
Phylogeny and evolution of wasps, ants and bees (Hymenoptera, Chrysidoidea, Vespoidea and Apoidea)

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The comprehensive cladistic study of family-level phylogeny in the Aculeata (*sensu lato*) by Brothers & Carpenter, published in 1993, is briefly reviewed and re-evaluated, particularly with respect to the sections dealing with Vespoidea and Apoidea. This remains the most recent general treatment of the subject, but several of the relationships indicated are only weakly supported, notably those of Pompilidae and Rhopalosomatidae. Characters used were almost entirely morphological, and re-evaluation of ground-plan states and hypotheses of character-state changes, specially from examination of different exemplars, is likely to lead to slightly different conclusions for some taxa, as is the use of additional or new characters, including molecular ones. The relationships of taxa within the Vespoidea are much better known than for those in the Apoidea, but recent work on the two major groups of bees (by Michener and colleagues) and various groups of sphecoid wasps (by Alexander and Melo) have provided greater clarity, for some families at least. A single cladogram showing the putative relationships of those taxa which should be recognized at the family level for the entire Aculeata is presented. These are, for the Chrysidoidea, Apoidea and Vespoidea, respectively (limits indicated by curly brackets): {Plumariidae + (Scolebythidae + ((Bethyidae + Chrysididae) + (Sclerogibbidae + (Dryinidae + Embolemidae))))} + ((Heterogynaidae + (Ampulicidae + (Sphecidae + (Crabronidae + Apidae))))} + {Sierolomorphidae + ((Tiphidae + (Sapygidae + Mutillidae)) + ((Pompilidae + Rhopalosomatidae) + (Bradynobaenidae + (Formicidae + (Vespidae + Scoliidae))))}. Current knowledge of the relationships within the families of Vespoidea is reviewed. A new analysis of the subtaxa of Mutillidae, based on that of Brothers published in 1975, is presented; the subfamilies to be recognized are: (Myrmosinae [= Myrmosini + Kudakrumiini] + (Pseudophotopsidinae + (Ticoplineae + (Rhopalomutillinae + (Sphaerophthalminae [= Dasylabrini + (Sphaerophthalmina + Pseudomethocina)] + (Myrmillinae + Mutillinae [= Ephutini + (Mutillina + Smicromyrmina)))))).

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Introduction

The first critical, cladistically based study of the phylogeny of the Aculeata was that of Brothers (1975). This dealt in detail with the taxa considered at the time to comprise the superfamilies Scoliidea, Pompiloidea, Vespoidea and Formicoidea, and in much less detail with those regarded as Bethyloidea (properly Chrysidoidea), Sphecoidea and Apoidea *s.s.* One of its major conclusions was that the previous seven superfamilies should be reduced to three: Chrysidoidea, Apoidea and Vespoidea. This has been followed in recent general reviews of the Hymenoptera, such as those by Gauld & Bolton (1988) and Goulet & Huber (1993). (In contrast, Genize (1986) felt that addi-

tional superfamilies beyond the traditional ones should be recognized, for a total of 11.) In addition, unexpected relationships, such as the sister-group relationship of Scoliidae and Vespidae, the placement of Formicidae, and the need for dismemberment of Tiphidae and Mutillidae, were found. That study was done before convenient computer programs for cladistic analysis were generally available and the data upon which the analysis was based were not presented in a form easily accessible to other workers. In order to rectify this, and also to re-evaluate and extend it in the light of subsequent work, Brothers & Carpenter (1993) presented an expanded analysis of the Chrysidoidea and Vespoidea. That paper scarcely dealt with the Apoidea

since very little new information was available on the phylogeny of the group, and it was the group dealt with in least detail in the Brothers (1975) paper. The present paper attempts to rectify that omission to some extent, and also discusses some more recent work on various vespoid taxa.

Material and methods

This paper is predominantly a review of work previously carried out by myself and others. However, some new analyses were done using the matrices of Brothers & Carpenter (1993) with a few modifications justified by subsequent work and the availability of a new program, Pee-Wee version 2.1 (Goloboff 1994), which uses weighting of variables according to their fit on the possible trees as influenced by their homoplasy levels and then retaining those trees with the highest implied weights (Goloboff 1993). New analyses of the subtaxa of Mutillidae, building on that by Brothers (1975), were also done. All analyses utilized an hypothetical ancestor with state 0 for all variables to provide roots for the trees. Polarization of character states was done by out-group comparison. Results obtained using the program Hennig86 version 1.5 (Farris 1988) for derivation of most-parsimonious trees and for successive-approximations character weighting (commands m*; bb*; xs w) were compared with those using Pee-Wee (commands hold* search=hold/20 mult*15). The trees obtained were analysed using Clados version 1.6.1 (Nixon 1994), optimizations of placements of derived states being done as for Brothers & Carpenter's (1993) study.

Phylogeny of Chrysoidea and Vespoidea

The analysis of Brothers & Carpenter (1993) was based on the characters used by Brothers (1975) and Carpenter (1986) (reinterpreted in some cases), additional characters investigated in various studies since 1975, and a few new characters discovered during the analysis. This resulted in postulated ground plans using 201 morphological variables of adults, 8 morphological variables of larvae and 10 behavioural variables for 34 taxa, ranging from single genera (such as *Olixon*, a specialized member of the Rhopalosomatidae), through tribes (such as Eotillini in the Bradynobaenidae), subfamilies (such as the seven comprising the Tiphidae), families (such as the seven comprising the Chrysoidea), to suprafamilial groups (the 'sphecids' and 'apids' of the Apoidea). This meant that some higher taxa were analysed in more detail than others. Attempts were made to compensate for this by analysing the relationships of the subtaxa of some families (particularly Tiphidae) in isolation, and also by deriving ground plans for families and analysing those separately. This approach made it obvious that partitioning of the data in different ways was likely to lead to somewhat different results when compar-

ing the most parsimonious trees found. Consequently, the final preferred tree (presented here as Fig. 1) was very slightly longer than the most parsimonious tree (length 692, consistency index 0.46, retention index 0.65 vs. length 689, consistency index 0.46, retention index 0.66). Apart from the additional data on Chrysoidea then included, and which confirmed the results of the analysis of Carpenter (1986), the only real changes from the conclusions of Brothers (1975) were in the placement of Sierolomorphidae as the most basal clade in the Vespoidea and placement of Pompilidae as the sister group of (Sapygidae + Mutillidae) rather than of Rhopalosomatidae.

Analysis of the full matrix used for our 1993 paper using Pee-Wee produced two trees (length 691, consistency index 0.46, retention index 0.65). These differed only in the placement of Formicidae (as the sister group of (Vespidae + Scolidae) as in Fig. 1, or as the sister group of Bradynobaenidae). However, both trees showed Pompilidae as the sister group of (rhopalosomatids + *Olixon*), agreeing with Brothers's (1975) conclusions. These trees are also one step shorter than the tree chosen in the 1993 paper, and thus are probably actually preferable.

Subsequent to publication of our 1993 paper, I started a more extensive analysis of the relationships of the genera of Mutillidae (as yet incomplete). It soon became evident that I had probably misinterpreted two of the characters used in the 1993 paper. These are variables 103 and 104. The latter (Hindwing vein Cu: Distinct distal to separation from vein M = 0; Obliterated distal to separation from vein M = 1) was scored as derived in Fedtschenkiinae, Sapyginae and Myrmosinae but as plesiomorphic in 'mutillids' (the rest of the family apart from the Myrmosinae) because it was presumed that the vein closing cell M + Cu apically and originating anteriorly directly from vein M + Cu in the first three taxa was cross-vein cu-e, there thus being no distinct separate vein Cu. This is exactly the condition in the next most basal subfamily of Mutillidae, the Pseudophotopsidinae, however (Brothers 1975). In the 'higher' subfamilies the venation tends to be reduced and broken and a vein which looks like a separate Cu often appears, which led me to the above scoring. In the Rhopalomutillinae (again a relatively basal subfamily) cell M + Cu is closed apically (as in Myrmosinae and Pseudophotopsidinae) by a continuous vein which is rather convex and from the apex of which there is often a spurlike sclerotized line in the membrane. This apparent free vein Cu is thus most probably a secondary development; in addition, this condition led me to consider that the apparently single apical 'cross-vein' may be compound, comprising an indistinguishable fusion of the free portion of vein Cu and the true cross-vein cu-e, and that this represents the ground-plan condition for 'mutillids'. This re-interpretation means

