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Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera)

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Abstract.—The development of ideas on the phylogeny of the aculeate Hymenoptera, especially Vespoidea and Chrysidoidea, since Brothers's 1975 and Carpenter's 1986 studies is reviewed. The results of their detailed analyses of aculeate higher taxa are re-evaluated in the light of new information and/or reinterpretations by subsequent workers. Almost all of their earlier results, including the relationships within the Chrysidoidea, the holophyly of Vespoidea (including Pompilidae), the sister-group relationship of Scoliidae (including Proscoliinae) and Vespidae, that of Sapygidae and Mutillidae (including Myrmosinae), and the composition of Bradynobaenidae are confirmed. The final preferred cladogram, using 219 variables and based on ground plans for all families of Chrysidoidea and Vespoidea and three taxa of Apoidea, indicates the following relationships (components of the superfamilies included within curly brackets): {Plumariidae + (Scolebythidae + ((Bethylidae + Chrysididae) + (Sclerogibbidae + (Dryinidae + Embolemidae)))) + ({Heterogynaidae + (Sphecidae s.l. + Apidae s.l.)} + {Sierolomorphidae + (Tiphiidae + (Pompilidae + (Sapygidae + Mutillidae))) + (Rhopalosomatidae + (Bradynobaenidae + (Formicidae + (Scoliidae + Vespidae)))))}).

INTRODUCTION

Current ideas on the phylogeny of the aculeate Hymenoptera date from the publication of Brothers's (1975) paper, which was the first attempt to apply cladistic principles in an analysis of the entire group. Since the initial purpose of that study was merely the elucidation of the relationships of the components of the Mutillidae s.l., the paper had limitations in that the component taxa were dealt with in differing detail (analysing tribes in some taxa but lumping families presumed to comprise holophyletic groups elsewhere) and the sample of exemplars used to derive taxon ground plans was probably inadequate for some taxa. Although not all of the conclusions of that study have been accepted, it has fulfilled one of its major functions in stimulating further investigations of the relationships among the various higher taxa of aculeates, Carpenter's (1986) analysis of the families of Chrysidoidea being particularly significant. The present paper aims to survey the relevant literature which has appeared on the topic since 1974, to analyze new characters and interpretations presented therein, and to modify and amplify the data base of Brothers (1975) and re-analyze it in the light of the new information. The final result is the best-supported cladogram available for the superfamilies of Aculeata and for the components of the Chrysidoidea and Vespoidea. We do not analyze the Apoidea in any detail since it is clearly a holophyletic group and analyses of some of its components are presented by Alexander (1990, 1992); that superfamily is in any case the group dealt with in least detail in the 1975 analysis.

Limits and names of the various taxa included in the Aculeata are sometimes problematic. Thus, Brothers's Bethyloidea and Sphecoidea should be Chrysidoidea and Apoidea respectively in terms of nomenclatural priority (Day 1977, Michener 1986), and the correct names are used below for these taxa even though other names may have been used by the authors of the papers under discussion. The abbreviations 's.l.' (*sensu lato*) and 's.s' (*sensu stricto*) are used to indicate more and less inclusive concepts where confusion could result, e.g., Vespoidea s.l. is more or less the concept of Brothers (1975), whereas Vespoidea s.s. comprises only Vespidae s.l. (Masaridae + Eumenidae + Vespidae s.s.).

PREVIOUS STUDIES

In the following survey of papers on this topic, we generally deal with them in chronological order, starting in 1975 with Brothers's study which examined 25 taxa and 92 characters of Aculeata. The cladogram he obtained is reproduced here (Fig. 1) in the format generated by CLADOS (Nixon 1992) from Hennig86 version 1.5 (Farris 1988), the computer programs used for our new analyses, for easier comparison with them. The distribution of derived character states on the various internodes of the 1975 cladogram is also provided (Appendix IA) to remedy a lack in the original paper; this is similar to the listing given by Wahl (1990) but with a few corrections. (Note that the distribution and numbering of variables shown in Fig. 1 results from one of our new analyses (see below) and is not the same as that used in the 1975 paper.) Major conclusions from the 1975 analysis were the establishment of the holophyletic nature of the Chrysidoidea, with Plumariidae as the sister taxon of the remaining chrysidoid families (exemplified by Scolebythidae and an amalgam of other taxa); the recognition of the polyphyletic nature of the traditional superfamily Scolioidea, with placement of the Scoliidae as the sister taxon of the Vespidae s.l. rather remote from the Tiphiidae; the acceptance of only three superfamilies (Chrysidoidea, Vespoidea and Apoidea) instead of the traditional seven; inclusion of Pompilidae in Vespoidea rather than close to Apoidea; inclusion of Myrmosinae in Mutillidae rather than Tiphiidae; and inclusion of Typhoctinae, Chyphotinae, Apterogyninae and Bradynobaeninae in a single newly constituted family (Bradynobaenidae) rather than in Mutillidae and Tiphiidae. Brothers (1976) further investigated the structure of the metapostnotum and second and third phragmata in various aculeates, finding corroboration for his earlier conclusions.

In 1977 Rasnitsyn described a new subfamily of Scoliidae based on a monotypic genus, *Proscolia* Rasnitsyn, which he considered indicated that "the ancestor of the family was at least as primitive as the Anthoboscinae (Tiphiidae)", and thus probably most closely related to that taxon. Such a conclusion does not necessarily follow, however, since it is based on shared plesiomorphies.

Over three years, Saini & Dhillon investigated various modifications of the metatibial spurs (1978), mouthparts (1979a, b) and metathorax (1980) in 22 varied families of Hymenoptera. Single and often relatively derived representatives were apparently used for each family, so that the studies were very limited, providing no information on intrafamilial variation. Furthermore, there was no differentiation between plesiomorphies and apomorphies, invalidating their conclusions. On the basis of number and development of the metatibial spurs, they linked Mutillidae and Formicidae (including their Dorylidae) in one line, and Chrysididae, Scoliidae, Sphecidae, Vespidae s.s., Eumenidae, Pompilidae and Apoidea s.s. in another. Looking at the mouthparts, they identified two lines of modification (in the maxillae involving the relative sizes of the galea and lacinia and in the labia the relative development of glossa and paraglossa), the first leading from Ichneumonoidea to Chrysididae, Mutillidae and Formicidae, and the other from Chalcidoidea to Scoliidae, Sphecidae, Vespidae s.s., Pompilidae, Eumenidae and Apoidea s.s. Their account of modifications of the metapleuron and metapostnotum could be interpreted to indicate close relationships between Chrysididae, Scoliidae and Sphecidae, a lineage including Vespidae s.s., Eumenidae, Formicidae and Apoidea s.s., and distinctness of the Pompilidae. They disagreed with Brothers's (1975, 1976) interpretation of the origin of the 'propodeal triangle' (as an expanded metapostnotum) in Apoidea s.l.

Königsmann (1978), in that part of his survey of hymenopteran phylogeny covering the Aculeata, based his treatment to a great extent on Brothers's (1975) analysis but indicated large areas of uncertainty (Fig. 2), usually where he felt that the characters given by Brothers in support of particular internodes were weak or homoplastic. He placed Sclerogibbidae as the sister group of all other aculeates (on the basis of the multisegmented antennae and apparent lack of synapomorphies with any particular aculeate group), excluding it from the Chrysidoidea, but otherwise accepted the division of the aculeates into three holophyletic groups. He analyzed the remaining taxa within the Chrysidoidea in greater detail than Brothers had, and suggested a sister-group relationship between

Plumariidae and Scolebythidae (based on the common reduction of the pronotal collar), between Embolemidae and Dryinidae (based on the 10-segmented antennae and single mesotibial spur in both) and between Chrysididae and Cleptidae (based on integumental sculpture, wing venation, form of the ovipositor and possibly the lack of articulation and sensillar fields between the first and second metasomal segments) but could not resolve the relationships among these pairs of taxa or Bethylidae and Loboscelidiidae, the other two taxa he included. Within the vespoid group he accepted a sister-group relationship between Scoliidae and Vespidae, rejected Scolioidea as polyphyletic, accepted a sister-group relationship of Pompilidae and Rhopalosomatidae, was uncertain of the position of Sierolomorphidae, and used more traditional superfamily names but left many taxa unassigned to superfamily. His treatment did not aim to be an original cladistic analysis of all characters for all taxa, but instead relied almost exclusively on data published by other workers; it is thus limited in providing new interpretations, but is useful in explicitly indicating the weakest points in Brothers's analysis.

Walther (1979) examined the types and arrangement of antennal sensilla of 25 species of aculeates in 12 higher taxa. He confirmed the 'monophyly' of Formicoidea (based on a single representative!), Pompiloidea (five Pompilidae only), Vespoidea s.s. (five Vespidae and Eumenidae) and Apoidea s.s. (three Andrenidae and Apidae) and found no evidence for holophyly of Scolioidea (11 species in 8 taxa). He confirmed a close relationship between Mutillidae (exemplified by three of the most derived species in that taxon) and female Myrmosinae, found evidence to link Anthoboscinae and Tiphiinae, but found no characters linking Scoliidae and Vespidae or Myzininae and Methochinae, and rejected any close relationships between Formicoidea and Anthoboscinae or Methochinae (relationships which had also been rejected by Brothers 1975). His study was very limited, however, in that he considered a single character complex to the exclusion of all others, his sample for each taxon was exceedingly small (often only one), and he seems often to have used inappropriate exemplar species (highly derived ones). He presented no simple coding of characters, so that his information cannot easily be included in any new cladistic analysis.

In his analysis of the evolution of the Hymenoptera, Rasnitsyn (1980) reinterpreted some of Brothers's (1975) characters and added a few new characters. In the Aculeata (his Vespomorpha; ignoring taxa known only from fossils, which were not considered by Brothers), he recognized the Chrysidoidea as a holophyletic group (including Sclerogibbidae), but split Brothers's Vespoidea into four superfamilies with Pompiloidea as the sister-group of Apoidea s.l. In the Chrysidoidea, he included Cleptinae and Loboscelidiinae in Chrysididae, rejected a close relationship between Embolemidae and Dryinidae (considering their similarities to be homoplastic), and postulated a sister-group relationship between Sclerogibbidae and Dryinidae. Although his figure (Fig. 3a) shows Scolebythidae as the sister taxon of (Embolemidae + (Bethylidae + Chrysididae)), this contradicts his discussion in which he stated that he preferred not to draw conclusions as to which of Plumariidae and Scolebythidae diverged the earlier from the stem leading to the remaining Chrysidoidea (implying a trichotomy as shown in Fig. 3b). His Scolioidea is a paraphyletic group giving rise to Formicoidea and Vespoidea s.s., and with Mutillidae remote from Sapygidae, and Scoliidae the sister-group of Tiphiidae + Mutillidae. In his discussion, Rasnitsyn implied that Tiphiidae is paraphyletic, with both Scoliidae and Mutillidae independently derived from within it. Although his figure left Bradynobaenidae floating within the Scolioidea, his discussion indicates that he considered it an early offshoot of the larger scolioid clade, but he could not decide which of Sapygidae and Bradynobaenidae had diverged first; this is shown as a trichotomy in our version of his phylogeny (Fig. 3b). Although he used the concept of synapomorphy, at least in part, in deriving his phylogeny, he did not do a general analysis considering all states for all characters over all taxa. He was also often not explicit in his definitions of the various states of characters, so that it is sometimes difficult to be certain of the significance to be placed on various features. In many cases his interpretations were very heavily influenced by, if not entirely based on, his impressions of features in

fossils, which were allocated to their extant taxa and used to polarize his characters. There seems to have been a general application of the principle that states seen in older fossils are necessarily more primitive than states in more recent fossils or modern species. Such an assumption cannot be justified since a plesiomorphic state can persist in one lineage long after an apomorphic state of the same character has arisen in a related lineage, and the fossil record is far too fragmentary to resolve such situations. In order to estimate how well Rasnitsyn's (1980) phylogeny is supported by the characters he cited, we did an analysis based on as many characters (38) and states as we could extract with reasonable certainty from his account, using his interpretations but correcting two or three straightforward errors. These were coded using nonredundant linear coding (O'Grady & Deets 1987) (Appendix II; Table I) and analyzed using Hennig86 for the modern taxa. The analysis produced three equally most parsimonious unweighted cladograms, with fewer steps than implied by his trees (Figs. 3a, b) for those characters used by us (lengths 94 versus 115 and 116). The strict consensus tree (Fig. 4) is considerably different from that given in his paper. The major differences are that Pompiloidea is now the sister-group of the remaining Vespoidea, Mutillidae and Sapygidae are sister groups, and Scoliidae is the sister-group of Vespidae + Formicidae. In many respects this tree is more similar to that of Brothers (1975) than Rasnitsyn's tree(s). We thus conclude that Rasnitsyn's (1980) treatment is highly subjective and that the tree he presented is not the one which explains his own data most efficiently.

Day, Else & Morgan (1981) provided a detailed analysis of *Proscolia*, pointing out that it lacks various of the putative synapomorphies, such as reniform eyes, dorsally produced clypeus and elongated ligula, previously used to establish the sister-group relationship of Scoliidae and Vespidae. They made no detailed analysis of the effect of making the necessary changes in ground-plan states on the relationship between these families, but suggested that they were unlikely to affect it significantly, and rejected Rasnitsyn's (1977) suggestion that the characters of *Proscolia* indicate a close relationship with Anthoboscinae (Tiphiidae).

The relationships within the Vespoidea s.s. were examined in detail by Carpenter (1981). He applied a numerical cladistic analysis to 50 varied characters and concluded that a single family (rather than three) should be recognized to include six subfamilies. In general he followed Brothers's (1975) interpretations of character state changes where he used similar characters, but the study was limited to the relationships within a group considefed as a single final taxon by Brothers, so that any differences of interpretation are of limited general applicability.

Osten (1982) investigated the structure and musculature of the head and mouthparts in 48 species of Hymenoptera, with the emphasis on 'Scolioidea'. He found that the separation of mandibular and oral cavities by a cuticular bridge, previously cited as a defining character of Scolioidea by Börner (1919), for example, is very variable within that grouping, even differing between the sexes of a single species of scoliid (present in female but entirely absent in male), and thus invalid. He agreed with Brothers (1975) in rejecting Scolioidea as polyphyletic, but saw a close relationship between Scoliidae and 'Myzinidae', and between Mutillidae and 'Tiphiidae' s.s. (*Tiphia* Fabricius). His conclusions were based entirely on a restricted number of characters and an inadequate sample of exemplars (these often being some of the most highly derived members of their taxa), however.

In 1984 Day clarified the position of *Heterogyna* Nagy, a genus which Brothers (1974, 1975) had tentatively placed in the Plumariidae (Chrysidoidea), based on the rather inadequate description and figures available to him. Day showed convincingly that this genus is an aberrant member of the Sphecidae s.l., for which he recognized a separate subfamily. Argaman (1985) reviewed the group (as a distinct family), and suggested a closer relationship with the Chrysidoidea, and Embolemidae in particular, but his ideas were mainly based on a somewhat confused mixture of shared plesiomorphies without any critical analysis of apomorphies. The correct name for this taxon was the subject of a ruling by the International Commission for Zoological Nomenclature (1987), which specified the stem to be '*Heterogyna-*' (to prevent

confusion with family-group names based on the lepidopteran genus *Heterogynis* Rambur).

Walther (1984) extended his examination of antennal sensilla in ants and proposed "a close phylogenetic relationship between the Formicoidea and the Scolioidea including the Scoliidae". Unfortunately, this paper is merely an abstract, and no further details or justifications have been published.

Gibson (1985) carried out a detailed examination of various structures of the pro- and mesothorax, especially in Parasitica, and most of this study is irrelevant in the context of aculeate phylogeny. However, he did show that the close association of the pro- and mesothorax in the Scoliidae and Vespidae must have been independently derived, rather than being a synapomorphy as Brothers (1975: Character 19) had postulated, but this did not invalidate the idea that the different forms of the prepectus in these taxa may have been derived from a common relatively derived condition (Brothers 1975: Character 29). The postulated sister-group relationship of these two taxa was thus weakened but not disproved.

The next major paper is that of Carpenter (1986) in which he analyzed the relationships of the families of Chrysidoidea. This is a detailed cladistic study based on 22 characters or character complexes, and including extensive analysis of previous interpretations of these characters and/or taxa, specially those of Rasnitsyn (1980). His cladogram (Fig. 5) is well-supported since most internodes have at least one unique synapomorphy. He unfortunately did not present a data matrix or explicit explanations of the codings of his characters, but he did list the inferred apomorphies for all nodes (components) and terminal taxa (terms). His analysis supported the traditional views of sister-group relationships between Chrysididae and Bethylidae and between Embolemidae and Dryinidae, placed Sclerogibbidae unequivocally and confirmed the inclusion of Plumariidae and the branching sequence of Plumariidae then Scolebythidae and the remaining Chrysidoidea, as suggested by Brothers (1975).

In his 1987 revision of *Bradynobaenus* Spinola, Genise suggested different ranks for the higher taxa of aculeates "in order to diminish the differences between the classification of Hymenoptera Aculeata proposed by Brothers and the classical one" and to facilitate the construction of keys. Genise accepted Brothers's (1975) analysis as being the best and most objective then available, and merely modified his classification by raising the ranks of almost all higher taxa by one level. So, for example, the three superfamilies became informal groups with '-formes' endings and included 11 superfamilies. This necessitated the proposition of four new superfamilies, Sierolomorphoidea (Sierolomorphidae only), Tiphioidea (Anthoboscidae, Thynnidae, Myzinidae, Tiphiidae s.s., Brachycistididae, Methochidae), Bradynobaenoidea (Chyphotidae, Typhoctidae, Apterogynidae, Bradynobaenidae s.s.) and Mutilloidea (Mutillidae, Sapygidae), and restriction of the Scolioidea to include Scoliidae only. The scheme thus ended up as being more different from the classical arrangement than was Brothers's.

Schönitzer & Lawitzky (1987) studied the antenna cleaner by scanning electron and light microscopy in Formicidae (seven subfamilies), Mutillidae (four subfamilies) and Tiphiidae (four subfamilies), by light microscopy alone in single or a few species each representing Bethylidae, Chrysididae, Bradynobaenidae, Eumenidae, Vespidae, Masaridae, Scoliidae, Pompilidae and Sapygidae, and also consulted descriptions and published figures of a few other taxa. They related their findings to Königsmann's (1978) phylogeny, and found some support for the holophyly of Formicidae, of (Sapygidae + Mutillidae) (although they indicated that the antenna cleaner in Myrmosinae is more similar to that in some Tiphiidae), and of the four subfamilies of Tiphiidae for which they had data. As the authors themselves admitted, too few characters (and too few representatives) were involved for them to draw any further conclusions.

