its presence has been confirmed within Leptanilloidinae (Brandão *et al.*, 1999). All three dissected species observed from *Aenictogiton* show a convex helcium similar in appearance to that of *Dorylus nigricans*. Baroni Urbani *et al.* (1992) did not include males in their coding and considered *Aenictogiton* unknown for this character; Bolton (1990b), however, did include the male caste in his observations (his character 15). Modified from character 18 in Baroni Urbani *et al.* (1992).

44. Worker and male. *Position of helcium*: (0) approximately midheight of abdominal segment III; (1) well above midheight, such that the dorsal surface of the helcium is approximately even with the dorsal surface of abdominal segment III.

The raised position of the helcium has been used to distinguish *Acanthostichus* from other cerapachyines (Bolton, 1990a, 1994). Several species of *Cylindromyrmex* also show a helcium clearly above the midheight (*C. meinerti* Forel and *C. longiceps* André). These two species, however, form a clade nested well within the genus (de Andrade, 1998b), which implies that character state 0 is ancestral for this genus. A raised helcium also occurs in *Amblyopone* and *Onychomyrmex*.

45. Worker. *Dorsal midline length of abdominal segment III excluding the helcium (i.e. length of post-tergite)*: (0) at least half as long as abdominal segment IV; (1) much less than half as long as abdominal segment IV.

In *Aenictus*, *Asphinctanilloides*, and all genera of Ectoninae, abdominal segment III is much less than half the length of abdominal segment IV. The relative size of abdominal segment IV varies considerably among *Leptanilla* species (e.g. Baroni Urbani, 1977), whereas the size of abdominal segment III varies in *Leptanilloides* (Brandão *et al.*, 1999); these two genera have thus been coded as polymorphic. Some 'Cerapachys lineage' species also show state 1, but the overwhelming majority

observed have state 0 and this taxon has been coded with this latter state.

46. Worker and queen. *Postsclerites of abdominal segment III*: (0) not completely fused; (1) completely fused.

Complete tergo-sternal fusion of abdominal segment III, posterior to the helcium, occurs in all dorylomorph, leptanilloid, and poneromorph females except *Adetomyrma* Ward (Bolton, 2003). This includes all taxa in the current study excluding *Myrmecia*. Character 22 in Baroni Urbani *et al.* (1992).

47. Worker. *Position of spiracle on abdominal segment III*: (0) in front of midlength of post-tergite; (1) shifted backwards on post-tergite, at or behind the midlength of post-tergite.

The spiracle of abdominal segment III is shifted posteriorly in *Aenictus* (Bolton, 1990b) and *Asphinctanilloides* (Brandão *et al.*, 1999). This spiracle is not substantially shifted backwards in *L. mckennae* (*contra* Longino, 2003).

48. Worker. *Degree of constriction of presclerites of abdominal segment IV*: (0) not constricted or at most very weakly constricted; (1) moderately to strongly constricted, but with a lateral height greater than that of abdominal segment III presclerites; (2) very strongly constricted, such that the lateral height is subequal to that of abdominal segment III presclerites.

This character compares the constriction of the postpetiole, if present, with that of the petiole. A very strongly constricted postpetiole, such that the degree of constriction is subequal to that of the petiole, occurs in all *Aenictus* (e.g. the observation in Bolton (1990b) of a narrow anterior neck in the postpetiole), *Asphinctanilloides*, and *Leptanilla* (also noted by Bolton, 1990c). The constriction is more moderate in all Ectoninae (except *Cheliomyrmex*), Cerapachyinae, *Myrmecia*, and poneromorphs, although it can be somewhat weak in this last group. The constriction is also more moderate in all species of *Leptanilloides*, except the newly discovered *L. mckennae* (Longino, 2003), in which it is strongly constricted. *Leptanilloides* has thus been coded polymorphic for states 1 and 2. In *Cheliomyrmex* and *Dorylus*, constriction of abdominal segment IV is essentially absent.

49. Worker and queen. *Tergosternal fusion of presclerites of abdominal segment IV*: (0) present; (1) absent.

This character has been previously considered to be polymorphic within Cerapachyinae (Baroni Urbani *et al.*, 1992). These presclerites are regularly fused in *Acanthostichus* and *Cylindromyrmex* (Bolton, 1990a), and our observations have failed to uncover any instances of lack of fusion within other cerapachyine genera. This character has thus been coded as fused for all genera of Cerapachyinae. The absence of fusion occurs in army ants and Leptanilloidinae (Baroni Urbani *et al.*, 1992; Brandão *et al.*, 1999). Modified from character 26 in Baroni Urbani *et al.* (1992).

50. Worker and queen. *Presclerites of abdominal segment IV*: (0) longer than one half of III and with parallel sides; (1) not longer than one half of III and ring-shaped.

Possessing 'tubulate' abdominal IV presclerites has been used repeatedly to help define a group of taxa called the 'poneroid complex' (Taylor, 1978; Bolton, 1990b; Ward, 1990). Because all taxa in the current study fall within this group, this character has been redefined to emphasize the relative size and shape of this feature (after Baroni Urbani *et al.*, 1992). A long abdominal segment IV presclerite with parallel sides occurs in all Cerapachyinae, poneromorphs (except *Adetomyrma*), and *Myrmecia*. Character 27 in Baroni Urbani *et al.* (1992).

51. Worker and queen. *Tergosternal fusion of postsclerites of abdominal segment IV*: (0) absent; (1) present.

Fusion in this character has been considered the only strong putative synapomorphy for poneromorphs (Bolton, 1990b, 2003), although it is absent in *Adetomyrma* (Ward, 1994). Character 29 in Baroni Urbani *et al.* (1992).

52. Worker. *Dorsal midline length of abdominal segment IV*: (0) much longer than abdominal segment V; (1) subequal to abdominal segment V.

Taxa in this study that possess an abdominal tergum IV subequal to abdominal segment V are *Dorylus*, *Leptanilloides* (except *L. mckennae*) and most *Sphinctomyrmex* (see also Bolton, 1990a). The length of abdominal segment IV varies considerably among *Leptanilla* species (e.g. figures in Baroni Urbani, 1977), but in the majority of cases it is substantially longer than abdominal segment V. This character has thus been coded polymorphic for *Leptanilloides*, *Sphinctomyrmex*, and *Leptanilla*.

53. Worker, queen, and male. *Distinct girdling constrictions between abdominal segments IV and VI*: (0) absent; (1) present.

The presence of deep constrictions between gastral segments occurs in all *Sphinctomyrmex* and *Leptanilloides*, except *L. mckennae* (Longino, 2003).

54. Worker. *Orifice of abdominal spiracles IV–VII*: (0) directed laterally; (1) directed posteriorly.

Spiracles on the gaster that are orientated posteriorly are an autapomorphy for Ecitoninae (Bolton, 1990b).

55. Worker and queen. *Spiracles of abdominal segments V–VII*: (0) not visible under normal gastric expansion; (1) visible under normal gastric expansion.

Exposed gastral spiracles are a putative synapomorphy for the dorylomorphs (Bolton, 1990b). Character 11 in Baroni Urbani *et al.* (1992).

56. Worker. *Orifice of abdominal spiracles V–VII*: (0) round; (1) oval to slit-shaped.

Character state 1 is an autapomorphy for Ecitoninae (Bolton, 1990b).

57. Worker. *Tergite of abdominal segment VI*: (0) not covering the pygidium; (1) covering the pygidium.

In workers, the pygidium is the tergite of abdominal segment VII. Concealment of the pygidium by the preceding tergite is an autapomorphy for Leptanilloidinae (Brown, 1975; Brandão *et al.*, 1999). Character 34 in Baroni Urbani *et al.* (1992).

58. Worker and queen. *Pygidium*: (0) unmodified; (1) bordered apically by a row of denticles or teeth; (2)

armed with a pair of lateral spines; (3) reduced to a narrow U-shaped sclerite.

We have considered all modifications to the pygidium to be states of the same character, unlike some previous treatments that separated this information into several discrete characters (Baroni Urbani *et al.*, 1992; Grimaldi *et al.*, 1997). Generally, in ants the pygidium is large, rounded, and lacks teeth or spines (state 0). The presence of denticles on the apex of the pygidium (state 1) is a putative synapomorphy for all genera of Cerapachyinae (Brown, 1954, 1975). A few species of poneromorphs, including *Paraponera* and some *Amblyopone*, possess denticles on the hypopygium (the sternite of abdominal segment VII), but these are readily distinguishable in form and location from the denticles seen in Cerapachyinae (see Discussions in Bolton, 1990a; Baroni Urbani *et al.*, 1992). A bispinose pygidium (state 2) has long been considered an autapomorphy for *Dorylus* (Emery, 1910; Bolton, 1990b). Pygidial reduction (state 3) occurs in *Aenictus*, Ecitoninae, and Leptanilloidinae (Jessen, 1987; Bolton, 1990b; Brandão *et al.*, 1999). Modified from characters 31, 32, and 33 in Baroni Urbani *et al.* (1992).

59. Worker. *Dufour gland epithelium*: (0) not crenellate; (1) crenellate.

The Dufour gland is crenellate in the Old World army ants *Aenictus* and *Dorylus*, but smooth in several genera of Ecitoninae and all other taxa studied to date (Hermann & Blum, 1966; Campione *et al.*, 1983; Billen, 1985, 1986, 1990; Billen & Gotwald, 1988). It is coded as not crenellate in *Rhytidoponera* on the strength of observations from several species in the same tribe, which are uniformly noncrenellate (Billen, 1986). Character 39 in Baroni Urbani *et al.* (1992).

