Army ants reassessed: the phylogeny and classification of the doryline section (Hymenoptera, Formicidae)

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Detailed comparative morphology of the ants continues to provide an abundance of new characters with great significance for our understanding of formicid phylogeny. This study discusses earlier phylogenies and goes on to show that the doryline section, nominated here to include the subfamilies Dorylinae, Aenictinae stat. n., Cerapachyinae and Ecitoninae, forms a monophyletic lineage within the poneroid group of subfamilies, with Leptanillinae as the sister-group. Numerous characters, both old and new, are considered, the section is defined and discussed, and diagnostic autapomorphies are given for each subfamily. The wider relationships of the doryline section are considered with respect to its position in the poneroid group and the poneroid complex, and the elevation of Aenictinae to subfamily status is justified. A provisional new-format key to ant subfamilies is provided at the end of the paper, and the phylogeny of the poneroid complex outlined in the light of this survey.

KEYWORDS: Formicidae, subfamilies, doryline section, phylogeny, classification, key.

Introduction

The earliest attempts at formulating a phylogeny of ant subfamilies tended to have a simple hub-and-spokes arrangement, with the Ponerinae centrally and the other subfamilies radiating out from it. In other words the Ponerinae was seen as the group ancestral to all other ant subfamilies, either directly or indirectly (e.g. Wheeler, 1920). This view persisted for many years, but was eventually challenged by Brown (1954). He decided that all the subfamilies could be divided roughly between those which bore an overall resemblance to the Ponerinae, and those which resembled the Myrmeciinae. He termed the former group the poneroid complex and the latter the myrmecioid complex of subfamilies.

Under the poneroid complex Brown (1954) grouped the subfamilies Leptanillinae, Dorylinae (which then included Ecitoninae and Aenictinae), Myrmicinae, Ponerinae, and Cerapachyinae. The myrmecioid complex contained Myrmeciinae (which then included Nothomyrmeciinae), Pseudomyrmecinae, Dolichoderinae (which then included Aneuretinae), and Formicinae. His tentative phylogenetic tree, despite its numerous unavoidable dotted lines and question marks indicating dubious or unproved relationships, was a great step forward. It rapidly acquired importance as a radical new approach to the problem of ant phylogeny.

The discovery of Upper Cretaceous ant fossils allowed Wilson, Carpenter and Brown (1967) to present a more detailed phylogenetic tree, based upon Brown's earlier model but with a number of justifying characters added. As before, the family was divided into poneroid and myrmecioid complexes, and contained the subfamily

distributions noted above. This phylogeny was reproduced almost exactly in Wilson's (1971) excellent book on social insects. As previously, many implied or suspected relationships were shown by dotted lines, and the version is dogged by a shortage of apomorphies to characterize the various subfamilies and their relationships.

The basic bifid structure of this Brown–Wilson phylogeny was challenged by Taylor (1978) following the rediscovery of *Nothomyrmecia* in Australia. Whilst studying this morphologically rather generalized ant he observed that the pre- and postsclerites of abdominal segment 4 were separated by a transverse constriction or incised groove, or both, in the genera *Myrmecia* (Myrmeciinae) and *Amblyopone* (Ponerinae), but were not so separated in *Nothomyrmecia*, which more closely resembled Formicinae and its allies. Concluding that this abdominal modification was of prime importance, he altered the Brown–Wilson phylogeny by shifting the subfamilies Myrmeciinae and Pseudomyrmecinae into the poneroid complex. This complex was thereafter characterized by the apomorphy of having a specialized fourth abdominal segment. *Nothomyrmecia*, now isolated in a subfamily of its own (Nothomyrmeciinae) was moved to a basal position on the Formicinae–Dolichoderinae–Aneuretinae branch, which Taylor (1978) renamed the formicoid complex. Unfortunately this action left the formicoid complex without an apomorphy and consequently paraphyletic with respect to the poneroids.

Dlussky (1988) retained the Taylor system, showing a basal bifurcation with formicoids (including Nothomyrmeciinae) on one side and poneroids (including Myrmeciinae and Pseudomyrmecinae) on the other. As before the same basic problem remained: there are no apomorphies justifying the major branches, and many terminate in question marks.

The version recently presented by Hölldobler and Wilson (1990) is equally weak in its treatment of the poneroids, presenting a number of characters which are dubious, many admittedly so, and others which are not autapomorphic for the groups thus delineated.

In a radical departure from the above line of thought, Baroni Urbani (1989) has produced a phylogeny which, as far as the poneroid complex is concerned, amounts to a major reshuffle. For many reasons, discussed below, I disagree most strongly with his arrangement and regard the Brown–Wilson–Taylor–Dlussky line of thought as more credible. Although their hypothesis contains much which is admittedly undecided, it has the merit of being based upon a very broad general knowledge and experience of large numbers of ant taxa, and does not present as solid evidence features which are debatable or definitely not so.

One of Baroni Urbani's (1989) clades includes the subfamilies Ecitoninae + Dorylinae (which includes Aenictinae) + Leptanillinae. Synapomorphies of these, according to Baroni Urbani, include the presence of dichthadiigyne queens, the lack of a true postpetiole in queens, and adult carrying behaviour where the carried individual is held under the head of the carrier. The first of these can be dismissed as it is certainly not a synapomorphy but the result of parallel evolution in response to the adoption of a particularly specialized lifeway. On the one hand, dichthadiigynes are now known not to be universal in subfamily Leptanillinae (Bolton, 1990b), and on the other hand dichthadiigynes are developed in some Ponerinae (e.g. Brown, 1960; Gotwald and Brown, 1967), from Baroni Urbani's alternative clade where they are not supposed to exist. Some subdichthadiigynes occur in the Cerapachyinae (Brown, 1975), a group included in the Ponerinae by Baroni Urbani (1989). The taxonomic distribution of dichthadiigyny is mentioned in Bolton (1990b) and under the definition of doryline section queens, later in this paper.

The lack of a true postpetiole in queens of this proposed clade fails as an apomorphy because in Leptanillinae postpetiolate queens occur in the genus *Anomalomyrma*. Further, Baroni Urbani's Ponerinae, in his alternative clade, shows two character states, both presence and absence of a postpetiolate queen. This reflects his inclusion of Cerapachyinae among the Ponerinae, but transferring the cerapachyines to the doryline branch does not, in this instance, solve any problems as some cerapachyine queens are postpetiolate whilst others are not. It seems most likely that the evolution of a separated postpetiole has occurred independently several times, as mentioned in the notes on doryline section worker characters, below.

As for carrying position, both Ponerinae and Myrmicinae, from his alternative clade, are indicated as showing variation in this aspect of their behaviour, so carrying behaviour of ants with a nomadic and group-predatory lifeway may have evolved in parallel, as a result of independent evolutions of that lifeway.

Baroni Urbani's (1989) second clade, Myrmeciinae + Ponerinae + Myrmicinae + Pseudomyrmecinae, is paraphyletic with respect to the one discussed above; this group of subfamilies has no synapomorphy to link them. Finally, his clade which contains all the remaining extant subfamilies, Nothomyrmeciinae + Dolichoderinae + Formicinae, is paraphyletic with respect to all the above. Thus nothing credible remains of the main features of Baroni Urbani's phylogeny, and it must be rejected. What it does indicate, however, is that if the database is incomplete, or is too small, then meaningful results will always be impossible to pin down.

The object of the present paper is to confirm the monophyly of the poneroid complex, to establish the monophyly of the poneroid group, and to establish and define the doryline section as a monophyletic group within the poneroids. The phylogeny of the poneroid group of subfamilies resulting from this study is indicated (Fig. 23) and all the included subfamilies receive some discussion. In a recent paper (Bolton, 1990a) I showed that the subfamily Cerapachyinae is monophyletic and should be regarded as distinct, separate from the Ponerinae with which it was previously associated (Brown, 1975). Elsewhere I have indicated (Bolton, 1990b) that the Leptanillinae is monophyletic and should be dissociated from the doryline lineage, with which it had traditionally been linked, and associated more closely with the Ponerinae. One or two ideas and hypotheses advanced in these two publications have since been revised, modified, or corrected. These are noted and discussed in the following text.

The establishment and definition of the doryline section of subfamilies occupies the main part of the study. Only one major change in status is put forward, the elevation of the doryline tribe Aenictini to subfamily rank. The section, as defined here, thus includes the subfamilies Ecitoninae, Dorylinae, Aenictinae, and Cerapachyinae. Association of the Cerapachyinae with the other three is not a new idea. It was first suggested by Emery (1901) but was later discarded, though not entirely forgotten (Brown, 1975; Bolton, 1990a).

Introductory notes on the doryline section

Through most of their history the subfamilies recognized here, with the exception of the Cerapachyinae, have been regarded as forming a single subfamily, originally called Dorylinae. These have commonly been referred to as army ants, driver ants, legionary ants, soldier ants, etc.; or, in the case of *Dorylus*, by one of a plethora of local African names for the larger members of the subgenus *Anomma*, which tend to be very conspicuous. Painful encounters with larger *Dorylus* species are a common talking point for everyone who has had the misfortune to be ambushed by them. In recent

years a tendency has developed to call the ecitonines army ants, and the dorylines driver ants. If common names are to be considered necessary, a view that I do not adhere to, then I would subscribe to this terminology. Aenictines and cerapachyines have no 'common' names, nor do they need them.

Because of their nomadic and group-predatory lifeways (Wilson, 1958) the biologies of ecitonines and dorylines have attracted much attention, though decidedly less in known of aenictines and cerapachyines. A good synopsis of 'army ant' life is given in Gotwald (1982), which includes an extensive bibliography. Other excellent publications for biological information include Raignier and van Boven (1955), Schneirla (1971), Wilson (1971), and Hölldobler and Wilson (1990). Species-level taxonomic coverage of the subfamilies is generally quite good, though the Afrotropical dorylines and aenictines remain as a glaring lacuna. For Cerapachyinae see Brown (1975); for Dorylinae and Aenictinae outside the Afrotropical region see Wilson (1964); for Ecitoninae see Borgmeier (1955) and Watkins (1976).