The relationships of *Proscolia* were again examined by Osten (1988). He compared various morphological structures, particularly the mouthparts, across 27 species, representing about 13 taxa at the subfamily level or above, in Scoliidae, Tiphiidae (including Bradynobaeninae and Myrmosinae!), Mutillidae and Sapygidae. His cladogram of the 'Scolioidea', based on a few characters of the head and mouthparts only, indicated the

Tiphiidae s.l. as extensively paraphyletic, giving rise separately to Mutillidae, Scoliidae and *Proscolia* (sister taxon of Anthoboscinae and remote from the Scoliidae) but not to Myrmosinae or Sapygidae. These results must be evaluated with the realization that they are based on a very limited data set in terms of number of exemplars, number of higher taxa and number of characters used, and exclude such classical characters used to associate *Proscolia* and Scoliidae as the tripartite propodeum, striolate wing membrane and widely separated meso- and metacoxae.

Johnson (1988) examined the mesocoxal articulations in a wide but unspecified variety of hymenopterons, and dissected the extrinsic musculature in a broad selection, including 27 species in 14 families of Aculeata. He obtained little critical information from the limited number of characters involved, but confirmed the holophyly of Chrysidoidea and of each of the three families Mutillidae, Bradynobaenidae and Formicidae, using the cladograms of Brothers (1975) and Carpenter (1986). Since he did not list all the taxa examined, it is difficult to evaluate the general validity of his results, however.

Also in 1988, Rasnitsyn produced an English summary of his ideas, some of which had changed since his 1980 paper. His phylogeny of the aculeates ('Vespomorpha') differs slightly from the previous one, in that the Scolebythidae are more basal in the Chrysidoidea, and the sequence of branches involving Sierolomorphidae, Falsiformicidae, Formicoidea and Vespoidea s.s. is different. In the text he indicated that the position of Bradynobaenidae was still obscure (referring to his 1980 paper for details), but now suggested common ancestry either with (Mutillidae + Tiphiidae) (his node 104) or with the clade including Sierolomorphidae (node 108); we have compromised and placed Bradynobaenidae as forming a trichotomy with both major branches involved (Fig. 6). As with his 1980 scheme, subjection of Rasnitsyn's own characters and states for the modern taxa (Appendix III; Table II) to a cladistic analysis using Hennig86, produces results which differ from his in many respects, and differ slightly from those produced by a similar treatment of his 1980 data (Fig. 4). Exact analysis produced six equally parsimonious cladograms, the strict consensus of which is shown in Fig. 7a, and successive approximations character weighting produced two cladograms (strict consensus shown in Fig. 7b, resolving an additional taxon in Chrysidoidea). Major differences between Figs. 6 and 7 are the holophyly of the Vespoidea s.l. (including Pompilidae and Rhopalosomatidae), the unresolved relationships amongst the components of the 'Scolioidea' and the Formicidae-Vespidae, and the sister-group relationship of Mutillidae and Sapygidae in Fig. 7. The major differences between the earlier and later reanalyses are the positions of Formicidae, Scoliidae and Vespidae and the degree of resolution of the 'Scolioidea'. The same problems and limitations of methodology and philosophy apply to the 1988 paper as to that of 1980 (Carpenter, 1990a). Rasnitsyn (1988) made explicit statements that he preferred searching for new characters and re-evaluation of the reliability of the evidence to criteria such as parsimony in dealing with homoplasy, and that he disagreed with 'cladistics ("phylogenetic systematics")' in so far as the derivation of classifications is concerned, preferring to accept ancestral paraphyletic groups as valid taxa, which explains some of the anomalies. Regardless of the merits of those viewpoints as stated in such broad terms, parsimony cannot legitimately be rejected out of hand, especially when the differences between the lengths of the trees being compared are as great as here (131 versus 118 for Figs. 6 and 7a respectively).

Day (1988), in a general account of the British Pompilidae, rejected some of Brothers's (1975) supposed synapomorphies of Pompilidae and Rhopalosomatidae, stating that the fine structure of the hindleg cleaning apparatus is very different in the two (something about which we are not convinced after reexamination), that the common loss of the second abscissa of vein 1A in the hindwing ignores the presence of a claval lobe in Rhopalosomatidae (but these are surely different characters); and that the basal hamuli in Rhopalosomatidae are more like those of the primitive Xyelidae (which could be the result of subsequent reduction in the ancestor of Pompilidae). Instead, Day cited several features of Rhopalosomatidae which "parallel those of the vespid (*s. str.*)

branch", including the shape of the eyes, formation of a trochantellus (although this is probably a plesiomorphy, and is weakly present in some Pompilidae), coadaptation of the pronotum and mesothorax, form of propodeal to metasomal articulation, and articulation between first and second metasomal segments. Many of these characters have relatively more plesiomorphic states (often fairly similar to those in Pompilidae) in the brachypterous genus *Olixon* Cameron, however, and these could represent the ground-plan states for Rhopalosomatidae. In addition, Day questioned Brothers's (1975) interpretation of the ground-plan state for the metapleuron in Pompilidae (another putative synapomorphy with Rhopalosomatidae); our re-examination has led to extensive reinterpretation of this character (see new analyses below). Day came to no firm conclusions, but retained Pompilidae as an early offshoot of the vespoid stock although probably not close to Rhopalosomatidae.

In a comprehensive general treatment of the British Hymenoptera, Gauld & Bolton (1988) followed Brothers's (1975) classification of the Aculeata (except that they reduced Spheciformes and Apiformes to a single family each), but unfortunately redrew his impressionistic tree of the relationships of the chrysidoid families in a formal manner instead of using the critically derived cladogram produced by Carpenter (1986). They stated that the Vespoidea was probably paraphyletic and suggested that the Pompilidae might have to be distinguished as a separate superfamily, without giving any evidence to support these ideas.

In a series of papers starting in 1987, Piek and his co-authors (Piek 1987, Piek et al. 1989, Piek 1989, Piek 1990) related their discoveries of novel components (kinins) in the venoms of various aculeates to Brothers's (1975) phylogeny, suggesting, in a stepwise fashion, how it should be modified to take their results into account. These papers are a particularly clear example of misguided attempts to invalidate a phylogeny based on numerous characters and taxa by consideration of only one or a few new characters which have been investigated in only a small number of taxa and apparently without taking the concepts of ground-plan analysis into account. The last tree proposed (Piek 1990) grouped Mutillidae (based on 3 species in 2 derived subfamilies), Formicidae (6 species in 2 subfamilies), Tiphiidae (2 species in 2 derived subfamilies), Scoliidae (3 species) and Vespidae s.s. (12 species) on the basis of the presence of kinins in their venoms (although these were not found in 2 of the 3 mutillids!). There is still insufficient information for the incorporation of this character into any general analysis of the Aculeata.

Kimsey (1991) re-evaluated the status and limits of the subfamilies of Tiphiidae delimited by Brothers (1975), and came to the conclusion, based on a cladistic analysis of 19 characters, that his Thynninae should be subdivided, with a relatively more primitive component (Diamminae) falling in the cladogram in the same position as Brothers's Thynninae (not surprising since *Diamma* Westwood was used as the main representative when he derived the ground plan for his Thynninae), and the other component falling as the sister-group of Myzininae. Her cladogram is identical to that presented by Brothers in all other respects. Kimsey's interpretations of some characters are questionable, however, and she sometimes did not clearly distinguish between the two sexes. Thus, enlargement of the ocelli in males is not universal in Brachycistidinae since species of *Brachycistellus* Baker and some *Quemaya* Pate have small ocelli, are black in colour and may even be diurnal (Wasbauer, 1968). Not all male Myzininae have emarginate eyes (simple in *Pterombrus* Smith), so that this feature is probably not part of the ground-plan of that subfamily. The differences between the frontal lobes of Diamminae and some Thynninae are far slighter than indicated by Kimsey; in these there is merely a frontal swelling which may be associated with a slight expansion of the dorsal rim of the socket itself, not very different from the condition in many Anthoboscinae; some male Methochinae (e.g. species from North America and Trinidad examined by DJB) have even less development of frontal lobes. The pronotum is not universally vertical in Brachycistidinae; there is a short but distinct dorsal surface in *Quemaya* at least, although the pronotum is strongly concave posteriorly. Not all Tiphiinae have only a single mesotibial spur; there are two in both sexes of *Paratiphia* Sichel at least. It is difficult to under-

stand how closed metacoxal cavities could be part of the ground plan of Thynninae when *Aelurus nigrofasciatus* Smith is illustrated as having distinctly open cavities; Kimsey gives no explanation or justification for her conclusion which is contradicted by her later study of some Thynninae (Kimsey 1992). Although most female Thynninae certainly have the metasomal apex considerably modified, this is not always the case (*Aelurus* Klug (Kimsey 1992), *Elaphroptera* Guérin and some unidentified Australian species examined by DJB have it similar to many other tiphiids) and so cannot be part of their ground plan. A bilobate eighth tergum is not universally present in male Myzininae; at least one *Pterombrus* sp. (from Trinidad) has it simple. In the absence of further justification, we are not convinced that the ground-plan state of the male hypopygium (metasomal sternum VIII) in the Thynninae is unciform; some thynnines (e.g., *Aelurus* (Kimsey 1992) have simple hypopygia (although not identical to those in Anthoboscinae) which is the groundplan condition for the family, most have a wide variety of modifications (including some with a single strong upcurved process but different in formation from the superficially similar condition in Myzininae and Methochinae), and apparently only one genus (not named by Kimsey) has it unciform. Kimsey's treatment of the form of the hypopygium as two separate characters, thus coding Thynninae as simultaneously unciform and "elaborately lobate and sculptured", is also illogical. Furthermore, we are not convinced of the validity of the proposed synapomorphy of volsellar elaboration in Myzininae and Thynninae: the digitus and cuspis are somewhat elaborate and well articulated in at least some tiphiines such as *Paratiphia* and Kimsey (1992) even stated that various thynnine genera have the same condition as considered primitive for the family.

Quicke, Fitton & Ingram (1992) examined ovipositor structure, with particular reference to the valvilli, in a wide variety of Hymenoptera, with particular emphasis on Ichneumonoidea but also including Chrysidoidea (6 species in 4 families), Vespoidea (24 species in 7 families, but mainly ants) and Apoidea (9 species, mainly various bees). Their findings confirmed those of Oeser (1961) and Brothers (1975) and provided additional justification for considering the presence of valvilli to be ancestral in Aculeata.

Also in 1992, Quicke, Ingram, Baillie & Gaitens examined sperm structure in a variety of Hymenoptera, including about 20 species of Aculeata in the following taxa: Chrysidoidea: Dryinidae; Apoidea: Andreninae, Anthophorinae, Megachilinae, Apinae, Xylocopinae, Astatinae, Larrinae, Nyssoninae, Pemphredoninae, Sphecinae; Vespoidea: Eumeninae, Vespinae, Polistinae, Pompilidae, Formicidae. Although some interesting results were obtained which indicated the potential usefulness of such studies for hymenopteron systematics, the data are still insufficient to be incorporated in any re-analysis of the aculeates as a whole.

NEW ANALYSES

For our new studies, various sets of data were subjected to analysis using different options of Hennig86 (Farris 1988) to obtain the most parsimonious cladograms and strict consensus trees with and without the application of successive approximations character weighting. Polarization of characters was based on outgroup comparison, using a wide variety of species of Ichneumonoidea and Symphyta, and the trees were rooted by the addition of an ancestral outgroup with all variables coded 0. Character weighting was applied to give some indication of which cladogram derived without weighting might be preferred. Tree plots and optimizations of placements of derived states were done using Clados (Nixon 1992) both using the accelerated transformation option (which applies the criteria of Farris (1970), maximizing reversals and minimizing parallelisms) and also using the delayed transformation option (which applies the criteria of Swofford & Maddison (1987), maximizing parallelisms and minimizing reversals). In all cases, variables for which values are unknown or inapplicable for some taxa were 'squeezed' (Nixon 1992) so that state changes were placed as far from the base of the tree as possible (distal to the points of origin of taxa for which the values are missing) to avoid the indication of apparent synapomorphies based only on the putative sharing of missing states (Platnick, Griswold & Coddington 1991). The plots and appendices giving state placements are

based on those produced by accelerated transformation (the optimization preferred on a theoretical basis by de Pinna (1991)), except that variables for which reversals are considered unlikely on evolutionary grounds (such as Dollo's law), are placed according to delayed transformation. Manual analysis of such optimizations on consensus trees based on successive weighting sometimes showed that different placements could further reduce the number of reversals without increasing the number of steps; this often lead to a resolution of tree topology and thus an indication of the fully dichotomous cladogram (from the set of underlying cladograms) to be preferred. In all cases, such a preferred cladogram was found to be identical to one from the initial set of cladograms derived without the application of character weighting. Choice of cladogram was also influenced by comparison with the results of the other analyses. The appropriate optimizations of variables on the preferred unweighted cladogram were then carried out; for a few 'irreversible' variables, manual modification of delayed transformation placements enabled reversals to be eliminated without increasing the number of steps.

The first attempt to subject Brothers's (1975) phylogeny to a critical analysis using modern techniques, particularly efficient computer derivation using Hennig86, was done by Carpenter (1990b). The cladogram which was presented, derived from Brothers's data as far as Carpenter was able to reconstruct them from the original paper and using nonredundant linear coding, agrees closely with Brothers's tree, although there are a few differences. That treatment was a preliminary one and unfortunately included a few errors, and also scored sexually dimorphic characters as missing. The data base was re-evaluated through consultation between both of us and an improved version, with a few changes to scoring and coding, was subjected to analysis. A list of the 162 variables, showing their derivation from the original 92 characters, is given in Appendix IV, and the data matrix appears as Table III. (Note that here (and in subsequent analyses) the variables refer to the conditions in the relatively least modified forms (e.g., to macropterous individuals where the taxon also contains brachypterous or apterous ones), unless there is a statement to the contrary.) Brothers's analysis had considered differential expression of character states in the two sexes in some detail, and this was particularly significant in his estimates of amounts of phenotypic divergence. In the present re-evaluation, however, for a taxon where there is sexual dimorphism in the expression of character states, such that for a particular taxon only one sex has a relatively apomorphic state which occurs elsewhere in the other or both sexes (whether in an entire taxon or only part of a taxon), the relatively plesiomorphic state was scored (in analogy with ground-plan analysis); if the relatively apomorphic state does not occur elsewhere in the other sex, however, then the relatively apomorphic state itself was scored. This simplification is unlikely to have any material effect on the estimates of the branching pattern.

Two sets of analyses were run, one using only those characters identified by Brothers (1975) as the most significant in deriving his phylogeny, and the other using all characters. Interestingly, the results using all characters were consistently more similar to the 1975 tree than those based on the restricted character set. Since there is no good reason to exclude any characters, the restricted data set was discarded and further analyses were based on the full set of 162 characters. When no weighting was used, eight equally parsimonious cladograms resulted. The strict consensus tree appears in Fig. 8a. The application of successive approximations character weighting produced two cladograms, each identical to one of the original eight. One of these two cladograms is preferred (Fig. 8b), both on the basis of manual optimization of states on the consensus tree (see above; Variables 72, 83 and 95), and also because this is the one most closely resembling the results of subsequent analyses (see Figs. 9a, 9b, 10a, 10b), and Brothers's (1975) tree, for the taxa showing ambiguity (Plumariidae placed as the sister group either of the remaining Chrysidoidea or of (Apoidea + Vespoidea)). It differs from Brothers's tree (Fig. 1) in a number of respects: Sierolomorphidae is basal in Vespoidea, (Pompilidae + Rhopalosomatidae) is polyphyletic, Formicidae is the sister group of Bradynobaenidae, and Thynninae s.l. is basal in Tiphiidae. Brothers's major conclusions on the polyphyly of 'Scolioidea', the sister-group relationship of Scoliidae and Vespidae, and

also of Sapygidae and Mutillidae (including Myrmosinae), and the composition of Bradynobaenidae are confirmed. The 1975 tree is, however, only about 2% longer than the most parsimonious cladogram (408 versus 401 steps, both lengths based on the distribution of states in Table III), and the differences found may thus be of little significance. There is no point in analysing them in greater detail since new data are now available. (Note, however, that the computer-derived optimization of states shown in Fig. 1 and Appendix IB differs in many respects from the placement of states used in 1975 (Appendix IA). In particular, the computer-derived scheme suggests that the polarities of at least four characters (25, 61, 62 and 82 = Variables 40, 103, 106 and 142) may be incorrect, since derived states of those characters are placed on the basal stem of the cladogram, and it entails 73 reversals (83 under accelerated transformation only and 48 under delayed transformation only) as compared with only 20 reversals in the 1975 scheme. The distribution of character states on Fig. 8b (Appendix V) suggests that Character 82 may be correctly polarized, however. In deriving his tree, Brothers (1975) used parsimony but rejected its strict application if contra-indicated on the basis of reasonable evolutionary expectations, including the reversal of complex characters.)

In order to take subsequent work and the discovery of new taxa into account, we extended the data matrix based on Brothers's (1975) paper to include those new characters and taxa used by Brothers (1976), Rasnitsyn (1980, 1988), Carpenter (1986), Johnson (1988) and Kimsey (1991) which we were able to code with reasonable certainty and considered to be valid (e.g., see above account of Kimsey's paper). We reinterpreted some characters where indicated by workers such as Gibson (1985) and our new insights, added a few characters, and corrected a few errors discovered in previous analyses. Sclerogibbidae, Embolemidae, Dryinidae, Bethylidae, Chrysididae, Heterogynaidae, Diamminae and Proscoliinae were entirely newly scored. *Olixon* was separately scored in order to check whether its placement in Rhopalosomatidae is correct, and Fedtschenkiinae was separately scored to check its association with Sapyginae. Scoliidae (now more properly Scoliinae) and Rhopalosomatidae (now only the macropterous species, including *Liosphex* Townes) were also rescored to reflect the addition of Proscoliinae and separation of *Olixon* respectively; Thynninae and Sapyginae were rescored to reflect their separation from Diamminae and Fedtschenkiinae respectively; and Scolebythidae was rescored to reflect consideration of *Ycaploca* Nagy (Appendix VI, Table IV). Ground-plan character states for taxa newly scored or rescored and new characters were based on the examination of representative specimens (most unfortunately unidentified), supplemented by reference to the papers cited above and to others such as Olmi (1984), Evans (1987) and Kimsey & Bohart (1990).

