

Higher classification of the ant subfamilies Aneuretinae, Dolichoderinae and Formicinae (Hymenoptera: Formicidae)

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Abstract. An analysis of the cladistic relationships among the ant subfamilies Aneuretinae, Dolichoderinae and Formicinae demonstrates the monophyly of these three subfamilies, and places Dolichoderinae and Formicinae as sister groups. This latter result differs from most previous studies which consider Aneuretinae and Dolichoderinae as sister groups.

Introduction

The ants of the subfamilies Aneuretinae, Dolichoderinae and Formicinae have been considered closely related for nearly 100 years. However, there has been considerable variability in the placement of these groups relative to each other, and to other subfamilies within the family Formicidae. In this paper I review the more important previous classifications, and propose a new one based on a cladistic analysis of twenty-eight worker and larval characters. In the proposed system, Aneuretinae is placed as the sister group of Dolichoderinae and Formicinae. This relationship is supported by a single, fully resolved, most-parsimonious tree and nine cladistically informative, uniquely derived characters.

Previous classifications of Aneuretinae, Dolichoderinae and Formicinae

Recent higher classifications of the family Formicidae are those of Brown (1954), Wilson *et al.* (1967), Taylor (1978), Lutz (1986), Dlussky & Fedoseeva (1988), Baroni Urbani (1989), Bolton (1990b), Hölldobler & Wilson (1990) and Ward (1990). These studies differ significantly in their treatment of the subfamilies Aneuretinae, Dolichoderinae, Formicinae and Nothomyrmecinae.

Brown (1954) grouped Dolichoderinae (which then included Aneuretinae) and Formicinae as a sister group to Nothomyrmecinae, and these three subfamilies as the sister group to Myrmeciinae and Pseudomyrmecinae (Fig. 1). These five taxa together formed the myrmecioid complex, a sister group to the remaining formicids (the

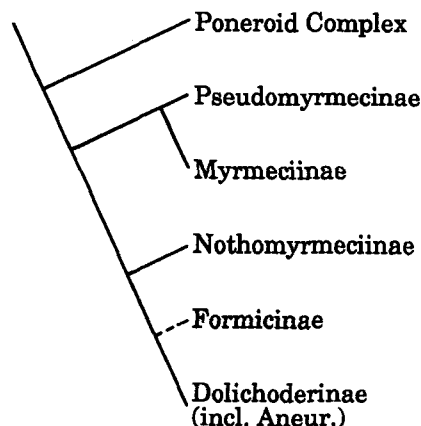


Fig. 1. Relationships among ant subfamilies proposed by Brown (1954).

poneroid complex). The complexes were apparently based on the overall resemblance of the taxa.

With the discovery of the fossil genus *Sphecomyrma*, Wilson *et al.* (1967) expanded on Brown's (1954) scheme (Fig. 2). Aneuretinae was treated as basal to Dolichoderinae, in part because of a terminal knob in the larva (Wilson *et al.*, 1956). However, while these knobs do occur in *Aneuretus* and some Dolichoderinae (*Tapinoma*, *Technomyrmex*, *Iridomyrmex glaber*-group), they are not present in all Dolichoderinae. Other characters used by Wilson *et al.* (1967) were too variable for reliable analysis in this study. Nothomyrmecinae was treated as ancestral to Myrmeciinae and Pseudomyrmecinae, and these three together as the sister group to Aneuretinae and Dolichoderinae. The placement of Formicinae was ambiguous, although it was thought to be near Nothomyrmecinae.

The rediscovery of *Nothomyrmecia* prompted Taylor

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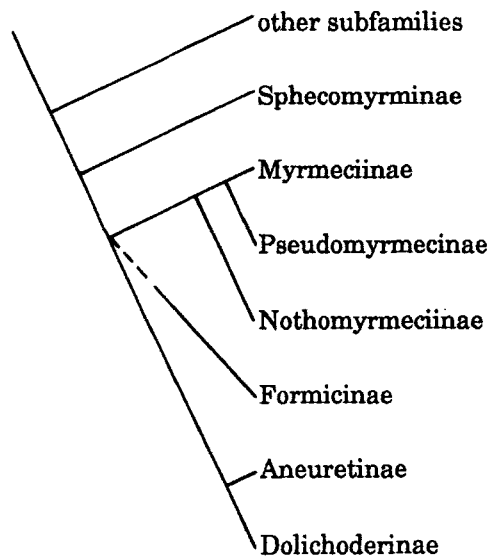


Fig. 2. Relationships among ant subfamilies proposed by Wilson *et al.* (1967).