60. Worker. *Pygidial gland*: (0) with definite reservoir; (1) without definite reservoir; (2) pygidial gland absent.

The pygidial gland possesses a reservoir in *Eciton*, *Neivamyrmex*, 'Phyracaces lineage', *Myrmecia*, *Paraponera*, *Rhytidoponera*, *Onychomyrmex*, and *Amblyopone*; it lacks one in *Aenictus* and *Dorylus* (Hölldobler & Haskins, 1977; Hölldobler & Engel, 1978; Hölldobler, 1982; Campione *et al.*, 1983; Hölldobler & Wilson, 1990). *Leptanilla* is missing a pygidial gland altogether, a condition only otherwise commonly found in the subfamily Formicinae (Hölldobler *et al.*, 1989). This character has not been studied yet for other taxa included in the present analysis.

61. Worker. *Specialized cuticular structure on pygidial gland*: (0) absent; (1) present.

The pygidial gland shows a specialized cuticular structure in *Dorylus*, and lacks such a structure in *Eciton*, *Neivamyrmex*, 'Phyracaces lineage', *Myrmecia*, *Rhytidoponera*, and *Amblyopone* (Hölldobler & Engel, 1978; Hölldobler, 1982). *Leptanilla* lacks a pygidial gland altogether (Hölldobler *et al.*, 1989). This character has not been studied yet for other taxa included in the present study.

62. Worker. *Postpygidial gland*: (0) absent; (1) small (\leq five cells) and without reservoir; (2) small with reservoir; (3) large (\geq fifteen cells) with reservoir.

This character was coded as a single multistate character (instead of several binary characters) due to the dearth of information in most taxa. The recent discovery of

consistency among six species of *Aenictus* (Billen *et al.*, 1999) in possessing a large gland with a reservoir suggests future potential for this character in ant systematics. This reservoir in *Aenictus* functions in at least one species to store trail pheromone that originates from the postpygidial gland (Oldham *et al.*, 1994; Billen & Gobin, 1996). Coded after Hölldobler & Engel (1978), Hölldobler *et al.* (1989), Hölldobler & Wilson (1990), and Billen *et al.* (1999).

63. Worker. *Abdominal segment VII sternum*: (0) without epithelium or gland; (1) with glandular epithelium; (2) with large sternal gland.

Among army ants, the few observed species of Ecitoninae and *Aenictus* possess a highly developed glandular epithelium on the internal surface of the sternite of abdominal segment VII. This epithelium appears to be absent from *Dorylus* and all other observed taxa in this study. It is also present in a few other genera (from several different subfamilies) not included in this study, including the ponerine *Leptogenys* Roger, which displays in some species obligate collective foraging similar to army ants. The genus *Leptanilla* is evidently unique in possessing a large, unpaired gland in this sternite. Coded after Hölldobler & Engel (1978), Hölldobler (1982), Jessen (1987), Hölldobler *et al.* (1989), Hölldobler & Wilson (1990), Billen & Gobin (1996), and Gobin *et al.* (2001).

64. Worker. *Convoluted poison gland*: (0) present; (1) absent.

With the exception of four genera within Amblyoponinae (including *Amblyopone* and *Onychomyrmex*), all ant taxa examined to date from at least ten subfamilies have a convoluted poison gland associated with the venom sac (Schoeters *et al.*, 1999). Coded after Hermann & Blum (1966), Hermann (1969), Blum & Hermann (1978), Billen (1990), Billen & Gobin (1996), and Schoeters *et al.* (1999).

65. Worker and queen. *Furcula*: (0) present and not fused to sting base; (1) present and fused to sting base; (2) absent.

The furcula, a structure on the anterior region of the sting, is absent from all observed *Aenictus*, *Dorylus*, Ecitoninae, and Cerapachyinae, presumably due to complete fusion with the sting base (Hermann, 1969; Bolton, 1990b). It is also absent from several other ant taxa not included in the present study (Baroni Urbani *et al.*, 1992). In Leptanilloidinae, the furcula is present but fused to the sting base and has lost the dorsal arm (Brandão *et al.*, 1999). The furcula is not fused in *Leptanilla* (Kugler, 1992), *Myrmecia* (Kugler, 1980), *Paraponera* (Hermann & Blum, 1966; Kugler, 1991), *Rhytidoponera* (Hermann & Chao, 1983), *Amblyopone*, and *Onychomyrmex* (Hermann, 1969; Ward, 1994). Modified from character 37 in Baroni Urbani *et al.* (1992).

66. Worker. *Gonostylus*: (0) separated into distal and proximal sclerites; (1) homogeneous and not separated into distal and proximal sclerites.

A homogeneous gonostylus (the third valvulae of the sting apparatus) occurs in all dorylomorphs so far examined; it is two-segmented in all other taxa in this study. It should be cautioned, however, that this character contained some degree of homoplasy in a comparative (but

nonphylogenetic) study of Myrmicinae (Kugler, 1978). Coded after Hermann & Blum (1966), Hermann (1969), Kugler (1980, 1991, 1992), Hermann & Chao (1983), and Brandão *et al.* (1999). It is also coded as state 0 in *Rhytidoponera* based on direct observations, consistent with the state in the related genera *Ectatomma* Smith and *Gnamptogenys* Roger (Kugler, 1991).

67. Worker. *Gonostylus*: (0) not fused along its width to the posterior arm of the oblong plate; (1) very wide and fused along its width to the posterior arm of the oblong plate.

A wide gonostylus that is fused to the posterior arm of the oblong plate is a putative synapomorphy of Leptanilloidinae (*Asphinctanilloides* + *Leptanilloides*) (Brandão *et al.*, 1999). It indeed appears unfused in other dorylomorphs and outgroups (Hermann & Blum, 1966; Hermann, 1969; Kugler, 1980, 1991, 1992; Hermann & Chao, 1983).

68. Worker. *Anterior portion of sting bulb*: (0) without extensions; (1) with a prominent anteromedial extension; (2) with prominent anterolateral extensions.

The sting bulb of Ecitoninae has a large anteromedial extension, although it is reduced in size somewhat in *Labidus* (Hermann, 1969). One of two *Leptanilloides* species for which sting dissections are available (material is too rare for other species) also displays a prominent anteromedial extension (Brandão *et al.*, 1999); this genus has been coded polymorphic. *Dorylus* and *Aenictus* conversely show a pair of anterolateral extensions, resulting in a concave border (Hermann, 1969; Gotwald, 1978). Other taxa in this analysis lack either character state, possessing instead a relatively flat anterior border (Hermann & Blum, 1966; Hermann, 1969; Kugler, 1980, 1991, 1992; Hermann & Chao, 1983; Brandão *et al.*, 1999).

69. Worker. *Sting*: (0) exsertile; (1) insertile.

The sting of *Dorylus* is reduced, spatulate, and positioned entirely within the gaster (Hermann, 1969; Bolton, 1990b). The sting of all other taxa in this study extrudes from the posterior region of the gaster.

70. Worker. *Lancet barbs*: (0) present; (1) absent.

The lancet of the sting lacks distinct barbs in all dorylomorphs (see also Hermann, 1969 and Brandão *et al.*, 1999) and possesses distinct barbs in *Leptanilla* (Kugler, 1992), *Myrmecia* (Kugler, 1980) and all poneromorph outgroups except *Rhytidoponera*.

71. Worker. *Base of sting shaft with a pair of long setae that almost reach the sting apex*: (0) absent; (1) present.

The presence of a pair of long setae on the base of the sting shaft is a putative synapomorphy of Leptanilloidinae within the dorylomorphs (Brandão *et al.*, 1999). These setae also appear to be absent from all outgroup taxa (Hermann & Blum, 1966; Kugler, 1980, 1991, 1992; Brandão *et al.*, 1999).

72. Queen. *Extreme dichthadiigyny*: (0) absent; (1) present.

The term dichthadiigyny is actually a surrogate for a complex of characters, including a gaster with the ability to greatly expand during egg production (physogastry), an enlarged postpetiole (abdominal segment III), the lack of wings or corresponding sclerites, a broadened and rounded

head, falciform mandibles, and vestigial or absent ocelli and eyes (see Schneirla, 1971; Hölldobler & Wilson, 1990; Gotwald, 1995 for a discussion). Such queens exist in *Aenictus*, *Dorylus*, Ecitoninae, *Leptanilla*, and *Onychomyrmex* (Brown, 1960; Bolton, 1990b, c; López *et al.*, 1994). Some species of *Acanthostichus* and *Sphinctomyrmex* have subdichthadiigyne queens that display some of these traits in less extreme form; these taxa have been coded as lacking extreme dichthadiigyny, per standard usage of this concept in ant taxonomy. Because the various components of dichthadiigyny are functionally linked (Gotwald, 1995), they have not been deconstructed into separate characters. Character 43 in Baroni Urbani *et al.* (1992).

73. Queen. *Abdominal segment II (petiole)*: (0) lacking extensions; (1) with paired lateral extensions; (2) with paired dorsal extensions.