The 64 most parsimonious cladograms which resulted from analysis of the 219 variables and 34 final taxa all confirm Apoidea as including Heterogynaidae, (Proscoliinae + Scoliinae) as holophyletic and (*Olixon* + rhopalosomatids) as holophyletic, as shown by the strict consensus tree (Fig. 9a). This also indicates five distinct lineages within the Vespoidea, the relationships between which are unresolved: Sierolomorphidae, Pompilidae, (Sapygidae + Mutillidae), Tiphiidae and (Rhopalosomatidae + ((Vespidae + Scoliidae) + (Formicidae + Bradynobaenidae)). The relationships between Fedtschenkiinae, Sapyginae and Mutillidae (including Myrmosinae) are also unresolved. Successive approximations character weighting resulted in two cladograms, one of which is identical to one of the original eight. That one (Fig. 9b) is additionally preferred on the basis of manual optimization of states on the consensus tree (see above; Variables 7 and 214), and also because it is the one most closely resembling the results of subsequent analyses (see Figs. 10a, 10b) for the taxa showing ambiguity (Thynninae s.s. placed as the sister group either of Diamminae or of (Tiphiinae to Methochinae)). It resolves the relationships of the major lineages of Vespoidea and agrees substantially with Brothers's (1975) tree (Fig. 1). It differs mainly in the basal position of Sierolomorphidae in Vespoidea, the association of Pompilidae with (Sapygidae + Mutillidae) and its separation from Rhopalosomatidae, and the sister-group relationship of Formicidae to Bradynobaenidae. The relationships of subfamilies within

families (including those of Tiphiidae, making allowance for the inclusion of Diamminae in Thynninae s.l. by Brothers) also agree with Brothers's tree, except that Myzininae is basal to Methochinae (but a tree differing only in showing Myzininae and Methochinae as sister-groups, as found by Brothers, has the same raw length, and such a relationship is shown in half of the original trees). Note that the placement of Thynninae s.s. differs from that suggested by Kimsey (1991) who showed it as the sister group of Myzininae; this is due to different treatment of some characters (see our above discussion of Kimsey's paper). Sapyginae and Fedtschenkiinae are now shown as holophyletic. The unexpected basal position of apids in the Apoidea probably reflects the inadequacy of these data for analysing the components of that superfamily. The relationships of the families of Chrysidoidea are identical to those found by Carpenter (1986) (Fig. 5), despite the fact that those taxa are now included within a much larger analysis, giving confidence in the correctness of this result. The distribution of the character states on Fig. 9b is given in Appendix VII.

In order to eliminate any influences on the parsimony analysis of homoplastic occurrences of states in taxa outside the Vespoidea, that taxon was then analyzed in isolation from the Chrysidoidea and Apoidea. Thirty most-parsimonious cladograms resulted (length 471, consistency index 0.51, retention index 0.62) and the strict consensus tree has a topology identical to that of the applicable portion of Fig. 9a except that Diamminae, Thynninae and the higher tiphiids form a trichotomy. Successive approximations character weighting produced one cladogram, identical to one of the original eight, and with a topology identical to the applicable portion of Fig. 9b, except that Myzininae and Methochinae are sister-groups, agreeing with Brothers (1975) and Kimsey (1991) when disregarding her placement of Thynninae, as discussed above. A sister-group relationship of Methochinae with (Tiphiinae + Brachycistidinae) is supported by one uniquely derived variable (137, form of mesosoma when apterous) which is not shown in the same state in Brachycistidinae and is not even expressed in Tiphiinae, whereas the sister-group relationship of Myzininae and Methochinae is supported by one uniquely derived and unreversed variable (1, sexual dimorphism in body proportions), which is probably a more significant character. We thus consider this latter arrangement of the subfamilies of Tiphiidae as preferable.

Examination of Fig. 9b and Appendix VII suggests that Variables 43 (prosternum, weight 0), 80 (metathoracic-propodeal pleural suture ventral to endophragmal pit, weight 2), 84 (extent of forewing venation, weight 1), 102 (hindwing empusal, anal and jugal veins, weight 2), 118 and 121 (meso- and metatibial spines, weight 2), 164 (male seventh metasomal sternum, weight 0), 193 (mesocoxal subdivision and insertion, weight 0), 197 (mandibles, weight 2), and 198 (female cerci, weight 10) may be incorrectly polarized since derived states of all of these are placed on the basal stem. Of these, only Variables 80 (but only State 2), 84, 102 and 198 are considered unlikely to show reversals; the rest are mostly highly plastic variables which ended up with relatively low weights (2 or less) and their polarities should probably be re-evaluated. Variable 80 also has low weight and should also probably be re-evaluated; it is placed without any reversal of its 'irreversible' state. Variable 198 is definitely correctly polarized, with State 1 found in all aculeates, contrary to Rasnitsyn's (1988) statement. Variables 84 and 102 are unlikely to be incorrectly polarized. State 1 of Variable 84 entails some reduction in the extent of the forewing venation, and is shown on the tree as having six derivations and two reversals; manual optimization ensuring no reversals would involve only a single extra step, so is perhaps preferable, especially since there may be a correlation between smaller size and reduction in venation in some taxa. Variable 102 involves sequential loss of the jugal, anal and empusal veins of the hindwing; an apparent jugal bar is present only in a few sphecids, and it is conceivable that it is not homologous with the same structure elsewhere, so that the reversal to the 0 state there may be reasonable; an anal vein forming a spur from the empusal vein is perhaps less likely to reappear after loss, but optimization ensuring no reversals of State 2 to State 1 would entail seven derivations instead of one derivation and two reversals and may thus be unlikely, since it is possible that the anal vein may persist fused with the empusal

vein at the base even when it has apparently been lost.

It is further evident that another four of the variables for which reversals are considered unlikely are placed with reversals having occurred (2, 96, 161 and 178). Variable 2 (sexual dimorphism in wing development) provides an interesting case where the first derivation of a state is placed at a point which indicates the potential for expression of the state rather than its actual expression, and reversals are thus more apparent than real; State 1 is derived within the Tiphiidae just below the point at which Diamminae branches off, and it is expressed in all taxa distal to that point with apterous females; taxa with macropterous females do not show the derived state and so are indicated as having reversals, but they probably nevertheless have the potential for expression of the derived state as shown by various apterous or brachypterous species, for example within Myzininae. State 1 of Variable 96 entails the loss of cell C in the hindwing through the distal reduction of vein C; manual optimization ensuring no reversals would involve nine derivations, so is difficult to evaluate, but may be preferable to the two derivations and five reversals shown. State 1 of Variable 161 entails the loss of the valvilli on gonapophysis VIII of the female; it is shown with five derivations and a single reversal (in Apterogyninae, the only member of the Bradynobaenidae with valvilli); optimization ensuring no reversals would involve another three derivations, but the likelihood of this being correct is difficult to evaluate in the absence of information on the function of these structures. Variable 178 (larval spiracles) is treated in the same way as by Brothers (1975), with an apparent reversal accepted in Sapygidae.

In order to remove any influences of homoplastic character state changes within families and to ensure that all of the taxa included were at a more or less consistent taxonomic level, family ground plans were derived for the Vespoidea, eliminating all subfamilies and single genera (Table V). For each family, the ground-plan state of each variable was specified as the relatively most plesiomorphic state found in any of its component taxa (unless there were *a priori* indications that some other state is more likely to have been that present in the ancestor) or as the known state where states are unknown in some component taxa. Analysis of the family ground plans of Vespoidea in isolation from the other taxa (except for an hypothetical ancestor) produced five most parsimonious cladograms (length 248, consistency index 0.65, retention index 0.43) and successive approximations character weighting resulted in three cladograms (weighted length 1088), all of which are amongst the initial five. Successive weighting was thus not very informative, and the strict consensus tree of the original five cladograms showed Tiphiidae as basal, with the remaining families forming a holophyletic group. The relationships of five lineages were unresolved: Sierolomorphidae, Pompilidae, Rhopalosomatidae, (Mutillidae + Sapygidae), and (Bradynobaenidae + (Formicidae + (Vespidae + Scoliidae))).

It would have been ideal if we could have treated the entire Aculeata in the same way, and derived similar family ground plans for the taxa of Apoidea, especially since there are strong indications that Sphecidae s.l. is paraphyletic with respect to the bees (Lomholdt 1982, Alexander 1990, 1992), but such data are not yet available. Analysis of the family ground plans of Chrysidoidea and Vespoidea and the three taxa of Apoidea together (20 taxa in total, as coded in Tables IV and V) produced four most parsimonious cladograms (strict consensus tree in Fig. 10a) and successive approximations character weighting produced two cladograms, one of which (Fig. 10b) is amongst the original four and is additionally preferred on the basis of manual optimization of variables (36, 126, 180, 193) on the consensus of the two, and because it has the same arrangement as the strict consensus tree (Fig. 10a) for the taxa showing ambiguity (Heterogynaidae or apids basal in Apoidea). The weighted tree agrees very closely with the comparable branches of its counterpart based on all taxa (Fig. 9b), differing only in the basal placement of Heterogynaidae in Apoidea, and the sister-group relationship of Formicidae to (Vespidae + Scoliidae) rather than to Bradynobaenidae (an arrangement also shown unequivocally in the analysis of vespoid family ground plans in isolation, see above). The relationships within the Apoidea are based on poor representation, but the arrangement shown in Fig. 10b is to be

preferred on a number of grounds: although the strict consensus tree based on all taxa (Fig. 9a) shows the structure of Apoidea unresolved, the strict consensus tree based on family ground plans (Fig. 10a) shows Heterogynaidae as always basal; furthermore, Heterogynaidae has a relatively basal position in Apoidea according to Alexander (1992), although it falls within the Sphecidae s.l. The sister-group relationship of Formicidae to (Vespidae + Scoliidae) is also to be preferred on various grounds: such a relationship is supported by three unique and unreversed derivations on Fig. 10b (34:1, truncate posterolateral angle of pronotum, although also derived within Mutillidae and Tiphiidae (Fig. 9b); 38:2, ventrally produced acute ventral angle of pronotum, although apparently reversed within Scoliidae (Fig. 9b); and 106:1, loss of basal hamuli, although also derived within Bradynobaenidae and Tiphiidae (Fig. 9b)), as contrasted with only one such derivation (150:1, petiolate metasoma, a rather variable character within many taxa; 55:1, shortened mesepimeron, is also derived in apids and within Rhopalosomatidae (Fig. 9b)) supporting a sister-group relationship between Formicidae and Bradynobaenidae, as found when altering the topology of Fig. 10b appropriately and as shown in Fig. 9b and Appendix VII; furthermore, this relationship agrees with that found in the analysis of Vespoidea family ground plans only, and with that previously found by Brothers (1975). The relationships within the Vespoidea differ from Brothers's (1975) tree (Fig. 1) only in the more basal position of Sierolomorphidae and the sister-group relationship of Pompilidae with (Mutillidae + Sapygidae) rather than Rhopalosomatidae. The relationships of the families of Chrysidoidea are still identical to those found by Carpenter (1986) (Fig. 5). Fig. 10b thus seems to be the best estimate that we now have of the relationships of the families of Chrysidoidea and Vespoidea, and of the relationships of the three superfamilies.

The distribution of the character states on Fig. 10b is given in Appendix VIII. This suggests (as for Fig. 9b, Appendix VII) that Variables 43, 80, 84, 102, 118, 121, 193, 197 and 198 may be incorrectly polarized since derived states of all of these are placed on the basal stem, and two additional 'irreversible' variables (96, closed cells in hindwing and 178, larval spiracles) have been placed showing reversals. The same comments apply here as were made above (in discussing Fig. 9b).

When the preferred intrafamilial relationships (as derived from Fig. 9b and analysis of all vespoid taxa in isolation, see above) are added to Fig. 10b, the cladogram shown in Fig. 11 results (distribution of character states given in Appendix IX). Despite the fact that it is slightly longer than the most parsimonious cladograms derived from the full analysis (692 vs 689 steps, a difference of 0.4%, resulting solely from the placement of Formicidae as the sister-group of (Vespidae + Scoliidae) which is strongly justified above), we consider it our current best estimate of the relationships of all of the groups analyzed.

CONCLUSION

Our re-evaluation of Brothers's (1975) and Carpenter's (1986) data and analyses and the incorporation of subsequent contributions and some new data, confirms their results and conclusions in all major respects. Chrysidoidea is definitely a holophyletic group which includes Plumariidae as its most basal taxon, Scolebythidae the next most basal, and (Bethylidae + Chrysididae) as the sister-group of (Sclerogibbidae + (Dryinidae + Embolemidae)). Apoidea s.l. and Vespoidea s.l. together form a holophyletic group, as does Vespoidea s.l. itself, although this is less strongly supported. Sierolomorphidae forms a distinct basal clade in Vespoidea. Rhopalosomatidae is probably the sister-group of (Bradynobaenidae + (Formicidae + (Scoliidae + Vespidae)), rather than of Pompilidae, which appears to be the sister-group of (Sapygidae (including Fedtschenkiinae) + Mutillidae (including Myrmosinae)). Tiphiidae is most likely the sister-group of (Pompilidae + (Sapygidae + Mutillidae)). Sierolomorphidae is thus probably more basal in Vespoidea than Brothers (1975) thought, and his suggested relationship of Pompilidae to Rhopalosomatidae was also probably incorrect.

It must be appreciated, however, that most of the characters and states used are essentially those of Brothers (1975) and Carpenter (1986). Although we have used various characters introduced by

Rasnitsyn (1980, 1988), we have often been unable to check their validity and generality of distribution over all of the taxa coded, but have had to rely on his interpretations and statements; these are difficult to evaluate because he did not list the species he had examined and often did not explain the characters fully. It is thus likely that our interpretations and/or codings are incorrect in at least some cases. For example, some Pompilidae have indications of posteromesal expansion of the metapostnotum, which might perhaps be interpreted as a stage intermediate between that in other Pompilidae and the Apoidea; does this mean that pompilids are closer to apoids, or is it an independent trend? Such questions can only be answered if other workers undertake more complete evaluations of particular taxa, looking at a greater variety of representatives than we were able to do, checking the validity of the characters and states used here, and finding new characters. We hope that this paper will stimulate such studies. Meanwhile, it is interesting that the full analysis produced results quite similar to the uncorrected Hennig86 analysis of Brothers's characters only (Fig. 8) and analysis of his taxa using only his characters but modified and corrected as above produced an arrangement essentially identical to that found using all characters, which indicates that the results will probably prove to be fairly stable to further investigations. We are thus satisfied that the present analysis, as presented in Fig. 11, represents the most complete and most rigorous estimate of relationships between the higher taxa of Aculeata (particularly the Chrysidoidea and Vespoidea) now possible.

Bearing in mind the limitations of the data base, uniquely derived and unreversed synapomorphies (sometimes with subsequent derivations) characterizing the superfamilies, families and other major lineages are as follows:

Chrysidoidea: all femora of female inflated (Variable 111: State 1), first metasomal tergum anteriorly narrowed and fused with sternum (152:1), gonocoxite IX of female with articulation within it (160:1), third phragma narrowed and muscles *2ph-3ph* with widely separated posterior attachments (186:1), prothoracic furca proclined (207:1), forewing vein Cu2 reduced (215:1).

Chrysidoids except for Plumariidae: forewing with seven (or fewer) cells (85:2), hindwing with one closed cell (98:1) which has been lost in all extant members, third phragma lost medially (186:2), second phragma scarcely oblique with anterior attachment of muscles *2ph-3ph* (191:1), and anterior pedicels of tentorium rodlike (206:1).

Plumariidae: mesosoma of apterous female uniquely modified (143:1), and seventh metasomal tergum of female concealed under sixth tergum but not desclerotized (159:1); in addition propleura forming short anterior necklike region (41:1, separately derived in Sclerogibbidae).

Remaining chrysidoids: posterior margin of metapostnotum mesally indistinct (64:1), inner metatibial spur calcariform with dorsal blunt longitudinal setose carina (136:1), and third phragma absent (186:3).

Scolebythidae: propleura widely separated posteriorly (42:1), protrochanter inserted near base of coxa (45:1), hindwing with vein C long and vein SC+R+S absent (98:2), meso- and metatibiae with long slender setae only (120:1, 123:1).

Bethylidae and Chrysididae: metapostnotum mesally shortened and hidden (64:2), vein C short but distinct and vein SC+R+S long (101:1), and gonocoxite IX and gonapophysis 1 IX in female not articulated (203:1).

Bethylidae: hindwing with vein C absent except at extreme base and vein SC+R+S very short (101:2), head prognathous of 'bethylid type' (209:1), and clypeus with median longitudinal carina (211:1).

Chrysididae: metasoma with only four exposed terga (157:1), and larval host Tenthredinoidea cocoon or Phasmida egg (204:3).

Sclerogibbidae, Dryinidae and Embolemidae: hindwing with empusal vein minute, anal and jugal veins absent (102:3), furcula in ovipositor absent (202:1).

Sclerogibbidae: frontal ledge overhanging ventrally-facing antennal socket (8:1), compound eye with dense pores and short setae (13:2), more than 14 antennomeres (19:1), prepectus fused midventrally but not to mesepisternum (53:1), forewing with six closed cells (87:1), hindwing with vein C short and vein SC+R+S

absent (100:1), profemur of female much swollen and protibia expanded (111:2), foreleg with arolium much enlarged (114:1), mesosoma of apterous female uniquely modified (144:1), seventh metasomal tergum of female hidden under expanded sixth sternum (158:1), larval host Embioptera (204:1), and prothoracic furca proclined and modified (207:2).

Dryinidae and Embolemidae: ten antennomeres (20:1), hindwing with veins C and SC+R+S long but fused (99:1), larval host Auchenorrhyncha (204:2), and larva initially endoparasitic but then forming external cyst (205:1).

Dryinidae: forewing with five closed cells (86:2).

Embolemidae: prepectus large and fused midventrally and to pronotum (32:2, 53:2), metapleuron uniquely modified (66:2), mesosoma of apterous female uniquely modified (144:2), anterior pedicels of tentorium rodlike with lamellar processes (206:2), antennal prominence present (212:1), pedicel-flagellum articulation fixed (213:1).

Aculeata *sensu stricto*: male with 13 and female with 12 antennomeres (18:1), and seventh metasomal tergum of female hidden and substantially desclerotized (156:1).

Apoidea (subordinate taxa not further analyzed because of inadequate data): pronotum with posterolateral angle reduced above spiracular lobe (35:1), ventral angle of pronotum considerably produced mesad (39:1), prepectus fused midventrally and to mesepisternum (52:1), metapostnotum expanded posteromesally to form 'propodeal triangle' (65:1), and second phragma scarcely oblique with posterior attachment of muscles *2ph-3ph* (192:1).

Vespoidea: no unique and unreversed derivations, but prepectus reduced (48:1, also in Chrysididae), and hypopharyngeal pubescence reduced (194:1, but reversed in Rhopalosomatidae and Pompilidae).

Sierolomorphidae: forewing with seven closed cells (88:1), hypopygium of male peglike (165:1), and third phragma weakly expanded laterally with muscles *2ph-3ph* small and attaching on somewhat separated areas of phragma (190:1).

Vespoidea except Sierolomorphidae: hindwing with jugal lobe moderately reduced (108:1); in addition, metapostnotum partially invaginated and mesally reduced (63:1, but reversed in Rhopalosomatidae and Pompilidae).

Rhopalosomatidae to Scoliidae: no unique and unreversed derivations, but prepectus further narrowed and shortened (48:2, separately derived in Brachycistidinae) and junction of first and second metasomal terga slightly constricted (149:1, but reversed in Vespidae and separately derived in Tiphiinae and Brachycistidinae).