(1978) to revise the higher-level classification of the formicids (Fig. 3). Taylor noted that tubulation of the fourth abdominal segment occurred in the poneroid complex, as well as the subfamilies Myrmeciinae and Pseudomyrmecinae. He therefore transferred these latter two subfamilies to the poneroid complex, and renamed the remaining subfamilies (Aneuretinae, Dolichoderinae, Formicinae, Nothomyrmeciinae) the formicoid complex. This latter group was defined by the plesiomorphic condition of lack of tubulation of the fourth abdominal segment. As in Wilson *et al.* (1967), *Sphecomyrma* was placed basal to all extant ants. Aneuretinae and Dolichoderinae were considered closely related, and the placement of Formicinae was ambiguous, although it was now thought to be near Aneuretinae rather than Nothomyrmeciinae.

The higher classification of the formicoid complex was next examined by Lutz (1986). He diagnosed the complex as those subfamilies without a dorsal stridulatory organ.

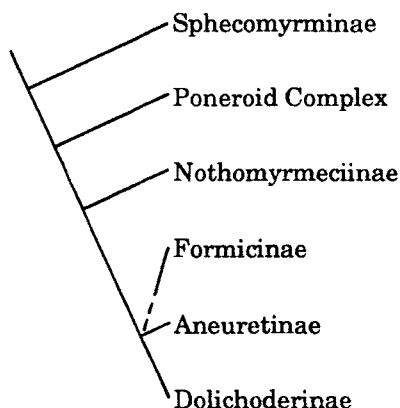


Fig. 3. Relationships among ant subfamilies proposed by Taylor (1976).

Within the complex, he placed Aneuretinae and Dolichoderinae as sister groups based on the structure of the furcula (an element of the sting). Formicinae was placed as the sister group to these two subfamilies, although no characters were given to support this conclusion. Finally, Nothomyrmeciinae was placed basal to Aneuretinae, Dolichoderinae and Formicinae.

Dlussky & Fedoseeva (1988) departed from previous authors in placing Dolichoderinae and Formicinae as sister groups, and Aneuretinae as the sister group of Nothomyrmeciinae (Fig. 4). However, the relationships between these two groups, and among the majority of the remaining subfamilies, were not resolved and data supporting the proposed relationships was minimal. As in previous studies, Sphecomyrminae was placed basal to all extant ants.

One of the first phylogenies for the entire family based on a cladistic character analysis was presented by Baroni Urbani (1989). His conclusions regarding the formicoid complex subfamilies are similar to those of Taylor (1978) and Lutz (1986) (i.e. Dolichoderinae (including Aneuretinae) formed the sister group to Formicinae; Nothomyrmeciinae was treated as basal to these subfamilies). However, there are several difficulties with the analysis and conclusions. No characters were given to support placing Nothomyrmeciinae with Aneuretinae, Dolichoderinae and Formicinae. Only a single character, the structure of the proventriculus, was given to unite Aneuretinae and Dolichoderinae with Formicinae. (Unfortunately, proventricular structure is diverse in these subfamilies and homologies are difficult to ascertain with certainty.) Additionally, a reanalysis of his data matrix conducted during the present study resulted in numerous equally most parsimonious trees being found, and the resulting strict consensus tree was uninformative regarding the subfamilies of interest in this study.

Recently, Hölldobler & Wilson (1990) introduced a classification in which Aneuretinae and Dolichoderinae

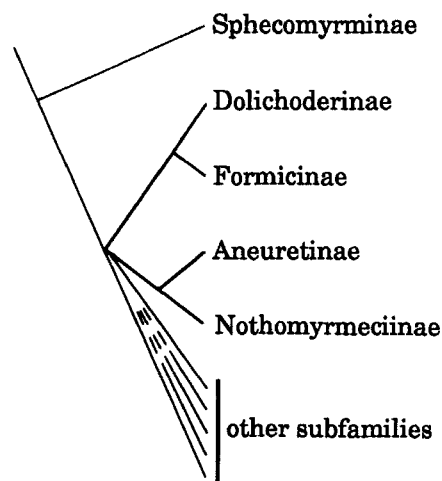


Fig. 4. Relationships among ant subfamilies proposed by Dlussky & Fedoseeva (1988).

were sister groups, Nothomyrmecinae was basal to these two subfamilies, and Formicinae was placed as the sister group of all other extant ants. The resulting 'formicoid' complex thus contained only Aneuretinae, Dolichoderinae and Nothomyrmecinae. Unfortunately, no characters were given to justify uniting Aneuretinae, Dolichoderinae and Nothomyrmecinae, and only a single character, the presence of a pygidial gland, was given to support the placement of all extant subfamilies as the sister group to Formicinae.