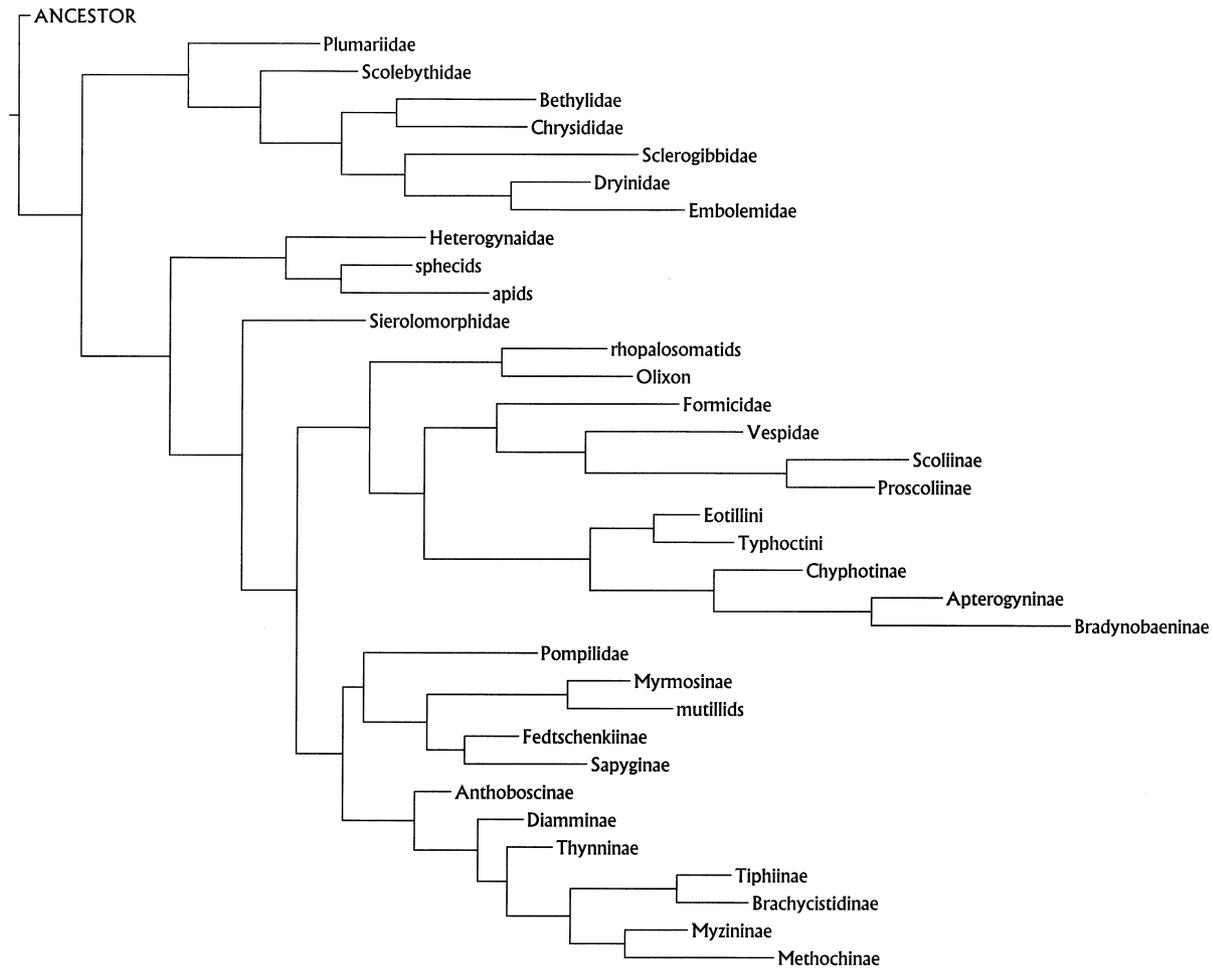


Fig. 1 Composite cladogram showing preferred results from the analyses of Brothers & Carpenter (1993) (length 692, consistency index 0.46, retention index 0.65). (sphecids = sphecoid wasps; apids = bees; rhopalosomatids + *Olixon* = Rhopalosomatidae; Scoliinae + Proscoliinae = Scolidae; Eotillini + Typhoctini = Typhoctinae; Typhoctinae + Chyphotinae + Apterogyninae + Bradynobaeninae = Bradynobaenidae; Myrmosinae + mutillids = Mutillidae; Fedtschenkiinae + Sapyginae = Sapygidae; Anthoboscinae + Diamminae + Thynninae + Tiphinae + Brachycistidinae + Myzininae + Methochinae = Tiphidae).

that variable 104 should be reformulated as follows: Hindwing vein Cu: Distinct distal to separation from vein M and distal to junction with cross-vein cu-e = 0; Indistinguishably fused with cross-vein cu-e distal to separation from vein M = 1. This results in scores of 1 for 'mutillids' in addition to Fedtschenkiinae, Sapyginae and Myrmosinae. This interpretation also means that Fedtschenkiinae, Sapyginae and Myrmosinae should now be scored as derived for Variable 103 (Hindwing cross-vein cu-e: Originating basal to separation of veins M and Cu = 0; Originating distal to separation of veins M and Cu = 1) rather than inapplicable, and 'mutillids' should also be scored 1. I have also discovered two coding errors for Myzininae: variables 133 and 145 should both be scored 0. Seven cells in

the matrix presented as Table 4 of Brothers & Carpenter (1993) have thus been changed.

When the data matrix was re-analysed after the above changes, using Hennig86 and Pee-Wee, the following results were obtained. Using Hennig86, 32 most-parsimonious trees were found (length 686, consistency index 0.47, retention index 0.66). After successive-approximations character weighting, 3 trees remained (length 2230, consistency index 0.83, retention index 0.89); these differed only in the arrangement of subfamilies within Tiphidae. Additionally, using the arguments of Brothers & Carpenter (1993) with reference to Tiphidae and relationships within Apoidea, one tree (of the most-parsimonious ones) was preferred. This, however, showed Formicidae as the sister

group of Bradynobaenidae. Again, following our earlier reasoning, the finally preferred tree (with Formicidae as sister group of (Vespidae + Scoliidae) (Fig. 2) turned out to be slightly longer (length 689, consistency index 0.46, retention index 0.66). The only difference from our earlier conclusions was that the position of Pompilidae changed to be more basal in the clade including Tiphidae and Mutillidae. Analysis by Pee-Wee produced two trees, differing only in the position of Formicidae. Both had Pompilidae as the sister group of Rhopalosomatidae; that preferred (length 688, consistency index 0.46, retention index 0.66) (Fig. 3) has Formicidae as the sister group of (Vespidae + Scoliidae) and is one step shorter than the finally preferred tree derived using Hennig86 (Fig. 2). It also agrees with the preferred tree derived using Pee-Wee for the uncorrected data.

The next step was to analyse the corrected data for all taxa of Vespoidea in isolation. Analysis using Hennig86 produced 10 most parsimonious trees (length 468, consistency index 0.51, retention index 0.63); successive-approximations character weighting resulted in two trees (length 1672, consistency index 0.83, retention index 0.85) only one of which (Fig. 4) was in the set of most-parsimonious trees. This differed from that preferred in the full analysis in that Pompilidae was now the basal taxon of the clade including Rhopalosomatidae, Vespidae, etc. rather than the clade including Tiphidae, Mutillidae, etc. (and it again showed Formicidae as the sister group of Bradynobaenidae). Analysis using Pee-Wee produced one tree, with Pompilidae as the sister group of Rhopalosomatidae and with Formicidae as sister group of (Vespidae + Scoliidae) (Fig. 5) (length 470, consistency index 0.51, retention index 0.63); it is the same as the relevant section of the tree derived in the full analysis (except for a slight difference within Tiphidae which does not alter the length). As a result, I now consider that the tree presented in Fig. 3 is our current best estimate of the phylogeny of Chrysidoidea and Vespoidea, based on the disparate taxa considered.

In order to obtain greater equivalence in the analysis across the two major superfamilies involved, a matrix of postulated ground-plan states for all families was produced from the corrected matrix. Usually, the relatively most plesiomorphic state for any component of a family, or the known state where it was unknown for some components, was considered to be the ground-plan state for the family, unless there were *a priori* indications that some other state should more reasonably be considered to be that present in the ancestral form. I tried to eliminate inapplicable or unknown states as far as possible, specially for those variables dealing with the form of the mesosoma in apterous females (which in 1993 had been considered inapplicable for those families where some females are fully winged)

and also changed a few states where I was not entirely happy with the previous decisions. The differences from Table 5 of Brothers & Carpenter (1993) are as follows: For Tiphidae, variables 137–144 now 10000000, variable 169 now 0; for Rhopalosomatidae, variable 94 now 2, variables 137–144 now 00000000; for Bradynobaenidae, variable 107 now 0, variable 118 and 121 now 2, variable 193 now 3. Analysis with Hennig86 produced 6 most-parsimonious trees (length 469, consistency index 0.53, retention index 0.60); successive-approximations character weighting resulted in a single tree (length 1648, consistency index 0.87, retention index 0.88) which was also one of the most-parsimonious trees. The relationships shown were the same as those for the full analysis using Hennig86, with Pompilidae the sister group of (Tiphidae + (Sapygidae + Mutillidae)) and Formicidae the sister group of Bradynobaenidae. Analysis using Pee-Wee produced a single tree (length 470, consistency index 0.53, retention index 0.60) showing the same relationships as for the finally preferred tree for the full corrected matrix (Fig. 3), except that (Pompilidae + Rhopalosomatidae) formed a clade basal to all Vespoidea except for Sierolomorphidae. However, making (Pompilidae + Rhopalosomatidae) the sister group of the Bradynobaenidae-to-Vespidae clade, to agree with Fig. 3, resulted in a tree of the same length (Fig. 6). In order to check whether these alternative positions of (Pompilidae + Rhopalosomatidae) were also equally parsimonious for the full analysis, the relationships shown in Fig. 3 were altered to show (Pompilidae + Rhopalosomatidae) in the more basal position; this increased the length by one step and is thus not to be preferred.