Rhopalosomatidae: forewing with cell C almost eliminated (92:1), female with tarsi flattened and forelegs swollen (112:1), larval host Gryllidae only (204:7), and larva entirely ectoparasitic with cyst formation (205:2).

Bradynobaenidae to Scoliidae: no unique and unreversed derivations, but mesad mesocoxal articulations posteriorly displaced (57:1, separately derived in Mutillidae).

Bradynobaenidae: mesocoxae somewhat separated and metasternum laterally depressed and slightly anteriorly produced (75:1, 78:1), mesosoma of apterous female uniquely modified (141:1), lateral felt line on second metasomal tergum only (146:1), first metasomal tergum overlapping sternum only posteriorly (151:1), and possibly larval host Solifugae (204:9) (uniquely derived paired stridulitra on fourth metasomal tergum (148:1) lost in two subfamilies).

Formicidae to Scoliidae: no unique and unreversed derivations, but ventral angle of pronotum acute and produced (38:2, but reversed in Proscoliinae).

Formicidae: caste of sterile females present (3:1), metapleural gland present (72:1), inner meso- and metatibial spurs calcariform with dorsal pectinate carina (128:1, 134:1), mesosoma of apterous female uniquely modified (144:3), larval food relocated and nest constructed but not closed (181:1).

Vespidae and Scoliidae: posterolateral angle of pronotum dorsally produced above anterior margin of tegula (34:2), and third phragma expanded laterally with muscles *2ph-3ph* very large (190:3); in addition, prey relocated, nest constructed and closed (180:2, separately derived in apids which use dissimilar provisions),

and head of larva with strong parietal bands (217:1, separately derived in Pompilidae).

Vespidae: pronotum fused with much-reduced hidden prepectus and closely abutting mesepisternum (32:1, 48:3), and posterolateral margin of pronotum acutely produced and much exceeding anterior margin of tegula (34:3).

Scoliidae: pronotum immovable with prepectus fused with mesepisternum (31:1), mesocoxae widely separated without shortening of mesosternum (59:1), metasternum broad and not depressed (76:1), metacoxae widely separated (79:1), protibial calcar inwardly curved and posteriorly hollowed (117:1), spines on meso- and metatibiae very strong and scattered (119:1, 122:1), hypopygium of male elongate and apically trilobed (166:1), and gonapophyses IX (penis valves) of male with dorsal membranous link over most of length (172:1).

Tiphiidae to Sapygidae: no unique and unreversed derivations, but second thoracic spiracle of larva reduced (178:1, reversed in Sapyginae).

Tiphiidae: hindwing with distal origin of crossvein cu-e (103:1); in addition, mesosternum with platelike projections posteromesally (56:2, lost in Methochinae, but also present in Rhopalosomatidae).

Pompilidae to Sapygidae: prepectus not shortened and fused with mesepisternum (51:1).

Pompilidae: larval prey relocated into pre-existing cavity which is then closed (182:1), and larval prey Araneae (204:6); in addition, inner metatibial spur calcariform with basal tuft of bristles and dorsal pectinate carina (132:1, separately derived in Rhopalosomatidae), and larval head with strong parietal bands (217:1, separately derived in Vespidae and Scoliidae).

Mutillidae and Sapygidae: hindwing with jugal lobe small (108:2), gonapophyses IX (penis valves) of male linked only basally by membrane (173:1), and larval host Aculeata larva or pupa (204:5).

Mutillidae: prepectus uniquely modified and fused with mesepisternum (51:2), mesosoma of apterous female uniquely modified (139:1), and third metasomal tergum with single small stridulitrum (147:1).

Sapygidae: no unique and unreversed derivations; but, prementum and stipes elongated (23:1, separately derived in apids).

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APPENDIX I

Distribution of derived character states for Aculeata on cladogram derived by Brothers (1975:Fig. 2). Internodes are referred to by numbers which designate the inferred ancestors subtending each internode in the original figure and taxon names referring to the range of taxa subtended. Character state code numbers are those used in the original text. Square brackets indicate an intermediate state not present but probably necessary for derivation of a more derived state; reversals are indicated by (r).

A. Distribution of states as derived by Brothers (1975) (NOT those plotted in Fig. 1). States occur in both sexes (or are consistently sexually dimorphic) unless otherwise indicated (for states which could occur in either sex—; F=female, M=male).

1-2 (Chrysidoidea): 42.1; 45.1; 46.1; 51.2; 56.2; 79.1
Plumariidae: 2.1; 7.3F; 9.3F; 10.1F; 13.1F; 16.1F; 17.1F; 18.1M; 20.1F; 24.2F; 25.1; 27.1M; 38.1; 38.1.1M; 57.1F; 59.1F; 61.1; 61.1.1F; 62.1; 69.4; 80.1; 82.1
2-3: 35.2; 46.1.1; 49.1; 50.3
Scolebythidae: 5.1; 7.3; 9.1; 20.1; 26.2; 34.2; 46.1.1.1; 49.1.1; 50.3.1; 57.2; 61.2; 62.2
bethylids ('higher' Chrysidoidea): 17.1
1-4: 12.1; 25.1; 26.1; 61.1; 62.1; 78.1
4-5 (Apoidea): 18.2; 21.2; 22.1; 23.2; 27.1; 29.2; 31.2; 33.1; 35.3; 36.3; 39.1; 47.1; [64.1;] 64.1.1; 81.2; 90.1
apids (Apidae s.l.): 4.1; 15.1; 30.2; 42.1; 45.1; 50.1; 51.1; 63.1; 78.1.1; [82.1;] 82.1.1; 84.2; 85.1; 87.2; 89.1; 90.1.1; 92.1
sphecids (Sphecidae s.l.): 21.2.1; 61.1.1; 62.1.1
4-6 (Vespoidea): 24.1; 29.1; 38.1; 51.2; 56.1
6-7: 31.1; 35.1; 52.1; 61.1.1; 62.1.1; 64.1F; 82.1; 88.1
7-8: 6.1; 29.1.2; 38.1.1; 50.1; 53.1; 55.1; 56.1.1; 64.1.1F; 66.1; 86.2; 90.2
Sapygidae: 15.3; 80.1; 87.2; 88(r)
8-9 (Mutillidae): 2.1; 13.1; 14.1; 29.1.2.1; 32.1; 36.1; [42.1;] 42.1.1; 54.1; 69.2; 71.1; 72.1; 76.1; 81.1
Myrmosinae: 9.2; 58.1F; 59.1F; 66.1.1; 69.2.1; 82(r); 84.2
mutillids ('higher' Mutillidae): 18.1; 21.1; 30.1; 34.1; 38.1.1.1; 45.1; 49.1; 69.2.2; 70.1
7-10 (Tiphiidae): 31.1.1; 57.1F
Anthoboscinae: 45.1F; 84.1
10-11: 69.1
Thynninae (s.l.): 2.1; 55.1; 66.1
11-12: 69.1.1; 72.1M; 76.1; 83.3
12-13: 1.1; 6.2; 82(r)
Myzininae: 35.1.1
Methochinae: 2.1; 7.3; 9.2; 22.1; 31.1(r); 42.1; 46.3; 50.1; 57(r); 61.1(r); 62.1(r); 63.1F; 65.2 ; 66.1M; 67.1; 68.4; 81.1; 90.2
12-14: 21.1; 22.1; 33.1; [36.1;] 36.1.1; 42.1; 44.1; 45.1; 49.1; 66.1; 72.1; 81.1; 82.1.1; 84.2; 85.1
Tiphiinae: 35.1.1; 42.1.1; 46.4
Brachycistidinae: 2.1; 5.1F; 7.3F; 8.1; 9.1M; 9.3F; 10.1F; 18.1M; 27.1M; 29.1.1; 54.2; 59.1; 63.1; 69.1.1.1
6-15: 22.1; 38.1.1; 55.1
Sierolomorphidae: 9.1; 31.1; 36.2; 42.1; 45.1; 46.2; 49.1; 50.1; 56.2; 66.1; 83.1; 84.2
15-16: 47.1; 54.1; 87.1
16-17: 31.1; 32.1; 36.2; 48.1; 50.1; 68.1; 82.1
Pompilidae: 29.1.2; 33.1; 61.1.1; 62.1.1; 64.1; 80.1; 88.1; [90.1;] 90.1.3
Rhopalosomatidae: 9.1; 18.1; 21.1; 27.1; 29.1.1; 31.1.1; 45.1; 46.1; 49.1; 55(r); 57.3F; 72.1; 81.2; [87(r);] 87.3
16-18: 29.1.1; 33.1; [35.1;] 35.1.1; 76.1
18-19: 18.1; 21.1; 23.1; 27.1; 36.1; 54.2; 90.1
Formicidae: 3.1; 9.1; 29.1.1.3; 30.2; 33.1.1; 37.1; 46.1; 50.1; [61.1.1;] 61.1.1.1; [62.1.1;] 62.1.1.1; 65.1; 68.3; 72.1; 73.1; 81.2; 89.1; 90.1.2; 91.1
19-20: 5.2; 7.2; 15.2; 19.1; 21.1.1; 25.1.1; 31.2; 48.1; 85.1
Scoliidae: 9.3; 29.1.1.2; 30.1; 32.2; 36.1.2; 38.1.1.2; 39.1; 41.1; 44.1; 45.1; 49.1; 55.1.1; 57.1F; 59.1; 60.2; 61.1.2; 62.1.2; 63.1; 64.1; 72.1; 83.2; 84.2; 86.1
Vespidae (s.l.): 21.1.1.1; 29.1.1.1; 32,1; 43.1; 68.2; 80.1; 82.1; 89.1; 90.1.1; 91.1
18-21 (Bradynobaenidae): 2.1; 9.1; 10.1F; 30.2; [38.1(r);] 38(r); 39.1; 40.1; 42.1; 45.1; 49.1; 55.1.1; 69.3; 70.2; 71.2; 72.1; 73.1; 74.1; 81.2; 82.1
21-22 (Typhoctinae): 4.1; 22(r); 36.2; 66.1; 69.3.1; 80.1
Eotillini: 47(r); 50.1; 55.1(r), 55(r); 58.1
Typhoctini: [56(r);] 56.2; 61.1.1; 62.1.1
21-23: 6.1; 7.1; [9(r)F;] 9.3F; 13.1; 18.1M; 23.1; 27.1M; 36.1; 57.1F; 58.1F; 61.1.1; [62.1.1;] 62.1.1.1; 64.1F; 69.3.2; 74.1.1; 75.1; 83.4
Chyphotinae: 7.1.1F; 8.1; 33.1.1; 47(r); 50.1; 66.1M; 75.1.1F; 80.1; 84.1
23-24: [9(r);] 9.3; 11.1; 28.1; 32.2 ; 34.1; 40.1.1; 45.1.1; 46.5; 47.1.1; 49.1.1; [54(r);] 54.2; 58.1; 60.1; 61.1.1.1; [64.1;] 64.1.2; 70.2.1F; 71(r); 85.1
Apterogyninae: 5.2M; 7.1.1F; 8.1; 66.1; 72.1.1; 77.1
Bradynobaeninae: 6.2; 15.4; 16.2; 17.1; 21.3; 28.1.1; 36.1.1; 43.1; 44.1; 46.5.1; 50.2; 59.1; 60.1.1; 61.1.1.1.1; 62.1.1.1.1; 63.2; 64.1.2.1; 64.1.2.1.1F; 70.2.1; 80.1; [81(r);] 81.1; 83.4.1

B. Distribution of states for data in Table III as applied to tree (Fig. 1) with topology identical to that of Brothers (1975); optimizations by Clados (Nixon 1992) using accelerated transformation (approach of Farris, 1970), except using delayed transformation (approach of Swofford & Maddison 1987) for variables considered unlikely to show reversals. For treatment of sexually dimorphic characters, see text. Placements which agree with those above (IA) are indicated in boldface.

Aculeata-1: 25.1; 61.1; 62.1; 82.1
1-2 (Chrysidoidea): **42.1; 45.1: 46.1; 51.2; 56.2; 79.1**
Plumariidae: **2.1; 10.1; 24.2; 25.1; 38.1; 57.1; 69.4; 80.1**
2-3: 25(r); **35.2; 46.1.1; 49.1; 50.3**; 61(r); 62(r); 82(r)
Scolebythidae: **5.1; 7.3; 9.1; 20.1; 26.2; 34.2; 46.1.1.1; 49.1.1; 50.3.1; 57.2; 61.2; 62.2**
bethylids ('higher' Chrysidoidea): **17.1**

1-4: **12.1;** 22.1; **26.1;** 50.1; 61.1.1; 62.1.1; **78.1**
4-5 (Apoidea): **18.2; 21.2; 23.2; 27.1; 29.2; 31.2; 33.1; 35.3; 36.3; 39.1; 47.1;** 51(r); **[64.1;] 64.1.1; 81.2; 90.1**
apids (Apidae s.l.): **4.1; 15.1; 30.2; 42.1; 51.1;** 61.1(r); 62.1(r); **63.1; 78.1.1; 82.1.1; 84.2; 85.1; 87.2; 89.1; 90.1.1; 92.1**
sphecids (Sphecidae s.l.): **21.2.1;** 50(r); 82(r)
4-6 (Vespoidea): **24.1; 29.1;** 31.1; **38.1; 51.2;** 55.1; 66.1
6-7: 22(r); **35.1; 52.1;** 56.1
7-8: **6.1; 29.1.2; 53.1; 56.1.1; 86.2**
Sapygidae: **15.3; 80.1; 87.2**
8-9 (Mutillidae): **2.1; 13.1; 14.1; 29.1.2.1; 32.1; 36.1; [42.1;] 42.1.1; 54.1; 69.2; 71.1; 76.1; 81.1;** 88.1; 90.2
Myrmosinae: **9.2; 66.1.1; 69.2.1; 82(r); 84.2**
mutillids ('higher' Mutillidae): **18.1; 21.1; 30.1; 34.1;** [38.1.1;] **38.1.1.1; 45.1; 49.1; 69.2.2; 70.1**
7-10 (Tiphiidae): **31.1.1**; 38(r); 50(r); 55(r); **57.1**; 88.1
Anthoboscinae: 66(r); **84.1**
10-11: 2.1
Thynninae (s.l.): **55.1;** 69.1
11-12: 22.1; 76.1; 81.1; **83.3**
12-13: **1.1; 6.2;** 66(r); **82(r)**
Myzininae: 2(r); 22(r); **35.1.1;** 81(r)
Methochinae: **7.3; 9.2; 31.1(r); 42.1; 46.3; 50.1; 57(r); 61.1(r); 62.1(r); 65.2; 67.1; 68.4;** [69.1;] 69.1.1; **90.2**
12-14: **21.1; 33.1; [36.1;] 36.1.1; 42.1; 44.1; 45.1; 49.1; 72.1; 82.1.1; 84.2; 85.1**
Tiphiinae: 2(r); **35.1.1; 42.1.1; 46.4**
Brachycistidinae: **8.1; 10.1; 29.1.1; 54.2; 59.1; 63.1;** [69.1;] [69.1.1;] **69.1.1.1**
6-15: 9.1; 36.2
Sierolomorphidae: **42.1; 45.1; 46.2; 49.1; 56.2;** 61.1(r); 62.1(r); 82(r); **83.1; 84.2**
15-16: 29.1.1; **47.1;** 56.1; 66(r); 72.1; 81.2; **87.1**
16-17: **32.1; 48.1;** 54.1; **68.1**
Pompilidae: 9(r); 29.1(r); **29.1.2; 33.1; 64.1;** 72(r); **80.1;** 81(r); **88.1; [90.1;] 90.1.3**
Rhopalosomatidae: **18.1; 21.1; 27.1; 31.1.1; 46.1; 49.1; 55(r); 57.3;** 61.1(r); 62.1(r); **87(r); 87.3**
16-18: 23.1; 30.2; 31(r); **33.1; [35.1;] 35.1.1;** 36(r); 36.1; 73.1; **76.1**, 89.1; 90.1
18-19: **18.1; 21.1; 27.1; 54.2;** 91.1
Formicidae: **3.1; 29.1.1.3; 33.1.1; 37.1; 46.1; 61.1.1.1; 62.1.1.1; 65.1; 68.3;** 82(r); **90.1.2**
19-20: **5.2; 7.2;** 9(r); **15.2; 19.1; 21.1.1; 25.1.1;** 30(r); **31.2; 48.1;** 50(r); 61.1(r); 62.1(r); 73(r); 81(r); **85.1**
Scoliidae: **9.3; 29.1.1.2; 30.1; 32.2; 36.1.2;** [38.1.1;] **38.1.1.2; 39.1; 41.1; 44.1; 45.1; 49.1; 55.1.1; 57.1; 59.1; 60.2; 61.1.2; 62.1.2; 63.1; 64.1;** 82(r); **83.2; 84.2; 86.1;** 89(r); 91(r)
Vespidae (s.l.): **21.1.1.1; 29.1.1.1; 32.1; 43.1; 68.2;** 72(r); **80.1; 90.1.1**
18-21 (Bradynobaenidae): **2.1; 10.1; 38(r); 39.1; 40.1; 42.1; 45.1; 49.1;** 54.1; **69.3; 70.2; 71.2; 74.1; 80.1**
21-22 (Typhoctinae): **4.1; 22(r);** 23(r); **36(r); 36.2; 66.1; 69.3.1**
Eotillini: **47(r); 55(r); 58.1;** 61.1(r); 62.1(r)
Typhoctini: 50(r); 55.1.1; **56(r); 56.2**
21-23: **6.1; 7.1;** 8.1; 9(r); **13.1;** 55.1.1; **57.1; 62.1.1.1; 69.3.2; 74.1.1; 75.1; 83.4**
Chyphotinae: **33.1.1; 47(r); 75.1.1; 84.1**
23-24: **9.3; 11.1; 28.1; 34.1; 40.1.1; 45.1.1; 46.5; 47.1.1; 49.1.1;** 50(r); **54(r); 54.2; 58.1; 60.1; 61.1.1.1; 64.1; 64.1.2; 71(r); 85.1**
Apterogyninae: **66.1; 72.1.1; 77.1;** 80(r)
Bradynobaeninae: **6.2;** 8(r); **15.4; 16.2; 17.1; 21.3; 28.1.1; 36.1.1; 43.1; 44.1; 46.5.1; 50.2; 59.1; 60.1.1; 61.1.1.1.1; 62.1.1.1.1; 63.2; [64.1.2.1;] 64.1.2.1.1; 70.2.1; 81(r); 81.1; 83.4.1**

APPENDIX II

Characters and states for Aculeata derived from Rasnitsyn (1980). Character states are linearly ordered except where noted, with the inferred primitive state listed first.