Ward (1990) conducted a detailed cladistic study of the relationships of Nothomyrmecinae, Myrmecinae, Pseudomyrmecinae, Myrmicinae, Cerapachyinae and Ponerinae. Applying his findings to the entire family, he concluded that Aneuretinae, Dolichoderinae and Formicinae were basal to the remaining extant subfamilies, including Nothomyrmecinae. As his study was concerned primarily with Pseudomyrmecinae, he did not comment on the relationships among Aneuretinae, Dolichoderinae or Formicinae, or their relationship to other subfamilies.

Finally, Bolton (1990b) examined the army ant subfamilies (Ecitoninae, Cerapachyinae, Aenictinae and Dorylinae) and discussed their placement relative to the remaining formicid subfamilies. He placed Aneuretinae, Dolichoderinae, Formicinae and Nothomyrmecinae basal to the remaining subfamilies, but did not support their monophyly or speculate on the relationships among them. He did, however, present numerous characters suggesting these and the remaining subfamilies are themselves monophyletic.

From this discussion, it is clear that Aneuretinae, Dolichoderinae, Formicinae, and to a lesser extent Nothomyrmecinae, have been considered closely related by most recent authors. However, little direct evidence has been used to support these views, and the exact relationships among these taxa have remained uncertain.

Cladistic analysis of relationships among Aneuretinae, Dolichoderinae and Formicinae

To resolve the relationships among Aneuretinae, Dolichoderinae and Formicinae, forty-three genera in eight subfamilies were examined for twenty-eight worker and larval characters. These data were analysed cladistically to hypothesize relationships among the subfamilies, and to demonstrate the monophyly of each.

Material examined. The following genera were studied: Aneuretinae: *Aneuretus*; Dolichoderinae: All genera (for a list of these genera see Hölldobler & Wilson (1990)); Dorylinae: *Dorylus*; Formicinae: *Acropyga*, *Camponotus*, *Formica*, *Melophorus*, *Myrmecorhynchus*, *Myrmoteras*, *Oecophylla*, *Paratrechina*, *Polyrhachis*; Myrmicinae: *Aphaenogaster*, *Pogonomyrmex*; Nothomyrmecinae: *Nothomyrmecia*; Ponerinae: *Ectatomma*, *Odontomachus*, *Onychomyrmex*, *Pachycondyla*, *Rhytidoponera*; Pseudomyrmecinae: *Tetraoponera*. Taxa in subfamilies other than those under direct study were included to allow assessment of character variability in the family as a whole.

Characters. The following characters were examined. Character states are given in square brackets and are not intended to indicate primitive or derived status. If no literature reference is given, the data are original. If a character state could not be determined (i.e. it was unknown or uncertain), it was coded as '?' (e.g. for the larvae of Sphecomyrminae). If more than one state was present for a given taxon, the character was recorded as 'P' (polymorphic).

1. The number of mandibular teeth is two [0] in *Sphecomyrma* (Wilson *et al.*, 1967). All other worker ants (excluding those with highly specialized mouthparts) have a minimum of three [1] teeth on the masticatory margin.

2. The worker scape in *Sphecomyrma* is very short [0] relative to the funiculus (at most 0.3 times the funicular length) (Wilson *et al.*, 1967). The scape is longer [1] in all extant ants, being generally about the same length as the funiculus, but never shorter than approximately 0.4 times the funicular length.

3. The hind coxal cavities are primitively open [0] in the Hymenoptera (Bolton, 1990a), and remain so in Aneuretinae and Nothomyrmecinae (condition unknown [?] in Sphecomyrminae). They are completely closed [1] in Dolichoderinae and Formicinae.

4. The anterior peduncle of the petiole is more than twice as long as the petiolar node [0] in Aneuretinae (Wilson *et al.*, 1956). The anterior peduncle is at most about as long as the node [1] in Dolichoderinae, Formicinae and Nothomyrmecinae.