Next, the Chrysidoidea was removed. Analysis of family ground plans of Apoidea and Vespoidea alone using Hennig86 resulted in six most-parsimonious trees (length 309, consistency index 0.59, retention index 0.50). Successive-approximations character weighting produced a single tree (length 1222, consistency index 0.88, retention index 0.81); it was one step longer than the most-parsimonious trees (raw length 310, consistency index 0.59, retention index 0.50) and showed the same relationships as in the relevant part of Fig. 6 except that sphecids were basal in the Apoidea and Rhopalosomatidae was the sister group of Sierolomorphidae rather than Pompilidae. Rearrangement to make Heterogynidae basal in the Apoidea increased the length by one step as did placement of Rhopalosomatidae as the sister group of Pompilidae. Analysis using Pee-Wee resulted in a single tree (length 311, consistency index 0.58, retention index 0.50), again agreeing in most respects with Fig. 6 except for sphecids being basal in the Apoidea and this time (Pompilidae + Rhopalosomatidae) being the sister group of Sierolomorphidae (placing (Pompilidae + Rhopalosomatidae) as in Fig. 6 caused no change in tree

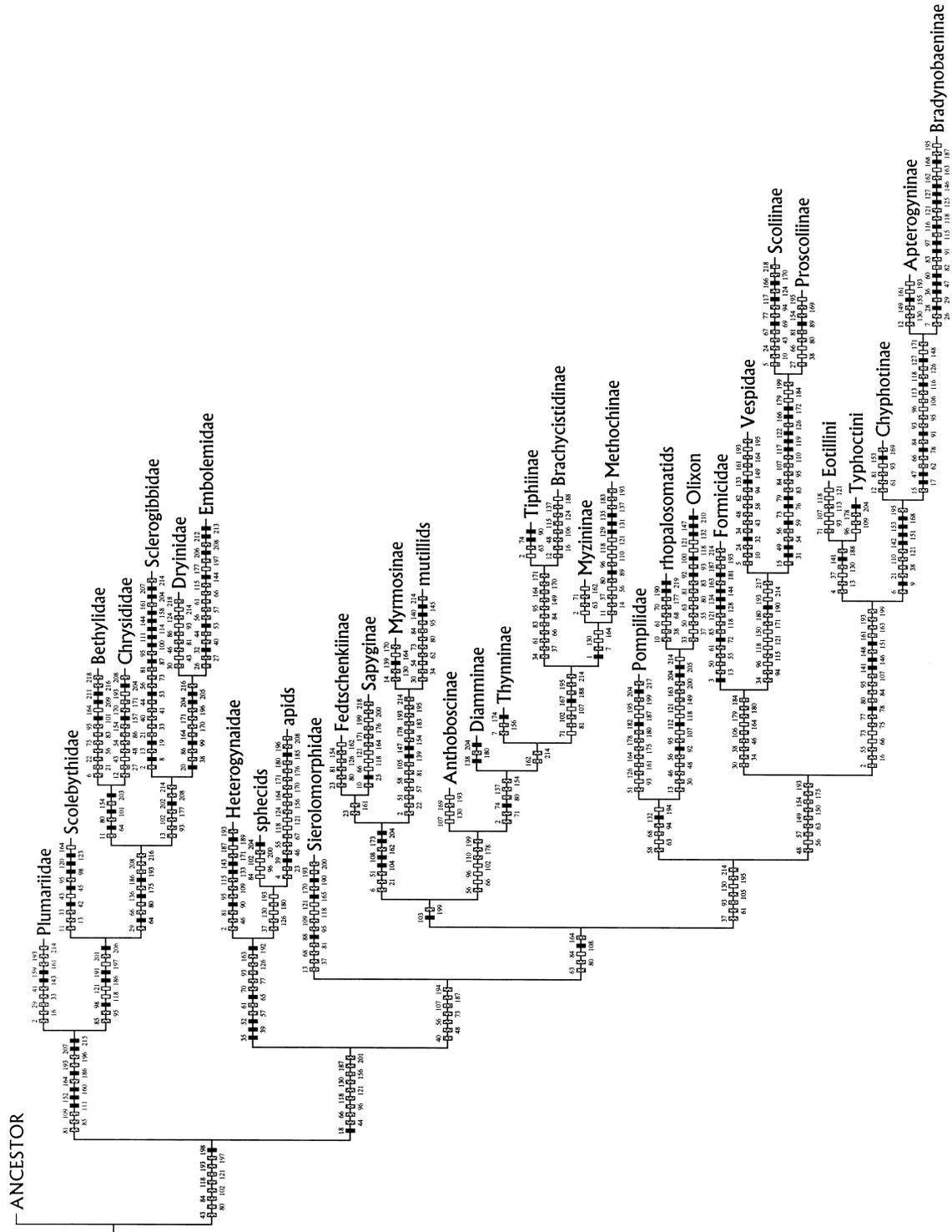


Fig. 3 Preferred cladogram (one of two found) for analysis of corrected matrix of all taxa of Aculeata using implied weighting (length 688, consistency index 0.46, retention index 0.66) (see Fig. 1 for explanation of taxa); regarded as our current best estimate of relationships in Chrysoidea and Vespoidea. Character hash-mark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent).

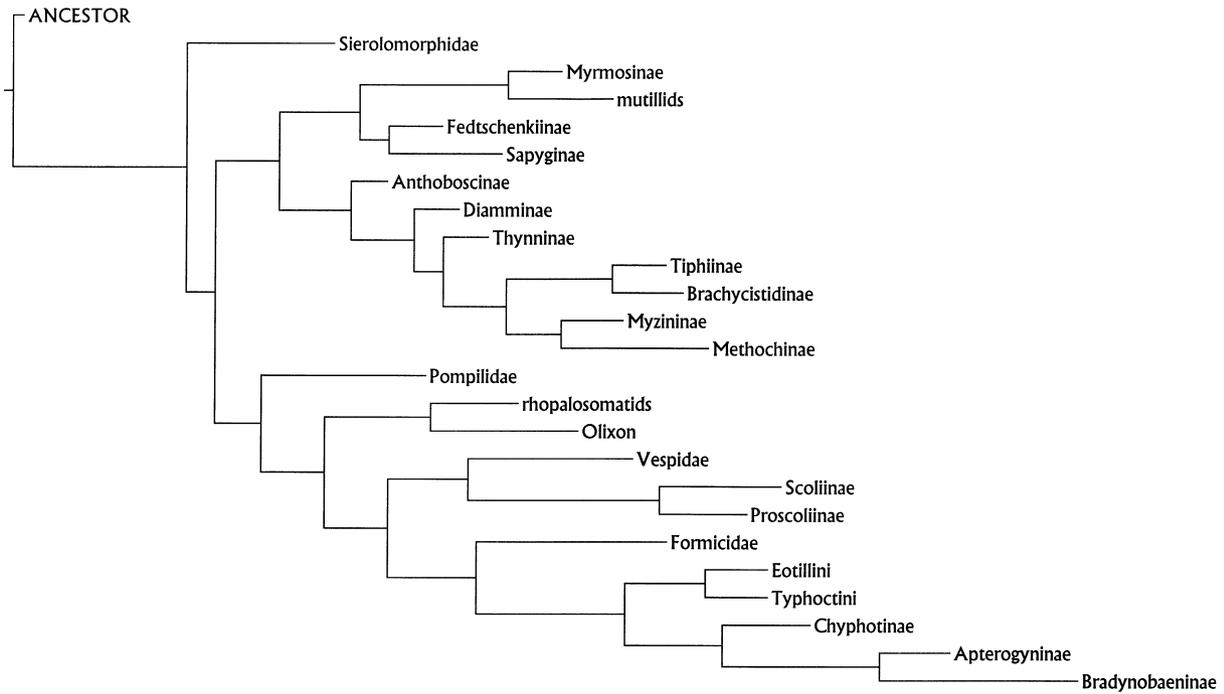


Fig. 4 Preferred cladogram (one of 10 most parsimonious trees found) for all taxa of Vespoidea using equal weighting and successive-approximations character weighting (length 468, consistency index 0.51, retention index 0.63) (see **Fig. 1** for explanation of taxa).