The scores for the taxa are given in Table I. Some corrections have been made, as noted, where these are matters of fact rather than interpretation. Characters are treated as nonadditive where we regard the ordering of states as unclear. Polarity was conferred by the addition of an all-primitive ancestral taxon to the matrix.

Rasnitsyn did not provide complete lists of diagnostic characters for his phylogenetic tree; where the state for a given taxon is unclear or unknown, we have usually scored it so as to provide the best support for Rasnitsyn's interpretation. Some scores may thus be erroneous. We have included characters dismissed solely on grounds of homoplasy by Rasnitsyn, again in order to assess most accurately the support for Rasnitsyn's scheme provided by all the evidence he discussed. 'Trends' are not included, only ground-plan states. We regard the polarities of Characters 2 and 15 as incorrect (see Brothers 1975, Carpenter 1986).

1. Valvifer 2: Not articulated = 0. Articulated = 1.
2. Hindwing jugal lobe: Absent = 0. Present = 1. Reduced = 2.

3. Anterior pedicels of tentorium: Thick = 0. Rodlike = 1. With lamellar processes = 2.
4. Prothoracic furca: Vertical = 0. Proclined = 1. 'Modified' in Sclerogibbidae = 2.
5. Reduction of forewing venation: 2m-cu present = 0. 2m-cu lost or present only as trace = 1.
6. Valves 2: Articulated with valvifer 2 proximally = 0. Not jointed with valvifer 2 proximally = 1. Secondary processes = 2.
7. Antenna: With 13 articles in both sexes = 0. With 13 articles in male and 12 in female = 1. With 10 articles = 2. With more than 14 articles = 3. NONADDITIVE.
8. Antennal pedicel: Mobile = 0. Fixed = 1.
9. Hosts: Beetles = 0. Embiidina = 1. Auchenorrhyncha = 2. Tenthredinoidea or Phasmida = 3. Melliferous = 4. Aculeata = 5. Araneae = 6. Gryllidae = 7. Wide host range (social foragers) = 8. Solifugae = 9. NONADDITIVE. [The host for Bradynobaenidae is based on new unpublished records.]
10. Host habitat: 'Confined' = 0. Free-living = 1.
11. Life style: Ectoparasitic = 0. Endoparasitic initially, with cyst formation = 1. [Rasnitsyn's original interpretation of complete endoparasitism in embolemids was an error; see Carpenter (1986), Wharton (1989).]
12. Furcula: Present = 0. Absent = 1. Vertical lamella = 2. NONADDITIVE.
13. Metasomal sternumI: Thin and overlapping sternumII = 0. Thick and abutting = 1. Forming lobules = 2. NONADDITIVE.
14. Metasomal sternum II: Curved anteriorly = 0. Straight with lateral notches = 1. Lateral desclerotized areas expanded = 2. Median notch = 3. NONADDITIVE.
15. Metasternum: Anteriorly narrow = 0. Carinate = 1. Two carinae = 2. Broad = 3. NONADDITIVE.
16. Female metasomal sternumVII: External = 0. Internated = 1.
17. Bilamellar stemming plates of ovipositor: Absent = 0. Present = 1.
18. Hypopharynx pubescence: Present = 0. Reduced = 1.
19. Pronotal lobes: Small = 0. Enlarged = 1.
20. Metapostnotum: Present and unmodified = 0. With propodeal suture obliterated = 1. Forming 'propodeal triangle' = 2. Medially shortened = 3. Medially invaginated = 4. NONADDITIVE. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 35).]
21 Metatibial calcar: Absent = 0. Basal brushes and chitinous modification = 1. Brushes lacking = 2. Brushes only = 3. Dorsally pectinate = 4. Dorsal carinate expansion = 5. NONADDITIVE. [We have supplemented Rasnitsyn' s account with reference to Brothers (1975: Character 68).]
22. Arolium and orbicula: Large = 0. Reduced = 1.
23. Metasomal sternumI and tergumII: Not articulated = 0. Articulated = 1.
24. Metasomal tergumI laterotergites: Wide = 0. Reduced = 1.
25. Propleura: Separated = 0. In contact along entire length = 1.
26. Prepectus (first variable): Not extended along pleurosternum = 0. Extended = 1. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 29).]
27. Prepectus (second variable): Broad = 0. Narrowed = 1. Shortened = 2.
28. Prepecti (third variable): Not fused = 0. Long and fused = 1. Line of fusion obliterated = 2.
29. Hindwing anal veins: Present = 0. Reduced = 1.
30. Hindwing axillary excision: Shallow = 0. Deepened = 1.
31. Basal hamuli: Scattered = 0. Closely spaced = 1.
32. Pterostigma: Large = 0. Small = 1.
33. Larval mandibles: Quadridentate = 0. Tridentate = 1.
34. Metaphragma: Narrow = 0. Expanded = 1.
35. Posterolateral angle of pronotum: Not produced = 0. Slightly produced = 1. Exceeding tegula = 2. Forming acute lobe = 3. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 21.)]
36. Mesotibial spines: Absent = 0. Strong scattered spines present = 1. Spines apical = 2. Very strong spines = 3. NONADDITIVE. [We

have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 61).]

37. Mesothoracic lamellae: Absent = 0. Small = 1. Large lobes = 2.
38. Dorsal aedeagal fusion: Sclerotized = 0. Desclerotized = 1.

APPENDIX III

Characters and states for Aculeata derived from Rasnitsyn (1988). Character states are linearly ordered except where noted, with the inferred primitive state listed first.

The scores for the taxa are given in Table II. Characters are treated as nonadditive where we regard the ordering of states as unclear. Polarity was conferred by the addition of an all-primitive ancestral taxon to the matrix. Rasnitsyn (1988) provided a diagnosis of his phylogenetic scheme, along with notes discussing some characters. This did not include all of the characters dismissed as homoplastic in Rasnitsyn (1980). These characters are included here as coded in Appendix II. Most of the characters mentioned are treated substantially as in Rasnitsyn (1980); the coding for these characters is as in Appendix II. One character from Appendix II is deleted (24, not included by Rasnitsyn, 1988), one is modified to include another state (23, specified more precisely by Rasnitsyn, 1988), and the scores are modified for four characters (17, 23, 36 and 37 in Appendix II). Eight new characters are included; generally, these are characters alluded to by Rasnitsyn (1980) but specified more precisely in 1988. We regard the polarity of Characters 2 and 15 as incorrect; see Brothers (1975), Carpenter (1986). We consider Character 45 as probably invalid; the sulcus referred to is the fused anteroadmedian lines (see Daly 1964, Matsuda 1970) seen in relatively more apomorphic members of the Apoidea s.l. (Alexander 1992); separate lines are present in most Aculeata (including the relatively more plesiomorphic Apoidea) and Parasitica.

1. Valvifer 2: Not articulated = 0. Articulated = 1.
2. Hindwing jugal lobe: Absent = 0. Present = 1. Reduced = 2.
3. Anterior pedicels of tentorium: Thick = 0. Rodlike = 1. With lamellar processes = 2.
4. Prothoracic furca: Vertical = 0. Proclined = 1. 'Modified' in Sclerogibbidae = 2.
5. Reduction of forewing venation: 2m-cu present = 0. 2m-cu lost or present only as trace = 1.
6. Valves 2: Articulated with valvifer 2 proximally = 0. Not jointed with valvifer 2 proximally = 1. Secondary processes = 2.
7. Antenna: With 13 articles in both sexes = 0. With 13 articles in male and 12 in female = 1. With 10 articles = 2. With more than 14 articles = 3. NONADDITIVE.
8. Antennal pedicel: Mobile = 0. Fixed = 1.
9. Hosts: Beetles = 0. Embiidina = 1. Auchenorrhyncha = 2. Tenthredinoidea or Phasmida = 3. Melliferous = 4. Aculeata = 5. Araneae = 6. Gryllidae = 7. Wide host range (social foragers) = 8. Solifugae = 9. NONADDITIVE. [The host for Bradynobaenidae is based on new unpublished records.]
10. Host habitat: 'Confined' = 0. Free-living = 1.
11. Life style: Ectoparasitic = 0. Endoparasitic initially, with cyst formation = 1. [Rasnitsyn's original interpretation of complete endoparasitism in embolemids was an error; cf. Carpenter (1986), Wharton (1989).]
12. Furcula: Present = 0. Absent = 1. Vertical lamella = 2. NONADDITIVE.
13. Metasomal sternumI: Thin and overlapping sternumII = 0. Thick and abutting = 1. Forming lobules = 2. NONADDITIVE.
14. Metasomal sternumII: Curved anteriorly = 0. Straight with lateral notches = 1. Lateral desclerotized areas expanded = 2. Median notch = 3. NONADDITIVE.
15. Metasternum: Anteriorly narrow = 0. Carinate = 1. Two carinae = 2. Broad = 3. NONADDITIVE.
16. Female metasomal sternumVII: External = 0. Internated = 1.
17. Bilamellar stemming plates of ovipositor: Absent = 0. Present = 1.
18. Hypopharynx pubescence: Present = 0. Reduced = 1.
19. Pronotal lobes: Small = 0. Enlarged = 1.

20. Metapostnotum: Present and unmodified = 0. With propodeal suture obliterated = 1. Forming 'propodeal triangle' = 2. Medially shortened = 3. Medially invaginated = 4. NONADDITIVE. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 35).]
21. Metatibial calcar: Absent = 0. Basal brushes and chitinous modification = 1. Brushes lacking = 2. Brushes only = 3. Dorsally pectinate = 4. Dorsal carinate expansion = 5. NONADDITIVE. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 68).]
22. Arolium and orbicula: Large = 0. Reduced = 1.
23. Metasomal sternumI and tergumII: Not articulated = 0. Articulated, with rotary mobility = 1. Hinged, no rotary mobility = 2. NONADDITIVE.
24. Propleura: Separated = 0. In contact along entire length = 1.
25. Prepectus (first variable): Not extended along pleurosternum = 0. Extended = 1. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 29).]
26. Prepectus (second variable): Broad = 0. Narrowed = 1. Shortened = 2.
27. Prepectus (third variable): Not fused = 0. Long and fused = 1. Line of fusion obliterated = 2.
28. Hindwing anal veins: Present = 0. Reduced = 1.
29. Hindwing axillary excision: Shallow = 0. Deepened = 1.
30. Basal hamuli: Scattered = 0. Closely spaced = 1.
31. Pterostigma: Large = 0. Small = 1.
32. Larval mandibles: Quadridentate = 0. Tridentate = 1.
33. Metaphragma: Narrow = 0. Expanded = 1.
34. Posterolateral angle of pronotum: Not produced = 0. Slightly produced = 1. Exceeding tegula = 2. Forming acute lobe = 3. [We have supplemented Rasnitsyn' s account with reference to Brothers (1975: Character 21).]
35. Mesotibial spines: Absent = 0. Strong scattered spines present = 1. Spines apical = 2. Very strong spines = 3. NONADDITIVE. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 61).]
36. Mesothoracic lamellae: Absent = 0. Small = 1. Large lobes = 2.
37. Dorsal aedeagal fusion: Sclerotized = 0. Desclerotized = 1.
38. Trochantellus: Present = 0. Absent = 1.
39. Prepecti (fourth variable): Separated = 0. In contact = 1.
40. Prosternum: Visible externally = 0. Reduced externally = 1. Almost lost externally = 2. Lost = 3.
41. Mesothoracic venter: Not produced caudally = 0. Produced caudally = 1.
42. Mandibles: 'Chewing type' = 0. 'Cutting type' = 1.
43. Female cerci: Present = 0. Absent = 1.
44. Mesocoxal base: Broad = 0. Narrow, tubular = 1.
45. Median scutal sulcus: Present = 0. Absent = 1.
46. Oviposition sequence: Prey first, then nest construction = 0. Nest construction first, then prey = 1.
47. Female metasomal sternumVI: Convex = 0. Depressed = 1.

[38-47 = characters added from Rasnitsyn (1988).]

APPENDIX IV

Variables used in analysis of Aculeata based entirely on Brothers (1975), showing equivalence with character states described there (using nonredundant linear coding); derived states not used because of sexually dimorphic occurrence (see text) enclosed within square brackets.

The scores for the taxa are given in Table III. Polarity was conferred by the addition of an all-primitive ancestral taxon to the matrix.

Variables considered unlikely to show reversals: 15, 16, 25-27, 30, 48, 49, 56, 69, 72, 75-80, 83-88, 90-92, 94, 95, 99, 105, 108, 109, 110, 116, 121-126, 133, 134, 137, 149, 152-155, 157-161.

1. Sexual dimorphism, general form: Brothers (1975) State 1 = 0. State 1.1 = 1.

2. Sexual dimorphism, aptery: State 2 = 0. State 2.1 = 1.
3. Sterile caste: State3 = 0. State 3.1 = 1.
4. Pubescence: State4 = 0. State 4.1 = 1.
5. Clypeus (first variable): State 5 (and 5.2) = 0. State 5.1 = 1.
6. Clypeus (second variable): State 5 (and 5.1) = 0. State 5.2 = 1.
7. Antennal socket (first variable): State 6 (and 6.2) = 0. State 6.1 = 1.
8. Antennal socket (second variable): State 6 (and 6.1) = 0. State 6.2 = 1.
9. Eye form (first variable): State 7 (and 7.2, 7.3) = 0. State 7.1 = 1. [State 7.1.1 = 2; Chyphotinae and Apterogyninae females and within other taxa.]
10. Eye form (second variable): State 7 (and 7.1, 7.1.1, 7.3) = 0. State 7.2 = 1.
11. Eye form (third variable): State 7 (and 7.1, 7.1.1, 7.2) = 0. State 7.3 = 1.
12. Eye contour: State 8 = 0. State 8.1 = 1.
13. Eye pores and setae (first variable): State 9 (and 9.2, 9.3) = 0. State 9.1 = 1.
14. Eye pores and setae (second variable): State 9 (and 9.1, 9.3) = 0. State 9.2 = 1.
15. Eye pores and setae (third variable): State 9 (and 9.1, 9.2) = 0. State 9.3 = 1.
16. Ocelli: State 10 = 0. State 10.1 = 1.
17. Genal organ: State 11 = 0. State 11.1 = 1.
18. Antennal dimorphism: State 12 = 0. State 12.1 = 1.
19. Radicle axis: State 13 = 0. State 13.1 = 1.
20. Radicle-scape insertion: State 14.1 = 0. State 14.1 = 1.
21. Labio-maxillary complex (first variable): State 15 (and 15.2, 15.3, 15.4) = 0. State 15.1 = 1.
22. Labio-maxillary complex (second variable): State 15 (and 15.1, 15.3, 15.4) = 0. State 15.2 = 1.
23. Labio-maxillary complex (third variable): State 15 (and 15.1, 15.2, 15.4) = 0. State 15.3 = 1.
24. Labio-maxillary complex (fourth variable): State 15 (and 15.1, 15.2, 15.3) = 0. State 15.4 = 1.
25. Maxillary palpus (first variable): State 16 (and 16.2) = 0. [State 16.1 = 1; Plumariidae female and within other taxa.]
26. Maxillary palpus (second variable): State 16 (and 16.1) = 0. State 16.2 = 1.
27. Labial palpus: State 17 = 0. State 17.1 = 1.
28. Hind margin of pronotum (first variable): State 18 (and 18.2) = 0. State 18.1 = 1.
29. Hind margin of pronotum (second variable): State 18 (and 18.1) = 0. State 18.2 = 1.
30. Pronotal articulation: State 19 = 0. State 19.1 = 1.
31. Pronotal collar: State 20 = 0. State 20.1 = 1.
32. Posterolateral angle of pronotum (first variable): State 21 (and 21.2, 21.2.1, 21.3) = 0. State 21.1 = 1. State 21.1.1 = 2. State 21.1.1 .1 = 3 .
33. Posterolateral angle of pronotum (second variable): State 21 (and 21.1, 21.1.1, 21.1.1.1, 21.3) = 0. State 21.2 = 1. State 21.2.1 = 2.
34. Posterolateral angle of pronotum (third variable): State 21 (and all others except 21.3) = 0. State 21.3 = 1.
35. Posteroventral margin of pronotum: State 22 = 0. State 22.1 = 1.
36. Ventral angle of pronotum (first variable): State 23 (and 23.2) = 0. State 23.1 = 1.
37. Ventral angle of pronotum (second variable): State 23 (and 23.1) = 0. State 23.2 = 1.
38. Propleural separation (first variable): State 24 (and 24.2) = 0. State 24.1 = 1.
39. Propleural separation (second variable): State 24 (and 24.1) = 0. State 24.2 = 1.
40. Prosternum: State 25 = 0. State 25.1 = 1. State 25.1.1 = 2.
41. Forecoxal contiguity (first variable): State 26 (and 26.2) = 0. State 26.1 = 1.
42. Forecoxal contiguity (second variable): State 26 (and 26.1) = 0. State 26.2 = 1.
43. Mesonotum: State 27 = 0. State 27.1 = 1.
44. Scutellum: State 28 = 0. State 28.1 = 1. State 28.1.1 = 2.
45. Prepectus (first variable): State 29 (and 29.2) = 0. State 29.1 (and 29.1.2, 29.1. 2.1) = 1. State 29.1.1 (and 29.1.1.2, 29.1. 1.3) = 2. State 29.1.1.1 = 3.
46. Prepectus (second variable): State 29 (and all others except 29.1.1.2) = 0. State 29.1.1.2 = 1.
47. Prepectus (third variable): State 29 (and all others except 29.1.1.3) = 0. State 29.1.1.3 = 1.