Distribution of the cerapachyines is worldwide, but aenictines and dorylines are restricted to the Old World tropics and subtropics whilst the ecitonines range through the tropics and subtropics of the New World. Dorylinae and Aenictinae are absent from Madagascar, and the former is also absent from the Australasian region.

The number of described species in each subfamily is shown in Table 1 by zoogeographical region. The figures given represent only the number of currently recognized species-level taxa. Infraspecific taxa are ignored and species which occur in more than one zoogeographical region are entered only under the region containing their type-localities. The figures given in parentheses indicate the number of species-level taxa in each group that are known only from males. The subfamilies are abbreviated as follows. Cerap. = Cerapachyinae; Aenict. = Aenictinae; Doryl. = Dorylinae; Ecit. = Ecitoninae.

Table 1

Region	Cerap.	Aenict.	Doryl.	Ecit.	Total
Nearctic	3 (1)	—	—	15 (5)	18 (6)
Neotropical	25 (1)	—	—	137 (67)	162 (68)
Palaearctic	5 (3)	7 (2)	1	—	13 (5)
Afrotropical	36 (4)	33 (19)	54 (23)	—	123 (46)
Malagasy	7 (1)	—	—	—	7 (1)
Oriental	15	25 (13)	3	—	43 (13)
Indo-Australian	45 (2)	39 (18)	2	—	86 (20)
Australasian	61 (2)	2 (1)	—	—	63 (3)
Total	197 (14)	106 (53)	60 (23)	152 (72)	515 (162)

The high number of male-based species is a major problem in all subfamilies except the Cerapachyinae. Males of the other three subfamilies are relatively large insects, nocturnal fliers which readily come to light and are thus easily collected, sometimes in considerable numbers. Unfortunately the discovery of males in association with workers is a fairly rare event. These features have led to the development of a dual taxonomy, one system being based on workers (and to a lesser extent queens), and the other based exclusively on males. This is an unsatisfactory state of affairs, and efforts must be made to collect males in association with workers, so that the available names in the two systems can be matched. It is undoubtedly the case that many real species-

level taxa will be found to have at least two names when worker-based species can be compared directly with male-based taxa, by comparison with samples containing both.

There has been, in the recent past, quite some speculation over whether the 'army ants', e.g. the dorylines, aenictines and ecitonines, are diphyletic or triphyletic. Through most of their history, when all of these groups were placed in one subfamily (Dorylinae) it was tacitly assumed, if it was ever considered at all, that the subfamily was monophyletic.

Brown (1954) was the first to suggest that diphyly was a possibility, and the huge study of Neotropical army ants by Borgmeier (1955) tended to support Brown's suggestion. The split was basically zoogeographical, the Old World dorylines and aenictines being separated from the New World ecitonines. The split was formalized by Brown (1973) and Snelling (1981), who recognized two subfamilies, Ecitoninae and Dorylinae, the latter containing both the dorylines and aenictines.

A detailed zoogeographical study by Gotwald (1979) suggested that triphyly was a possibility, and this suggestion was supported by Jessen's (1987) study of gastral exocrine glands. But diphyly was reverted to after Billen and Gotwald (1988) found that dorylines and aenictines had a crenellate Dufour gland lining, whilst in ecitonines the lining was simple. The condition of the gland lining remains unknown in Cerapachyinae, but I will predict that it is simple, as in Ecitoninae and Ponerinae. The current survey, based on comparative anatomy with emphasis on the abdomen, indicates that the group Ecitoninae + Cerapachyinae + Dorylinae + Aenictinae is monophyletic, and that the Leptanillinae is the sister-group of this assemblage. The reasons for these conclusions form the remainder of this paper.

The poneroid complex

This major division of the Formicidae includes the subfamilies Myrmicinae, Pseudomyrmecinae, Myrmeciinae, Ponerinae, Leptanillinae, Cerapachyinae, Dorylinae, Aenictinae and Ecitoninae.

The synapomorphy linking all these subfamilies is that first proposed by Taylor (1978) and recently reinforced by Ward (1990), concerning the structure of the fourth abdominal segment. In these subfamilies abdominal segment 4 is tubulate. This means that the presclerites and postsclerites of the segment are sharply delineated on both tergum and sternum, at least in the worker caste. The presclerites are somewhat to much narrower than the postsclerites and fit tightly within the posterior end of the third abdominal segment, with which they form an articulation with enhanced mobility. The presclerites and postsclerites are separated by at least a transverse groove or impression, or the separation may be more marked, with a sharp transverse rim followed by a girdling groove or constriction.

The remaining subfamilies within the Formicidae, namely Formicinae, Dolichoderinae, Aneuretinae and Nothomyrmeciinae, together form the formicoid complex. Currently they lack a synapomorphy and as a group are, therefore, paraphyletic with respect to the poneroid complex (Fig. 23).

The poneroid group

Within the poneroid complex the subfamilies Ponerinae + Leptanillinae + Cerapachyinae + Dorylinae + Aenictinae + Ecitoninae form the *poneroid group*.

The synapomorphy of these six subfamilies is tergosternal fusion of the third abdominal segment, a feature first noted by Gotwald (1969) and extended here to all included genera. In all workers and queens this fusion is complete, so that the tergal

and sternal portions of both the presclerites and postsclerites are firmly fused together. In males the condition is slightly different. Complete fusion is exhibited by most males but in the Ecitoninae only the presclerites of abdominal segment 3 are fused, the postsclerites remaining unfused and mobile. Whilst it is possible that the lack of fusion of the postsclerites in ecitonine males is a reversal from an earlier fused condition, it seems most parsimonious to accept that it is a persistent plesiomorphic state, and to treat it as such.

No synapomorphy has yet been detected to link those subfamilies of the poneroid complex that are excluded from the poneroid group (Myrmicinae, Myrmeciinae, Pseudomyrmecinae, Fig. 23) although each of those subfamilies has several apomorphies demonstrating that each represents a monophyletic taxon (e.g. Ward, 1990 for Pseudomyrmecinae).

The doryline section

Four subfamilies within the poneroid group form a monophyletic lineage and can be referred to as the *doryline section*: Cerapachyinae + Dorylinae + Aenictinae + Ecitoninae. These possess a series of eight synapomorphies which are listed below and discussed individually.

Apart from the four subfamilies of the doryline section the poneroid group also contains the subfamilies Leptanillinae and Ponerinae (Fig. 23). The phylogeny and classification of the Leptanillinae has recently been reviewed by Bolton (1990b). A single strong apomorphy has been found for the Ponerinae, tergosternal fusion of the fourth abdominal segment, which is universal in workers of all ponerine genera (B. Bolton, unpublished data).

Synapomorphies of doryline section subfamilies

The characters listed apply to workers unless otherwise stated.

1   Abdominal spiracles 5–7.
2   Metatibial gland.
3   Pygidium.
4   Metapleural gland orifice.
5   Helcium (all castes).
6   Furcula.
7   Cerci (males).
8   Subgenital plate (males).

1. *Abdominal spiracles 5–7* (Figs 1, 3, 4, 8, 13, 17, 20).   Workers throughout the doryline section have the spiracles of abdominal segments 5–7 shifted backwards on the posttergites. The spiracles are visible in ordinarily mounted specimens without artificial distension or disarticulation of the abdominal segments. This means that all abdominal spiracles, from segment 1 (propodeum) to segment 7 (pygidium) can be seen, unlike the situation which prevails in subfamilies Leptanillinae and Ponerinae. In these only the spiracles of abdominal segments 1–4 are normally visible. Sometimes in Ponerinae the spiracle of abdominal segment 5 is very close to the pre-posttergital boundary and may just be visible with very little distension of the abdomen. However, both here and in Leptanillinae the spiracles of abdominal segments 6 and 7 are always concealed. Concealment of abdominal spiracles 5–7 is the plesiomorphic condition (Bolton, 1990b).
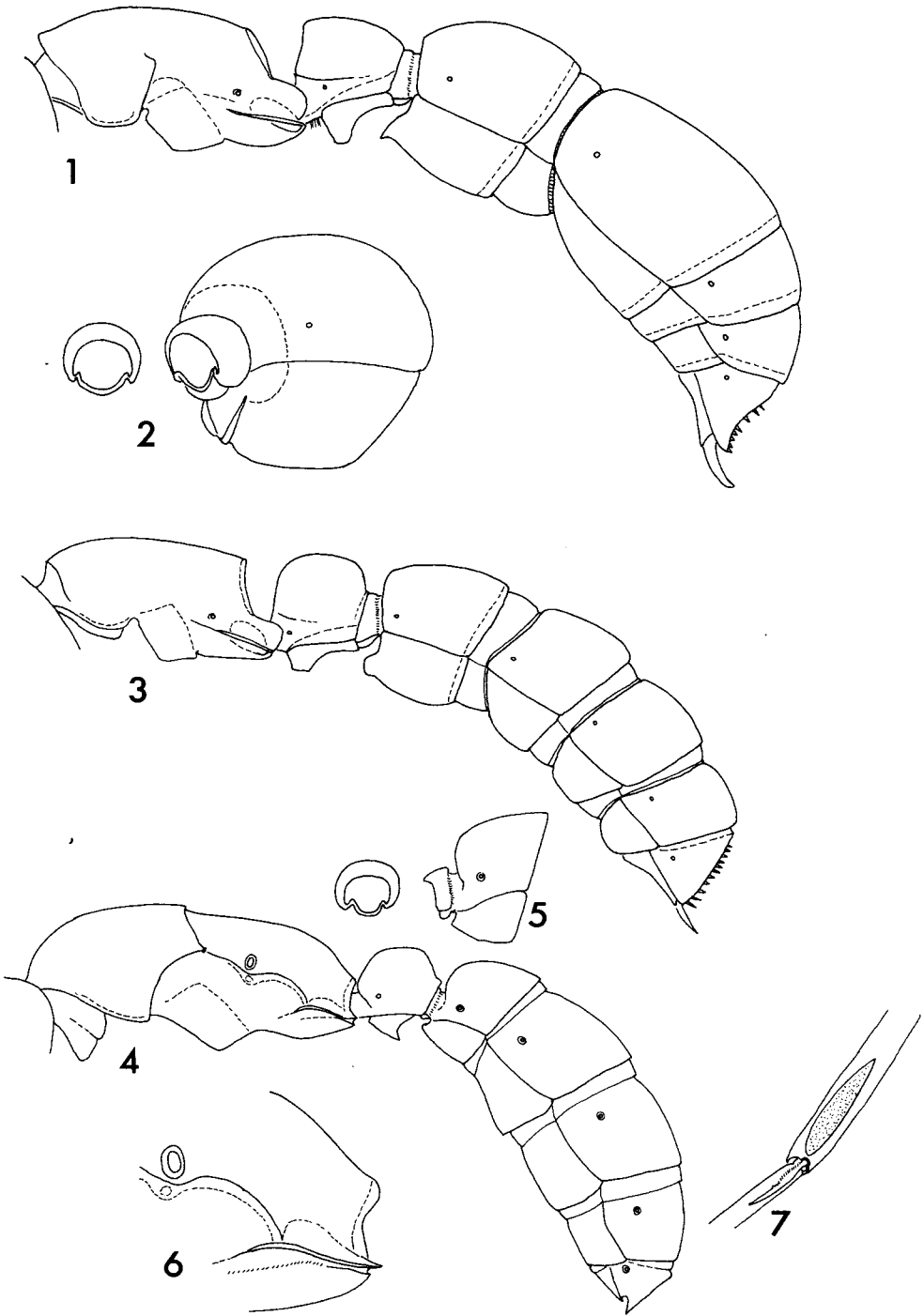
FIGS 1–7.   1–3: Cerapachyine workers: 1, thorax and abdomen of *Cerapachys sulcinodis*; 2,
third abdominal segment of *Sphinctomyrmex turneri* to show helcium, frontal view of
helcium offset; 3, thorax and abdomen of *Sphinctomyrmex rufiventris*. 4–7: *Dorylus opacus*
worker: 4, thorax and abdomen; 5, disarticulated abdominal segment 3, frontal view of
helcium offset; 6, propodeum and metapleuron; 7, metatibial gland. Sculpture, pilosity
and legs omitted.