5. The anterodorsal margin of the helcium (Bolton, 1990a) is excised [0] in Dolichoderinae and Formicinae (although only weakly so in some *Polyrhachis* species); it is entire [1] in Aneuretinae and Nothomyrmecinae.

6. In Dolichoderinae and Formicinae the lateral regions of the helcium sternite are retracted posteriorly relative to the lateroventral helcium tergite, and fusion of the sternite and tergite occurs for a length less than one half the tergite length [0]. In other ants, including Aneuretinae and Nothomyrmecinae, the helcium sternite is approximately the same length as the tergite and lateral fusion of the plates occurs for a length greater than one half the tergite length [1].

7. The complete fusion of the second abdominal tergite and sternite (the petiole) [0] has occurred in Aneuretinae, Dolichoderinae and Formicinae (and Myrmicinae, most Leptanillinae and some Ponerinae (Bolton, 1990c; Ward, 1990)). The sclerites are not fully fused [1] in Nothomyrmecinae, and their condition is uncertain [?] in Sphecomyrminae.

8. Differentiation of the fourth abdominal segment into pre- and post-tergites and sternites [0] is weakly developed but distinct in Nothomyrmecinae (Ward, 1990). (Differentiation of this segment is strongly developed in most members of the poneroid complex (Bolton, 1990a, b).) The other groups considered in this study have the fourth abdominal segment undifferentiated [1].

9. The pygidial (=anal) gland, although originally reported from only Aneuretinae and Dolichoderinae, is now known to be present [0] in all ants except Formicinae

[1] (Hölldobler & Engel, 1979). (Its occurrence in the formicine genus *Polyergus* is thought to be convergent with other ants rather than homologous (Hölldobler, 1985).)

10. Cyclopentanoid monoterpene production by the pygidial glands [0] is known only from Dolichoderinae (Blum & Hermann, 1978b) and is unknown from others [1]. Unfortunately, detailed information is lacking [?] for Nothomyrmecinae. The limited data concerning Aneuretinae suggests that pygidial gland secretions differ in their biological activity from those of Dolichoderinae, and are probably not the same compounds [1] (Traniello & Jayasuriya, 1981).

11. Postpygidial glands are present [0] in Nothomyrmecinae (and Dorylinae, Ecitoninae, Myrmecinae, Ponerinae, and Pseudomyrmecinae), and are absent [1] in Aneuretinae, Dolichoderinae and Formicinae (and Myrmicinae) (Hölldobler & Engel, 1979).

12. Distinct Pavan's gland cellular structure (Billen, 1986) and the development of an associated reservoir sac [0] (Hölldobler & Engel, 1979) is unique to Aneuretinae and Dolichoderinae and lacking in others [1].

13. The formation of an acidopore [0] is unique to Formicinae (Hung & Brown, 1966) and is absent [1] in all others.

14. Formic acid production [0] is known only in Formicinae (Blum & Hermann, 1978a) and is absent [1] in others.

15. The sting is greatly reduced and non-functional [0] in Dolichoderinae and Formicinae. It is fully developed [1] in other ants, although some do not sting (e.g. some army ants (Gotwald, 1982)).

16. In most Hymenoptera, the furcula is free from the sting base [0]. However, in Aneuretinae and Dolichoderinae (and Cerapachyinae, Ecitoninae, Dorylinae and Aenictinae), the furcula is fused with the sting base [1] (Hermann & Chao, 1983). In Formicinae, the furcula is free [0] but considerably reduced (Hermann & Chao, 1983), and the condition before reduction is uncertain.

17. The number of hind tibial spurs is two [0] in Sphecomyrminae (Wilson *et al.*, 1967) and Nothomyrmecinae (Taylor, 1978); it is one [1] in Aneuretinae, Dolichoderinae and Formicinae.

18. A sulcus on the hind basitarsus [0] occurs only in Nothomyrmecinae (and members of the poneroid complex) (Ward, 1990). It is absent [1] in Sphecomyrminae (Ward, pers. comm.) and the other subfamilies considered in this study.

19. The tarsal claws are toothed [0] in Sphecomyrminae and Nothomyrmecinae. Simple claws [1] occur in Aneuretinae, Dolichoderinae and Formicinae.

20. A well-defined neck [0] occurs in the larvae of Aneuretinae, Formicinae and Nothomyrmecinae (Wheeler & Wheeler, 1976). The neck is reduced [1] in Dolichoderinae.