The queens of *Dorylus* possess a pair of extended lobes that extend posteriorly from the lateral surface of the petiole, leaving the dorsum flat (see Raignier & Boven, 1955 and Barr *et al.*, 1985 for examples). In Ecitoninae, paired extensions instead protrude from the dorsum, creating a concave dorsal surface. *Aenictus* queens lack petiolar extensions, with one observed exception (*A. aratus* Forel; Wilson, 1964).

74. Queen. *Petiolar horns*: (0) absent; (1) lobelike; (2) hornlike.

This character varies among genera of Ecitoninae. In *Neivamyrmex*, lobes protrude from the dorsum, creating a concave dorsal surface. These structures appear modified in *Eciton* and *Labidus* as prominently raised horns (examples illustrated in Borgmeier, 1955, 1958). These horns are most pronounced in *Eciton*, in which they may serve as an anchor for the male during mating (Schneirla, 1949, 1971; but see also Rettenmeyer, 1963).

75. Queen. *Bursa copulatrix*: (0) not exposed; (1) exposed.

The bursa copulatrix is exposed in *Dorylus* and *Leptanilla*. Character 46 in Baroni Urbani *et al.* (1992).

76. Queen. *Abdominal segment VII (hypopygium)*: (0) not hypertrophied and not bilobate; (1) hypertrophied, extremely long and bilobate posteriorly.

A hypertrophied, bilobate abdominal segment VII is an autapomorphy of *Dorylus* (Barr *et al.*, 1985; Bolton, 1990b).

77. Male. *Tufts of long, fine, flexuous hairs on various parts of the body*: (0) absent; (1) present (1).

Aenictogiton is characterized by a quite bizarre arrangement of tufts of long hairs scattered throughout the body, especially on the scapes, mandibles, front half of the head dorsum, front femora, posterior margins of the pronotum, propodeum, undersides of the petiole, and the apex of the gaster (Brown, 1975).

78. Male. *Antennal sockets*: (0) behind the anterior margin of the head, leaving visible at least a trace of the clypeus between the socket and the anterior head margin; (1) at the anterior margin of the head, leaving no portion of the clypeus visible.

Taxa that show state 1 for this character are *Aenictus*, *Dorylus*, *Aenictogiton*, *Leptanilloides*, and *Leptanilla* (Baroni Urbani *et al.*, 1992). Although the clypeus in a

very few *Cerapachys* and *Sphinctomyrmex* closely approaches the anterior head margin, in the vast majority of these species the clypeus is still clearly visible; these two genera have thus been coded as state 0. Modified from character 47 in Baroni Urbani *et al.* (1992).

79. Male. *Length of antennal scape relative to head length*: (0) one-third the length of the head or less; (1) exceeding one-third the length of the head.

The following taxa possess short scapes relative to head length: *Acanthostichus* and *Cylindromyrmex* (see also measurements in MacKay, 1996 and de Andrade, 1998b); *Aenictogiton* (in part due to its unusually elongated head); most species of *Leptanilla* (e.g. Baroni Urbani, 1977; Ogata *et al.*, 1995); some *Simopone* (which has been coded polymorphic); and all outgroup taxa. The scape in all army ant genera, *Cerapachys*, and *Sphinctomyrmex* is comparatively much longer.

80. Male. *Length of antennal segment II*: (0) subequal to or shorter than each of the following two segments; (1) distinctly elongate, much longer than each of the following two segments.

An elongate antennal segment II is an autapomorphy for *Aenictogiton* (see also Brown, 1975).

81. Male. *Antennal segments II and III*: (0) together longer than or subequal to the antennal scape; (1) together much shorter than the antennal scape.

A similar version of this character as used in Baroni Urbani *et al.* (1992) contains an error in the coding of Leptanillini. The sum of antennal segments II and III is clearly much greater than the scape length in all *Yavnella* Kugler observed, including type material from two species. This sum is subequal to or slightly greater than the scape length in all *Leptanilla* observed except for one undescribed species from the Ivory Coast (which itself appears highly bizarre, even for a *Leptanilla*). See also the figures in Baroni Urbani (1977), Kugler (1987), and Ogata *et al.* (1995). Another inaccuracy in Baroni Urbani *et al.* (1992) occurs in Cerapachyinae, which is actually polymorphic for this character. The genus *Cylindromyrmex* (see also figures in de Andrade, 1998b) and some species of *Simopone* possess state 0. Modified from character 49 in Baroni Urbani *et al.* (1992).

82. Male. *Antennal segments I, II, and III*: (0) not smooth, and relatively indistinct from remaining antennal segments; (1) smooth, shiny, and clearly distinct from remaining antennal segments.

Within *Dorylus*, the first three antennal segments are characteristically distinct from the remaining antennomeres, representing an autapomorphy for this taxon. Note that in many other taxa, the first two antennal segments may appear moderately distinct, but this never includes the third segment.

83. Male. *Deep median posterodorsal impression in head*: (0) absent; (1) present.

The presence of this character is an autapomorphy for *Aenictogiton* (Brown, 1975). Character 48 in Baroni Urbani *et al.* (1992).

84. Male. *Forewing pterostigma*: (0) present; (1) absent.

Among included taxa, the stigma of the male forewing is absent only in *Leptanilla* (Bolton, 1990b; Ogata *et al.*, 1995). Character 50 in Baroni Urbani *et al.* (1992).

85. Male. *Forewing veins M and Cu diverging*: (0) slightly proximal, adjacent, or distal to crossvein cu-a; (1) considerably proximal to cu-a, by a distance greater than the length of the cu-a vein.

This character was first discussed by Brown & Nutting (1950) and modified by Gotwald (1982), who also commented on the variation within *Dorylus*. In virtually all Ecitoninae, the distance along the vein connecting M and cu-a is much greater than the length of the cu-a vein itself. Several species of *Eciton*, however, show the M vein separated by only the length of the cu-a, which is a condition also seen in some *Dorylus* (subgenus *Alaopone*) and some *Aenictus*. Thus, *Eciton* has been coded as polymorphic. Other subgenera of *Dorylus*, as well as all other taxa in this study, have the M vein originating approximately adjacent or distal to the cu-1 vein. This character has been coded as unknown for *Leptanilla* in consideration of the near total absence of wing venation in this genus.

86. Male. *Forewing vein Rsf2 + 3*: (0) present; (1) absent.

This vein is present in Ecitoninae and *Aenictogiton*, creating two submarginal cells. The vein is absent from *Aenictus* and *Dorylus*. This difference is remarkably consistent as there were no observed exceptions to this pattern within these four taxa. It is interesting to note that in *Aenictogiton* this vein is usually detached at its base from Rs + M (Brown, 1975), perhaps representing the initial stages of loss of this vein. This vein is also present in most (but not all) species within *Acanthostichus*, *Cylindromyrmex*, and *Sphinctomyrmex*. It is absent in some species of *Cerapachys*, *Simopone*, and *Amblyopone* as part of a general pattern of wing vein reduction, but is clearly present in other species from these genera. The groundplan for these taxa has been coded as present, based on the assumption of progressive, unidirectional venational reduction (see also Brown & Nutting, 1950; Perfil'eva, 2002). The vein is absent in *L. mckenna*. This character has been coded as unknown for *Leptanilla* in consideration of the near total absence of wing venation in this genus.

87. Male. *Hindwing jugal lobe*: (0) present; (1) absent.

This character is present in only two outgroup taxa, *Myrmecia* and *Paraponera*. Modified from character 52 in Baroni Urbani *et al.* (1992), which incorrectly considered *Paraponera* to lack a jugal lobe.

88. Male. *Mandibles*: (0) triangulate and truncated; (1) falcate and elongate; (2) lobate; (3) straplike.

Army ant males are frequently characterized as having specialized mandibles (e.g. Gotwald, 1982). All three army ant subfamilies and *Aenictogiton* show sickle-shaped mandibles in the male that are as long or longer than the length of the head. (In some species of *Eciton*, this basic shape has been modified by torsion at the mandibular tips and additional ridges.) By contrast, Cerapachyinae and most other groups have mandibles that are triangular and much shorter than the head length. A few *Sphinctomyrmex* have falcate mandibles (Brown, 1975), but in these cases

they are shorter than the length of the head. A single exception occurs in an undescribed *Cerapachys* species from Madagascar that has falcate mandibles about the length of the head. Lobate mandibles, often vestigial, are an autapomorphy for Leptanillinae, including *Leptanilla* (Bolton, 1990c; Ogata *et al.*, 1995). *Amblyopone* and *Onychomyrmex* are characterized by slender, curved, 'straplike' mandibles that are relatively short and are typically tucked under the clypeus in a resting position (Brown, 1960).

89. Male and queen. *Number of labial palps*: (0) more than one; (1) one.

The genera *Aenictogiton*, *Aenictus*, *Dorylus*, and *Leptanilla* have only a single labial palp in the queen (unknown for *Aenictogiton*) and male (Gotwald, 1969; Ogata *et al.*, 1995). Other taxa in the analysis, including Ecitoninae (Borgmeier, 1957), have two or more labial palps in these castes.

90. Male. *Shape of pronotum in lateral view*: (0) quadrangular; (1) triangular.

All known males of *Aenictus*, *Dorylus*, Ecitoninae, *Aenictogiton*, and *Leptanilloides* display a characteristic triangular-shaped pronotum. The sclerite in these taxa possesses an angular posterior apex and a dorsolateral side that remains approximately parallel to the long axis of the body, when seen in lateral view. In Cerapachyinae and all other taxa in the analysis, the pronotum is quadrangular, without this sharp apex and with a dorsolateral side that is directed dorsally towards the head. The male of the extinct *Cerapachys ammosus* (Wheeler) also has a quadrangular pronotum (Wheeler, 1915).