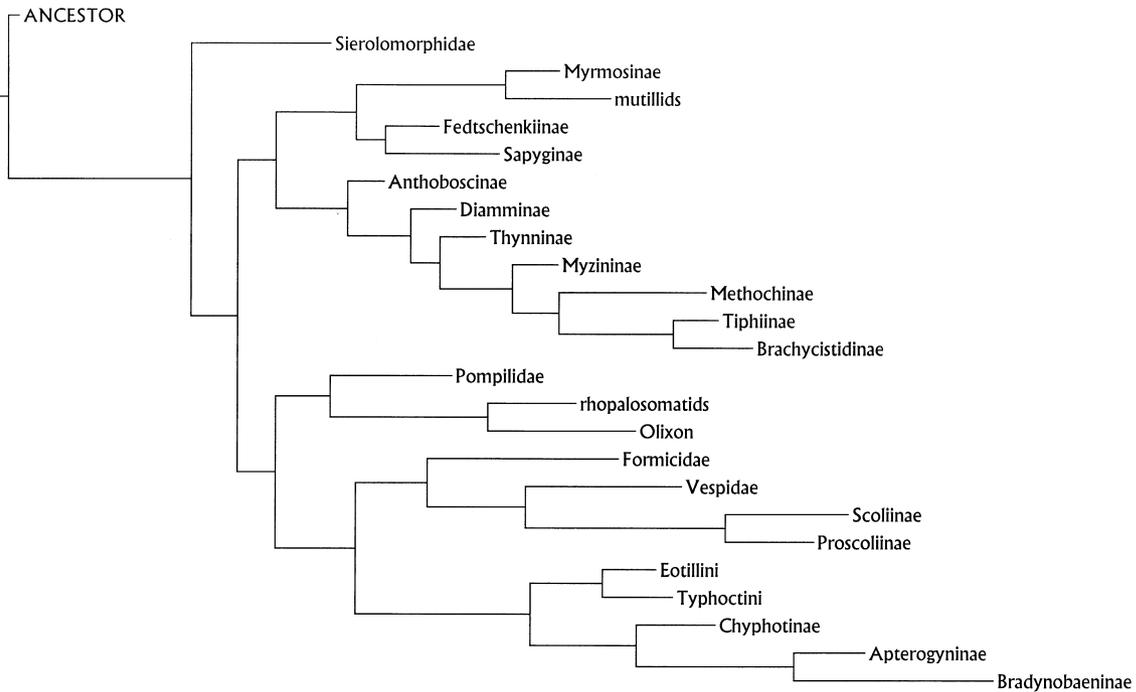


Fig. 5 Preferred cladogram (one of two found) for all taxa of Vespoidea using implied weighting (length 470, consistency index 0.51, retention index 0.63) (see **Fig. 1** for explanation of taxa).

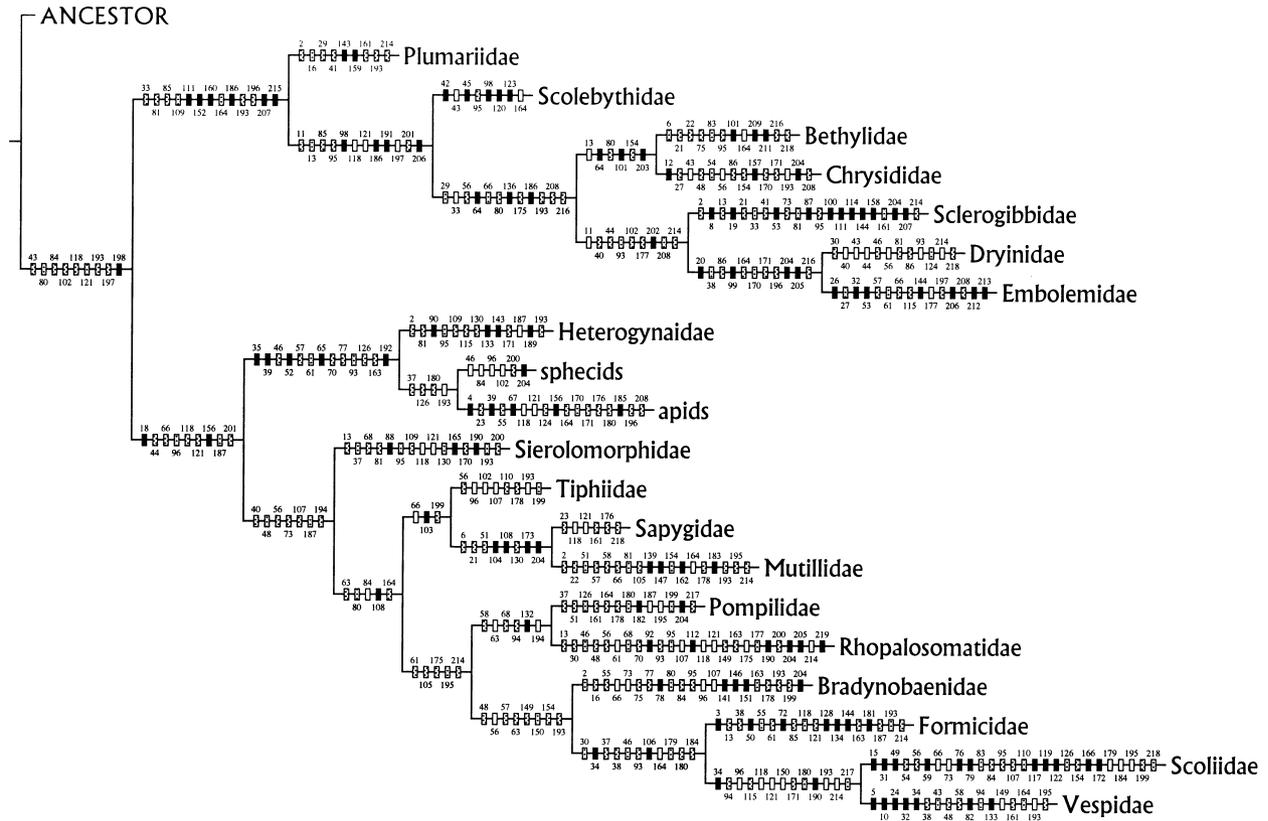


Fig. 6 Preferred cladogram for corrected ground plans of all families of Aculeata (one step longer than most-parsimonious trees and of equal length to single tree found using implied weights) (length 470, consistency index 0.53, retention index 0.60); regarded as our current best estimate of relationships in Chrysoidea and Vespoidea. Character hash-mark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent).

statistics, however). Making Heterogynaidae basal in the Apoidea increased the length by two steps this time and subsequent placement of (Pompilidae + Rhopalosomatidae) as in Fig. 6 reduced the length by one step and so should be preferred (length 312, consistency index 0.58, retention index 0.49).

The last analysis was of family ground plans for the Vespoidea alone. Analysis using Hennig86 produced 11 most-parsimonious trees (length 251, consistency index 0.64, retention index 0.43), one of which remained after successive-approximations character weighting; this showed the same relationships as found by Pee-Wee in the previous analysis. Interestingly, the analysis of Vespoidea ground plans using Pee-Wee produced the same relationships as found by Hennig86 for the previous analysis, a single tree which was also one of the most-parsimonious ones. Shifting (Pompilidae + Rhopalosomatidae) to agree with their position in Fig. 6 increased the tree length by one step, as did placing them basal to all Vespoidea except Sierolomorphidae.

Although Pompilidae and Rhopalosomatidae share only a single unique and unreversed synapomorphy (variable 132, the form of the hind tibial calcar), and these two families are sometimes dissociated in the analyses of the smaller data sets, they do appear to form a monophyletic group in most of the analyses. Their position with respect to the rest of the Vespoidea varies, however, trees of identical or very similar length resulting from rather different placements of these families. Sierolomorphidae forms a distinct basal clade in the Vespoidea in almost all analyses, and that is thus our best estimate of its position. My impression after all of the analyses is that the relationships of the families as shown in Fig. 6 (and of all taxa as shown in Fig. 3) are those to be preferred based on all of the available data. A case could be made, however, for the use of a slightly less resolved tree (Fig. 7) which emphasizes the greater uncertainty about the placement of the Pompilidae and Rhopalosomatidae than the other groups, but such a tree is one step longer.