2. *Metatibial gland* (Figs 7, 10, 15, 19, 22).   An apparently glandular area on the worker hind tibia, located ventrally on the leg segment immediately behind the metatibial median spur. The length and width of the gland varies considerably through the doryline section, being quite broad and short in some, but narrow and running almost the length of the ventral metatibia in others.

In its presumed most generalized form the gland appears as an elongate strip, running from close behind the spur towards the base of the tibia, and filled with or roofed by whitish to yellowish modified cuticle which appears as relatively dull, frequently granular to spongiform, tissue. This condition is seen in *Dorylus*, *Ctenopyga*, *Labidus*, and *Cheliomyrmex*, and is also present in some *Cerapachys*, *Sphinctomyrmex*, *Aenictus*, *Eciton*, and *Neivamyrmex*.

Modifications of the gland away from this state are as follows. The direction of evolutionary change is conjectural but the scheme outlined here fits current observations the best.

(i)   The outer surface of the glandular area is covered by an extremely thin sheet of translucent cuticle, the shape and size of the gland remaining clearly visible. The thin cuticular cover is glossy and may be convex, blister-like, or depressed. Tissue paler than the surrounding tibia may be visible through the translucent cuticle, which itself is usually paler in colour than tibial cuticle proper. (Some to many species in *Acanthostichus*, *Cylindromyrmex*, *Cerapachys*, *Sphinctomyrmex*, *Aenictus*, *Eciton*, and *Neivamyrmex*.)

(ii) The gland is completely secondarily concealed by thick cuticle so that it is not discernible externally. This is envisaged as a continuation of the process initiated in (i), where the originally thin cuticle covering the gland is progressively thickened. (Both species of *Nomamyrmex*, some *Cerapachys* and *Acanthostichus*, a few species of *Neivamyrmex*.)

In some *Cerapachys* species the gland retains an open pit, or a pit in a depression, immediately behind the spur. This is presumably an orifice for the gland products, but in some species even this is lost. *Leptanilloides* appear to fall here, but suitably prepared material of this extremely rare genus is not available. Of the genera included in the doryline section subfamilies, the greatest variation in form of the metatibial gland is seen in *Cerapachys*.

(iii) In the cerapachyine genus *Simopone* either a patch of pale thin cuticle occurs behind the metatibial spur or no external sign of the gland remains. However, the metabasitarsus has a longitudinal groove or trench ventrobasally, which appears glandular in some species. I suspect that this is a development separate from the metatibial gland, rather than a shifting of the gland to an adjacent leg segment. Philip Ward has informed me that in Pseudomyrmecinae, and some other members of the poneroid complex, there is a metabasitarsal groove, mostly lost in higher poneroids. It seems reasonable to suspect that the metabasitarsal groove or trench seen in *Simopone* is a retention of or development from this condition, rather than an autapomorphy of this genus.

Outside the doryline section, but within the poneroid group, the metatibial gland in the form described above is absent. An analogous but apparently not homologous glandular area is present on the metatibia of some Ponerini (Ponerinae). In this tribe a roughly oval-shaped glandular patch can be seen in about 25 species of *Pachycondyla* (in the broad sense of Brown, 1973), in four species of *Hagensia* (a genus almost certainly a junior synonym of *Pachycondyla*), and in most species of the closely related
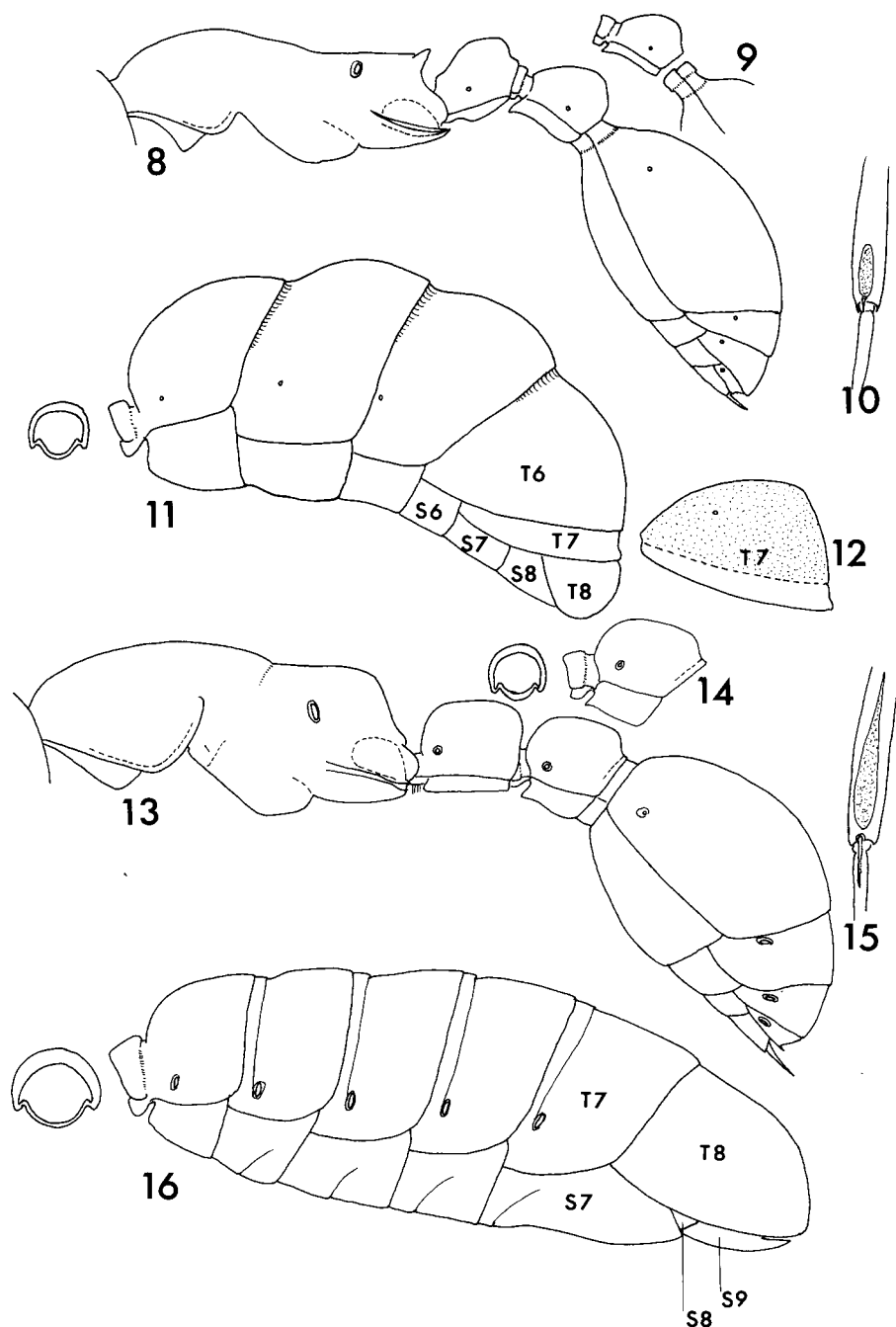
FIGS 8–16.   8–10: *Aenictus dentatus*, worker: 8, thorax and abdomen; 9, disarticulated abdominal segment 3 and anterior end of segment 4; 10, metatibial gland. 11–12: *Aenictus feae*, male: 11, abdominal segments 3–8 (S = sternite, T = tergite), frontal view of helcium offset; 12, isolated tergite 7 to show internal desclerotised portion (stippled). 13–15: *Neivamyrmex nigrescens*, worker: 13, thorax and abdomen; 14, disarticulated abdominal segment 3, frontal view of helcium offset; 15, metatibial gland. 16: *Neivamyrmex harrisi*, male: abdominal segments 3–8 (S = sternite, T = tergite), frontal view of helcium offset. Sculpture, pilosity and legs omitted.

genus *Diacamma*. In all of these the glandular patch is lateral, on the inner face of the metatibia basally and away from the articulation of the main spur. Metatibial glands are lacking in other ponerines, in leptanillines, and elsewhere throughout the Formicidae; their absence is the plesiomorphic state.