91. Male. *Mesothoracic spiracle*: (0) near dorsal posterior lobe of pronotum; (1) positioned halfway, or closer, towards the ventral margin of the pronotum.

The normal position of the male mesothoracic spiracle is near the dorsal posterior lobe of the pronotum, next to the tegula (Tulloch, 1935). However, this spiracle is shifted down in *Dorylus* and *Aenictogiton* so that it is exposed much closer to the ventral portion of the pronotum.

92. Male. *Tegula*: (0) small and flaplike; (1) large and bulbous.

Most ant males have a small, flaplike tegula, which is located anterodorsal to the attachment of the wing to the thorax (Tulloch, 1935). In all Cerapachyinae except *Acanthostichus*, however, the tegula is much larger and bulbous in appearance, and covers much more of the anterior portion of the wing attachment.

93. Male. *Parascutal carina*: (0) reaches transcutal cleft at lateral margin of notum; (1) curves over tegula and terminates before transcutal cleft.

The parascutal carina is a prominent ridge that separates the dorsal surface of the mesoscutum from the lateral surface. It curves over the tegula and ends before the transcutal suture in males of *Aenictogiton*, *Aenictus*, *Dorylus*, Ecitoninae, and *Leptanilloides*. In all other taxa in the analysis the parascutal carina extends to meet the transcutal suture at the lateral margin of the notum. This latter condition is also evident in other ant groups not included in the present analysis, as first recognized by Tulloch (1935).

94. Male. *Axilla*: (0) consisting of two lateral plates connected medially or represented medially by a broad furrow; (1) consisting of two reduced lateral plates, not connected medially.

The transcutal suture directly abuts the scutellum, without an intermediary axilla or axillary furrow, in *Aenictus*, *Dorylus*, and *Aenictogiton*. In Cerapachyinae and all other taxa in the analysis these lateral plates are connected medially by a broad furrow and are usually much larger in dorsal view. The distinction between *Dorylus* and other taxa was first observed by Tulloch (1935). State 1 also occurs in many other ants not in the present analysis, including some pseudomyrmecines, formicines, dolichoderines, and poneromorphs.

95. Male. *Mesopleuron*: (0) divided by a distinct posterior transverse sulcus; (1) not divided by a posterior transverse sulcus.

In many ant taxa the mesopleuron is divided by a distinct posterior oblique sulcus to form an anepisternum and katepisternum (Tulloch, 1935). In army ants, *Aenictogiton*, *Cylindromyrmex*, *Leptanilloides*, and *Myrmecia*, however, the mesopleuron is not so divided, and instead forms one large plate with no trace of a suture (or, in a few cases within *Myrmecia*, only a weak broad furrow; Ward & Brady, 2003). The sulcus is evident only in some *Simopone* and *Leptanilla*, and so has been coded as polymorphic in these two genera.

96. Male. *Number of apical hind tibial spurs*: (0) two; (1) one; (2) none.

Most taxa in the analysis have males with one metatibial spur. *Cylindromyrmex* is unusual among dorylomorphs by possessing two pectinate spurs, although rare occurrences of two spurs have been reported in Cerapachyini (Brown, 1975). The species of *Aenictus* observed were quite variable, with a single spur (but see Bolton, 2003) that is greatly reduced or lost in some species. The genus *Leptanilla* is coded as having two spurs, based on López *et al.* (1994) and Ogata *et al.* (1995).

97. Male. *Shape of propodeal spiracle*: (0) round to elliptical; (1) slit-shaped.

The propodeal spiracle is slit-shaped in *Aenictus*, *Dorylus*, all genera of Ecitoninae, *Myrmecia*, and *Paraponera*. Note that the distribution of states in males is considerably different from that in the worker caste (character 22). Character 53 in Baroni Urbani *et al.* (1992).

98. Male. *Orifice of abdominal spiracles III and IV*: (0) round and directed laterally; (1) elliptical to slit-shaped and directed posteriorly.

The orifices of abdominal spiracles III and IV are directed posteriorly in all army ant genera and *Aenictogiton*. The shape of the orifice in these taxa, however, is correlated with body size, becoming more slitlike as body size increases. This gradation, for example, is evident in comparing small vs. large species of *Neivamyrmex*. In Cerapachyinae and other taxa in this analysis, the spiracles are round and directed laterally.

99. Male. *Abdominal sclerites III–VIII with conspicuous rows of long dense setae*: (0) absent; (1) present.

The presence of conspicuous rows of setae along the length of the gaster is an autapomorphy of *Nomamyrmex*.

100. Male. *Tergosternal fusion of abdominal segment III postsclerites*: (0) absent; (1) present.

Abdominal segment III is fused in *Aenictus*, *Dorylus*, *Aenictogiton*, all genera of Cerapachyinae, *Leptanilla*, *Leptanilloides*, and poneromorph outgroups; it is unfused elsewhere (Bolton, 1990b; Baroni Urbani *et al.*, 1992; P.S. Ward, unpublished). Character 54 in Baroni Urbani *et al.* (1992).

101. Male. *Abdominal segments IV–VII*: (0) tapering posteriorly; (1) cylindrical with parallel sides, the segments of approximately similar width.

Army ant males are well known for their unusually robust gasters. All males of *Aenictus*, *Aenictogiton*, *Dorylus*, and Ecitoninae have stout, cylindrical gasters. All other taxa possess gasters that taper considerably across the posterior abdominal segments.

102. Male. *Abdominal segment IV*: (0) with convex presclerites differentiated by a deep constriction, and over whose length the sternite of abdominal segment III does not completely overlap; (1) with differentiated presclerites that are not strongly constricted from the postsclerites, and over whose length the sternite of abdominal segment III completely overlaps; (2) without differentiated presclerites.

Differentiated presclerites on abdominal segment IV occur in Cerapachyinae, *Myrmecia*, and most poneromorphs as part of a 'ball-and-socket' arrangement in which a portion of these presclerites is visible in specimens under normal gastric distension. Their rounded morphology is evident in disarticulated specimens. In Ecitoninae and *Leptanilloides*, disarticulation reveals clearly demarcated presclerites that nevertheless are not separated from the postsclerites by a strong constriction. Under normal distension of the gaster these presclerites are completely occluded by the overlap of the sclerites of abdominal segment III. Differentiation of the presclerites in any form is absent from *Aenictus*, *Dorylus*, and *Aenictogiton*. Modified from character 55 in Baroni Urbani *et al.* (1992).

103. Male. *Tergite of abdominal segment VII*: (0) sclerotized and normally developed; (1) desclerotized and concealed by segment VI.

Character state 1 is an autapomorphy of *Aenictus* (Bolton, 1990b). Character 56 in Baroni Urbani *et al.* (1992).

104. Male. *Sternite of abdominal segment VII*: (0) in proportion with rest of gaster and not hypertrophied; (1) hypertrophied, longer in ventral view compared with preceding segments and largely concealing abdominal segment VIII.

The presence of a hypertrophied abdominal segment VII is an autapomorphy of Ecitoninae (Bolton, 1990b).

105. Male. *Long anterior apodemes on sternite of abdominal segment VIII*: (0) absent; (1) present.

Only *Aenictogiton*, *Aenictus*, and *Dorylus* have an abdominal segment VIII with long anterior apodemes (Bolton,

1990b; Baroni Urbani *et al.*, 1992). Character 57 in Baroni Urbani *et al.* (1992).

106. Male. *Sternite of abdominal segment IX (subgenital plate)*: (0) largely or entirely concealed in ventral view; (1) mostly or entirely exposed in ventral view.

The ninth abdominal sternum of males is also known as the subgenital plate or hypopygium. An exposed subgenital plate is an autapomorphy of Ecitoninae (Bolton, 1990b).

107. Male. *Sternite of abdominal segment IX (subgenital plate)*: (0) posterior margin not strongly biaculeate; (1) posterior margin strongly biaculeate.

A subgenital plate with a pair of posterior sharp spines occurs in all army ant genera (Bolton, 1990b; Baroni Urbani *et al.*, 1992). Very similar structures are also found in Cerapachyinae, although these spines are highly reduced on occasion (Brown, 1975). Even though Baroni Urbani *et al.* (1992) cited *Amblyopone santschii* (Menozzi) as having a bifid subgenital plate, this condition appears not to be typical of the genus (Brown, 1960). *Paraponera* has a long projecting limb with a clawlike bifurcation that has also been coded as state 1. In *Leptanilla*, however, the subgenital plate is only 'sometimes bifurcate posteriorly' (Ogata *et al.*, 1995), and in these cases the bifurcation is often weakly developed (e.g. figures in Petersen, 1968; Baroni Urbani, 1977; Kugler, 1987; Ogata *et al.*, 1995). For these reasons, this genus has been coded with state 0. Modified from character 59 in Baroni Urbani *et al.* (1992).

108. Male. *Constriction in middle of sternite of abdominal segment IX (subgenital plate), forming two expanded lobes distally and proximally*: (0) absent; (1) present.