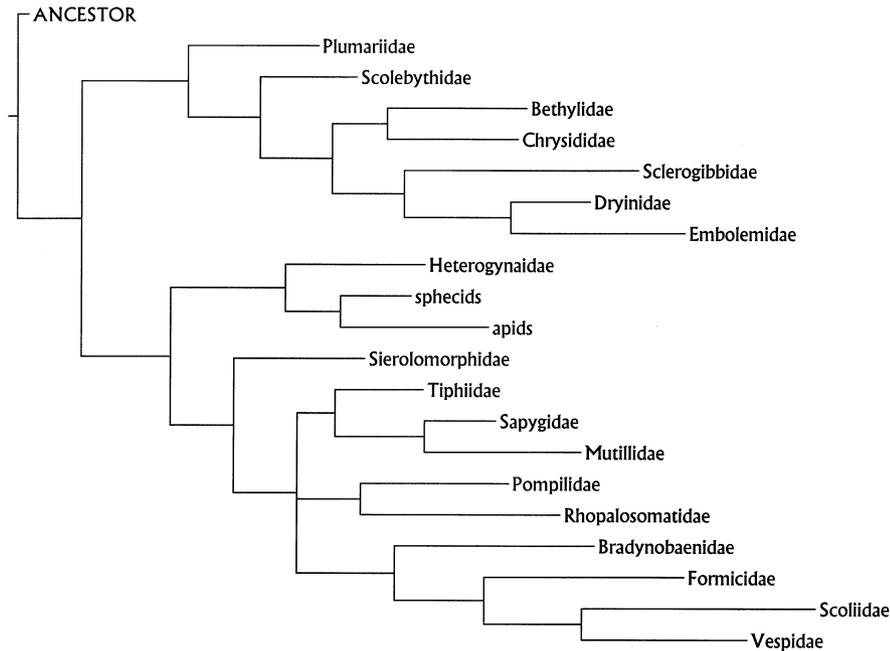


Fig. 7 Cladogram for corrected ground plans of all families of Aculeata emphasising uncertainty regarding position of (Pompilidae + Rhopalosomatidae).

Phylogeny of Apoidea

Brothers (1975) demonstrated unequivocally that the Apoidea is a holophyletic group. The common division of the members of the group into 'sphecoid wasps' and 'bees' has implied that the superfamily itself comprised two monophyletic groups. Traditional usage by workers specialising in one of these components has unfortunately meant that their component taxa have been recognized at different taxonomic levels; the 'sphecoids' have often been considered to comprise a single family, particularly recently (e.g. Bohart & Menke 1976), whereas the bees have been regarded by all bee specialists as comprising several families. Brothers (1975) suggested that rough equivalence across the Aculeata would require the recognition of several families of sphecoids, an approach followed by Krombein (1979a) and Finnermore (1993), for example, but Gauld & Bolton (1988) preferred to recognize a single family for the sphecoids and one for all bees. Alexander (1992) also commented on this disparity of approach, and suggested that consistency was required, recommending that strictly cladistic principles be applied when making decisions about ranks. The few critical analyses of the group as a whole, such as those by Lomholdt (1982) and Alexander (1990, 1992), have provided strong indications that the wasp component is probably paraphyletic, as did the very limited consideration of Apoidea by Brothers & Carpenter (1993). If this is true, then several family-level

taxa should be recognized within the old 'Sphecidae'. None of the studies mentioned above provided any more than indications, however, because of inadequate sampling of taxa and/or characters. Similar reservations apply to the study by Plant & Paulus (1987) who used a single character complex in analysing the bees.

Two subsequent studies, focused on the long-tongued and the short-tongued bees (Roig-Alsina & Michener 1993 and Alexander & Michener 1995), have clearly demonstrated that the bees form a holophyletic group derived from within the sphecoids, and have provided some indications of relationships amongst the groups of bees. Neither of these papers came to unequivocal conclusions, but they do provide the results of several analyses which imply somewhat different relationships, and they also supply suggestions for changes in the classification of the bees to take their findings into account. I have attempted to summarise these here, but it must be recognized that the final tree produced is a tentative one.

Roig-Alsina & Michener (1993) examined the adults of 82 taxa of long-tongued bees and their putative sister group, the 'Melittidae', and scored them for 131 characters. In addition, 77 characters of larvae were scored for 71 taxa, much of those data being derived from an earlier study by McGinley (1981). They concluded that the long-tongued bees form a holophyletic group which itself comprises two sister groups. Consequently, only two

higher taxa should be recognized: Megachilidae (including Fideliinae) and Apidae (including Xylocopinae and Nomadinae, thus comprising several groups previously recognized as distinct families). Alexander & Michener (1995) examined adults of 48 taxa of short-tongued bees, 9 of long-tongued bees and 8 of spheciform wasps, scoring them in two series of analyses for 109 and 114 characters, and analysed them using exemplars and also using 'family' ground plans. The holophyly of the bees as a whole was strongly confirmed in all analyses. The results were otherwise rather inconsistent, but the authors did come to some conclusions which necessitated alterations to previous groupings. The major uncertainty revolved around the position of the 'Melittidae', which was confirmed as the group from within which the long-tongued bees were derived (and which is thus paraphyletic, necessitating its dismemberment into three components), but which could be considered either as the sister group to most of the other short-tongued bees, or else as the sister group of the Andrenidae (in which case the Halictidae is the sister group to the rest). The genus *Ctenocolletes*, representing the Stenotritidae, fell in many different positions and so could not be placed anywhere with any confidence. Combination of all of these results produces a poorly resolved consensus tree for all bees (Fig. 8), although there seems to have been some greater certainty about the relationships within the taxa considered as families. Despite the finding that several subfamilies are evidently paraphyletic, no recommendations for formal recognition of their components were made since the results were regarded as tentative.

The situation regarding the sphecoids has been even less clear. The studies of Alexander (1990, 1992) were very preliminary and enabled him to draw few conclusions. He did suggest that the subfamilies Ampulicinae and Sphecinae were probably valid monophyletic groups, and found that some components of the subfamilies 'Philanthinae' and 'Nyssoninae' consistently appeared to fall as monophyletic groups. He also confirmed the monophyly of the bees. More recently, Melo (1997) presented an as yet unpublished study of the phylogeny of the sphecoids with emphasis on the crabronids. This work is being expanded at present, but some conclusions which are unlikely to change are as follows. (I am extremely grateful to Gabriel Melo for providing me with a copy of his abstract, discussing his work briefly with me and giving me permission to share it more widely.) The analysis considered 105 characters of adult morphology, 6 of larval morphology and 1 involving adult behaviour, using various parsimony approaches. The results under implied weighting were preferred, and demonstrated that the sphecoids are almost certainly paraphyletic, the bees having originated as the sister group of the crabronids. Melo (1997) recommended

the recognition of only five families for the entire Apoidea: Heterogynaidae, Ampulicidae, Sphecidae, Apidae (all bees) and Crabronidae (itself with five subfamilies). His conclusions, with the addition of subordinate taxa for the bees (considering the family-level groups recognized above as subfamilies), are summarised in Fig. 9; the names are those which are correct in terms of the review provided by Menke (1997). These are certainly the best estimate we have at present of the relationships between all these groups.

Relationships of all families of Aculeata

The results for the Apoidea may now be amalgamated with those obtained for the Chrysoidea and Vespoidea. A good case could be made for recognizing more taxa at the family level in the Apoidea than suggested by Melo (1997), since both his Crabronidae and even more so his Apidae are very large groups (much larger than almost all families in the Chrysoidea and Vespoidea) and such an approach would agree with the recommendations of Brothers (1975). This would require 17 families of Apoidea, based on the above results. This number could be halved were the bees considered to comprise four families, Stenotritidae, Halictidae, Andrenidae (including Colletinae) and Apidae (including Mellitinae, Dasypodinae, Meganomiinae and Megachilinae), based on the basal tetrachotomy of Fig. 8. This would be dangerous, however, since those relationships are uncertain and such family groupings may prove incorrect, but this could be reconsidered when greater clarity is reached.

Classifications should be constructed with the needs of nonsystematists in mind since they are their main users, so a proliferation of taxa which are difficult to recognize is likely to prove less generally useful than fewer taxa which are fairly easily distinguishable. The almost universal use of the single family Formicidae for the ants, despite the size of the group (e.g. Bolton 1995), recognizes the functional similarities amongst its members. The recognition of a single family for bees on a similar functional basis would thus not be inappropriate, and would acknowledge the fact that many of its components, even at the subfamily level, are difficult to distinguish. Amongst the sphecoids, the Heterogynaidae, Ampulicidae and Sphecidae s.s. are the groups most easily recognized, whereas the subtaxa of Melo's Crabronidae are easily distinguished only by experts in the group.

Taking these considerations into account, I suggest that our best current estimate of relationships at the family level across the Aculeata is shown in Fig. 10. Somewhat ironically, this recognizes several families of sphecoids and only one of bees, the opposite of the current situation amongst most specialists in these groups.