48. Prepectus (fourth variable): State 29 (and all others except 29.1.2, 29.1.2.1) = 0. State 29.1 .2 = 1. State 29.1.2.1 = 2.
49. Prepectus (fifth variable): State 29 (and all others except 29.2) = 0. State 29.2 = 1.
50. Mesepimeron (first variable): State 30 (and 30.2) = 0. State 30.1 = 1.
51. Mesepimeron (second variable): State 30 (and 30.1) = 0. State 30.2 = 1.
52. Mesosternum (first variable): State 31 (and 31.2) = 0. State 31.1 = 1. State 31.1.1 = 2.
53. Mesosternum (second variable): State 31 (and 31.1, 31.1.1) = 0. State 31.2 = 1.
54. Mesocoxal contiguity (first variable): State 32 (and 32.2) = 0. State 32.1 = 1.
55. Mesocoxal contiguity (second variable): State 32 (and 32.1) = 0. State 32.2 = 1.
56. Meso-metapleural suture: State 33 = 0. State 33.1 = 1. State 33.1.1 = 2.
57. Metanotum (first variable): State 34 (and 34.2) = 0. State 34.1 = 1.
58. Metanotum (second variable): State 34 (and 34.1) = 0. State 34.2 = 1.
59. Metapostnotum (first variable): State 35 (and 35.2, 35.3) = 0. State 35.1 = 1. State 35.1 .1 = 2.
60. Metapostnotum (second variable): State 35 (and 35.1, 35.1.1, 35.3) = 0. State 35.2 = 1.
61. Metapostnotum (third variable): State 35 (and 35.1, 35.1.1, 35.2) = 0. State 35.3 = 1.
62. Metapleuron (first variable): States 36 (and 36.2, 36.3) = 0. State 36.1 (and 36.1.2) = 1. State 36.1.1 = 2.
63. Metapleuron (second variable): State 36 (and all others except 36.1.2) = 0. State 36.1.2 = 1.
64. Metapleuron (third variable): State 36 (and all others except 36.2) = 0. State 36.2 = 1.
65. Metapleuron (fourth variable): State 36 (and all others except 36.3) = 0. State 36.3 = 1.
66. Metapleural gland: State 37 = 0. State 37.1 = 1.
67. Metasternum (first variable): State 38 = 0. State 38.1 = 1. State 38.1.1 (and 38.1.1.2) = 2. State 38.1.1.1 = 3.
68. Metasternum (second variable): State 38 (and 38.1, 38.1.1, 38.1.1.1) = 0. State 38.1.1.2 = 1.
69. Metasternal differentiation: State 39 = 0. State 39.1 = 1.
70. Metasternal anterior production: State 40 = 0. State 40.1 = 1. State 40.1.1 = 2.
71. Metacoxal contiguity: State 41 = 0. State 41.1 = 1.
72. Metathoracic-propodeal pleural suture: State 42 = 0. State 42.1 = 1. State 42.1.1 = 2.
73. Propodeal length: State 43 = 0. State 43.1 = 1.
74. Discal distinction: State 44 = 0. State 44.1 = 1.
75. Extent of forewing venation: State 45 = 0. State 45.1 = 1. State 45.1.1 = 2.
76. Cells of forewing (first variable): State 46 (and 46.2, 46.3, 46.4, 46.5, 46.5.1) = 0. State 46.1 = 1. State 46.1.1 = 2. State 46.1.1.1 = 3.
77. Cells of forewing (second variable): State 46 (and all others except 46.2) = 0. State 46.2 = 1.
78. Cells of forewing (third variable): State 46 (and all others except 46.3) = 0. State 46.3 = 1.
79. Cells of forewing (fourth variable): State 46 (and all others except 46.4) = 0. State 46.4 = 1.
80. Cells of forewing (fifth variable): State 46 (and all others except 46.5 and 46.5.1) = 0. State 46.5 = 1. State 46.5.1 = 2.
81. Pterostigmal size: State 47 = 0. State 47.1 = 1. State 47.1.1 = 2.
82. Pterostigmal sclerotization: State 48 = 0. State 48.1 = 1.
83. Extent of hindwing venation: State 49 = 0. State 49.1 = 1. State 49.1.1 = 2.
84. Cells of hindwing (first variable): State 50 (and 50.2, 50.3, 50.3.1) = 0. State 50.1 = 1.
85. Cells of hindwing (second variable): State 50 (and 50.1, 50.3, 50.3.1) = 0. State 50.2 = 1.
86. Cells of hindwing (third variable): State 50 (and 50.1, 50.2) = 0. State 50.3 = 1. State 50.3.1 = 2.
87. Hindwing anal and jugal veins (first variable): State 51 (and 51.2) = 0. State 51.1 = 1.
88. Hindwing anal and jugal veins (second variable): State 51 (and 51.1) = 0. State 51.2 = 1.
89. Hindwing cross-vein cu-e: State 52 = 0. State 52.1 = 1.
90. Hindwing vein Cu: State 53 = 0. State 53.1 = 1.
91. Basal hamuli (first variable): State 54 (and 54.2) = 0. State 54.1 = 1.

92. Basal hamuli (second variable): State 54 (and 54.1) = 0. State 54.2 = 1.
93. Plical lobe: State 55 = 0. State 55.1 = 1. State 55.1.1 = 2.
94. Jugal lobe (first variable): State 56 (and 56.2) = 0. State 56.1 = 1. State 56.1.1 = 2.
95. Jugal lobe (second variable): State 56 (and 56.1, 56.1.1) = 0. State 56.2 = 1.
96. Leg form (first variable): State 57 (and 57.2, 57.3) = 0. State 57.1 = 1.
97. Leg form (second variable): State 57 (and 57.1, 57.3) = 0. State 57.2 = 1.
98. Leg form (third variable): State 57 (and 57.1, 57.2) = 0. State 57.3 = 1.
99. Arolium: State 58 = 0. State 58.1 = 1.
100. Claws: State 59 = 0. State 59.1 = 1.
101. Foretibial calcar (first variable): States 60 (and 60.2) = 0. State 60.1 = 1. State 60.1.1 = 2.
102. Foretibial calcar (second variable): State 60 (and 60.1, 60.1.1) = 0. State 60.2 = 1.
103. Midtibial spines (first variable): State 61 (and 61.2) = 0. State 61.1 (and 61.1.2) = 1. State 61.1.1 = 2. State 61.1.1.1 = 3. State 61.1.1.1.1 = 4.
104. Midtibial spines (second variable): State 61 (and all others) except 61.1.2 = 0. State 61.1.2 = 1.
105. Midtibial spines (third variable): State 61 (and all others) except 61.2 = 0. State 61.2 = 1.
106. Hindtibial spines (first variable): State 62 (and 62.2) = 0. State 62.1 (and 62.1.2) = 1. State 62.1.1 = 2. State 62.1.1.1 = 3. State 62.1.1.1.1 = 4.
107. Hindtibial spines (second variable): State 62 (and all others except 62.1.2) = 0. State 62.1.2 = 1.
108. Hindtibial spines (third variable): State 62 (and all others except 62.2) = 0. State 62.2 = 1.
109. Midtibial spur number (first variable): State 63 (and 63.2) = 0. State 63.1 = 1.
110. Midtibial spur number (second variable): State 63 (and 63.1) = 0. State 63.2 = 1.
111. Basic form of mid and hindtibial spurs (first variable): State 64 = 0. State 64.1 (and 64.1.2, 64.1.2.1, 64.1.2.1.1) = 1. State 64.1.1 = 2.
112. Basic form of mid and hindtibial spurs (second variable): State 64 (and 64.1, 64.1.1) = 0. State 64.1.2 = 1. [State 64.1.2.1 = 2, Bradynobaeninae male only is precursor to state 3]. State 64.1.2.1.1 = 3.
113. Midtibial calcar (first variable): State 65 (and 65.2) = 0. State 65.1 = 1.
114. Midtibial calcar (second variable): State 65 (and 65.1) = 0. State 65.2 = 1.
115. Form of hindcoxa: State 66 = 0. State 66.1 = 1. State 66.1.1 = 2.
116. Hindtibial spur number: State 67 = 0. State 67.1 = 1.
117. Hindtibial calcar (first variable): State 68 (and 68.2, 68.3, 68.4) = 0. State 68.1 = 1.
118. Hindtibial calcar (second variable): State 68 (and 68.1, 68.3, 68.4) = 0. State 68.2 = 1.
119. Hindtibial calcar (third variable): State 68 (and 68.1, 68.2, 68.4) = 0. State 68.3 = 1.
120. Hindtibial calcar (fourth variable): State 68 (and 68.1, 68.2, 68.3) = 0. State 68.4 = 1.
121. Modified mesosoma of apterous female (first variable): State 69 (and 69.2, 69.2.1, 69.2.2, 69.3, 69.3.1, 69.3.2, 69.4) = 0. State 69.1 = 1. State 69.1.1 = 2. State 69.1.1.1 = 3.
122. Modified mesosoma of apterous female (second variable): State 69 (and 69.1, 69.1.1, 69.1.1.1, 69.3, 69.3.1, 69.3.2, 69.4) = 0. State 69.2 (and 69.2.2) = 1. State 69.2.1 = 2.
123. Modified mesosoma of apterous female (third variable): State 69 (and all others except 69 .2.2) = 0. State 69.2.2 = 1.
124. Modified mesosoma of apterous female (fourth variable): State 69 (and 69.1, 69.1.1, 69.1.1.1, 69.2, 69.2.1, 69.2.2, 69.4) = 0. State 69.3 (and 69.3.2) = 1. State 69.3.1 = 2.
125. Modified mesosoma of apterous female (fifth variable): State 69 (and all others except 69.3.2) = 0. State 69.3.2 = 1.
126. Modified mesosoma of apterous female (sixth variable): State 69 (and all others except 69.4) = 0. State 69.4 = 1.
127. 'Felt lines' (first variable): State 70 (and 70.2, 70.2.1) = 0. State 70.1 = 1.
128. 'Felt lines' (second variable): State 70 (and 70.1) = 0. State 70.2 = 1. State 70.2.1 = 2.
129. Stridulitra (first variable): State 71 (and 71.2) = 0. State 71.1 = 1.

130. Stridulitra (second variable): State 71 (and 71.1) = 0. State 71.2 = 1.
131. Constriction of metasomal tergumI: State 72 = 0. State72.1 = 1. State 72.1.1 = 2.
132. Metasomal petiole: State 73 = 0. State 73.1 = 1.
133. Lateral margin of metasomal tergumI: State 74 = 0. State 74.1 = 1. State 74.1.1 = 2.
134. Width of metasomal tergumI: State 75 = 0. State 75.1 = 1. State 75.1.1 = 2.
135. Differentiation of metasomal sternumI: State 76 = 0. State 76.1 = 1.
136. Constriction of second metasomal segment: State 77 = 0. State 77.1 = 1.
137. Metasomal tergumVII of female: State 78 = 0. State 78.1 = 1. State 78.1.1 = 2.
138. Gonocoxite IX of female: State 79 = 0. State 79.1 = 1.
139. GonapophysisVIII of female: State 80 = 0. State 80.1 = 1.
140. Gonapophysis IX of female (first variable): State 81 (and 81.2) = 0. State 81.1 = 1.
141. Gonapophysis IX of female (second variable): State 81 (and 81.1) = 0. State 81.2 = 1.
142. Metasomal sternumVII of male: State 82 = 0. State 82.1 = 1. State 82.1.1 = 2.
143. Form of male hypopygium (first variable): All states except 83.1 = 0. State 83.1 = 1.
144. Form of male hypopygium (second variable): All states except 83.2 = 0. State 83.2 = 1.
145. Form of male hypopygium (third variable): All states except 83.3 = 0. State 83.3 = 1
146. Form of male hypopygium (fourth variable): State 83 (and 83.1, 83.2, 83.3) = 0. State 83.4 = 1. State 83.4.1 = 2.
147. Concealment of male hypopygium (first variable): State 84 (and 84.2) = 0. State 84.1 = 1.
148. Concealment of male hypopygium (second variable): State 84 (and 84.1) = 0. State 84.2 = 1.
149. Cercus of male: State 85 = 0. State 85.1 = 1.
150. Gonapophysis IX of male (first variable): State 86 (and 86.2) = 0. State 86.1 = 1.
151. Gonapophysis IX of male (second variable): State 86 (and 86.1) = 0. State 86.2 = 1.
152. Larval mandibular teeth (first variable): State 87 (and 87.2, 87.3) = 0. State 87.1 = 1.
153. Larval mandibular teeth (second variable): State 87 (and 87.1, 87.3) = 0. State 87.2 = 1.
154. Larval mandibular teeth (third variable): State 87 (and 87.1, 87.2) = 0. State 87.3 = 1.
155. Larval spiracles: State 88 = 0. State 88.1 = 1.
156. Number of prey: State 89 = 0. State 89.1 = 1.
157. Nest construction (first variable): State 90 (and 90.2) = 0. State 90.1 (and 90.1.2, 90.1.3) = 1. State 90.1.1 = 2.
158. Nest construction (second variable): State 90 (and 90.1, 90.1.3, 90.2) = 0. State 90.1.2 = 1.
159. Nest construction (third variable): State 90 (and 90.1, 90.1.2, 90.2) = 0. State 90.1.3 = 1.
160. Nest construction (fourth variable): State 90 (and 90.1, 90.1.2, 90.1.3) = 0. State 90.2 = 1.
161. Oviposition sequence: State 91 = 0. State 91.1 = 1.
162. Type of provisions: State 92 = 0. State 92.1 = 1.

APPENDIX V

Distribution of derived character states on preferred cladogram (see text) of Aculeata (Fig. 8b) resulting from analysis of data from Brothers (1975) (Table III); optimization by accelerated transformation, except delayed transformation for variables considered unlikely to show reversals and manual for Variables 72 and 83. Unnamed internodes are referred to by listing the subtended superfamilies, families or lower taxa. Character numbers refer to the variables in Appendix IV; transformations are denoted by listing the ancestral and derived states separated by a '>'.

Final weights of variables (10 is maximum):

Weight = 10: 1, 3, 5, 6, 9, 10, 17, 18, 20, 21, 22, 23, 24, 25, 26, 29, 30, 31, 33, 34, 37, 38, 39, 40, 41, 42, 44, 46, 47, 49, 55, 58, 60, 61, 63, 65, 66, 68, 70, 71, 77, 78, 79, 80, 85, 86, 87, 89, 90, 97, 98, 101, 102, 104, 105, 107, 108, 110, 112, 113, 114, 116, 118, 119, 120, 122, 123, 124, 125, 126, 127, 128, 129, 132, 133, 134, 136, 137, 138, 143, 144, 145, 146, 150, 151, 154, 158, 159, 162

Weight = 6: 45

Weight = 5: 48, 94

Weight = 4: 7, 36, 51, 155

Weight = 3: 19, 52, 53, 59, 67, 76, 131, 152
Weight = 2: 4, 8, 15, 16, 32, 43, 56, 57, 62, 69, 81, 88, 99, 103, 106, 111, 130, 135, 140, 141, 157, 160
Weight = 1: 28, 74, 75, 82, 83, 92, 93, 95, 96, 115, 149
Weight = 0: 2, 11, 12, 13, 14, 27, 35, 50, 54, 64, 72, 73, 84, 91, 100, 109, 117, 121, 139, 142, 147, 148, 153, 156, 161

(Aculeata): 40:0>1, 75:0>1, 103:0>1, 106:0>1
(Plumariidae, bethylids, Scolebythidae): 72:0>1, 76:0>1, 88:0>1, 95:0>1, 138:0>1
Plumariidae: 2:0>1, 16:0>1, 39:0>1, 67:0>1, 96:0>1, 126:0>1, 139:0>1, 142:0>1
(bethylids, Scolebythidae): 40:1>0, 60:0>1, 76:1>2, 83:0>1, 86:0>1, 103:1>0, 106:1>0
bethylids ('higher' Chrysidoidea): 27:0>1
Scolebythidae: 5:0>1, 11:0>1, 13:0>1, 31:0>1, 42:0>1, 58:0>1, 76:2>3, 83:1>2, 86:1>2, 97:0>1, 105:0>1, 108 :0>1
(Apoidea, Vespoidea): 18:0>1, 35:0>1, 41:0>1, 81:0>1, 137:0>1
(Apoidea): 29:0>1, 33:0>1, 37:0>1, 43:0>1, 49:0>1, 53:0>1, 56:0>1, 61:0>1, 65:0>1, 69:0>1, 111:0>2, 141:0>1, 157:0>1
sphecids (Sphecidae s.l.): 33:1>2, 75:1>0, 103:1>2, 106:1>2
apids (Apidae s.l.): 4:0>1, 21:0>1, 51:0>1, 72:0>1, 84:0>1, 87:0>1, 109:0>1, 137:1>2, 142:0>2, 148:0>1, 149:0>1, 153:0>1, 156:0>1, 157:1>2, 162:0>1
(Vespoidea): 13:0>1, 38:0>1, 45:0>1, 52:0>1, 64:0>1, 67:0>2, 84:0>1, 88:0>1, 93:0>1
Sierolomorphidae: 72:0>1, 77:0>1, 81:1>0, 83:0>1, 95:0>1, 115:0>1, 143:0>1, 148:0>1
(Rhopalosomatidae, Scoliidae, Vespidae, Formicidae, Bradynobaenidae, Pompilidae, Sapygidae, Mutillidae, Tiphiidae): 82:0>1, 94:0>1, 142:0>1
(Rhopalosomatidae, Scoliidae, Vespidae, Formicidae, Bradynobaenidae): 28:0>1, 32:0>1, 43:0>1, 45:1>2, 131:0>1, 141:0>1
Rhopalosomatidae: 52:1>2, 54:0>1, 76:0>1, 83:0>1, 91:0>1, 93:1>0, 98:0>1, 117:0>1, 154:0>1
(Scoliidae, Vespidae, Formicidae, Bradynobaenidae): 36:0>1, 52:1>0, 56:0>1, 59:0>2, 62:0>1, 64:1>0, 135:0>1, 152:0>1, 156:0>1, 157:0>1
(Scoliidae, Vespidae): 6:0>1, 10:0>1, 13:1>0, 22:0>1, 30:0>1, 32:1>2, 40:1>2, 53:0>1, 84:1>0, 92:0>1, 141:1>0, 149:0>1
Scoliidae: 15:0>1, 46:0>1, 50:0>1, 55:0>1, 63:0>1, 68:0>1, 69:0>1, 71:0>1, 74:0>1, 83:0>1, 93:1>2, 96:0>1, 100:0>1, 102:0>1, 104:0>1, 107:0>1, 109:0>1, 111:1>2, 142:1>0, 144:0>1, 148:0>1, 150:0>1, 156:0>1
Vespidae: 32:2>3, 45:2>3, 54:0>1, 73:0>1, 75:1>0, 118:0>1, 131:1>0, 139:0>1, 157:1>2, 161:0>1
(Formicidae, Bradynobaenidae): 51:0>1, 82:1>0, 103:1>2, 106:1>3, 132:0>1, 161:0>1
Formicidae: 3:0>1, 47:0>1, 56:1>2, 66:0>1, 75:1>0, 76:0>1, 92:0>1, 103:2>3, 113:0>1, 119:0>1, 142:1>0, 158:0>1
(Bradynobaenidae): 2:0>1, 16:0>1, 28:1>0, 32:1>0, 43:1>0, 67:2>0, 69:0>1, 70:0>1, 72:0>1, 83:0>1, 93:1>2, 124:0>1, 128:0>1, 130:0>1, 133:0>1, 139:0>1
(Typhoctinae): 4:0>1, 35:1>0, 36:1>0, 62:1>0, 64:0>1, 91:0>1, 106:3>2, 115:0>1, 124:1>2
Eotillini: 81:1>0, 93:2>0, 99:0>1, 103:2>1, 106:2>1
Typhoctini: 84:1>0, 94:1>0, 95:0>1
(Chyphotinae, Apterogyninae, Bradynobaeninae): 7:0>1, 9:0>1, 12:0>1, 13:1>0, 19:0>1, 96:0>1, 125:0>1, 133:1>2, 134:0>1, 146:0>1
Chyphotinae: 56:1>2, 81:1>0, 91:0>1, 134:1>2, 147:0>1
(Apterogyninae, Bradynobaeninae): 15:0>1, 17:0>1, 44:0>1, 57:0>1, 70:1>2, 75:1>2, 80:0>1, 81:0>2, 83:1>2, 84:1>0, 92:0>1, 99:0>1, 101:0>1, 103:2>3, 111:0>1, 112:0>1, 130:1>0, 149:0>1
Apterogyninae: 115:0>1, 131:1>2, 136:0>1, 139:1>0
Bradynobaeninae: 8:0>1, 12:1>0, 24:0>1, 26:0>1, 27:0>1, 34:0>1, 44:1>2, 62:1>2, 73:0>1, 74:0>1, 80:1>2, 85:0>1, 100:0>1, 101:1>2, 103:3>4, 106:3>4, 110:0>1, 112:1>3, 128:1>2, 140:0>1, 141:1>0, 146:1>2
(Pompilidae, Sapygidae, Mutillidae, Tiphiidae): 13:1>0, 75:1>0, 103:1>2, 106:1>2, 155:0>1
Pompilidae: 48:0>1, 54:0>1, 56:0>1, 91:0>1, 111:0>1, 117:0>1, 139:0>1, 152:0>1, 159:0>1
(Sapygidae, Mutillidae, Tiphiidae): 35:1>0, 59:0>1, 64:1>0, 81:1>0, 82:1>0, 89:0>1, 115:0>1
(Sapygidae, Mutillidae): 7:0>1, 48:0>1, 90:0>1, 94:1>2, 151:0>1
Sapygidae: 23:0>1, 139:0>1, 153:0>1, 155:1>0
(Mutillidae): 2:0>1, 19:0>1, 20:0>1, 48:1>2, 54:0>1, 62:0>1, 72:0>2, 91:0>1, 122:0>1, 129:0>1, 135:0>1, 140:0>1, 160:0>1
Myrmosinae: 14:0>1, 115:1>2, 122:1>2, 142:1>0, 148:0>1
mutillids ('higher' Mutillidae): 28:0>1, 32:0>1, 50:0>1, 57:0>1, 67:2>3, 75:0>1, 83:0>1, 123:0>1, 127:0>1
(Tiphiidae): 52:1>2, 67:2>1, 84:1>0, 96:0>1
Thynninae (s.l.): 2:0>1, 121:0>1
(Anthoboscinae, Tiphiinae, Brachycistidinae, Myzininae, Methochinae): 93:1>0, 115:1>0