In genera of Ecitoninae the middle of the subgenital plate is strongly constricted, resulting in expanded regions on either end of the sternite (Krafchick, 1959). This condition is absent from all other taxa in the present analysis.

109. Male. *Anterior margin of sternite of abdominal segment IX (subgenital plate)*: (0) with mesal apodeme longer than or subequal to lateral apodemes; (1) with mesal apodeme much shorter than lateral apodemes; (2) apodemes absent; (3) anterior margin fused to basal ring or ring-shaped tergum.

Leptanilloides, most genera of Cerapachyinae, and all outgroup taxa except *Leptanilla* have a mesal apodeme that is as long as or longer than the flanking, lateral apodemes. The mesal apodeme by contrast is much shorter than the lateral apodemes in Ecitoninae, *Aenictus*, and *Simopone* (although very few dissected specimens of this last genus were available). The subgenital plate in *Aenictogiton* and *Dorylus* lacks apodemes altogether. In *Leptanilla*, apodemes are not observable due to fusion of the anterior margin of the subgenital plate to a ringlike structure, which either represents the basal ring or the ninth abdominal tergite (Petersen, 1968; Ogata *et al.*, 1995).

110. Male. *Basal ring (i.e. lamina annularis)*: (0) thin; (1) enlarged.

An enlarged, egg-shaped basal ring is an autapomorphy of Ecitoninae (Bolton, 1990b). Character 60 in Baroni Urbani *et al.* (1992).

111. Male. *Cerci*: (0) present; (1) absent.

Cerci are missing from all dorylomorphs (Bolton, 1990b), *Leptanilla* (Ogata *et al.*, 1995), and some *Amblyopone* (Baroni Urbani *et al.*, 1992). Character 58 in Baroni Urbani *et al.* (1992).

112. Male. *Size of genitalia*: (0) not larger than rest of gaster; (1) larger.

Known males of Leptanillinae, including *Leptanilla*, are characterized by unusually hypertrophied genitalia (Baroni Urbani, 1977, 1989; Bolton, 1990c). Character 62 in Baroni Urbani *et al.* (1992).

113. Male. *Genitalia*: (0) not retractile; (1) retractile.

The genitalia are retractile in dorylomorphs and not retractile elsewhere (Bolton, 1990b). Character 61 in Baroni Urbani *et al.* (1992).

114. Male. *Paramere*: (0) lobelike or digitiform; (1) rectangular; (2) frondlike with a distinct neck; (3) sickle-shaped with an arching neck; (4) large, valvelike with a thin, flattened apex.

Most taxa in this analysis, including outgroups, all genera of Cerapachyinae, *Leptanilloides*, *Aenictus*, and *Aenictogiton*, possess approximately lobelike or digitiform parameres. Some army ant taxa have parameres that are very distinct from this presumed groundplan. The parameres in *Dorylus* are large, sickle-shaped objects with a smoothly arching neck. In *Neivamyrmex*, they are rectangular with approximately parallel sides, whereas in the remaining genera of Ecitoninae they are frondlike, with a distinct neck and a flattened, paddle-shaped posterior. The paramere of *Leptanilla* is a large, tubular structure with a thin, flattened posterior that is sometimes armed with teeth (Petersen, 1968; Ogata *et al.*, 1995).

115. Male. *Dense, long hair around entire lateral perimeter of paramere*: (0) absent; (1) present.

All members of Ecitoninae have long, dense hairs surrounding the entire paramere in lateral view, representing a putative synapomorphy for this subfamily. Other taxa only have hair concentrated towards the distal end of the paramere.

116. Male. *Prominent sulcus connecting paramere to basal ring*: (0) absent; (1) present, showing a long sulcus between paramere and basal ring; (2) present, showing a short sulcus between paramere and basal ring.

Ecitoninae is characterized by the presence of a distinct sulcus at the point of attachment between the paramere and the basal ring (Wheeler, 1921). In *Cheliomyrmex* and *Neivamyrmex*, this is a long sulcus that connects the paramere along the basal ring far down into its interior. In *Eciton*, *Labidus*, and *Nomamyrmex*, the paramere is narrowly attached to the basal ring, such that a sulcus forms only at the posterior margin of the basal ring.

117. Male. *Digitus of volsella*: (0) not tapered distally to form a thin, sharp point, even if rodlike or bent distally; (1) curving and tapering distally to form a thin point; (2) with a distal lateral arm or wedge that is serrated with irregular teeth.

The apex of the digitus in *Neivamyrmex* and *Cheliomyrmex* curves distally and tapers to a thin point, although in a few *Neivamyrmex* it forms a sharpened apex without a

bend. The digitus in *Labidus* is unique in possessing a pickaxelike morphology with a series of distal jagged teeth. In other taxa examined, the apex of the digitus remains blunt, or at most is bent or curved into a hooklike structure that does not taper distally into a sharp point.

118. Male. *Aedeagal plates*: (0) not flattened; (1) flattened.

In males of *Leptanilla* the aedeagus is flattened and usually forms a broad shield, a condition evidently unique among ants (Petersen, 1968; Ogata *et al.*, 1995).

119. Male. *Setae on apex of aedeagus*: (0) absent; (1) present.

Setae are present on the apex of the aedeagus in *Cheliomyrmex*, *Labidus*, and *Nomamyrmex* (Watkins, 1976) and absent from all other taxa. An exception occurs in *Dorylus nigricans*, but setae are absent from all other *Dorylus* species examined (including several other species from the subgenus *Anomma*).

120. Male. *Accessory gland*: (0) not tightly coiled, subequal to or shorter than the vasa deferens; (1) tightly coiled, much longer than the vasa deferens.

The accessory gland and vasa deferens (also called the seminal vesicle in army ants due to its saclike morphology) are components of the male internal reproductive system. In *Eciton*, *Neivamyrmex*, and *Nomamyrmex* the accessory gland is tightly coiled and when unfurled much longer than the vasa deferens (Forbes, 1958; Forbes & Do-Van-Quy, 1965; Hung & Vinson, 1975; Gotwald & Burdette, 1981). This condition does not occur in *Cheliomyrmex*, *Labidus*, *Aenictus*, *Dorylus*, or *Rhytidoponera* (Mukerjee, 1927; Hung & Vinson, 1975; Ford & Forbes, 1980; Gotwald & Burdette, 1981; Shyamalanath & Forbes, 1984). This character remains unexamined for all other terminal taxa.

121. Male. *Ejaculatory duct*: (0) subequal to or shorter than the vasa deferentia; (1) much longer than the vasa deferentia.

The ejaculatory duct (which includes the bound accessory duct) connects the accessory gland to the genital capsule. In *Eciton* and *Neivamyrmex* the ejaculatory duct is very elongate, such that it is many times longer than the vasa deferens (Forbes, 1958; Forbes & Do-Van-Quy, 1965; Hung & Vinson, 1975; Gotwald & Burdette, 1981). In the other Ecitoninae genera (*Cheliomyrmex*, *Labidus*, and *Nomamyrmex*) as well as *Aenictus* and *Dorylus*, the ejaculatory duct is not elongated (Mukerjee, 1927; Ford & Forbes, 1980; Gotwald & Burdette, 1981; Shyamalanath & Forbes, 1984).

122. Larva. *Profile*: (0) pogonomyrmecoid; (1) aphaenogasteroid; (2) myrmecoid; (3) leptanilloid.

Larval profile refers to the shape of the body outline in lateral view. These profiles have been defined and categorized into twelve distinct types (Wheeler & Wheeler, 1976). Three of the four poneromorphs in this analysis have a pogonomyrmecoid profile, whereas the fourth (*Onychomyrmex*) is aphaenogasteroid. All other taxa in the analysis for which larvae are known have myrmecoid profiles, except *Leptanilla* and *Leptanilloides*, which are leptanilloid.

123. Larva. *Number of antennal sensilla*: (0) three; (1) two.

The antennae of ant larvae possess between one and five sensilla, each of which bears a minute spinule. Most ant genera have three such sensilla on each antenna (Wheeler & Wheeler, 1976), which is true for all Cerapachyinae and outgroups observed to date except *Leptanilla* and some *Onychomyrmex*. The number of antennal sensilla is usually very consistent within a given genus; for example, all thirteen species of *Rhytidoponera* in the literature have three sensilla. All army ants, *Leptanilloides*, *Leptanilla*, and some *Onychomyrmex* have two sensilla. Coded after Emery (1899), Wheeler (1916) and Wheeler & Wheeler (1965, 1976, 1984).

124. Larva. *Haemolymph feeding organ on abdominal segment III*: (0) absent; (1) present.

This character was originally mistaken for an enlarged larval spiracle (Wheeler & Wheeler, 1965). It has now been shown to function as an organ that allows the queen to feed from larval haemolymph (Masuko, 1989). This organ appears to be unique to *Leptanilla*. Character 63 in Baroni Urbani *et al.* (1992).

125. Larva. *Location of teeth on masticatory margins of mandibles*: (0) inner margin; (1) outer margin; (2) teeth absent.

Larvae of both *Leptanilla* (Wheeler & Wheeler, 1965) and *Leptanilloides* (Brandão *et al.*, 1999) bear teeth on the outer border of the larval mandibles. Teeth are completely absent from *Dorylus*, *Cheliomyrmex* (Wheeler & Wheeler, 1984) and *Acanthostichus* (Bruch, 1925). In all other taxa, the masticatory surface bears teeth on the inner margin, although in some cases these teeth can be minute. See character 123 for additional references.