3. *Pygidium* (Figs 1, 3, 4, 8, 13, 17, 20). Gross modification of the worker pygidium (abdominal tergite 7) is absent in most subfamilies of Formicidae but universally present in the doryline section. A simple relatively large arched pygidium, which is convex in both directions and without adornment or armament, is plesiomorphic in the Formicidae as a whole. In the doryline section (Cerapachyinae + Dorylinae + Aenictinae + Ecitoninae) the pygidium is always much modified.

Specialization of the pygidium takes two forms, the second seemingly derived from the first. The first, seen in Dorylinae and Cerapachyinae (except *Leptanilloides*), leaves the sclerite relatively large. In these subfamilies the pygidial posttergite slopes steeply posteriorly and tends to be flattened or even concave over part or most of its length. Usually the lateral rims of the flattened or depressed area are marginate or otherwise emphasized, and some form of dentiform or spiniform armament is present on the rims. Earlier I was of the opinion (Bolton, 1990a) that this pygidial form was not a synapomorphy of Cerapachyinae + Dorylinae, but now I suspect that it may be.

The second form of pygidial modification, seen in Aenictinae, Ecitoninae, and the cerapachyine genus *Leptanilloides*, is more uniform and appears to be a reduction from that just described. In these taxa the pygidium is small or very small, usually reduced to a narrow U-shaped sclerite, frequently with a shallow transverse impression running its width at about its midlength, or with its short dorsum somewhat concave. In some species of *Labidus* and *Neivamyrmex* (Ecitoninae) the apex of the pygidium has one or more pairs of small spines or teeth, reminiscent of the armament characteristic of dorylines and most cerapachyines. Whether this is a separate development or a retained character cannot be decided at present. I suspect that the ecitonine–aenictine–*Leptanilloides* form of pygidium has evolved independently in each taxon from a cerapachyine–doryline-like ancestral form, but would be hard-pressed to prove it.

As pointed out previously (Bolton, 1990a) only one other poneroid, *Pachycondyla crassinoda*, has a doryline-section-like pygidium, although a number possess armament on the hypopygium (abdominal sternite 7). *P. crassinoda* is a ponerine with all the apomorphies of the tribe Ponerini, and is the only member of its genus (and its subfamily) to have the pygidium so modified. It shows no other doryline section specializations and therefore the pygidial form must be regarded as an autapomorphy of *P. crassinoda*, and not a homologue of the doryline section pygidium.

4. *Metapleural gland orifice* (Figs 1, 3, 4, 6, 8, 13, 17, 20). The evolution of the metapleural gland is one of the major features of the Formicidae, and has been cited as an apomorphy of the family. Primitively the gland orifice is envisaged as a simple pore, without external adornments, situated in the lower posterior corner of the metapleuron above and slightly behind the metacoxa, and posterior to the metacoxal cavity in ventral view. Developments from this condition involve changes in shape, size and position of the orifice, the acquisition of various cuticular flanges, rims, tumuli, or plates around or over the orifice, and secondary loss of any visible orifice for the gland or loss of the gland itself in some groups.

The structure of the gland orifice in the doryline section is very characteristic and highly specialized. The orifice retains its primitive position in the extreme lower corner
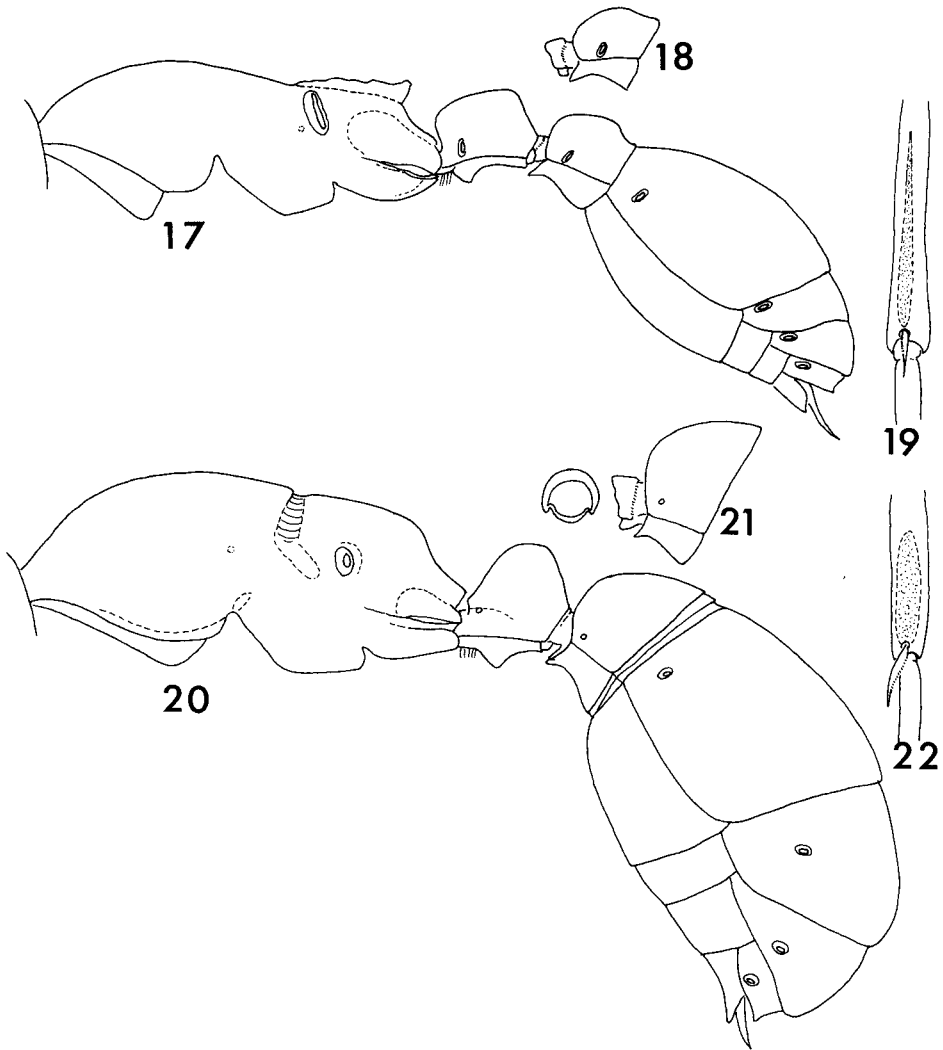
FIGS 17–22.   17–19: *Eciton hamatum*, worker: 17, thorax and abdomen: 18, disarticulated
abdominal segment 3; 19, metatibial gland. 20–22: *Cheliomyrmex andicolus*, worker: 20,
thorax and abdomen; 21, disarticulated abdominal segment 3, frontal view of helcium
offset; 22, metatibial gland. Sculpture, pilosity and legs omitted.

of the side, and it opens laterally. However, the orifice is covered or masked from above
by a ventrally directed cuticular flange or lip so that it is usually not visible in profile,
but can be seen in ventrolateral view by looking upwards, under the projecting flange
or lip. The cuticular flange or lip which conceals the orifice is extended obliquely
upwards in anterior direction, ascending the side of the metapleuron as a ridge, narrow
cuticular lamella or carina. It is subtended and paralleled on the side by a narrow
shallow impression. In some taxa the cuticular ridge is quite broad, lamellate, directed
ventrally and partially or entirely concealing the impression. Elsewhere it is
represented only as a low carina which leaves the impression exposed. I suspect that the
products of the metapleural gland spread along this impression and are scraped off by

the ant or allowed to evaporate. The side of the metapleuron below the gland orifice projects slightly outwards forming a prominence or small plate immediately below the orifice. The cuticular rim of this area anteriorly may form the base of the ascending impression. Finally either the dorsal cuticular lip or the ventral small plate, above and below the orifice respectively, may project backwards slightly beyond the posterior limits of the metapleuron.

5. *Helcium* (Figs 2, 5, 9, 11, 14, 16, 18, 21). The four subfamilies of the doryline section (Cerapachyinae, Dorylinae, Aenictinae, Ecitoninae) exhibit a unique and very characteristic form of the helcium (Bolton, 1990a) in all castes and both sexes. The helcium sternite (i.e. the presternite of the third abdominal segment which articulates within the ventral portion of the posterior foramen of abdominal segment 2) is well developed and convex, bulging ventrally. In standard card point-mounted specimens the convex helcium sternite is usually clearly visible without artificial distension of the segments, and without disarticulation. The sternite is fused on each side to the inner surface of the inverted U-shaped tergal collar, some distance above the apices of the tergal arms. Elsewhere in the poneroid complex, and generally in the Formicidae as a whole, the helcium sternite is reduced and concealed by the inverted U-shaped arms of the tergite, and cannot normally be seen without disarticulation of abdominal segments 2 and 3. In the Myrmicinae the sternite of the helcium forms a convex plate which is attached at the ventral apices of the tergal arms but is not fused to them.