21 & 22. Larval hairs are abundant [char. 21, state 0] and denticulate [char. 22, state 0] in Aneuretinae and Nothomyrmecinae, abundant [char. 21, state 0] and denticulate or bifurcate [char. 22, state P] in Formicinae, and sparse [char. 21, state 1] and simple [char. 22, state 1] in Dolichoderinae (Wheeler & Wheeler, 1976).

23 & 24. Larval mandibles are heavily sclerotized [char. 23, state 0] and with three teeth [char. 24, state 0] in Aneuretinae and Nothomyrmecinae, heavily sclerotized and with one or two teeth [char. 24, state 1] in Formicinae, and lightly sclerotized [char. 23, state 1] and with a single tooth in Dolichoderinae (Wheeler & Wheeler, 1976).

25. Larval spinules are abundant [0] in Aneuretinae, and sparse [1] in Dolichoderinae, Formicinae and Nothomyrmecinae (Wheeler & Wheeler, 1976).

26. The larval maxillary palp and galea are paxilliform [0] in Aneuretinae, Formicinae and Nothomyrmecinae, and are reduced to sensilla [1] in Dolichoderinae (Wheeler & Wheeler, 1976).

27. Larval sericteries are wide [0] in Aneuretinae, Formicinae and Nothomyrmecinae, and small [1] in Dolichoderinae (Wheeler & Wheeler, 1976).

28. Pupal cocoons are present [0] in Aneuretinae and Nothomyrmecinae, and are completely lost [1] in Dolichoderinae. Formicinae pupae have cocoons [0], although several groups lack them, apparently in response to arboreal nesting habits.

Cladistic methods. Character states for the subfamilies Aneuretinae, Dolichoderinae, Formicinae, Nothomyrmecinae, and Sphecomyrminae are summarized in Table 1. All characters were discrete and binary. Of the twenty-eight characters studied, nine were cladistically informative (chars. 3, 5, 6, 12, 15, 16, 17, 19, 24).

The computer program Hennig86 (Ver. 1.5), written by S. Farris, was used to determine the most parsimonious tree(s) (as an unrooted network) for the dataset. The 'ie*' option was utilized to assure finding all most-parsimonious trees. A single tree was found (length = 30, consistency index = 0.93, retention index = 0.77) (Fig. 5). To assist interpretation of the tree, character state changes (where possible) have been indicated. As character states were not explicitly polarized, the tree was rooted using the outgroup Sphecomyrminae. Sphecomyrminae, known only from Cretaceous fossils, is thought to represent the archetypal ant and has been placed basal to all extant taxa within the family Formicidae (Wilson *et al.*, 1967). The subfamily Nothomyrmecinae was examined to assist in placing the subfamilies Aneuretinae, Dolichoderinae and Formicinae in the family as a whole, and to test for the monophyly of this group.

Table 1. Character coding for the analysis of subfamily relationships (see text for explanation of character numbers and states). A '?' is used for 'unknown' states and a 'P' indicates polymorphism.

Character	1	11	21
Sphecomyrminae	00?1????1??	??1?1?010?	?????????
Nothomyrmecinae	110111100?	0111100000	00001000
Aneuretinae	1100110101	1011111110	00000000
Dolichoderinae	1111000100	1011011111	11111111
Formicinae	1111000111	1100001110	0P011000

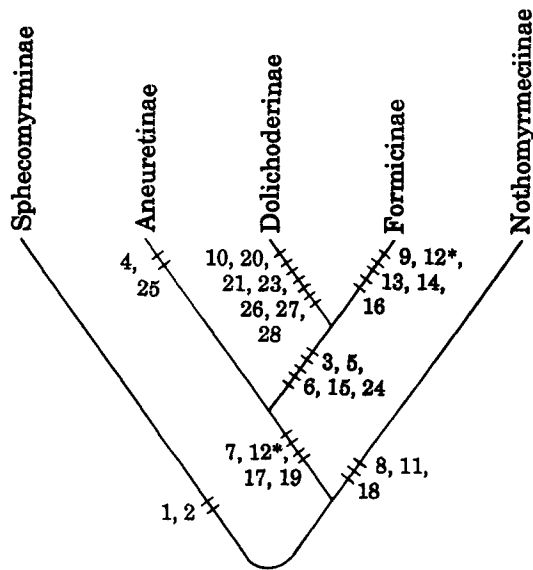


Fig. 5. Relationships among ant subfamilies proposed in this study. Numbers indicate character state changes (see text). Character 12 (indicated by an asterisk) is thought to have been secondarily lost in Formicinae. Character 22 is ambiguous in its placement and is not shown.