126. Pupa of worker. *Cocoon*: (0) present; (1) absent.

Among taxa in the analysis for which worker pupae are known, only *Aenictus*, *Dorylus*, *Neivamyrmex*, and *Leptanilla* do not spin cocoons (Rettenmeyer, 1963; Wheeler & Wheeler, 1976; Gotwald, 1982; Masuko, 1990). Naked pupae have rarely been reported in *Amblyopone* (e.g. Mann, 1919), but a cocooned pupa is much more common and has been considered the groundplan for this genus. Modified from character 66 in Baroni Urbani *et al.* (1992).

Results

We described and scored a total of 126 characters (ninety-eight parsimony informative) for twenty-two taxa (Appendix). These characters can be partitioned based on the castes from which they were defined: female only (sixty-one characters); male only (forty-four characters); queen only (five characters); female and male (ten characters); queen and male (one character), and immature castes (larvae or pupae) only (five characters). The 'female' category combines characters observed either in workers alone or in workers and queens. We classified two terminal taxa as containing a large proportion of missing character data: *Aenictogiton* (59% of characters coded as unknown)

and *Asphinctanilloides* (51%). All other taxa in the analysis were missing fewer data (mean 5%; range 0–13%).

Parsimony analysis of the complete dataset resulted in a single MP tree (Fig. 1; length = 273, consistency index (CI) including all characters = 0.697, CI including only parsimony-informative characters = 0.657, retention index (RI) = 0.796). The monophyly of the New World army ants (Ecitoninae) was very strongly supported (100% bootstrap support; Fig. 1). Within Ecitoninae, there was good bootstrap support (75%) for a clade containing *Labidus*, *Eciton*, and *Nomamyrmex*. The genus *Neivamyrmex* resolved as sister to the rest of Ecitoninae, but with weak support. The Old World army ant genus *Dorylus* formed a clade with *Aenictogiton* (77%), and this clade in turn was sister to the other Old World army ant genus *Aenictus* (79%). A clade including all army ant genera together with *Aenictogiton* occurred with good bootstrap support (81%). The monophyly of Leptanilloidinae was strongly supported (99%). This analysis suggested that (Leptanilloidinae + Leptanillinae) was sister to the army ant clade, but without strong bootstrap support. Likewise, the paraphyly of Cerapachyinae, the monophyly of (*Acanthostichus* + *Cylindromyrmex*), and the monophyly of *Sphinctomyrmex* and the two *Cerapachys* taxa were all indicated by the MP tree without strong bootstrap support.

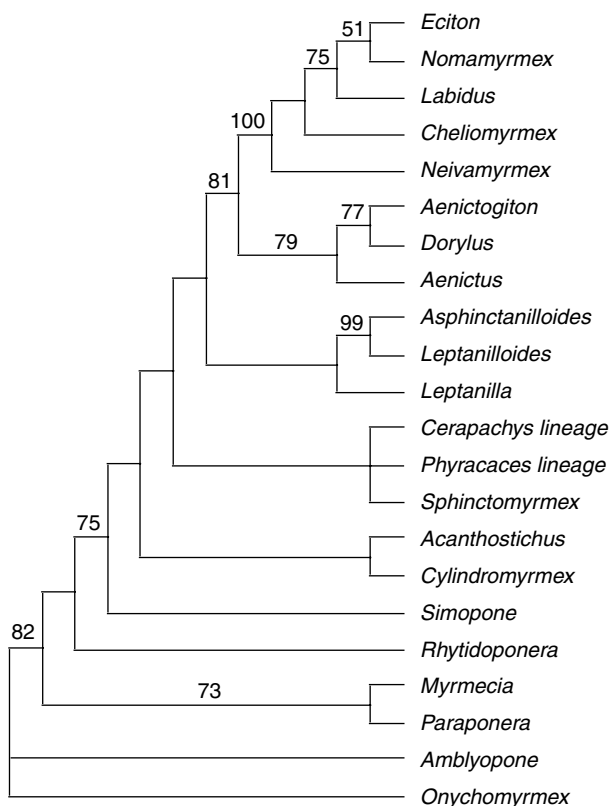


Fig. 1. The single most-parsimonious tree from the analysis of the complete dataset. The numbers above the branches are bootstrap values (>50%).

We conducted a second analysis in which all characters missing ~50% or more data entries were excluded. A total of eight characters were removed (characters 59–64 and 120–121). This analysis resulted in a single MP tree (length = 257; CI including all characters = 0.693, CI including only parsimony-informative characters = 0.650, RI = 0.800) whose topology was identical to that from the complete dataset, except that in this analysis (*Eciton* + *Labidus*) formed the sister group to *Nomamyrmex*.

After restoring the data matrix to its full complement of characters, we conducted another analysis in which the two taxa (*Aenictogiton* and *Asphinctanilloides*) missing a considerable proportion of character information were removed. This analysis produced seventeen MP trees (length = 267, CI including all characters = 0.704, CI including only parsimony-informative characters = 0.657, RI = 0.789). The strict consensus of these trees (Fig. 2A) failed to resolve any dorylomorph clades outside the army ants, and no new clades or substantial changes in bootstrap proportions resulted from the deletion of these incomplete taxa.

Discussion

The morphological evidence gathered and analysed in this study indicates that army ants together with *Aenictogiton* form a monophyletic group. In our analysis, the army ant clade (including *Aenictogiton*) is supported by ten or eleven inferred apomorphies, depending on the mode of ancestral state reconstruction used. The seven unambiguous state changes on the branch leading to the army ant common ancestor are: a spiracle positioned high and far forwards on the propodeum (worker, character 22); metatibial spur with a thin comb (worker, character 38); elongate, falcate mandibles (male, character 88); posteriorly orientated and slit-shaped abdominal spiracles (male, characters 97 and 98); a stout, cylindrical gaster (male, character 101); and a short or absent mesal apodeme on the subgenital plate (male, character 109). Additionally, if accelerated transformation (ACCTRAN) is assumed, the following three apomorphies are also reconstructed under all possible polytomy resolutions: endophragmal pit present (worker, character 28); flaring, crescent-shaped comb on foretibial spur present (worker, character 32); the abdominal segment VII sternum with a glandular epithelium (worker, character 63). On the other hand, if delayed transformation (DELTRAN) is assumed, these additional four apomorphies are reconstructed: absence of tergosternal fusion of presclerites of abdominal segment IV (workers, character 49); antennal segments II and III together much shorter than antennal scape (male, character 81); triangular pronotum (male, character 90); a parascutal carina that curves over tegula and terminates before transcutal cleft (male, character 93). The apomorphies inferred under only ACCTRAN or DELTRAN are subject to convergence and/or reversal and thus are not diagnostic. Also note that the reconstructions of all worker characters make assumptions about their condition in *Aenictogiton*, a taxon for

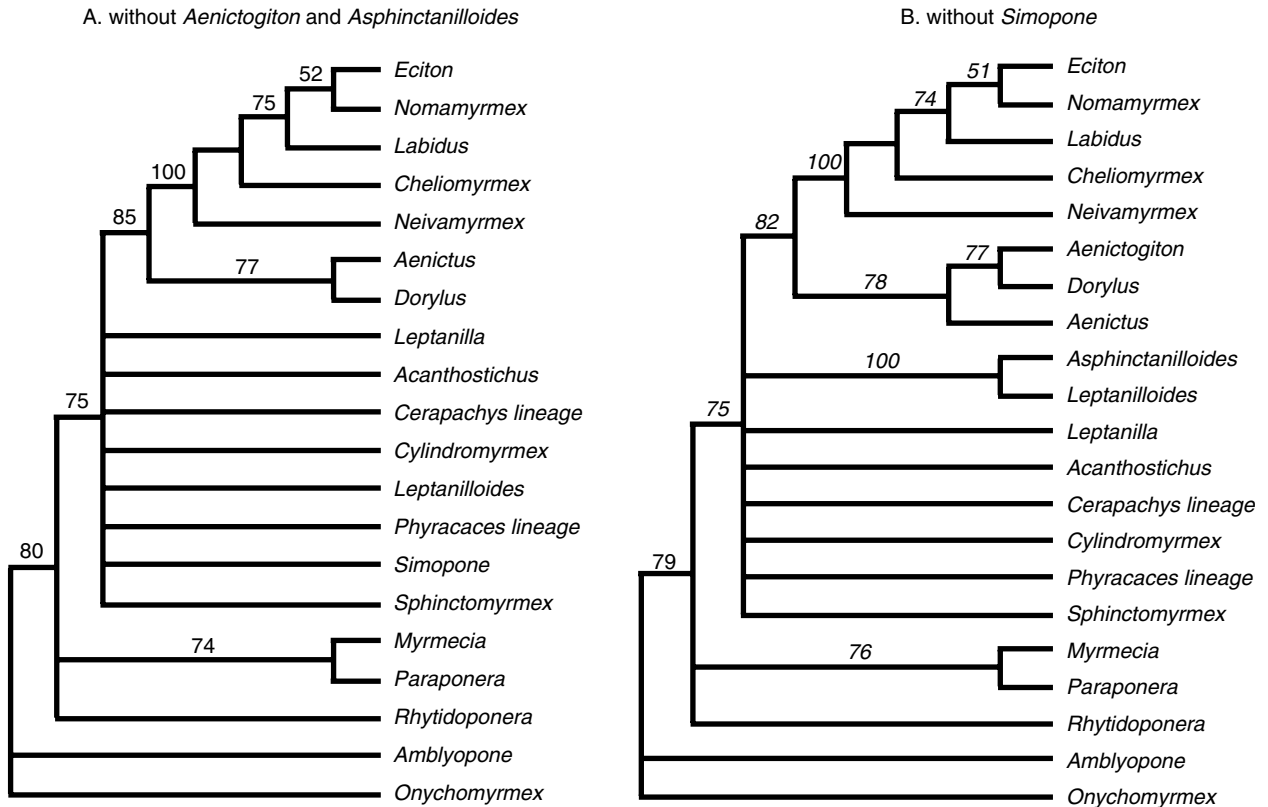


Fig. 2. Exploratory analyses examining the effect of incompletely known taxa. A, The strict consensus of the seventeen most-parsimonious trees from the analysis excluding two taxa (*Aenictogiton* and *Asphinctanilloides*) missing >50% character data. The numbers above the branches are bootstrap values (>50%); B, the strict consensus of the sixteen most-parsimonious trees from the analysis excluding *Simopone*. The numbers above the branches are bootstrap values (>50%).