Initially I was of the opinion (Bolton, 1990a) that members of the doryline section, represented in that paper by the Cerapachyinae, exhibited the plesiomorphic helcium state. This was based on the reasoning that the helcium in cross-section showed the approximate shape of a reduced segment, with tergosternal fusion. Since then I have had a number of very useful exchanges with Philip Ward in which we discussed this feature in some detail. His hypothesis, now accepted, is that in the plesiomorphic condition the helcium sternite is relatively broad in anterior view, and slightly convex ventrally, as is seen in most amblyoponine Ponerinae. If this is the case then the condition seen in the doryline section subfamilies is apomorphic by decreased width and increased convexity. The condition seen elsewhere in the Formicidae, where the helcium sternite is much reduced and lapped around by the tergite, is also apomorphic.

6. *Furcula.* The furcula is a small inverted Y-shaped sclerite associated with the base of the sting. It appears to be derived from the fused bases of the gonapophyses and projects dorsally internally from the sting base (Kugler, 1978 and included references).

Within the poneroid complex the presence of the furcula is plesiomorphic. The sclerite is found in the sting apparatus of subfamilies Myrmeciinae and No-thomyrmeciinae (Kugler, 1980), Ponerinae (Hermann, 1969) and Myrmicinae (Kugler, 1978). The furcula appears, apomorphically, to be universally lost in the four subfamilies of the doryline section (Hermann, 1969 and current investigation).

Among members of the poneroid group of subfamilies only *Simopelta*, outside the doryline section, has lost the furcula (Hermann, 1968). Indubitably this is a parallelism between *Simopelta* and the doryline section subfamilies, as the former possesses the major apomorphy of the subfamily Ponerinae (tergosternal fusion of abdominal segment 4) and the apomorphies of tribe Ponerini within that subfamily. Conversely, *Simopelta* lacks all apomorphies of the doryline section except for this convergent loss of the furcula.

7. *Cerci* (males).   The absence of cerci from the fully retractile male genitalia is one of the oldest characters invoked to isolate the doryline section subfamilies from the other poneroids. It dates back at least to Emery (1901) and is consistent. Presence of cerci on genitalia which are not fully retractile is the plesiomorphic state. Loss of the cerci and the acquisition of the ability to retract the genitalia completely into the abdominal cavity are apomorphic developments.

Cerci are absent in known males of subfamily Leptanillinae, but here the genitalia are hypertrophied, sometimes bizarrely modified, and not capable of retraction into the abdomen. Cercal loss in leptanillines is therefore most likely to be a parallelism.

8. *Subgenital plate* (males).   The subgenital plate (sternite of the ninth abdominal segment) is biaculeate in all members of the doryline section, simple elsewhere throughout the poneroids except for males of *Nothomyrmecia macrops* (Taylor, 1978) and *Paraponera clavata* (Brown, 1958). Like the above, this is another character invoked very early (Emery, 1901) to isolate the doryline-like groups.

It is just possible, given its occurrence in the two species mentioned above, that the biaculeate subgenital plate is a symplesiomorphy among the poneroids, with apomorphic reduction to a simple form almost universal elsewhere in the group. I do not favour this hypothesis, as it seems most parsimonious to accept that a biaculeate subgenital plate is a synapomorphy of the doryline-section subfamilies, which has been independently evolved in the two other, isolated, species. The alternative seems hard to digest, especially in the case of *Paraponera clavata*, where one would have to postulate the independent loss of a biaculate plate in every other Ponerinae lineage, including all other members of the tribe Ectatommini, to which *P. clavata* belongs.

Conclusion
These eight synapomorphies demonstrate the monophyly of the doryline section subfamilies within the poneroid group of subfamilies.

Definition of the doryline section
Ant subfamilies with the following combination of characters.

Workers
1. Clypeus reduced, narrow from front to back especially in front of the antennal insertions, bringing the antennal sockets close to the anterior margin of the head. (See notes below.)
2. Antennal socket horizontal, in the plane of the transverse axis of the head, mostly or wholly exposed in full-face view. (See notes below.)
3. Frontal lobes rarely weakly present (some Cerapachyinae) but generally vestigial to absent; usually very narrow vertical carinae are all that are present. (See notes below.)
4. Narrow neck joining condylar bulb of antennal scape to shaft of scape proper straight, not sharply angled or bent downwards in frontal or full-face view. (See notes below.)
5. Promesonotal suture usually absent, if present the suture is normally rigidly fused and inflexible (*Dorylus*, some *Cerapachys*); only extremely rarely is a somewhat flexible suture retained (*Leptanilloides*). (See notes below.)
6. Metapleural gland orifice with associated structures specialized (synapomorphy 4 above).
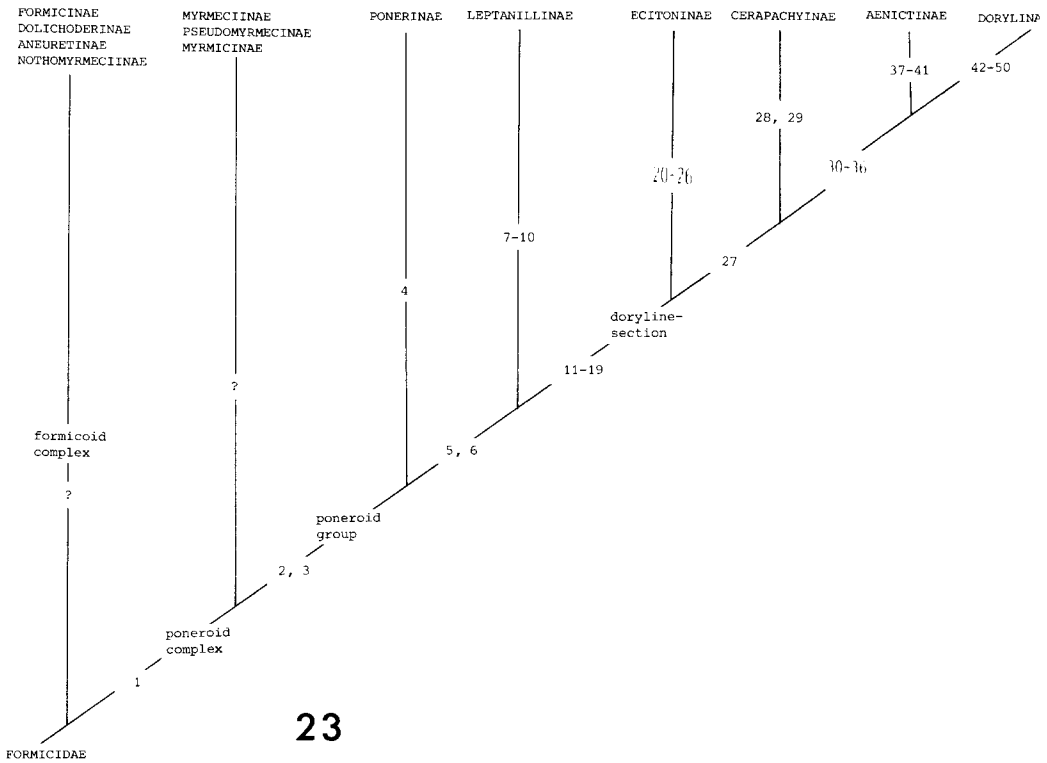
FIG. 23. Phylogeny of doryline section and related subfamilies implied from this study. Index of numerically represented apomorphies in Fig. 23 as follows. Apomorphies not discussed in the text are followed by their plesiomorphic states, in parentheses. Castes and sexes indicated by w = worker, q = queen, m = male. 1, Abdominal segment 4 tubulate (w); 2, presclerites of abdominal segment 3 fused (m); 3, postsclerites of abdominal segment 3 fused (w,q); 4, tergosternal fusion of abdominal segment 4 (w,q); 5, metacoxal cavities closed (w,q,m) (metacoxal cavities open or sutured); 6, jugal lobe of hindwing lost (m) (jugal lobe present); 7, sternite of helcium reduced and retracted (w); 8, spiracle of abdominal segment 3 large and shifted far forward (w,q) (spiracle not enlarged, in usual position); 9, abdominal segment 2 with tergosternal fusion (w) (not fused); 10, pterostigma absent (m) (present); 11, abdominal spiracles 5–7 exposed (w); 12, metatibial gland present (w); 13, pygidium specialized (w); 14, metapleural gland orifice specialized (w); 15, sternite of helcium convex and bulging ventrally (w,q,m); 16, furcula lost from sting (w); 17, genitalia completely retractile (m); 18, cerci lost from genitalia (m); 19, abdominal sternite 9 biaculeate (m); 20, orifice of abdominal spiracles 4–7 directed posteriorly (w); 21, orifice of abdominal spiracles 5–7 not round (w); 22, strongly developed presclerites on abdominal segments 5–7 (m); 23, abdominal sternite 7 hypertrophied (m); 24, abdominal sternite 8 internalized and bilobate (m); 25, abdominal sternite 9 mostly or entirely exposed (m); 26, basal ring of genital capsule hypertrophied (m); 27, postsclerites of abdominal segment 3 fused (m); 28, propodeal spiracle shifted low down and posteriorly on sclerite (w,q); 29, enhanced mobile ball-joint of presclerites of abdominal segment 4 (w,q); 30, Dufour gland epithelium crenellate (w); 31, pupae naked (w,q,m) (pupae in cocoons); 32, propodeal spiracle elliptical to slit-shaped (m); 33, abdominal sternite 8 with long anterior apodemes (m); 34, basal ring of genital capsule extremely reduced (m); 35, eyes lost (w) (present); 36, proprioceptor zone on abdominal sternite 2 reduced or absent (w) (zone conspicuously present); 37, abdominal spiracle 3 shifted posteriorly (w); 38, postsclerites of abdominal segment 4 forming a narrow anterior neck (w); 39, abdominal tergite 6 enlarged (m); 40, abdominal tergite 7 mostly internalized and desclerotized (m); 41, abdominal tergite 8 bulging outward (m); 42,

7. Metatibial glands present (synapomorphy 2 above).

8. Metacoxal cavities closed; cuticular annulus around each cavity complete, the annulus not broken medioventrally or with a suture traversing the annulus from the metacoxal cavity to the cavity in which the petiole articulates.