Anthoboscinae: 147:0>1
(Tiphiinae, Brachycistidinae, Myzininae, Methochinae): 35:0>1, 135:0>1, 140 >1, 145:0>1
(Tiphiinae, Brachycistidinae): 32:0>1, 56:0>1, 62:0>2, 72:0>1, 74:0>1, 75:0>1, 83:0>1, 115:0>1, 131:0>1, 142:1>2, 148:0>1, 149:0>1
Tiphiinae: 59:1>2, 72:1>2, 79:0>1
Brachycistidinae: 2:0>1, 12:0>1, 16:0>1, 45:1>2, 92:0>1, 100:0>1, 109:0>1, 121:0>3
(Myzininae, Methochinae): 1:0>1, 8:0>1, 142:1>0
Myzininae: 35:1>0, 59:1>2, 140:1>0
Methochinae: 2:0>1, 11:0>1, 14:0>1, 52:1>0, 72:0>1, 78:0>1, 84:0>1, 96:1>0, 103:2>1, 106:2>1, 114:0>1, 116:0>1, 120:0>1, 121:0>2, 160:0>1

APPENDIX VI

Variables used in final analyses of Aculeata, based on characters and states from Brothers (1975), Brothers (1976), Rasnitsyn (1980, 1988), Carpenter (1986), Johnson (1988), Kimsey (1991), new interpretations and new characters; all refer to adults unless otherwise specified.

The scores for the taxa are given in Tables IV and V. Characters are treated as additive except as noted. Polarity was conferred by the addition of an all-primitive ancestral taxon to the matrix.

Variables 1-18 and 21-185 are those used to score the 92 characters from Brothers (1975) given in Appendix IV and Table III, except that the following three variables of Appendix IV have been deleted for the reasons stated: 5 (very short clypeus, supposed autapomorphy of Scolebythidae, not shown in *Ycaploca*), 29 (U-shaped posterior pronotal margin duplicates Variable 33 of Appendix IV), 58 (much constricted metanotum, supposed autapomorphy of Scolebythidae, not shown in *Ycaploca*). New characters are Variables 19-20 and 186-219. The majority of the characters used by Rasnitsyn (1980, 1988) (Appendices II and III) are subsumed in the coding for the characters in Appendix IV, which is based on fuller study (examination of more characters and taxa than done by Rasnitsyn); where the inferred polarities of major features differed between Brothers (1975) and Rasnitsyn (1980, 1988), we have re-evaluated them and sometimes treated the polarity of the states of such characters as nonadditive.

Newly scored taxa (not considered separately by Brothers, 1975) are Bethylidae, Chrysididae, Sclerogibbidae, Embolemidae, Dryinidae, Heterogynaidae, Diamminae, Thynninae, *Olixon*, macropterous rhopalosomatids (including *Liosphex*), Proscoliinae, Scoliinae, Fedtschenkiinae and Sapyginae; Scolebythidae has been rescored to include *Ycaploca*. Other changes of interpretation from those in Appendix IV and the source publications are noted where relevant. In order to permit this new analysis to stand on its own, all variables and states are specified here, including those which are unchanged from Brothers's (1975) treatment, but the descriptions are shorter and often differ for greater clarity or as a result of the different system of coding used; because of the consideration of more taxa, new states have been added to some characters. To aid comparison, the equivalent characters in Brothers (1975) (C) and variables in Appendix IV (above) (V) are specified. The terminology of Brothers (1975) has been maintained for consistency, although different terminology for some features (e.g., wing veins) has been more generally adopted since that paper. Sexually dimorphic states used by Brothers (1975) but not included in this analysis (see text), are indicated by comments.

Variables considered unlikely to show reversals: 2, 15, 16, 27-29, 31, 32, 48 (State 3), 49-53, 61 (State 2), 77, 80 (State 2), 81 (State 2), 84-92, 95-102, 104-106, 109, 113, 124, 125, 131, 137-144, 151 (State 2), 152, 153, 156, 157, 161, 171, 178, 196, 198, 201, 202, 204, 215, 216 (State 2).

1. Sexual dimorphism in body proportions: None or slight although dimorphism in wing development may be considerable = 0. Male very much more slender than female = 1. (C1, V1)
2. Sexual dimorphism in wing development: Both sexes fully winged or equally brachypterous = 0. Male macropterous and female strongly brachypterous or apterous = 1. (C2) [Modification of V2 to account for conditions in *Olixon* and Heterogynaidae.]
3. Sterile caste: All females fertile = 0. Some females sterile and forming specialized caste = 1. (C3, V3)

4. Pubescence: Simple = 0. Some plumose = 1. (C4, V4)
5. Clypeus height: Moderate (or very short) = 0. Dorsally produced = 1. (C5, V6)
6. Antennal socket (first variable): Rim simple (or frontal ledge present) = 0. Rim produced dorsally to form differentiated 'tubercle' = 1. (C6, V7)
7. Antennal socket (second variable): Rim simple (or modified differently from State 1) = 0. Frons expanded as frontal ledge overhanging anteriorly-facing socket = 1. (C6, V8)
8. Antennal socket (third variable): Rim simple (or modified differently from State 1) = 0. Frons and socket produced as frontal ledge with ventrally-facing socket = 1. (C6) [Addition of variable for condition in Sclerogibbidae.]
9. Compound eye form (first variable): Oval with inner margin shallowly sinuate (or inner margin emarginate or convex) = 0. Rounded with inner margin shallowly sinuate = 1. [State 2, Chyphotinae and Apterogyninae females only, deleted.] (C7, V9)
10. Compound eye form (second variable): Oval (or rounded) with inner margin shallowly sinuate (or convex) = 0. Oval with inner margin emarginate = 1. (C7, V10)
11. Compound eye form (third variable): Oval with inner margin shallowly sinuate (or emarginate, or eye rounded) = 0. Oval with inner margin convex = 1. (C7, V11)
12. Compound eye contour: Following general contours of head = 0. Highly differentiated, eye protuberant = 1. (C8, V12)
13. Compound eye pores and setae (first variable): Scattered pores with setae minute (or long, or no pores or setae) = 0. Scattered pores with short setae = 1. Dense pores with short setae = 2. (C9, V13) [Addition of state for condition in Sclerogibbidae.]
14. Compound eye pores and setae (second variable): Pores with setae minute (or short, or no pores or setae) = 0. Scattered pores with long setae = 1. (C9, V14)
15. Compound eye pores and setae (third variable): Present = 0. Absent = 1. (C9, V15)
16. Ocelli: Present in both sexes = 0. Absent in one or both sexes = 1. (C10, V16)
17. Genal organ: Absent = 0. Present = 1. (C11, V17)
18. Sexual dimorphism in antennomere number: None = 0. Male with 13 and female with 12 antennomeres = 1. (C12, V18)
19. Antennomere number (first variable): Fewer than 14 antennomeres = 0. More than 14 antennomeres = 1.
20. Antennomere number (second variable): More than 11 antennomeres = 0. Ten antennomeres = 1.

(Variables 19-20: new character for conditions in various Chrysidoidea; see Carpenter (1986).]

21. Radicle axis: Scape and radicle sharing a common axis = 0. Axis of radicle at a distinct angle to that of scape = 1. (C13, V19)
22. Radicle-scape insertion: Simple annular constriction = 0. Radicle inserted under flangelike expansion of scape = 1. (C14, V20)
23. Labio-maxillary complex (first variable): Short and adapted for lapping (or modified differently from States 1 and 2) = 0. Elongated by production of prementum and stipes only = 1. Elongated by production of prementum and stipes and of glossa = 2. (C15, V21 & V23)
24. Labio-maxillary complex (second variable): Short and adapted for lapping (or modified differently from State1) = 0. Elongated by production of glossa and paraglossa only = 1. (C15, V22)
25. Labio-maxillary complex (third variable): Short and adapted for lapping (or modified differently from State 1) = 0. Elongated by production of prementum and stipes but glossa and paraglossa much reduced = 1. (C15)
26. Labio-maxillary complex (fourth variable): Short and adapted for lapping (or elongated) = 0. Much reduced = 1. (C15, V24)

[Variables 23-26: modification of C15 to reflect conditions in Fedtschenkiinae and Sapyginae more accurately.]

27. Maxillary palpus (first variable): Six-(or two-) segmented = 0. Five-segmented = 1. (C16, V25)
28. Maxillary palpus (second variable): Six- (or five-) segmented = 0. Two-segmented = 1. (C16, V26)
29. Labial palpus: Four-segmented = 0. Three-segmented = 1. (C17, V27)
30. Posterior margin of pronotum (first variable): Nearly straight, shallowly evenly concave or broadly U-shaped = 0. V-shaped, pronotum shortened medially = 1. (C18, V28)
31. Pronotal articulation (first variable): Pronotum freely articulating with mesothorax (or pronotum fused with prepectus and closely abutting mesepisternum) = 0. Pronotum closely abutting prepectus which fused with mesepisternum = 1. (C19)
32. Pronotal articulation (second variable): Pronotum freely articulating with mesothorax (or pronotum closely abutting prepectus which fused with mesepisternum) = 0. Pronotum fused with hidden prepectus and closely abutting mesepisternum = 1. Pronotum fused with large exposed prepectus which closely abutting mesepisternum = 2. NONADDITIVE (C19)

[Variables 31-32: addition of variable to differentiate between separate derivations of immovable pronotum in scoliids and vespids, see Gibson (1985:1417); and for condition in Embolemidae.]

33. Anterior collar of pronotum: Present and concealing anteriorly separated propleura from above = 0. Absent or greatly reduced and exposing anteriorly contiguous propleura from above = 1. (C20, V31)
34. Posterolateral angle of pronotum (first variable): Evenly rounded and reaching tegula (or modified differently from States 1, 2 or 3) = 0. Slightly dorsally produced, truncate and reaching tegula = 1. Dorsally produced, notched and slightly exceeding anterior margin of tegula = 2. Dorsally produced, acute and much exceeding anterior margin of tegula = 3. (C21, V32)
35. Posterolateral angle of pronotum (second variable): Evenly rounded and reaching tegula (or modified differently from State 1) = 0. Reduced dorsally above and anterior to differentiated spiracular operculum and reaching tegula = 1. [State 2, supposed autapomorphy of sphecids, deleted since not shown in Dolichurini] (C21, V33)
36. Posterolateral angle of pronotum (third variable): Evenly rounded and reaching tegula (or modified differently from State 1) = 0. Posteriorly produced below tegula = 1. (C21, V34)
37. Posteroventral margin of pronotum: Approximately straight = 0. Distinctly concave = 1. (C22, V35)
38. Ventral angle of pronotum (first variable): Broadly rounded and scarcely exceeding base of procoxa (or produced mesad and approaching its counterpart midventrally) = 0. Very narrowly rounded and slightly produced ventrally beyond base of procoxa and lateral to it = 1. Acute and produced ventrally beyond base of procoxa and lateral to it = 2. (C23, V36)
39. Ventral angle of pronotum (second variable): Scarcely exceeding base of procoxa (or produced ventrally beyond base of procoxa and lateral to it) = 0. Greatly produced mesad and approaching its counterpart midventrally although well separated from it = 1. Greatly produced mesad and closely approaching its counterpart midventrally = 2. (C23, V37)

[Variables 38-39: reformulation and addition of intermediate states as found in Proscoliinae and Heterogynaidae.]

40. Propleural separation (first variable): Propleura separated posteriorly = 0. Propleura mesally contiguous posteriorly with posterior margins forming more or less straight line = 1. (C24, V38)
41. Propleural separation (second variable): Propleura separated and exposing medial membranous areas anterodorsally = 0. Propleura contiguous or fused over some distance anterodorsally, forming short tubular necklike region = 1. (C24) [New variable, reformulation of V39 to avoid overlap with V144.]

42. Propleural separation (third variable): Propleura narrowly separated or contiguous posteriorly = 0. Propleura very widely separated posteriorly and exposing enlarged prosternum = 1. (C24) [Addition of extreme state for condition in Scolebythidae, see Carpenter (1986).]
43. Prosternum: Forming an even plane and not sunken except at most for very short region posteriorly = 0. Forming different planes and sunken except for short region anteriorly = 1. Entirely sunken = 2. (C25, V40)
44. Procoxal contiguity: Somewhat separated basally by broad prosternum = 0. Contiguous basally through reduction in prosternum = 1. (C26, V41)
45. Protrochanteral insertion: Apical on coxa = 0. Near base of coxa = 1. (C26, V42)
[Variables 44-45: reformulation of V41 and V42 as separate characters.]
46. Mesonotum: Scarcely extending anterior to tegulae = 0. Extending far anterior to tegulae = 1. (C27, V43)
47. Scutellum: Flattened and poorly differentiated = 0. Posterodorsally swollen and protuberant = 1. Posterodorsally produced and overhanging metanotum = 2. (C28, V44)
48. Prepectus (first variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or halves fused midventrally) = 0. Free with each half narrowed and widely separated from its counterpart = 1. Each half narrowed and shortened as a small elongate strip articulating with (or fused to) anterior margin of mesepisternum = 2. Each half very narrow and short, extending over dorsal half or less of mesepisternum, fused with pronotum and concealed under its posterolateral angle = 3. (C29, V45) [Reformulation to include reinterpretation of condition in Vespidae, see Gibson (1985).]
49. Prepectus (second variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from State 1) = 0. Each half very narrow and short, extending over less than dorsal half of mesepisternum, fused with mesepisternum and concealed under posterolateral angle of pronotum = 1. (C29, V46)
50. Prepectus (third variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from State 1) = 0. Each half very short but extending over most of height of mesepisternum, fused with mesepisternum and concealed under posteroventral margin of pronotum = 1. (C29, V47)
51. Prepectus (fourth variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from States 1 and 2) = 0. Not shortened, extending over most of height of mesepisternum and fused with it, line of fusion forming distinct sulcus = 1. Not shortened, extending over most of height of mesepisternum and fused with it, line of fusion obliterated except at two ventral pits = 2. (C29, V48)
52. Prepectus (fifth variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from State 1) = 0. Transverse with halves fused midventrally and to meso-pleurosternum = 1. (C29, V49)
53. Prepectus (sixth variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from States 1 and 2) = 0. Transverse with halves fused midventrally but not fused with mesopleurosternum = 1. Transverse with halves fused midventrally, fused with pronotum but not fused with mesopleurosternum = 2. NONADDITIVE (C29) [Addition of variable for conditions in some Chrysidoidea.]
54. Mesepimeron (first variable): Extending full height of mesopleuron and differentiated by complete pleural sulcus (or modified differently from State 1) = 0. Extending full height of mesopleuron and differentiated only dorsally by pleural sulcus = 1. (C30, V50)

55. Mesepimeron (second variable): Extending full height of mesopleuron = 0. Restricted to dorsal half of mesopleuron with pleural sulcus coincident with meso-metapleural suture ventrally = 1. (C30, V51)
56. Mesosternum (first variable): Smoothly truncate posteriorly = 0. With short transverse carina or weak tooth anteromesal to mesocoxal cavity = 1. With lamella anteromesal to mesocoxal cavity and projecting over it = 2. (C31, V52)
57. Mesosternum (second variable): Not posteriorly produced mesally = 0. Posteromesally produced and carrying mesal articulations of mesocoxae = 1. Posteromesally acutely produced without affecting mesal articulations of mesocoxae = 2. (C31, V53) NON-ADDITIVE [Reformulation to account for condition in some Chrysidoidea.]
58. Mesocoxal contiguity (first variable): Mesocoxae slightly (or widely) separated basally = 0. Mesocoxae contiguous as result of reduction in intercoxal region of mesosternum = 1. (C32, V54)
59. Mesocoxal contiguity (second variable): Mesocoxae slightly separated basally (or modified differently from State 1) = 0. Mesocoxae widely separated as a result of lateral expansion without shortening of intercoxal region of mesosternum = 1. (C32)
60. Mesocoxal contiguity (third variable): Mesocoxae slightly separated basally (or modified differently from State 1) = 0. Mesocoxae very widely separated as a result of lateral expansion and shortening of intercoxal region of mesosternum = 1. (C32)

[Variables 59-60: reformulation of V55 and addition of new variable to differentiate between apparently independent processes causing separation of mesocoxae in Scoliidae and some Bradynobaenidae.]