Results and Discussion

The results of this study show that (i) each subfamily is monophyletic, (ii) the subfamilies Aneuretinae, Dolichoderinae and Formicinae form a monophyletic group supported by four characters, and (iii) the internal structure of this group is completely resolved and supported by five characters.

Monophyly of each subfamily

Aneuretinae, Dolichoderinae and Formicinae were each found to possess uniquely derived characters, demonstrating that each subfamily is monophyletic. Two synapomorphic characters support the subfamily Aneuretinae: an elongate anterior petiolar peduncle (char. 4), and abundant spinules in the larvae (25). Other, more trivial characters exist (i.e. colour, pilosity, sculpturing) but these are presumably species-level differences and are not considered here.

The following seven characters support the monophyly of Dolichoderinae: loss of pupal cocoons (char. 28), reduction of the larval neck (20), reduced number of larval hairs (21), lightly sclerotized larval mandibles (23), larval maxillary palp and galea reduced to sensilla (26), small larval sericteries (27), and cyclopentanoid monoterpene production (10). Although most of these characters are from the larval stage, the extensive research of G. C. and J. Wheeler increases their reliability greatly. The chemical characters, however, have not been as thoroughly studied and additional documentation would increase their dependability.

The monophyly of Formicinae is supported by four characters: loss of the pygidial gland (char. 9), development of an acidopore (13), formic acid production (14), and reduction of the furcula (16). All these characters appear unique to Formicinae. However, a 'pygidial gland' does occur in the formicine genus *Polyergus*, but this structure is thought to be the result of the specialized slave-raiding behaviour of the genus and only convergently similar to, not homologous with, the pygidial gland of other ants (Hölldobler, 1985). Thus the loss of the gland is autapomorphic for the subfamily, and the development of a 'pygidial gland' in *Polyergus* is autapomorphic for the genus.

Monophyly of the group Aneuretinae, Dolichoderinae and Formicinae

This study demonstrates not only the monophyly of each subfamily, but also that Aneuretinae, Dolichoderinae and Formicinae together form a monophyletic group. The group is supported by three characters: complete fusion of the second abdominal tergite and sternite (char. 7), reduction of the number of tibial spurs (17), and simple tarsal claws (19).

The complete fusion of the second abdominal tergite and sternite occurs in these three subfamilies, as well as Myrmicinae, most Leptanillinae and some Ponerinae. However, this similarity is most likely convergent as these groups are morphologically very divergent and likely distantly related (Ward, 1990).

The two remaining characters (loss of the second tibial spur and loss of teeth on the tarsal claws) both occur in other groups of ants, but these groups are only distantly related to those under consideration here and the losses are likely to be convergently similar rather than synapomorphic among these groups.

Finally, the occurrence of the postpygidial glands (char. 11) at first appears to be informative about the relationships among these taxa, but it is actually ambiguous. The gland occurs in Nothomyrmecinae and most other ants, but it is absent from Aneuretinae, Dolichoderinae, Formicinae and Myrmicinae. Two alternate hypotheses are possible for this pattern. The first is that the gland was primitively present in formicids, and lost independently in Aneuretinae + Dolichoderinae + Formicinae, and Myrmicinae. This would require three evolutionary steps: a single origination (in the ancestor of all extant ants) and two losses (one in the ancestor of Aneuretinae + Dolichoderinae + Formicinae and one in the ancestor of Myrmicinae). The second hypothesis is that the gland arose after the split of Aneuretinae + Dolichoderinae + Formicinae from Nothomyrmecinae and the remaining ants. This would require two evolutionary steps: a single origination (in the ancestor of Nothomyrmecinae and the remaining subfamilies) and a single loss (in the ancestor of Myrmicinae). The first hypothesis would support the monophyly of the Aneuretinae + Dolichoderinae +

Formicinae, while the latter would be uninformative concerning these taxa. A strict parsimony analysis would support the second hypothesis as it requires fewer evolutionary events, and it is adopted in this paper. The gland, therefore, is not suggested as supporting the monophyly of the group Aneuretinae + Dolichoderinae + Formicinae.