9. Waist of one or two separated segments. Second abdominal segment (petiole) sessile to subsessile, the tergite and sternite not fused; sternite with a simple posterior margin and simple articulation to third abdominal segment. (See notes below.)

10. Abdominal stridulatory system absent.

11. Abdominal spiracles 5–7 shifted backwards, on posttergites, not concealed by preceding tergites and visible without distension of the segments (synapomorphy 1 above).

12 Helcium sternite large and convex, bulging ventrally, visible in profile in normally mounted specimens; tergite of helcium lacking a deep U- or V-shaped notch in its dorsal margin anteriorly (synapomorphy 5 above).

13. Abdominal segment 3 with tergosternal fusion (apomorphy of poneroid group, discussed above).

14. Abdominal segments 4–7 without tergosternal fusion.

15. Abdominal segment 4 tubulate anteriorly (apomorphy of poneroid complex, discussed above).

16. Pygidium (tergite of abdominal segment 7) modified and specialized (synapomorphy 3 above).

17. Furcula absent from sting apparatus (synapomorphy 6 above); sting always present but sometimes reduced and not functional as a weapon (*Dorylus*).

Notes on worker characters. Characters synapomorphic in the doryline section subfamilies are given in detail prior to the definition. A few others noted in the definition merit discussion.

(1) Extensive reduction of the clypeus is universal in the Dorylinae, Aenictinae and Ecitoninae but the reduction is morphoclinal in the Cerapachyinae. In the cylindromyrmecine cerapachyines the clypeus remains relatively broad; in acanthostichines it is narrower and in tribe Cerapachyini narrower still. The condition in *Leptanilloides* shows the closest approach to the other subfamilies, where the antennal sockets almost abut the anterior margin of the head. A parallel reduction in clypeal width is seen in Leptanillinae where the clypeus is relatively broad in Anomalomyrmini, reduced in Apomyrmini and extremely narrow in Leptanillini.

(2–4) The possession of horizontal antennal sockets is a symplesiomorphy retained by the doryline section subfamilies (and by Leptanillinae), as is the presence of a straight neck-like section between the condylar bulb of the scape and the scape shaft. In Ponerinae horizontal sockets are present but the neck between condylar bulb and scape shaft is sharply bent or angled downwards (best seen in anterior view). This appears to be in response to the development of frontal lobes above the antennal

propodeal spiracle subtended by longitudinal impression (w); 43, metapleural lobes lost (w); 44, sternite of abdominal segment 2 shortened (w); 45, presclerites of abdominal segments 5–7 strongly differentiated (w); 46, sting reduced and non-functional as weapon (w,q); 47, abdominal spiracles 2–8 slit-shaped (m); 48, bursa copulatrix permanently open (q); 49, abdominal sternite 7 hypertrophied, bilobate posteriorly (q); 50, spiracles of abdominal sternite 8 visible through bursa copulatrix (q).

sockets. Whilst protecting the scape articulations the presence of frontal lobes compels the scapes to project sideways from their insertions rather than straight out, and also prevents the scapes from being directed vertically from their insertions. Elsewhere in the poneroid complex the antennal sockets are vertical (at a near right-angle to the plane of the head's transverse axis) or are inclined, with their inner margins, closest to the cephalic midline, elevated above the level of the outer margin. This angling of the sockets allows the scapes to project laterally from beneath the frontal lobes without the need for a bend in the scape neck, and thus achieves the scape shaft attitude seen in the Ponerinae but by a different evolutionary mechanism.

(5) In ants of the doryline section the promesonotal suture is much modified by reduction. The suture retains flexibility only in *Leptanilloides* (plesiomorphic). In Dorylinae and some Cerapachyinae the track of the suture may be clearly defined, but here the pronotum and mesonotum are firmly fused together so that the suture is rigid and immobile. Elsewhere in the section reduction is taken still further, the site of the former suture being reduced to a weakly marked cuticular impression or completely lost (most Cerapachyinae, all Aenictinae and Ecitoninae).

In other subfamilies of the poneroid group the suture is plesiomorphically generally well developed and freely flexible. It is universally so in Leptanillinae and in the ponerine tribes Ponerini, Amblyoponini and Typhlomyrmecini. However, one genus of tribe Platythreini (*Probolomyrmex*) has lost the suture, and in tribe Ectatommini the situation is quite complex. The tribe as a whole shows a finely stepped morphoclinal reduction of the suture, with the 'lower' ectatommines (*Acanthoponera*, *Heteroponera*) having it complete and mobile. Intermediate genera, for example *Gnamptogenys*, show presence, fusion, diminution or loss of the suture, whilst 'higher' ectatommines (*Proceratium*, *Discothyrea*) have no trace of it.

(9) It seems reasonable to assume that the development of a separated postpetiole, by which I mean the isolation and usually reduction of the third abdominal segment, has evolved independently at least five times, and possibly even seven times, in the Formicidae. A differentiated postpetiole is always present in workers of Myrmeciinae, Myrmicinae, Pseudomyrmecinae, and Aenictinae. It is developed in some, but not all, Leptanillinae, Ecitoninae, and Cerapachyinae. The minimal figure of five is arrived at by accepting the possibility that postpetioler isolation may represent a unique event in Myrmeciinae + Myrmicinae + Pseudomyrmecinae, but is certainly independently achieved in the other subfamilies.

Support for the second part of this assumption is given by the fact that in Aenictinae, some Ecitoninae, and some Leptanillinae there is worker/queen dimorphism in the number of waist segments (see under discussion of queens). Further, in Leptanillinae, Cerapachyinae, and Ecitoninae the workers of some taxa have only one separated waist segment whilst those of others have two. Support for the first part of the assumption is not yet available, but Ward (1990) suggests that Pseudomyrmecinae and Myrmicinae may be sister-groups.

Queens

Characters 1–4, 8, 9, and 12–14 of the worker diagnosis also apply to the queens. Promesonotal suture (5) is as in workers in Dorylinae, Aenictinae and Ecitoninae, but is usually present and flexible in Cerapachyinae, only rarely fused. Except in cerapachyines and aenictines, where it is similar to or the same as in workers, the metapleural gland orifice (6) is simpler in queens than in workers. The metatibial gland (7) is absent from queens. The number of separated waist segments (character 9) is the

same in queens and workers of Cerapachyinae, either one or two being present; but worker/queen dimorphism is characteristic of several taxa in the doryline section (and also occurs in the leptanilline tribe Leptanillini). In *Dorylus* and *Cheliomyrmex* workers and queens each have a single waist segment (petiole, = abdominal segment 2), but in *Eciton, Labidus, Nomamyrmex, Neivamyrmex,* and *Aenictus* the queen has one waist segment (petiole), the workers two (petiole + postpetiole, = abdominal segments 2 and 3). Character (11), abdominal spiracles 5–7, is the same in workers and queens of Cerapachyinae, but shows much variation in the other three subfamilies, often being visible but sometimes remaining concealed. A tubular fourth abdominal segment (15) is universal in cerapachyine queens but may be secondarily reduced or lost elsewhere. Similarly, in the form of the pygidium (16) cerapachyine queens match their workers, but elsewhere the sclerite is variously modified. The condition of character 17 is not known in queens.

Queens of the subfamily Cerapachyinae mostly retain a generalized poneroid habitus, but throughout the Dorylinae, Aenictinae and Ecitoninae all known queens are ergatoid dichthadiigynes of monstrous and bizarre appearance. In these forms the eyes are vestigial or more usually absent, the mandibles are falcate, the head swollen and subglobular; the alitrunk is large, without trace of wings; the petiole is hypertrophied and the gaster (abdominal segments 3–7) is enormously enlarged (Gotwald, 1982; Hölldobler and Wilson, 1990).

Full dichthadiigyny has not yet been detected in the Cerapachyinae, where in general the queen reflects the morphology of the workers but possesses ocelli, has larger eyes, and a full complement of flight sclerites. However, Brown (1975) records the presence of ergatoid queens in some *Cerapachys* species, and of ergatoid to subdichthadiigyne queens in both *Sphinctomyrmex* and *Acanthostichus.*

It is safe to conclude that dichthadiigyny is not a synapomorphy of the doryline section subfamilies. In its fully developed form it is lacking in cerapachyines, where normal alate queens are the rule, but several lines appear to be evolving towards dichthadiigyny in this subfamily. Outside the doryline section evolution towards a subdichthadiigyne or fully dichthadiigyne queen has independently occurred several times, for instance in *Leptanilla* (Leptanillinae; Baroni Urbani, 1977; Bolton, 1990b) and in the Ponerinae genera *Leptogenys* (Wilson, 1958) *Onychomyrmex* (Brown, 1960), and *Simopelta* (Gotwald and Brown, 1967).

It can be postulated that the evolution of dichthadiigyny is a result of the adoption of a nomadic and group-predatory lifeway. (The reverse may also be postulated, that the evolution of a dichthadiiform queen initiates the development of nomadism; but this seems most unlikely.) Therefore could the appearance of universal dichthadiigyny be the result of a single evolutionary event in a group consisting of Dorylinae + Aenictinae + Ecitoninae, within the doryline section? I tend to think not, because apart from the fact that the condition has arisen independently in parts of two subfamilies outside the doryline section, and is lacking in the cerapachyines within the section, the Ecitoninae appear to be more widely taxonomically separated from the group Cerapachyinae + Dorylinae + Aenictinae than any member of that group is from the other two.

Males

Characters 2–4, 8, 10, 12, and 14 as in workers. The width of the clypeus (1) tends to be similar or greater in males than in the female castes. A flexible promesonotal suture (5) is always present but metapleural glands (6) and metatibial glands (7) are lacking.