which workers remain unknown. Even in light of these deficiencies, the overall weight of morphological evidence argues forcefully for army ant monophyly. Recent molecular phylogenetic analysis of data from four genes also supported army ant monophyly (Brady, 2003), although molecular data for *Aenictogiton* were not available in that study.

Some have suggested that many characteristics shared by the three army ant subfamilies are the products of convergent evolution (e.g. Gotwald, 1979; Franks & Hölldobler, 1987; Perfil'eva, 2002). It is true that some morphological traits of army ants clearly originated more than once over the course of ant evolution. A commonly cited example involves dichthadiiform queens, which occur in distantly related lineages (e.g. army ants, *Onychomyrmex*, *Leptanilla*, *Simopelta* Mann) and undoubtedly evolved multiple times. The existence of subdichthadiigynes in other groups (e.g. some species of *Acanthostichus* and *Sphinctomyrmex*) underscores the lability of this morphology. In our analysis, dichthadiigyny is reconstructed most parsimoniously as arising in the most recent common ancestor of *Leptanilla*, Leptanilloidinae, and army ants together. However, given that queens of Leptanilloidinae are still unknown and the weak support for the phylogenetic placement of Leptanil-

loidinae and *Leptanilla*, this reconstruction must be taken with caution. However, the evidence supporting army ant monophyly in our analysis implies that dichthadiiform queens only evolved once in this group.

Another character sometimes used to support multiple origins of army ants is the worker postpetiole. The third abdominal segment is typically called a postpetiole only if it is highly reduced and narrowly attached to both the second and fourth abdominal segments (Bolton, 1994). This condition is absent in *Cheliomyrmex* and *Dorylus*, and is present in *Aenictus* and all other genera of Ecitoninae. Our phylogeny suggests that the postpetiole either (1) evolved at least twice within the army ants; or (2) evolved once in this group and then was subsequently (and separately) lost in *Dorylus* and *Cheliomyrmex*. In *Cheliomyrmex*, although the third abdominal segment is certainly not narrowly attached to the fourth abdominal segment, it is much more reduced relative to the fourth abdominal segment than it is in *Dorylus* and most other ant taxa that lack a postpetiole. This situation in *Cheliomyrmex* may represent the partial evolution of a postpetiole or secondary fusion from a postpetiolate state. Several other ant taxa also show intermediate forms of the postpetiole, including a range of such cases in *Cerapachys* (Bolton, 1990a).

The unusual morphology of *Cheliomyrmex* has often elevated this genus to a central role in discussions of the internal phylogeny of army ants (e.g. Wheeler, 1921; Brown & Nutting, 1950; Gotwald & Kupiec, 1975; Hölldobler & Wilson, 1990; Gotwald, 1995). These rarely observed ants have the most restricted known distribution of any army ant genus (Watkins, 1976; Gotwald, 1995; Villareal *et al.*, 1995). Early taxonomists judged *Cheliomyrmex* to possess some features in common with *Dorylus* (e.g. lack of postpetiole), some with *Eciton* (e.g. toothed tarsal claws), and some unique to itself (e.g. prominent mandibular teeth), concluding that this mosaic phenotype represented the most archaic form of army ant (Wheeler, 1921). This line of argument suffers obvious shortcomings when viewed in a cladistic context. Brown & Nutting (1950) argued that the manifestation of the 1r crossvein in *Cheliomyrmex*, also present in other 'primitive' ant taxa such as Myrmeciinae and some poneromorphs, further supported this notion. This vein, however, is not present in most *Cheliomyrmex* specimens observed and also occurs on an inconsistent basis in several other ant genera (see also Brown & Nutting, 1950), making interpretation of this character problematic.

Although our knowledge of *Cheliomyrmex* biology is still quite meagre, this genus has also been considered to represent a primitive stage of army ant behaviour and colony bionomics, in terms of being strictly hypogaecic, foraging as specialized column raiders on social insects, and not having strongly polymorphic workers (Gotwald, 1995). However, the monophyly of Ecitoninae, suggested by previous work (Reid, 1941; Gotwald, 1969, 1971; Hermann, 1969; Gotwald & Kupiec, 1975; Bolton, 1990b; Brady, 2003) and overwhelmingly validated by our study, means that *Cheliomyrmex* cannot be viewed as sister to all other army ants. Thus, if this genus has retained any traits primitive within army ants, then their derived states must have evolved convergently in the Old World army ants and in the remaining New World army ants. The evolution of these putatively derived states – an epigaeic lifestyle, generalist foraging, swarm raiding, and pronounced polymorphism – almost assuredly did occur multiple times in army ant lineages, given the patchy taxonomic distribution of each of these traits. However, accurate assessment of these claims will require more detailed phylogenetic and biological information, both among army ants and their immediate relatives, than currently available.

Our study provides the most robust phylogenetic placement of the enigmatic subfamily Aenictogitoninae to date. These ants were originally included within Dorylinae (*sensu lato*), which at the time included all army ants (Ashmead, 1905, 1906; Emery, 1910). They were later transferred to the poneromorphs (Ponerinae *sensu lato*) in spite of their recognized similarities to army ant males (Brown, 1975). After a phylogenetic analysis concluded that *Aenictogiton* formed a polytomy with Aenictinae and Dorylinae, it was removed from Ponerinae and elevated to subfamily status in order to eliminate the possibility of defining a paraphyletic taxon (Baroni Urbani *et al.*, 1992). Our study supports the position of *Aenictogiton* within the Old World army ants

with 79% bootstrap support and further indicates that it is sister to Dorylinae with 77% support.

The placement of Aenictogitoninae as nested within the Old World army ants strengthens the idea that workers and queens of this subfamily should display the army ant adaptive syndrome of obligate collective foraging, nomadism, and dichthadiiform queens. The origin of the army ant syndrome is placed most parsimoniously at the most recent common ancestor of Aenictinae, Dorylinae, Ecitoninae (see also Brady, 2003), an ancestor that, according to our results, later gave rise to Aenictogitoninae as well. Because none of the approximately 320 currently described species belonging to these first three subfamilies is known to have lost any component of the army ant syndrome, it seems likely that this syndrome has been retained in the few described species of Aenictogitoninae as well. We must await the future discovery of females from this subfamily to test this prediction.

The monophyly of Cerapachyinae is not supported in our analyses. Our parsimony results from the primary dataset indicate the paraphyly of this subfamily, but bootstrap support for this conclusion is weak. Molecular data also yielded ambiguous results on cerapachyine monophyly (Brady, 2003). Furthermore, relationships within the subfamily are not resolved with strong bootstrap support in our study, although the parsimony tree does indicate clades consisting of (*Acanthostichus* + *Cylindromyrmex*) and (*Sphinctomyrmex* + *Cerapachys*). The first clade, but not the second, has also been recovered in two separate molecular phylogenies (Brady, 2003; Ward, 2005). The genera *Sphinctomyrmex* and *Cerapachys* are placed with *Simopone* into the tribe Cerapachyini on the basis of possessing carinate genae (Brown, 1975; Bolton, 2003). Of all Cerapachyinae genera, *Simopone* is the most incompletely known, especially considering that the few putative specimens of the male caste are not definitively associated with the genus. One might take the view that our knowledge of this genus is so incomplete as to be misleading. If we remove this genus from the primary dataset and re-run the analysis, the strict consensus of the MP trees shows a polytomy consisting of (in part) all remaining cerapachyine terminal taxa (Fig. 2B). In summary, our knowledge of the phylogeny of Cerapachyinae remains essentially unknown, and more taxonomic, morphological, and molecular work will be necessary to resolve relationships within this subfamily.