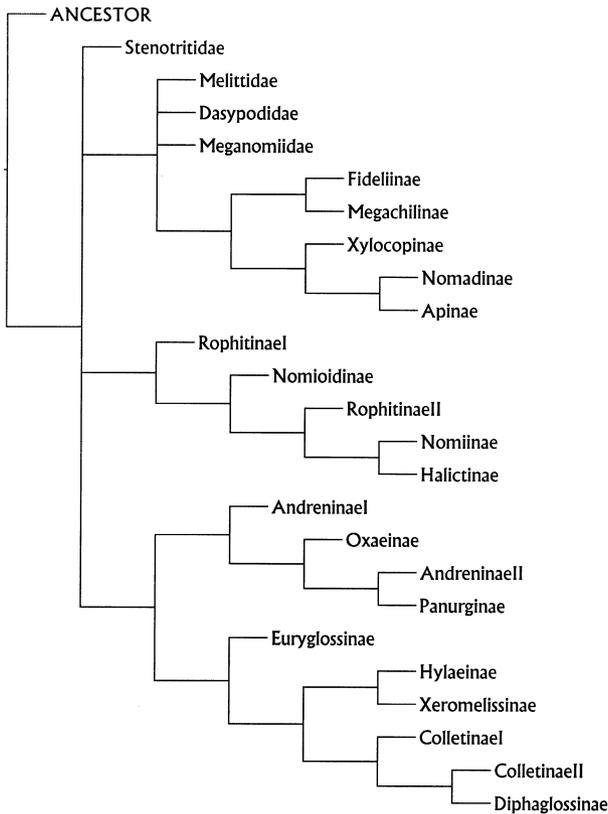


Fig. 8 Consensus cladogram for all taxa of bees, emphasising uncertainty about relationships of taxa of short-tongued bees and showing para- or polyphyletic nature of Rophitinae, Andreninae and Colletinae (interpreted from Roig-Alsina & Michener 1993 and Alexander & Michener 1995). (Fideliinae + Megachilinae = Megachilidae; Xylocopinae + Nomadinae + Apinae = Apidae; Rophitinae + Nomioidinae + Nomiinae + Halictinae = Halictidae; Andreninae + Oxaeinae + Panurginae = Andrenidae; Euryglossinae + Hylaeinae + Xeromelissinae + Colletinae + Diphaglossinae = Colletidae)

Intra-familial relationships within the Vespoidea

The studies of Brothers (1975), Brothers & Carpenter (1993) and the present one have dealt with taxa at various taxonomic levels within the Vespoidea. Three of the families recognized there, Tiphidae, Sapygidae and Bradynobaenidae, were analysed to subfamily level (or even below) as part of the larger analysis. There have been critical analyses of relationships within some of the other families also, and this section attempts to indicate some of those. The families Sierolomorphidae and Rhopalosomatidae are both small and relatively little known, and no subfamily groups have as yet been proposed for them. The Pompilidae is a larger group, with three subfamilies currently recognized (Pompilinae, Pepsinae and Ceropalinae) (Day 1988; Brothers & Finnamore 1993), but I am unaware of any critical analy-

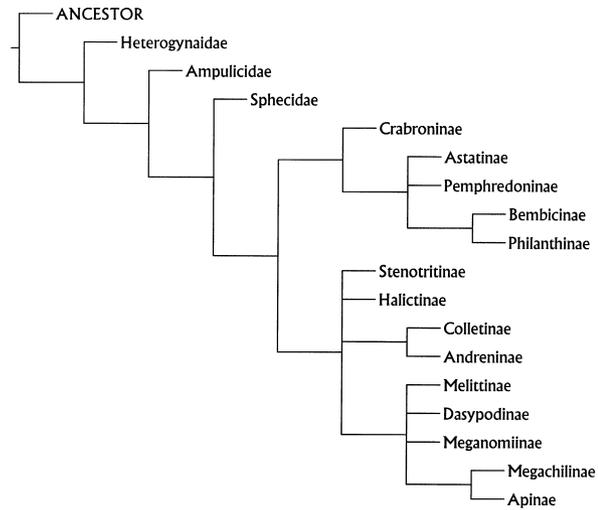


Fig. 9 Cladogram showing relationships and taxa of sphecids wasps and bees recognized by Melo (1997), with bee families of Fig. 8 as subfamilies. (Crabroninae + Astatinae + Pemphredoninae + Bembicinae + Philanthinae = Crabronidae; Stenotritinae + Halictinae + Colletinae + Andreninae + Melittinae + Dasypodinae + Meganomiinae + Megachilinae + Apinae = Apidae).

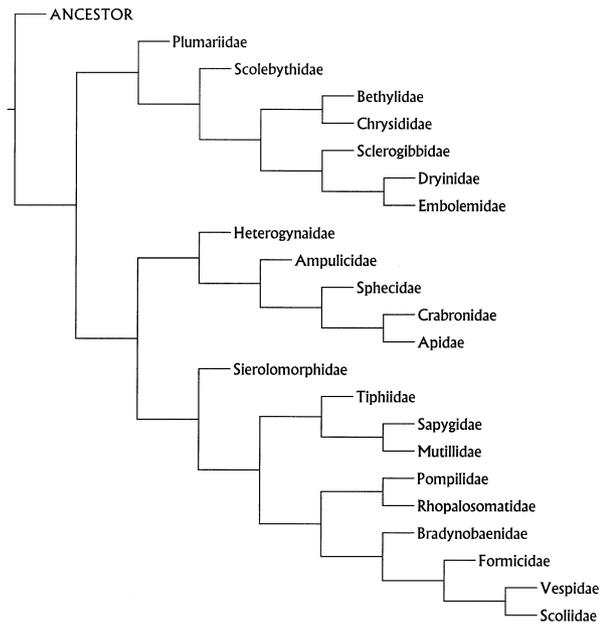


Fig. 10 Composite cladogram showing relationships of taxa of Aculeata which should be recognized at the family level, derived from previous figures.

sis of a broadly representative number of genera across the family which could throw light on their validity and/or relationships. The other families are dealt with in turn below.

Tiphiidae

The subfamilial classification of Tiphiidae has changed considerably over the years. The relationships of the most generally accepted subfamilies are shown in Fig. 3. These are slightly different from the conclusions reached by Kimsey (1991) but were justified by Brothers & Carpenter (1993) and I have no reason to alter our earlier conclusions. This is a very diverse family, with most of the subfamilies morphologically easily distinguishable and thus immediately recognizable. Apart from the work of Kimsey who has more recently been concentrating on the Thynninae (e.g. Kimsey 1992), Argaman has produced treatments of some of the subfamilies but treating them as valid at the family level (e.g. Argaman 1994a). In the process he has recognized many new subtaxa (3 new 'subfamilies' and 13 new 'tribes' for his Myzinidae, for example) in addition to describing many new genera, but has not done any critical phylogenetic analyses. I strongly suspect that many of the taxa which Argaman has proposed will not withstand the test of critical scrutiny. Apart from that aspect, should his lead be followed by other workers, the number of families of aculeate Hymenoptera would increase drastically, something for which I can see no justification. Indeed, the trend has been for a reduction in the number of families recognized.

Mutillidae

The initial purpose of Brothers's (1975) study was the clarification of the relationships of the members of the Mutillidae. The second part of that paper dealt with this topic in detail and proposed a cladogram and classification which recognized seven subfamilies. Subsequently, Krombein (1979b) described a new subfamily (Kudakrumiinae) and Lelej (1981) transferred several of the genera previously considered to belong to the Myrmosinae into it. Brothers & Finnamore (1993) preferred to regard the Myrmosinae as comprising two tribes (Myrmosini and Kudakrumiini), however. In order to investigate this, I recently performed a cladistic analysis of the taxa used in my 1975 study with

the addition of the kudakrumiines (considering them a group distinct from the myrmosines), based on the characters used at that time (Appendix I and Table 1). Several of Brothers's (1975) characters (which dealt with the two sexes separately) have identical distributions of states across the taxa and such characters were now considered to be the same character; however, where characters which describe the same feature in the two sexes have different distributions across the taxa, they were kept as separate characters. The result of this re-analysis, using Hennig86 (which produced a single most-parsimonious tree, length 66, consistency index 0.87, retention index 0.91) and Pee-Wee (which found the same tree), is shown in Fig. 11. This supports the recognition of Kudakrumiini as a tribe of Myrmosinae.