The waist (9) is one-segmented throughout Dorylinae, Aenictinae and Ecitoninae, but is sometimes of two segments in Cerapachyinae. Spiracles of abdominal segments 5–7 (character 11) may be visible or concealed; in some taxa the segments are more telescopic than in workers and it is difficult to tell what is the usual state of affairs. The spiracle of abdominal segment 8 appears always to be concealed. Tergosternal fusion of the third abdominal segment (13) is complete in cerapachyines, dorylines and aenictines, but only the presclerites are fused in Ecitoninae males, the postsclerites remaining free.

In all males of the doryline section mandibles are well developed, varying from triangular to enormously elongate and falcate; in all cases mandibles are edentate except for the apical tooth. Eyes and ocelli are universally present, the former may be very large. On the alitrunk a few cerapachyines retain notauli, but elsewhere these are absent. Venation is strong to reduced; a pterostigma is always present, large in cerapachyines and aenictines but reduced in ecitonines and dorylines. The hindwings lack a jugal (= anal) lobe. Characters of the male genitalia include the ability to retract them completely into the abdomen, loss of cerci and the development of a biaculeate subgenital plate (abdominal sternite 9), discussed under the synapomorphies of the doryline section.

Male cerapachyines approximate to the female castes in size, and in general have a rather ponerine habitus. In other subfamilies males tend to be massive, as compared to workers, and may be quite bizarre, as illustrated by the strange 'sausage fly' males of *Dorylus*.

Monophyly of the doryline section subfamilies
Subfamily CERAPACHYINAE

Cerapachysii Forel, 1893: 162. (Ponerinae, tribe Cerapachysii.)
   Type-genus: *Cerapachys* Smith, 1857: 74.
Cerapachyi: Emery, 1895: 765; Emery, 1901: 34. (as a tribe of subfamily Dorylinae.)
Cerapachyinae: Wheeler, 1902: 185. (As a group within subfamily Ponerinae.)
Prodorylinae Emery, 1909: 355. (Ponerinae, Hauptgruppe Prodorylinae.) Unavailable name, not based on a genus-level taxon (see Wheeler, 1920: 51).
Cerapachyinae: Wheeler, 1920: 51. (Raised to subfamily status.)
Eusphinctinae Clark, 1951: 15 (diagnosis in key). Type-genus: *Eusphinctus* Emery, 1893: cclxxv. (Junior synonym of *Sphinctomyrmex* Mayr, 1866: 895; synonymy by Brown, 1975: 31.) Synonymy by Bolton, 1990a: 66.
Cerapachyinae: Brown, 1975: 14. (As a synonym of Ponerinae.)
Cerapachyinae: Bolton, 1990a: 66. (Reinstated as subfamily.)

Diagnosis.   With apomorphic characters of poneroid complex, poneroid group, and doryline section as given above, and with the following autapomorphies within these limits. (Plesiomorphic states exhibited by other doryline section subfamilies given in parentheses.)

(i) Propodeal spiracle in worker and queen shifted to a position low down on the side of the sclerite, and shifted posteriorly so that it is at or behind the midlength (Figs 1, 3). (Propodeal spiracle high on side of sclerite and far forward.)

(ii) Worker and queen with enhanced ball-joint formed from presclerites of abdominal segment 4, particularly by the presternite (Figs 1, 3). (Enhanced ball-joint absent. Extreme reduction of presclerites of abdominal segment 4 by separation of segment 3 as a postpetiole is an alternative apomorphic condition seen in some Ecitoninae and all Aenictinae.)

Included genera and number of species examined in this survey.

Tribe Acanthostichini. Genus: *Acanthostichus* (6).
Genus: *Ctenopyga* (1).
Tribe Cylindromyrmecini. Genus: *Cylindromyrmex* (3).
Tribe Cerapachyini. Genus: *Cerapachys* (94).
Genus: *Leptanilloides* (2).
Genus: *Simopone* (8).
Genus: *Sphinctomyrmex* (10).

For systematic, taxonomic and other information see Brown (1975), Bolton (1990a).

Subfamily ECITONINAE

Ecitonii Forel, 1893: 163. (As a tribe of subfamily Dorylinae.)
  Type-genus: *Eciton* Latreille, 1804: 179.
Metadorylinae Forel, 1917: 240. (Dorylinae, section Metadorylinae.) Unavailable name, not based on a genus-level taxon.
Ecitoninae: Brown, 1973: 166. (Raised to subfamily.)

Diagnosis. With apomorphic characters of poneroid complex, poneroid group, and doryline section as given above, and with the following autapomorphies within these limits. (Plesiomorphic states exhibited by other doryline section subfamilies given in parentheses.)

(i) Abdominal spiracles 4–7 in workers with orifice directed posteriorly. (Orifices of abdominal spiracles 4–7 directed laterally.)
(ii) Abdominal spiracles 5–7 in workers with orifice oval to slit-shaped, not round. The cuticular annulus surrounding each spiracular meatus broader anteriorly than posteriorly (Figs 13, 17, 20). (Round spiracular orifices on abdominal segments 5–7, the cuticular annulus surrounding each spiracular meatus of approximately equal width all round.)
(iii) Sharply defined presclerites present on abdominal segments 5–7 of males (Fig. 16). (Abdominal segments 5–7 of males without sharply defined presclerites.)
(iv) Abdominal sternite 7 of males hypertrophied (Fig. 16). (Male abdominal sternite 7 of normal size, in proportion with rest of abdomen.)
(v) Abdominal sternite 8 of males internalized and bilobate apically (Fig. 16). (Male abdominal sternite 8 exposed and simple apically.)
(vi) Abdominal sternite 9 (subgenital plate) of males mostly or entirely exposed (Fig. 16). (Male abdominal sternite 9 concealed or at most with distal part of apical fork projecting.)
(vii) Basal ring of male genital capsule hypertrophied. (Basal ring of male genital capsule of moderate size.)

Included genera and number of species examined in this survey.

Tribe Cheliomyrmecini. Genus: *Cheliomyrmex* (3).
Tribe Ecitonini Genus: *Eciton* (10).
Genus: *Labidus* (3).
Genus: *Neivamyrmex* (42).
Genus: *Nomamyrmex* (2).

For taxonomic, systematic and other information see Borgmeier (1955), Watkins (1976), Schneirla (1971), Gotwald (1982).

Subfamily **DORYLINAE**

Dorylida Leach, 1815: 147. (Mutillarides. Family 1. Dorylida.)
   Type-genus: *Dorylus* Fabricius, 1793: 365.
Dorylidae: Haliday, 1836: 331.
Dorylinae: Dalla Torre, 1893: 1. (As subfamily of Formicidae.)
Eudorylinae Forel, 1917: 239. (Dorylinae section Eudorylinae.) Unavailable name, not based on
   a genus-level taxon.

Diagnosis. With apomorphic characters of poneroid complex, poneroid group and
doryline section as given above, and with the following autapomorphies within these
limits. (Plesiomorphic states exhibited by other doryline section subfamilies given in
parentheses.)

  (i) Propodeal spiracle in workers subtended by a longitudinal impression (Figs 4, 6).
       (Worker propodeal spiracle not subtended by a longitudinal impression.)
 (ii) Metapleural lobes (= inferior propodeal plates) lost in workers (Figs 4, 6).
       (Metapleural lobes present in workers.)
(iii) Sternite of abdominal segment 2 (petiole) short in workers, so that abdominal
       segments 3–7 (gaster) are held at a downflexed angle with respect to petiole.
       (Sternite of petiole relatively long, the gaster aligned with the petiole.)
 (iv) Abdominal segments 5–7 of worker with strongly differentiated pre- and
       postsclerites (Fig. 4). (Pre- and postsclerites of abdominal segments 5–7 not or
       extremely feebly defined in worker.)
  (v) Sting of worker reduced and non-functional as a weapon. (Sting of worker large
       and functional as a weapon.)
 (vi) Bursa copulatrix of queen permanently open. (Bursa copulatrix closed.)
(vii) Abdominal sternite 7 (hypopygium) of queen hypertrophied, extremely long and
       bilobate posteriorly. (Hypopygium of queen not hypertrophied, not bilobate.)
(viii) Abdominal sternite 8 of queen sclerotized, the plate and its spiracles visible in
       posterior view through the permanently open bursa copulatrix. (Abdominal
       sternite 8 of queen desclerotised, not visible.)

Included genus and number of species examined in this survey.

Tribe Dorylini.   Genus: *Dorylus* (35).

The genus *Dorylus* has six currently recognized subgenera, namely *Dorylus*, *Dichth-*
adia, *Anomma*, *Typhlopone*, *Rhogmus*, and *Alaopone*, some or all of which may be
worthy of elevation to genus-level. For taxonomic, systematic and other information
see Raignier and van Boven (1955), Wilson (1964), Gotwald (1982), Gotwald and
Schaefer (1982), Barr and Gotwald (1982), Hölldobler and Wilson (1990).

Subfamily **AENICTINAE** stat. n.

Aenictii Emery, 1901: 36. (As tribe of subfamily Dorylinae.)
   Type-genus: *Aenictus* Shuckard, 1840: 266.
Aenictii: Emery, 1910: 28. (As synonym of Ecitoni.)
Aenictini: Borgmeier, 1955: 15. (Reinstated as a tribe of subfamily Dorylinae.)

Diagnosis. With apomorphic characters of poneroid complex, poneroid group and
doryline section as given above, and with the following autapomorphies within these
limits. (Plesiomorphic states exhibited by other doryline section subfamilies given in
parentheses.)

  (i) Spiracle of abdominal segment 3 (postpetiole) in workers shifted backwards on

posttergite, usually behind the midlength (Fig. 8). (Spiracle of abdominal segment 3 in workers in front of midlength of posttergite.)

(ii) Postsclerites of abdominal segment 4 in workers constricted anteriorly, forming a narrow neck behind the articulatory presclerites (Fig. 8). (Postsclerites of abdominal segment 4 not constricted anteriorly in workers.)