In the primary dataset, the subfamily Leptanilloidinae together with the nondorylomorph *Leptanilla* resolves as sister to the army ants. We view this result with some scepticism, however, given the lack of substantial bootstrap support. The position of *Leptanilla*, in particular, may be a spurious result due in part to the missing castes of *Aenictogiton* and *Asphinctanilloides*. These unknown castes generate a large number of missing character state values in the data matrix, which may compromise parsimony analysis because of ambiguous character optimizations (Huelsenbeck, 1991; Nixon & Wheeler, 1992; Novacek, 1992; Kearney & Clark, 2003). Adding these highly incomplete taxa to our study reduces the number of MP

trees from seventeen down to one, contrary to the usual effect of incomplete taxa inflating the number of MP trees. Their inclusion (Fig. 1) does not overturn any clades compared with the analysis where these two taxa were excluded (Fig. 2A), but *Leptanilla* in the strict consensus now falls in a polytomy at the root of the dorylomorphs. The removal of *Simopone* alone, which is not missing an inordinate amount of character data in the matrix, also shifts the position of *Leptanilla* in the same manner (Fig. 2B), further highlighting the sensitivity of this taxon to the overall context of our dataset. Another factor contributing to this instability may be that we did not include other genera from the subfamily Leptanillinae because their taxonomy is still in a state of flux and they are represented by incomplete castes (e.g. *Protanilla* known from workers only; *Phaulomyrma* and *Yavnella* from males only; *Anomalomyrma* from queens only).

A sister-group relationship between Leptanilloidinae alone and army ants may be more plausible. The only published observation of a species of Leptanilloidinae in the field, that by J. L. M. Diniz of *Asphinctanilloides anae*, noted that these ants were 'walking in columns similar to those of army ants' (Brandão *et al.*, 1999: 22). Although this is a tantalizing observation, the degree to which these ants might share the army ant adaptive syndrome remains unknown. If they indeed share some of these traits with army ants and form their sister group, then they may provide a critical link in studying the origins of this adaptive syndrome. However, we regard a sister-group relationship between army ants and Leptanilloidinae as an intriguing but unsubstantiated hypothesis, in consideration of (1) the potentially confounding effects in our analysis of *Leptanilla* and the two incompletely known taxa; (2) the poor bootstrap support in this region of the tree; and (3) our knowledge of very few males and no queens of Leptanilloidinae. Our results do not rule out the possibility that some or all members of Cerapachyinae instead form the sister group to army ants.

A recent phylogeny including data from five nuclear genes (Ward, 2005) offered several conclusions relevant to the phylogeny of the dorylomorph ants. This molecular study, focused on inferring the phylogenetic placement of *Leptanilloides*, robustly placed this genus within the dorylomorph clade, but was unable to provide much further resolution within this clade. Most relationships with the dorylomorphs were poorly resolved; army ant monophyly was recovered, but without strong bootstrap and Bayesian support. However, these molecular data did yield strong evidence that *Leptanilla* does not belong to the dorylomorph clade and in fact is probably only distantly related to the dorylomorphs. Even accounting for these molecular results, secure hypotheses regarding the relationships among some dorylomorph taxa remain elusive, most notably those involving genera within Cerapachyinae and Leptanilloidinae. Additional morphological and molecular data will be required to resolve these outstanding issues in dorylomorph phylogeny.

Acknowledgements

We are grateful to the following curators for access to specimens: Barry Bolton (Natural History Museum, London), Roberto Brandão (Museu de Zoologia da Universidade de São Paulo), Stefan Cover (Museum of Comparative Zoology), William Gotwald (personal collection), James Liebherr (Cornell University Insect Collection), Roy Snelling (Los Angeles County Museum), and Steve Shattuck (Australian National Insect Collection). Jack Longino generously provided two male specimens of *Leptanilloides*. We thank Barry Bolton, Peter Cranston, Chris Marshall, and Ted Schultz for helpful discussion and comments on the manuscript. An earlier version of this project formed a portion of the doctoral dissertation by SGB at the University of California, Davis, and SGB thanks Michael Sanderson and H. Bradley Shaffer for their input. We acknowledge support from the Center for Population Biology and the Center for Biosystematics, both at the University of California, Davis, and the National Science Foundation (grants INT-9904233 to SGB and PSW and DEB-9903650 to PSW).

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Accepted 29 October 2004

First published online 28 February 2005

Appendix Morphological data matrix. The first six taxa are outgroups. Polymorphisms are indicated by letters: a = 0, 1; b = 1, 2; c = 0, 1, 2; d = 2, 3; e = 1, 2, 3. The symbol '?' indicates an unknown character state.

	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890
<i>Amblyopone</i>	2a10000000	0000100000	0010010000	0000000210	1001010100	10000000?0
<i>Leptanilla</i>	0100100000	000?310000	0011100001	1010000310	1000a10201	0a000000?2
<i>Myrmecia</i>	0001000000	0000000000	0000100000	0000100000	0000000100	0000000000
<i>Onychomyrmex</i>	0010000000	0000200000	0011010000	00b000b210	1001010100	10000000?0
<i>Paraponera</i>	0000000010	0000100101	0000000000	?000100000	1000010100	1000000000
<i>Rhytidoponera</i>	0000000000	0000200011	0010000000	1010001000	0000010100	1000000000
<i>Acanthostichus</i>	0100010001	0010100002	2011100000	1011011110	0011010100	00001001??
<i>Aenictogiton</i>	??0???????	???1?????0?	???1???????	1?1???????	0?10???????	??0???????
<i>Aenictus</i>	0100100000	0010210003	2111100000	111001b010	0010111211	0000100311
<i>Asphinctanilloides</i>	1100100000	101?210000	?011100001	1010001110	101011121?	00001013??
<i>Cerapachys</i> lineage	010010010a	101010000e	1011100000	10100aa1a0	0010010100	00001001??
<i>Cheliomyrmex</i>	0100100000	0010110003	2111100100	1110011000	0010110011	00011103?a
<i>Cylindromyrmex</i>	0000010001	0110100002	1011100000	1000010110	0010010100	00001001??
<i>Dorylus</i>	0100100000	0011210001	2111101101	1010011010	0110010011	0100100211
<i>Eciton</i>	0100101000	0010101003	2101100110	1110011000	0010110111	0001110300
<i>Labidus</i>	0100100000	0010101003	2101100100	1110011000	0010110111	000111030?
<i>Leptanilloides</i>	1100100000	101?210000	0011100001	1010001110	1010a10b11	0aa01013??
<i>Neivamyrmex</i>	0100100000	001010a003	21a1100100	1110011010	0010110111	0001110300
<i>Nomamyrmex</i>	0100100000	0010101003	2101100100	1110001000	0010110111	00011103??
<i>Phyracaces</i> lineage	010000000a	101010000d	1011100000	1010011111	0010010100	00001001?0
<i>Simopone</i>	0100000000	1010000002	2011100000	1020201100	0010010100	00001001??
<i>Sphinctomyrmex</i>	0100100000	1010100003	1011100000	1010011110	0010010100	0a101001??

	1 6666666667 1234567890	1111111111 7777777778 1234567890	1111111111 8888888889 1234567890	1111111111 9999999990 1234567890	1111111111 0000000001 1234567890	1111111111 1111111112 1234567890	111111 222222 123456
<i>Amblyopone</i>	0001000000	0000000000	0000001300	0000000001	0000000000	a00000000?	?00000
<i>Leptanilla</i>	0020000000	0100100100	0001??1210	0000a00001	0?00000030	110400010?	?31111
<i>Myrmecia</i>	0100000000	0000000000	0000000000	0000101000	0000000000	000000000?	?20000
<i>Onychomyrmex</i>	?001000000	0100000000	0000011300	0000010001	0000000000	000000000?	?1a000
<i>Paraponera</i>	??00000000	0000000000	0000000000	0000001001	0000001000	000000000?	?00000
<i>Rhytidoponera</i>	0100000001	0000000000	0000001000	0000010001	0000000000	0000000000	000000
<i>Acanthostichus</i>	????210001	0000000000	1000001000	0000010001	0000001000	101000000?	?2?000
<i>Aenictogiton</i>	???????????	??????1101	1010001111	1011110101	1200101020	101000000?	??????
<i>Aenictus</i>	?310210201	0100000110	1000011111	00111a1101	1210101010	1010000000	021001
<i>Asphinctanilloides</i>	????111001	1?????????	???????????	???????????	???????????	???????????	??????
<i>Cerapachys</i> lineage	????210001	0000000010	1000001000	0100010001	0000001000	101000000?	?20000
<i>Cheliomyrmex</i>	????210101	0?????0010	1000101101	0010111100	1101011111	1012111010	02102?
<i>Cylindromyrmex</i>	??0?????01	0000000000	0000001000	0100100001	0000001000	101000000?	???00?
<i>Dorylus</i>	1100210211	0110110110	1100011111	1011111101	1200101020	1013000000	021021
<i>Eciton</i>	0210210101	0122000010	1000a01101	0010111100	1101011111	1012120001	121000
<i>Labidus</i>	????210101	0122000010	1000101101	0010111100	1101011111	1012122010	021000
<i>Leptanilloides</i>	????111a01	1?????0110	00000110?1	0010110001	0100000000	10?000000?	?3101?
<i>Neivamyrmex</i>	0210210101	0121000010	1000101101	0010111100	1101011111	1011111001	021001
<i>Nomamyrmex</i>	????210101	0121000010	1000101101	0010111110	1101011111	1012120011	12?0?0
<i>Phyracaces</i> lineage	0?0?210001	0000000010	1000001000	0100010001	0000001000	101000000?	?20000
<i>Simopone</i>	?????????01	00000000a0	a000001000	0100a10001	0000001010	101000000?	?20000
<i>Sphinctomyrmex</i>	????210001	0000000010	1000001000	0100010001	0000001000	101000000?	?20000