Lelej & Nemkov (1997) recently also examined the subfamily classification of the Mutillidae. They used 89 characters scored for 15 taxa, analysed cladistically using two different programs (PAUP 3.1 and Hennig86 1.5). Many characters were different from those used by Brothers (1975), and even where essentially the same characters were used they were often treated somewhat differently. For some of their characters the coding appears incorrect, with different derived states both coded the same, and a few characters are redundant. Because of inadequate material for some taxa, specially Rhopalomutillinae, their matrix also had several missing values. They did not derive ground plans for the taxa analysed but instead coded polymorphic characters as inapplicable for the particular taxon. This meant that their data matrix had a large number of missing values. Their final result, which was used to justify the recognition of several additional subfamilies and which reflects somewhat different relationships from those found by Brothers (1975 and Fig. 11), was based on analyses using only 71 of the 89 characters, those judged by some unspecified criteria to be 'most important' (50) and 'valuable' (21), the former being assigned twice the weight of the latter. No analyses using implied weighting or successive-approximations character weighting were done. Preli-

Table 1 Data matrix for analysis of Mutillidae using 42 characters of Appendix 1, derived from Brothers (1975). Variables 6,11,14,17,22,24,25,27,28,30, 33 and 40 are non-additive

Ancestor	0000000000	0000000000	0000000000	0000000000	00
Kudakrumiini	1000000000	1000110000	0002001000	0000000000	00
Myrmosini	0000000000	1001110000	0000001000	0000000000	00
Pseudophotopsidinae	0010001100	1010000101	0001000000	1000000001	10
Ticopliinae	1000002000	2110100100	0002100100	1001110101	01
Rhopalomutillinae	1011122000	2110101100	0212210200	1000100201	00
Dasylabrini	1010012010	2112100101	0112212100	1000100211	00
Sphaerophthalmina	1110012010	2112100111	1112212100	1000100211	00
Pseudomethocina	1110012010	2112100111	1112212100	1000100211	00
Myrmillinae	1010002010	2112100101	0012212100	1110100221	00
Mutillina	1010002011	2112100101	0212212111	1200100221	00
Smicromyrmina	1010002011	2112100101	0212212111	1200100221	00

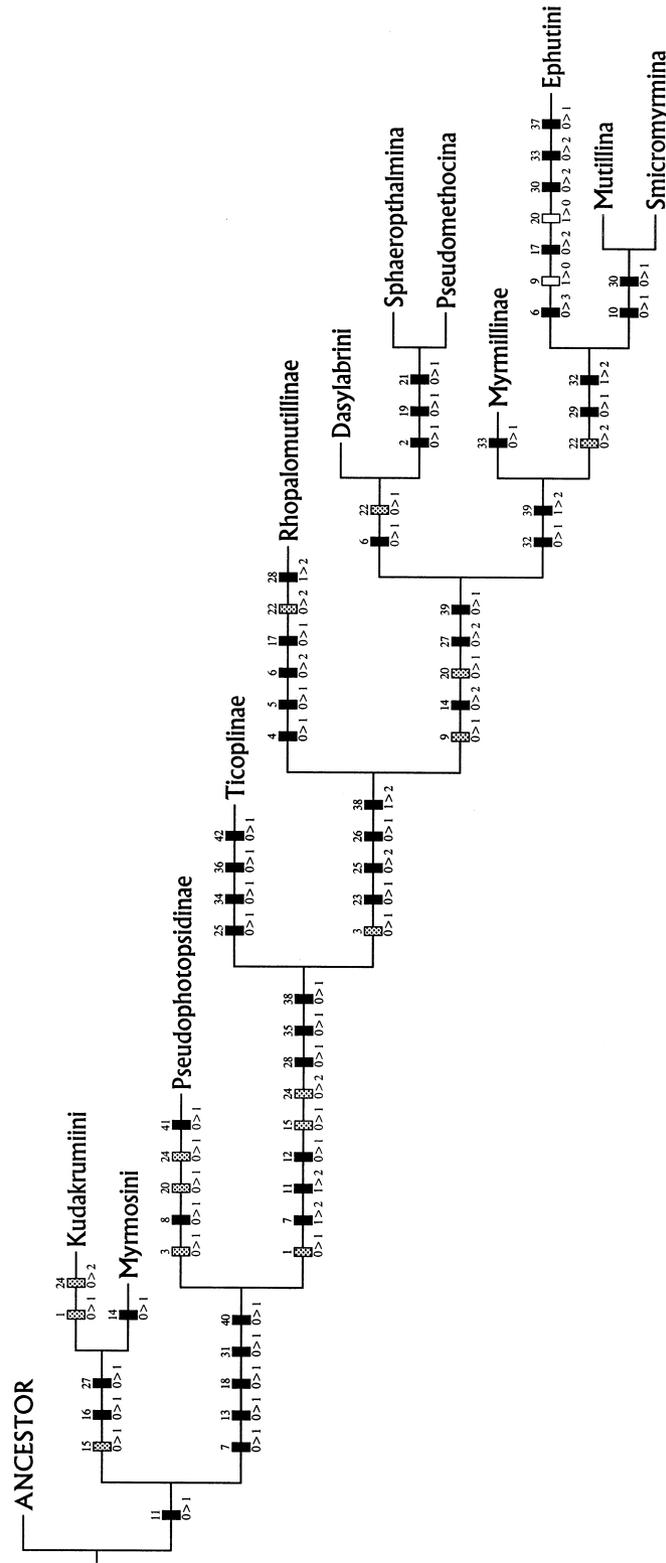


Fig. 11 Single most-parsimonious cladogram of 12 taxa of Mutillidae (based on 42 characters in Appendix I and data of Table 1, derived from Brothers 1975) (length 66, consistency index 0.87, retention index 0.91). Character numbers above, state changes below hash marks. Character hash-mark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent). (Kudakrumiini + Myrmosini = Myrmosinae; Sphaerophthalmina + Pseudomethocina = Sphaerophthalmini; Dasylabrini + Sphaerophthalmini = Sphaerophthalminae; Mutillina + Smicromyrmina = Mutillini; Ephutini + Mutillini = Mutillinae).

minary re-analyses of their data after supplying missing information and correcting some characters have produced results more similar to mine. I intend to pursue this further, but regard Lelej & Nemkov's (1997) conclusions as questionable, and so consider the relationships shown in Fig. 11 currently to be our best estimate.

Bradynobaenidae

The relationships of the component taxa of the Bradynobaenidae were established by Brothers's (1975) study. They are shown in Fig. 3 (Eotillini and Typhoctini together comprise the subfamily Typhoctinae). As for the Tiphidae, the subfamilies are very distinct and rather dissimilar. Argaman (1994b) reviewed the Apterogyninae, describing four new tribes and seven new genera, but provided no phylogenetic analysis. I am not aware of any other recent work looking at higher-level relationships in the family. Argaman (1994b) used the family name Apterogynidae although he also included Bradynobaeninae in the family. He gave no explanation, but attributed Apterogynidae to André (1899) and Bradynobaeninae to Ashmead (1903). However, de Saussure (1892) recognized the 'Tribu des Bradynoboeniens [sic]' within the 'Sous-famille des Scolines' of the 'Famille des Hétérogynes'. The tribal name was based on the genus '*Bradynoboenus* [sic] Spinola', and despite being slightly misspelled and not fully Latinized, it fulfils the requirements of Article 11(f)(iii) of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1985) for recognition from that date. Bradynobaenidae de Saussure, 1892 is thus the proper name for the family.

Formicidae

The ants comprise a large and distinct group which has previously often been recognized at the superfamily level. Much work has been done on the relationships of the various subfamilies and tribes, but there is still considerable uncertainty about the true situation. In particular, the discovery of enigmatic species with unusual combinations of characters (e.g. by Ward 1994) has caused problems. The latest complete catalogue of the family (Bolton 1995) recognized the modern subfamilies Aenictinae, Aenictogitoninae, Aneuretinae, Apomyrminae, Cerapachyinae, Dolichoderinae, Dorylinae, Ecitoninae, Formicinae, Leptanillinae, Leptanilloidinae, Myrmeciinae, Myrmicinae, Nothomyrmeciinae, Ponerinae and Pseudomyrmecinae and the fossil subfamilies Armaniinae, Formiciinae, Palaeosminthurinae and Sphecomyrminae. No details about relationships were given, but they are apparently those set out in the paper by Baroni Urbani *et al.* (1992) in which two large clades were recognized. At about the same time as the latter, Shattuck (1992) published a paper treat-

ing a small section of the family, in which he obtained the same results as Baroni Urbani *et al.* (1992) of a close relationship between Aneuretinae, Dolichoderinae and Formicinae. Most recently, Grimaldi *et al.* (1997) re-analysed the data of Baroni Urbani *et al.* (1992) in the light of new information gleaned from recently discovered fossils as well as a few taxa not included originally. That study confirmed without doubt that the fossil Sphecomyrminae are true ants, confirmed the close relationship of Aneuretinae, Dolichoderinae and Formicinae, and also confirmed the close relationship of the army ants (Apomyrminae, Leptanillinae, Leptanilloidinae, Cerapachyinae, Ecitoninae, Aenictinae and Dorylinae). Other relationships, including the monophyly of the Ponerinae, remained unclear. One must thus recognize that, although knowledge of the internal phylogeny of the ants is expanding, no firm conclusions are yet possible, except for a few components of the group.