(iii) Abdominal tergite 6 of males enlarged (Fig. 11). (Abdominal tergite 6 not enlarged in males.)

(iv) Abdominal tergite 7 of males mostly overlapped and concealed by tergite 6, so that only a small portion of 7 is visible; internalized portion of tergite 7 desclerotized (Figs 11, 12). (Abdominal tergite 7 of males not mostly overlapped by tergite 6, not mostly concealed, not largely desclerotized.)

(v) Abdominal tergite 8 (pygidium) of males bulging outwards (Fig. 11). (Pygidium of males not bulging outwards.)

Included genus and number of species examined in this survey.

Tribe Aenictini.   Genus: *Aenictus* (56)

For taxonomic, systematic and other information see Wilson (1964), Gotwald (1982).

After much deliberation it seems best to regard the aenictines as constituting a separate subfamily. The taxonomic history of the group is quite straightforward. The aenictines began as a tribe of subfamily Dorylinae (Emery, 1901), in the broad sense of that subfamily then current, but were later regarded (Emery, 1910; Wheeler, 1922) as a component of the tribe Ecitonini within subfamily Dorylinae. Borgmeier (1955) again treated the aenictines as tribe, within Dorylinae but separate from tribe Ecitonini. When Brown (1973) rightly elevated Ecitoninae to subfamily rank he left Dorylinae with two tribes: Dorylini and Aenictini. The latest move is that proposed here, the elevation of Aenictini to subfamily rank (Aenictinae) based on the autapomorphies listed above and contrasting with those given under Dorylinae. Other comparative morphological features separating the two subfamilies are as follows.

DORYLINAE	AENICTINAE
Worker (Figs 4–7)	*Worker* (Figs 8–10)
Antennae 7–12 segmented.	Antennae 8–10 segmented.
Gena outside antennal fossa not carinate.	Gena outside antennal fossa carinate.
Promesonotal suture present but fused and inflexible.	Promesonotal suture absent.
Mesothoracic spiracle (or a vestige) visible in profile.	Mesothoracic spiracle not visible.
Propodeal spiracle subtended by an endophragmal pit.	Propodeal spiracle not subtended by a pit.
In posterior view the petiolar foramen with a thickened sternal flange.	In posterior view the petiolar foramen lacking a thickened sternal flange.
Waist of a single segment.	Waist of two segments. ′
Abdominal segments 4–7 together longitudinal and subcylindrical in profile.	Abdominal segments 4–7 together subglobular in profile.
Abdominal tergites 4 and 5 subequal in size.	Abdominal tergite 4 enlarged, much larger than 5.

Pygidium large and flattened to concave posterodorsally; armed with a pair of spines.

Pygidium small, not concave, not armed with a pair of spines.

Queen

Propodeal spiracle huge, vertical and with a slit-shaped orifice.

Propodeal endophragmal pit present.

Bulla of metapleural gland not widely separated from spiracle.

Metapleural gland groove runs posteriorly, not constructed as in workers.

Abdominal tergites 3–7 about the same size or increasing in size posteriorly.

Abdominal spiracles 2–7 slit-shaped.

Sting very reduced, apparently not excertile, non-functional.

Queen

Propodeal spiracle of moderate size, orifice not slit-shaped.

Propodeal endophragmal pit absent.

Bulla of metapleural gland widely separated from spiracle.

Metapleural gland groove runs anteriorly, constructed as in workers.

Abdominal tergite 4 by far the largest, tergites decreasing in size posteriorly.

Abdominal spiracles 2–7 subcircular.

Sting not reduced, excertile, functional.

Male

Dorsum of petiole convex.

Abdominal spiracles 2–8 large, slit-shaped, easily visible.

Abdominal segments 3–8 telescopic. At full retraction apparently spiracles 3–4 always visible, 5–8 concealed; but often 5, 6, or 7 also visible according to degree of extension of segment.

Abdominal tergites 4–8 without division into pre- and postsclerites.

Male (Figs 11, 12)

Dorsum of petiole broadly transversely concave.

Abdominal spiracles 2–8 very small, often difficult to see, circular to elliptical.

Abdominal segments 3–8 not telescopic. At full retraction spiracles 3–6 visible, 7–8 concealed.

Abdominal tergites 4–8 with feeble differentiation into pre- and post-sclerites.

New format key to subfamiles (workers)

This is a first, provisional, attempt to construct a key to ant subfamilies that is based, as far as possible, on subfamily-level apomorphies. It appears radically different from previous keys (e.g. Hölldobler and Wilson, 1990) which are based mostly or entirely upon differentiating characters observable without dissection or disarticulation of specimens. The key is presented here for testing and comment.

Thirteen extant subfamilies are recognized. Most of these are not currently the subject of debate as regards their taxonomic level. Subfamily Cerapachyinae was resurrected by Bolton (1990a) and Aenictinae is proposed as a valid subfamily earlier in this paper. Only Aneuretinae presently needs a little discussion.

The status of this taxon, which has only a single extant species but an extensive fossil representation, has been undecided in recent years. It was first described as Aneuretini, a tribe of subfamily Dolichoderinae, by Emery (1912), and was retained as such by, for instance, Forel (1917), Wheeler (1922), Carpenter (1930) and Brown (1973). However, Clark (1951), Wilson (1971), Snelling (1981) and Dlussky (1988) regarded it as a valid subfamily.

The latest opinion was voiced by Baroni Urbani (1989), who considered Aneuretinae a junior synonym of Dolichoderinae, because of a supposed lack of apomorphic characters. I propose the formal reinstatement of Aneuretinae (stat. rev.) here, based on the following apomorphies, so far discovered in the worker caste of each taxon.

Apomorphies of Dolichoderinae

(i) Metacoxal cavities closed. (Plesiomorphically open in Aneuretinae.)
(ii) Anterodorsal margin of helcium deeply excised or notched. (Plesiomorphically entire in Aneuretinae.)
(iii) Sting reduced or vestigial. (Plesiomorphically large and functional in Aneuretinae.)

Apomorphies of Aneuretinae

(i) Helcium fused in posterior foramen of abdominal segment 2. (Plesiomorphically very mobile in Dolichoderinae.)
(ii) Postsclerites of abdominal segment 3 reduced. (Plesiomorphically large in Dolichoderinae.)
(iii) Petiole with a long anterior peduncle. (Plesiomorphically sessile or subsessile in Dolichoderinae.)

1 Abdominal segment 4 with tergosternal fusion . . . . . . PONERINAE
— Abdominal segment 4 with tergite and sternite not fused 2

2 Abdominal segment 3 with tergosternal fusion 3
— Abdominal segment 3 with tergite and sternite not fused 7

3 Abdominal spiracles 5–7 on posttergites, visible without distension of abdomen. Pygidium specialized by armament, depression of posttergite posteromedially, extreme reduction, or a combination of these. Sternite of helcium large, convex and bulging ventrally, visible in profile 4
— Abdominal spiracles 5–7 on pretergites, not visible without distension of abdomen. Pygidium unspecialized, large, evenly biconvex, unarmed. Sternite of helcium small, concealed, not bulging ventrally, not visible in profile . . . LEPTANILLINAE

4 Propodeal spiracle situated low down on side and behind the midlength of the sclerite
                                                                  CERAPACHYINAE
— Propodeal spiracle situated high up on side and in front of the midlength of the sclerite 5

5 Tergite of abdominal segment 7 a reduced U-shaped sclerite, small and often somewhat overhung by the tergite of abdominal segment 6 6
— Tergite of abdominal segment 7 large, the posttergite indented or depressed postero-medially and bidentate laterally . . . . DORYLINAE

6 Posttergite of abdominal segment 4 with a neck-like anterior constriction. Spiracle of abdominal segment 3 (postpetiole) behind midlength of segment . AENICTINAE
— Posttergite of abdominal segment 4 without a neck-like anterior constriction. Spiracle of abdominal segment 3 (postpetiole) in front of, or very rarely at, the midlength of the segment . . . . ECITONINAE

7 Metacoxal cavities open 8
— Metacoxal cavities closed 10

8 Abdomen constricted between segments 3 and 4; abdominal segment 4 tubulate anteriorly . . . . MYRMECIINAE
— Abdomen not constricted between segments 3 and 4; abdominal segment 4 not tubulate anteriorly 9

9 Stridulitrum present ventrally on abdominal segments 3 and 4. Helcium mobile in posterior foramen of abdominal segment 2. Mandibles elongate
NOTHOMYRMECIINAE
— Stridulitrum absent from abdomen. Helcium fused in posterior foramen of abdominal segment 2. Mandibles short . . . . ANEURETINAE

10 Helcium with emarginate to deeply indented anterodorsal margin. Abdomen not constricted between segments 3 and 4; abdominal segment 4 not tubulate anteriorly . 11
— Helcium with entire anterodorsal margin. Abdomen constricted between segments 3 and 4; abdominal segment 4 tubulate anteriorly 12

11 Acidopore present. Tergite of abdominal segment 7 large. Pavan's gland and pygidial glands absent . . . . FORMICINAE
— Acidopore absent. Tergite of abdominal segment 7 small. Pavan's gland and pygidial glands present . . . . DOLICHODERINAE

12 In frontal view the sternite of the helcium meeting the inverted U-shaped tergite at the apices of the tergal arms on each side; the sternite evenly transversely convex ventrally. Abdominal segment 2 with tergosternal fusion. Pronotum fused to mesonotum . . . . MYRMICINAE
— In frontal view the sternite of the helcium meeting the inverted U-shaped tergite some distance up the inner surface from the apices of the tergal arms on each side; the sternite sinuate, not evenly transversely convex ventrally. Tergite and sternite of abdominal segment 2 not fused. Pronotum not fused to mesonotum
PSEUDOMYRMECINAE

Acknowledgement

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