A few recent studies have proposed that Aneuretinae, Dolichoderinae and Formicinae are not most closely related to themselves (Dlussky & Fedoseeva, 1988; Hölldobler & Wilson, 1990). However, the relationships suggested by these authors were not supported by the data examined in the present study. It is unlikely that the four characters listed above as uniting Aneuretinae, Dolichoderinae and Formicinae evolved independently as required by the Hölldobler & Wilson (1990) model. It is more reasonable that the pygidial gland has been lost in Formicinae, rather than gained in all other ants. The hypothesis proposed here allows placement of the subfamily without conflict with any of the other characters so far discovered. Similarly, the model of Dlussky & Fedoseeva (1988) is not supported, as the data suggest Aneuretinae + Dolichoderinae + Formicinae form a monophyletic group. Unfortunately, their model is difficult to evaluate in detail as it contains numerous unresolved relationships involving subfamilies not considered in this study.

Relationships within the group Aneuretinae, Dolichoderinae and Formicinae

One of the most controversial aspects of previous studies has been the relationships among the group Aneuretinae, Dolichoderinae and Formicinae. As mentioned above, most recent higher-level classifications of the family have placed Aneuretinae as either a sister group to Dolichoderinae (as a separate subfamily or a tribe within Dolichoderinae) (Brown, 1954; Lutz, 1986; Baroni Urbani, 1989; Hölldobler & Wilson, 1990), or in an unspecified position basal to it (Wilson *et al.*, 1967; Taylor, 1978). One notable exception is Dlussky & Fedoseeva (1988), who placed Dolichoderinae and Formicinae as sister groups. This latter viewpoint is supported by the results found here.

In this study, Dolichoderinae and Formicinae are found to be sister groups based on five adult and larval characters: helcium tergite excised (5), helcium sternite laterally retracted (6), reduction of sting (15), hind coxal cavities closed (3) and reduced number of larval mandibular teeth (24).

Three of these characters (helcium tergite excised, helcium sternite laterally retracted and reduction of sting) are unique to Dolichoderinae and Formicinae and strongly suggest these subfamilies are sister groups. The helcium is the modified pretergite and presternite of the third abdominal segment (Bolton, 1990a). In most ants the dorsal and ventral margins are more or less flat or weakly convex. In Dolichoderinae and Formicinae (weakly so in some *Polyrhachis*) the tergite is concave mediodorsally, and in all species the sternite has the lateral edge retracted.

It seems plausible that the helcium originated with even constriction of both the tergite and sternite along their entire circumference. The posterior retraction of the dorsal and ventral margins was a secondary development, possibly allowing for enhanced dorsal and ventral movement of the gaster, a movement commonly found in these ants. This movement has been accomplished in many other groups of ants by the development of a postpetiole.

The remaining two characters (hind coxal cavities closed and reduced number of larval mandibular teeth) occur in Dolichoderinae, Formicinae, and in other more distantly related groups of ants outside those studied here, and are also evidence of this relationship. However, the method of closure of the coxal cavities differs between Dolichoderinae and Formicinae and other ants with a similar condition. In Dolichoderinae and Formicinae, the closure consists of a simple, narrow band of cuticle, while in the remaining ants the cuticular strip is broad and more strongly developed (Bolton, pers. comm.). This indicates a separate, convergently similar formation between these groups.

A sixth character, the larval hair type, is difficult to interpret. Larval hairs are denticulate in *Nothomyrmecinae* and Aneuretinae, and are simple in Dolichoderinae. In Formicinae, both denticulate and bifurcate hairs occur. Thus hairs in both Dolichoderinae and some Formicinae have become somewhat simplified. Unfortunately, the pattern is too variable to determine if this simplification is homologous or convergent.

Two of the characters examined in this study suggest that Aneuretinae and Dolichoderinae, rather than Dolichoderinae and Formicinae, are sister groups. The first is the presence of a reservoir sac for the Pavan's gland. Although this gland (or type of gland) is known from several groups, the similar cellular structure and the development of a reservoir sac suggest a single, unique origin within at least Aneuretinae and Dolichoderinae (Billen, 1986). If the relationships among these three subfamilies proposed here are correct, there must have been a loss of this gland in Formicinae. It is possible that the development of formic acid as a defensive compound in Formicinae reduced the usefulness or effectiveness of Pavan's gland products, and therefore led to its reduction.