Vespidae

Carpenter's (1981) paper dealing with the subfamily classification has not been superseded. Six subfamilies are recognized, and their relationships have been established with greater confidence than for most of the other families of Vespoidea. They are (Euparagiinae + (Masarinae + (Eumecinae + (Stenogastrinae + (Vespiniae + Polistinae))))). It is possible that the placement of Stenogastrinae is incorrect and that they may have originated more basally, as indicated by Schmitz & Moritz (1998) using molecular studies, but their results should be viewed with caution since they did not include representatives of Euparagiinae or Masarinae. Furthermore, their results placed two species of *Apis* (Apoidea) within the Vespidae!

Scoliidae

The discovery of the relatively plesiomorphic genus *Proscolia* by Rasnitsyn (1977) necessitated the recognition of a new subfamily (Proscoliinae), and the changing of the status of the two previously recognized subtaxa to that of tribes (Campsomerini and Scoliini) within the Scoliinae (Brothers & Finnamore 1993). (One of the reviewers of this paper questioned whether Campsomeridini should not be the proper spelling. In the monograph in which the subfamily was proposed, Betrem & Bradley (1972) used the shorter form; Bradley was a longstanding member of the International Commission on Zoological Nomenclature and would have been aware of such matters. This form is also supported by the probable derivation of the name, given by Dalla Torre (1897) as from *καμπός* (kampsos, curved) and *μηρός* (meros, thigh or femur), an appropriate description of the female; the stem of 'meros' is 'mer-' (genitive 'merous'), so that Campsomerini is correct.) No phylogenetic analyses of the relationships

within the Scoliinae have been done, so the validity of those taxa remains to be tested. Rasnitsyn (1993) has recently recognized another subfamily, Archaeoscoliinae, based on fossils, which he stated is probably paraphyletic.

Conclusions

From the above, it is clear that our estimates of the phylogeny and evolution of the Aculeata are quite varied in terms of the degree of confidence one can place in them. It is gratifying that the broad conclusions of Brothers (1975) for the Vespoidea continue to be supported as analyses become more refined, but it must be stated that the subsequent studies by Brothers & Carpenter (1993) and in this paper have relied in the main on Brothers's original data. It will only be possible to have greater confidence in those results should they be confirmed by other studies which consider different characters, and preferably even different types of characters, such as molecular ones. As far as the Apoidea are concerned, advances have been made recently, but additional studies across all taxa of sphecoid wasps and bees are needed. Ultimately, analysis of all taxa of Aculeata together should prove even more informative. However, it is already clear that the three superfamilies are almost certainly each holophyletic, so analyses in isolation should provide useful information. This is not to say that combination and partitioning of the data in different ways should not be done. We have found in the earlier analyses, and in the work presented in this paper, that exclusion of some groups, even if they are sister groups of the group of interest, often has marked effects on the results. This was particularly seen when comparing the results of the analysis of all taxa of aculeates with those obtained for family ground plans, and even more when only the families of Vespoidea were analysed in isolation. Such analyses at different levels are particularly useful in highlighting those areas where estimates of relationships are weakest.

Since good estimates of phylogeny are required for the proper investigation of many other topics of particular interest in the context of the aculeates, notably behavioural and physiological adaptations such as sociality, nesting behaviour, host switching, etc., and the possible times of their origin, it is important that further work in this area be pursued.

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Appendix I

Variables used in the analysis of Mutillidae based on Brothers (1975) (with relevant character numbers from that paper; characters for both sexes with identical distributions of states combined; F = female, M = male). Variables considered unlikely to show reversals: 1, 4, 5, 7, 16, 31, 35, 42

1 = *F1. Ocelli: Present = 0. Absent = 1.

2 = *F2. Eye form: Oval and weakly convex = 0. Almost circular and strongly convex = 1.

3 = *F3. Eye pubescence and pores: Present = 0. Absent = 1.

4 = F4. Maxillary palpus: Six-segmented = 0. Two-segmented = 1.

5 = F5. Labial palpus: Four-segmented = 0. Two-segmented = 1.

6 = F6. Form of mesosoma: More or less parallel-sided = 0. Mesopleuron protuberant anterior to metathoracic spiracle and propodeum narrower than prothorax = 1. Mesopleuron slightly protuberant at metathoracic spiracle and propodeum narrower than prothorax = 2. Mesopleuron weakly convex and propodeum as broad as prothorax = 3. NONADDITIVE.

7 = F7. Pro-mesonotal suture: Very weakly concave and freely articulating = 0. Distinct, concave and fused = 1. Obliterated or very indistinct and concave = 2.

8 = F8, M24. Pronotal pubescent pit: Absent = 0. Present = 1.
 9 = F9. Length of pronotum: About as long as distance between pronotal and propodeal spiracles = 0. About two-thirds or less length of distance between pronotal and propodeal spiracles = 1.
 10 = F10. Meso-metapleural suture: Almost straight and separate from mesopleural ridge = 0. Strongly angled and joining mesopleural ridge = 1.
 11 = F11. Mesosternum anterior to mesocoxae: Paired simple transverse carinae = 0. Paired toothlike projections = 1. Simple = 2. NONADDITIVE.
 12 = *F12. Contiguity of mesocoxae: Contiguous mesally = 0. Slightly separated mesally = 1.
 13 = *F13, *M28. Metasternum: Simple and flattened = 0. With paired processes anterior to metacoxae = 1.
 14 = *F14. Metacoxa dorsally: With carinate tubercle = 0. With lamellate process = 1. Simple = 2. NONADDITIVE.
 15 = *F15. Tarsal claws: Ventrally toothed = 0. Simple = 1.
 16 = *F16. Arolia: Present = 0. Absent = 1.
 17 = F17. First metasomal segment: Gradually broadened posteriorly, less than half length of second = 0. Parallel-sided posteriorly, more than half length of second = 1. Parallel-sided, less than quarter length of second = 2. NONADDITIVE.
 18 = F18. Metasomal base: Simple = 0. With paired 'auricles' = 1.
 19 = *F19, *M38. Pubescence of first metasomal tergum: Simple = 0. Some plumose = 1.
 20 = *F20, *M39. Tergal felt line: Absent = 0. Present = 1.
 21 = *M21. Eye form: Weakly convex = 0. Strongly convex = 1.
 22 = *M22. Eye shape: Broadly oval with inner margin weakly sinuate = 0. Subcircular with inner margin convex = 1. Broadly oval with inner margin acutely emarginate = 2. NONADDITIVE.
 23 = *M23. Eye pubescence and pores: Present = 0. Absent = 1.
 24 = M25. Mesosternum anterior to mesocoxae: Paired simple transverse carinae = 0. Paired toothlike projections = 1. Simple = 2. NONADDITIVE.
 25 = M26. Meso-metapleural suture: Almost straight = 0.

Posteriorly convex = 1. Sinuate = 2. NONADDITIVE.
 26 = *M27. Meso-metapleural 'bridge': Absent = 0. Present, fused = 1.
 27 = *M29. Metacoxa dorsally: With carinate tubercle = 0. With lamellate process = 1. Simple = 2. NONADDITIVE.
 28 = *M30. Tarsal claws: Ventrally toothed = 0. Simple = 1. Lamellate and cleft basally = 2. NONADDITIVE.
 29 = M31*a*. Tegula (first variable): Short = 0. Elongate = 1.
 30 = M31*b*. Tegula (second variable): Evenly convex = 0. Posteriorly recurved = 1. Longitudinally angulate = 2. NONADDITIVE.
 31 = *M32. Extent of forewing venation: Reaching distal margin = 0. Ending before margin = 1.
 32 = *M33*a*. Pterostigmal sclerotization: Entirely sclerotized = 0. Sclerotization reduced anteriorly = 1. Unsclerotized = 2.
 33 = M33*b*. Pterostigmal delimitation: Completely delimited by distinct veins = 0. Vein SC lost or much reduced, pterostigma not delimited basally = 1. Vein R lost or fused with SC, pterostigma not delimited apically = 2. NONADDITIVE.
 34 = M34. Forewing cell 1S: Sessile anteriorly = 0. Petiolate anteriorly = 1.
 35 = *M35. Jugal lobe of hindwing: Present = 0. Absent = 1.
 36 = M36. Propodeal disc: Evenly sculptured = 0. With four longitudinal carinae linked posteriorly by zigzag transverse carina = 1.
 37 = M37. First metasomal segment: Gradually broadened posteriorly, less than half length of second = 0. Parallel-sided, less than quarter length of second = 1.
 38 = M40*a*. Gonostylus form: Short, lamellate with rounded apex = 0. Short, tapered with narrow apex = 1. Elongate, tapered with acute apex = 2.
 39 = M40*b*. Gonostylus curvature: Straight = 0. Apically upcurved = 1. Apically downcurved = 2. NONADDITIVE.
 40 = M41. Gonapophysis IX: Apex dorsally produced and tooth about halfway along ventral margin = 0. Apex dorsally simple and tooth on apical half of ventral margin = 1.
 41 = M42. Gonapophyseal spines: Absent = 0. Present = 1.
 42 = M43. Digitus: Present = 0. Absent = 1.