The second character relating Aneuretinae and Dolichoderinae is the fusion of the furcula with the sting base. This structure is fully fused in Aneuretinae and Dolichoderinae. In Formicinae the furcula is free from the sting base but has been greatly reduced in size and is apparently used in manipulation of the acidopore (Hermann, 1983). It is difficult to determine the condition of the furcula before its apparently more recent reduction in this subfamily. It may have been fused, and secondarily became free during its modification in relation to acidopore functioning, or it may have always been free from the sting base. The latter scenario would suggest that Aneuretinae and Dolichoderinae are closely related. However, the former scenario is consistent with other characters examined and produces a more parsimonious tree. Therefore, the first model is assumed to be correct.

Conclusions

A cladistic analysis of the subfamilies Aneuretinae, Dolichoderinae, Formicinae, Nothomyrmecinae and Sphecomyrminae results in a single, fully resolved, most-parsimonious tree (Fig. 5). The analysis supports the close relationship of Aneuretinae, Dolichoderinae and Formicinae, which is in agreement with most recent higher-level classifications of the family. However, Aneuretinae was found to be a sister group of Dolichoderinae and Formicinae, a relationship not generally suggested by previous authors.

Characters supporting the close relationship of Dolichoderinae and Formicinae include the closed hind coxal cavities, the configuration of the anterior helcium tergite, the loss of a functional sting, and the simplification of larval mandibles. Characters contradicting this arrangement include the development of a Pavan's gland reservoir sac and the fusion of the furcula to the sting base. It is suggested that the Pavan's gland has undergone reduction

and loss in Formicinae as a result of the development of formic acid as a defensive secretion. The furcula is present in a highly modified form in Formicinae, and is therefore of reduced value in determining relationships in this group of subfamilies. Additionally, it is involved in defensive activities and may have coevolved with the Pavan's gland.

Several recent papers have hypothesized higher-level relationships for sets of subfamilies within the Formicidae (Bolton, 1990b; Ward, 1990). Combining the results of this study with these, a phylogeny for the entire family can be constructed (Fig. 6). While this phylogeny is not completely resolved, it is explicit in the methods used for its construction and the lists of characters supporting it. As with all studies of this type, it can only benefit from further investigation and addition of new and expanded data sets.

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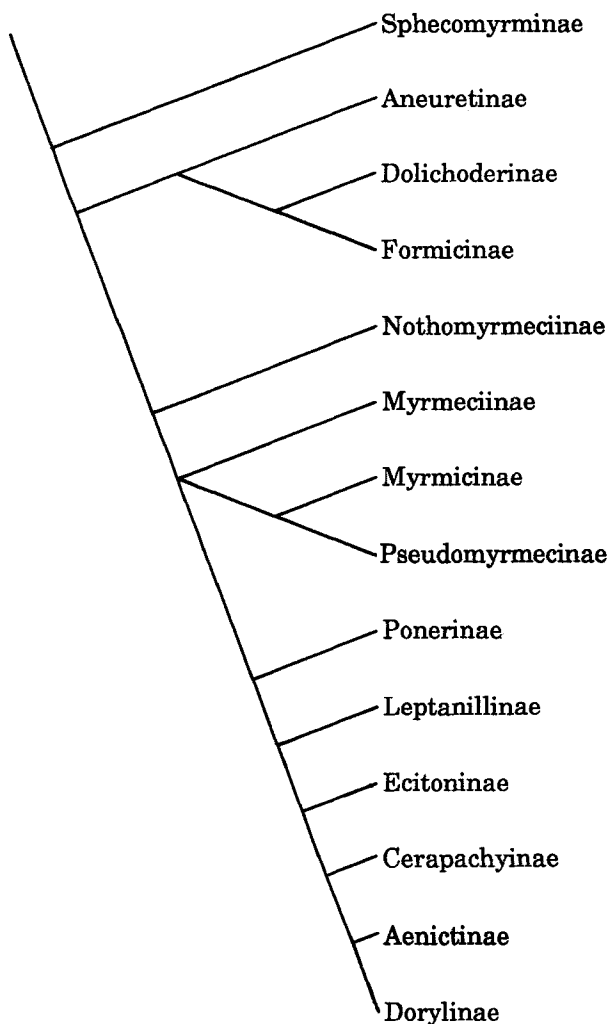


Fig. 6. Relationships among ant subfamilies based on this study, Bolton (1990b) and Ward (1990).

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