61. Meso-metapleural suture: Freely articulating = 0. Immovable but not fused = 1. Entirely or only dorsally fused although distinct = 2. (C33, V56)
62. Metanotum: About as long laterally as mesally = 0. Nearly twice as long laterally as mesally = 1. (C34, V57)
63. Metapostnotum (first variable): Transverse, depressed and distinct mesally between metanotum and propodeum (or modified differently from States 1 and 2) = 0. Partially invaginated and barely visible mesally between metanotum and propodeum = 1. Invaginated and not visible mesally between metanotum and propodeum = 2. (C35, V59)
64. Metapostnotum (second variable): Transverse, depressed and distinct mesally between metanotum and propodeum (or modified differently from States 1, 2 or 3) = 0. Transverse, visible mesally and not invaginated, depressed with posterior margin indistinct mesally = 1. Transverse, very much shortened and hidden mesally but not invaginated, depressed with posterior margin indistinct = 2. (C35, V60) [Addition of state and reformulation to describe conditions in Chrysidoidea more accurately; Carpenter (1986) corrected.]
65. Metapostnotum (third variable): Transverse, depressed and distinct mesally between metanotum and propodeum (or shortened) = 0. Strongly expanded posteromesally to form 'propodeal triangle' = 1. (C35, V61)
66. Metapleuron of macropterous form (first variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from States 1 and 2) = 0. With anterodorsal part of pleural sulcus curved (or angled) and only partly coincident with meso-metapleural suture, posteroventral part convex or straight (or strongly concave) and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and some distance posterior to straightish meso-metapleural suture at or above mid-height = 1. With anterodorsal part of pleural sulcus curved and partly coincident with

meso-metapleural suture, posteroventral part convex and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to posteriorly convex meso-metapleural suture at or above mid-height = 2. (C36)

67. Metapleuron of macropterous form (second variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture, endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus curved and partly coincident with meso-metapleural suture, posteroventral part strongly concave and coincident with metapleural-propodeal suture and passing through ventral pit; true endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and some distance posterior to straightish meso-metapleural suture at or above mid-height = 1. (C36)
68. Metapleuron of macropterous form (third variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture, endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus almost entirely coincident with meso-metapleural suture but extended anteroventral to endophragmal pit, posteroventral part curved and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture slightly below mid-height = 1. (C36)
69. Metapleuron of macropterous form (fourth variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture, endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part angled and coincident with metapleural-propodeal suture only posteroventrally; endophragmal pit within pleural sulcus and close to straightish meso-metapleural suture at about mid-height = 1. (C36)
70. Metapleuron of macropterous form (fifth variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture, endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus coincident with meso-metapleural suture only anterodorsally but extended anteroventral to endophragmal pit and angled, posteroventral part angled and coincident with metapleural-propodeal suture only posteroventrally; endophragmal pit within pleural sulcus and some distance posterior to straightish meso-metapleural suture at about mid-height = 1. (C36)
71. Metapleuron of macropterous form (sixth variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture

at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part straight orweakly concave and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture below mid-height = 1. (C36)

[Variables 66-71: total re-evaluation and recoding consequential on observation of conditions in taxa not examined by Brothers (1975) and different interpretations, see Rasnitsyn (1980).]

72. Metapleural gland: Absent = 0. Present = 1. (C37, V66)
73. Metasternum (first variable): Depressed anterolaterally but not medially nor posteriorly (or modified differently from States1 and 2) = 0. Entirely depressed without teeth (or with separated small teeth just anterior to metacoxal cavities, or depressed only laterally) and mesocoxae more or less contiguous = 1. Entirely depressed with medially fused small teeth just anterior to metacoxal cavities and mesocoxae contiguous = 2. (C38)
74. Metasternum (second variable): Depressed anterolaterally but not medially nor posteriorly (or modified differently from States 1 and 2) = 0. Entirely depressed with separated small teeth just anterior to metacoxal cavities and mesocoxae contiguous = 1. Depressed only laterally and mesocoxae more or less contiguous = 2. (C38)
75. Metasternum (third variable): Depressed anterolaterally but not medially nor posteriorly (or modified differently from State 1) = 0. Depressed only laterally and mesocoxae separated = 1. (C38)
76. Metasternum (fourth variable): Partly or entirely depressed = 0. Broad, not depressed and mesocoxae widely separated = 1. (C38)

[Variables 73-76: reformulation of V67-68 to take new interpretations into account; see Rasnitsyn (1980), Carpenter (1986), Kimsey (1991).]

77. Metasternal differentiation: Meso- and metasterna distinctly differentiated by a deep sulcus or difference in level = 0. Meso- and metasterna scarcely differentiated through fusion and loss of any sulcus, at least mesally = 1. (C39, V69)
78. Metasternal anterior margin: Approximately straight and at a level posterior to anterior extremities of mesocoxae = 0. Slightly anteromesally produced to level of anterior extremities of mesocoxae = 1. Anteromesally produced to level anterior to mesocoxae = 2. (C40, V70)
79. Metacoxal contiguity: Contiguous or nearly so = 0. Broadly separated = 1. (C41, V71)
80. Metathoracic-propodeal pleural suture (first variable): Distinct and complete ventral to endophragmal pit = 0. Reduced but partly discernible ventral to endophragmal pit = 1. Obliterated ventral to endophragmal pit = 2. NONADDITIVE (C42)
81. Metathoracic-propodeal pleural suture (second variable): Distinct and complete dorsal to endophragmal pit = 0. Reduced but partly discernible dorsal to endophragmal pit = 1. Obliterated dorsal to endophragmal pit = 2. NONADDITIVE (C42)

[Variables 80-81: reformulation of V72 and addition of a variable to permit independent losses and intermediate states.]

82. Propodeal length: At least as long as high = 0. Much shorter than high = 1. (C43, V73)
83. Propodeal disc: Merging evenly with declivity = 0. Distinct from declivity = 1. (C44, V74)
84. Extent of forewing venation: Reaching apical margin = 0. Extending into apical half of membrane but not reaching apical margin = 1. Restricted to basal half of membrane = 2. (C45, V75)
85. Closed cells in forewing (first variable): Ten (or modified differently from States 1, 2 and 3) = 0. Eight (C not much reduced) = 1. Seven (C, SC+R+S, SC+R, R, S+M, M+Cu, 1Cu) (or six but unlike State2) = 2. Six (C, SC+R+S, SC+R, R, S+M, M+Cu) = 3. (C46, V76)

86. Closed cells in forewing (second variable): Ten (or modified differently from State 1) = 0. Six (C, SC+R+S, R, S+M, M+Cu, 1Cu) = 1. Five (C, SC+R+S, R, M+Cu, 1Cu) = 2. (C46)
87. Closed cells in forewing (third variable): Ten (or modified differently from State 1) = 0. Six (C, SC+R+S, SC+R, R (not subdivided), M+Cu, 1Cu) = 1. (C46)
88. Closed cells in forewing (fourth variable): Ten (or modified differently from State 1) = 0. Seven (C, SC+R+S, (SC+R)+1S, R, S+M, M+Cu, 1Cu) = 1. (C46, V77)
89. Closed cells in forewing (fifth variable): Ten (or modified differently from States 1 and 2) = 0. Nine (C, SC+R+S, R, (SC+R)+1S (vein S obliterated just proximal tofusion with vein r-s), 2S, S+M, 1M, M+Cu, 1Cu) = 1. Nine (C, SC+R+S, SC+R, R, 1S, S+M, 1M, M+Cu, 1Cu) = 2. NONADDITIVE (C46)
90. Closed cells in forewing (sixth variable): Ten (or modified differently from States 1 and 2) = 0. Nine (C, SC+R+S, R, (SC+R)+1S (vein S obliterated just distal to separation from vein M), S+M, 1M, M+Cu, 1Cu) = 1. Six (C, SC+R+S, SC+R, R (subdivided), M+Cu, 1Cu)=2. NONADDITIVE (C46)
91. Closed cells in forewing (seventh variable): Ten (or modified differently from States 1 and 2) = 0. Five (C, SC+R+S, SC+R, M+Cu, 1Cu) = 1. Three (C, SC+R+S, M+Cu)=2. (C46, V80)
92. Closed cells in forewing (eighth variable): Ten (or modified differently from States 1 and 2) = 0. Eight (C present but almost eliminated through partial fusion of veins C and SC) = 1. Three (probably SC+R+S, SC+R, R; C eliminated) = 2. (C46)

[Variables 85-92: addition of states and variables for conditions in various Chrysidoidea, Proscoliinae, Heterogynaidae and *Olixon*, see Carpenter (1986) and others; 1Cu considered as a closed cell if vein Cu1 well-developed, even when vein Cu2 reduced or absent and/or vein E apically weakened.]

93. Pterostigmal size: Large and prominent = 0. Medium to small but distinct = 1. Very small and not distinct = 2. (C47, V81)
94. Pterostigmal sclerotization: Complete = 0. Reduced apically, pterostigma partially cell-like = 1. Entirely reduced, pterostigma completely cell-like = 2. (C48, V82) [Addition of intermediate state for condition in Proscoliinae.]
95. Extent of hindwing venation: Reaching apical margin = 0. Extending into apical half of membrane but not reaching apical margin = 1. Restricted to basal half of membrane = 2. (C49, V83)
96. Closed cells in hindwing (first variable): Three (or two (C, (SC+R+S)+(M+Cu)) or none) = 0. Two (SC+R+S, M+Cu) = 1. (C50, V84)
97. Closed cells in hindwing (second variable): Three (or two (SC+R+S, M+Cu) or none) = 0. Two (C, (SC+R+S)+(M+Cu)) = 1. (C50, V85)
98. Closed cells in hindwing (third variable): Three (or two) = 0. One (C, hypothetical intermediate state) (or none but unlike State 2) = 1. None, vein C long, vein SC+R+S absent (vein running along margin and abruptly narrowed at base, weak longitudinal crease in membrane indicating position of separate SC+R+S) = 2. (C50)
99. Closed cells in hindwing (fourth variable): One or more (or none but unlike State 1) = 0. None, veins C and SC+R+S long but fused (vein running along margin and of even broad thickness, no longitudinal crease in membrane indicating separate SC+R+S) = 1. (C50)
100. Closed cells in hindwing (fifth variable): One or more (or none but unlike States 1 and 2) = 0. None, vein C short and vein SC+R+S absent (vein running along margin and weak longitudinal crease in membrane indicating position of separate SC+R+S) = 1. None, no veins distinguishable = 2. NONADDITIVE (C50)
101. Closed cells in hindwing (sixth variable): One or more (or none but unlike States 1 and 2) = 0. None, vein C short but distinct and vein SC+R+S long (veins running along and some distance from margin, latter continuous with crease in membrane indicating po-

sition of SC+R+S) = 1. None, vein C absent except at extreme base and vein SC+R+S short (vein running some distance from margin and continuous with longitudinal crease in membrane indicating position of SC+R+S) = 2. (C50)

[Variables 98-101: modification of V86 and addition of variables for conditions in Chrysidoidea and *Olixon*; Carpenter (1986, considering nebulous veins also) corrected.]

102. Hindwing empusal, anal and jugal veins: All three present = 0. Empusal well-developed, anal present, jugal absent = 1. Empusal well-developed, anal and jugal absent = 2. Empusal minute, anal and jugal absent = 3. [Reformulation of C51 and addition of state for conditions in various Chrysidoidea; Brothers (1975) and Carpenter (1986) corrected.]
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. (C52, V89)
104. Hindwing vein Cu: Distinct distal to separation from vein M = 0. Obliterated distal to separation from vein M = 1. (C53, V90)
105. Basal hamuli (first variable): Dispersed along costal margin (or absent) = 0. Concentrated into a basal cluster = 1. (C54, V91)
106. Basal hamuli (second variable): Present = 0. Absent = 1. (C54, V92)
107. Plical lobe: Indicated by moderate incision = 0. Indicated by shallow notch = 1. Not indicated on margin = 2. (C55, V93)
108. Jugal lobe (first variable): Long and indicated by a notch (or absent) = 0. Moderately long and indicated by incision extending about half length of lobe = 1. Small and indicated by incision extending almost to base of wing = 2. (C56, V94)
109. Jugal lobe (second variable): Present = 0. Absent = 1. (C56, V95)
110. Leg form of female (first variable): All similar, slender and generalized (or modified differently from State 1) = 0. Mid- and hindlegs stout with femora and tibiae expanded; foreleg and all tarsi fairly slender = 1.
111. Leg form of female (second variable): All similar, slender and generalized (or modified differently from State 1) = 0. All femora inflated and fusiform although midfemur often less so; tibiae and tarsi fairly slender = 1. Profemur greatly swollen and protibia much expanded; other femora inflated and fusiform; tibiae and tarsi fairly slender = 2.
112. Leg form of female (third variable): All similar, slender and generalized (or modified differently from State1) = 0. Profemur swollen; other femora and all tibiae slender; all tarsi flattened and expanded = 1.

[Variables 110-112: limitation of C57 to female for clarity and elaboration for conditions in some Chrysidoidea.]

113. Arolium (first variable): Well-developed = 0. Not distinguishable = 1. (C58, V99)
114. Arolium (second variable): Similar on all legs = 0. Much enlarged on foreleg only = 1. [Variable added for condition in Sclerogibbidae.]
115. Claws: Ventrally toothed or cleft = 0. Ventrally simple = 1. (C59, V100)
116. Protibial calcar (first variable): Approximately straight and parallel-sided or triangular with an elongate inner lamina or pectination (or inwardly curved and hollowed along posterior surface) = 0. Strongly inwardly curved, not hollowed along posterior surface and more or less even in width with a small outer spine at apex = 1. Strongly inwardly curved, not hollowed along posterior surface and more or less even in width with apex obtuse = 2. (C60, V101)
117. Protibial calcar (second variable): Approximately straight and parallel-sided or triangular with an elongate inner lamina or pectination (or strongly inwardly curved and not hollowed along posterior surface) = 0. Inwardly curved, hollowed along posterior surface and with apex acute = 1. Inwardly curved, hollowed along posterior surface and with apex obtuse = 2. (C60)

[Variables 116-117: reformulation for clarity and addition of intermediate state in V102 for condition in Proscoliinae.]

118. Mesotibial spines (first variable): Many scattered spiniform setae (or neither spines nor spiniform setae) = 0. Scattered weak (or very strong) spines = 1. Scattered moderately strong spines = 2. Spines moderate and present only apically = 3. Spines very strong and present only apically = 4. (C61, V103)
119. Mesotibial spines (second variable): Spines weak or absent (or strong but present only apically) = 0. Scattered very strong spines = 1. (C61, V104)
120. Mesotibial spines (third variable): Spiniform setae or spines present = 0. Neither spines nor spiniform setae but some slender setae much elongated = 1. (C61, V105)
121. Metatibial spines (first variable): Many scattered spiniform setae (or neither spines nor spiniform setae) = 0. Scattered weak (or very strong) spines = 1. Scattered moderately strong spines = 2. Spines moderate and present only apically = 3. Spines very strong and present only apically = 4. (C62, V106)
122. Metatibial spines (second variable): Spines weak or absent (or strong but present only apically) = 0. Scattered very strong spines = 1. (C62, V107)
123. Metatibial spines (third variable): Spiniform setae or spines present = 0. Neither spines nor spiniform setae but some slender setae much elongated = 1. (C62, V108)
124. Mesotibial spur number (first variable): Two (or none) = 0. One = 1. (C63, V109)
125. Mesotibial spur number (second variable): Two (or one) = 0. None = 1. (C63, V110)
126. Basic form of meso- and metatibial spurs (first variable): Simple, narrowly conical and circular in cross-section = 0. Slightly flattened dorsally with margins simple (or dorsally flattened with margins dentate or simple) = 1. Dorsally flattened with margins serrate = 2. (C64, V111)
127. Basic form of meso- and metatibial spurs (second variable): Simple, narrowly conical and circular in cross-section (or modified differently from States 1 and 2) = 0. Dorsally flattened with margins deeply dentate = 1. Dorsally flattened and elongate with few or no teeth on margins = 2. [States 2 and 3, Bradynobaeninae male and female respectively, combined.] (C64, V112)
128. Mesotibial calcar (first variable): Spurs similar and neither modified as calcar (or calcar formed by dorsal pectination only) = 0. Inner spur modified as calcar by dorsal pectinate carina = 1. (C65, V113)
129. Mesotibial calcar (second variable): Spurs similar and neither modified as calcar (or calcar formed by dorsal pectinate carina) = 0. Spur modified as calcar by dorsal pectination only = 1. (C65, V114)
130. Form of metacoxa: Smoothly rounded dorsally = 0. With dorsal longitudinal carina = 1. With dorsal longitudinal lamella = 2. (C66, V115)
131. Metatibial spur number: Two = 0. One = 1. (C67, V116)
132. Metatibial calcar (first variable): Spurs similar and neither modified as calcar (or modified differently from States 1 and 2) = 0. Inner spur modified as calcar by formation of dorsal tuft of bristles with little modification of cuticular portion = 1. Inner spur modified as calcar by formation of dorsal tuft of bristles and development of finely pectinate dorsal carina = 2. (C68)
133. Metatibial calcar (second variable): Spurs similar and neither modified as calcar (or modified differently from States 1 and 2) = 0. Inner spur modified as calcar by dorsal carinate expansion of cuticle over a considerable length = 1. Inner spur modified as calcar by dorsal carinate expansion of cuticle over less than half its length = 2. NONADDITIVE (C68)

    [Variables 132-133: addition of states to V117 and V118 for conditions in *Olixon* and Heterogynaidae.]
134. Metatibial calcar (third variable): Spurs similar and neither modified as calcar (or modified differently from State1) = 0. Inner spur modified as calcar by pectinate elaboration of dorsal carina = 1. (C68, V119)
135. Metatibial calcar (fourth variable): Spurs similar and neither modified as calcar (or modified differently from State 1) = 0. Inner

spur modified as calcar by dorsal pectination without carina = 1. (C68, V120)

136. Metatibial calcar (fifth variable): Spurs similar and neither modified as calcar (or modified differently from State 1) = 0. Inner spur modified as calcar with dorsal blunt longitudinal setose carina = 1. [Variable added for condition in some Chrysidoidea.]
137. Mesosoma of apterous or micropterous female (first variable): Similar to that of male or macropterous female (or modified differently from States 1, 2 and 3) = 0. Proportions different from those of male or macropterous female, with pro-meso- and meso-metathoracic articulations functional, mesonotal subdivisions distinguishable but scutum reduced, metapostnotum very short, propleura free and not swollen, prepectal sclerite small and free, mesepimeron distinct and metepimeron well-developed = 1. As for State 1 but mesepimeron not distinguishable externally = 2. As for State 2 but mesonotal subdivisions not distinguishable and prepectal sclerite reduced = 3. (C69, V121)
138. Mesosoma of apterous or micropterous female (second variable): Similar to that of male or macropterous female (or modified differently from State1) = 0. As for Variable 137 State 1 but mesepimeron not distinguishable externally and metepimeron much reduced and visible only at dorsal extremity = 1. (C69)
139. Mesosoma of apterous or micropterous female (third variable): Similar to that of male or macropterous female (or modified differently from States 1 and 2) = 0. Proportions different from those of male, with pleura flattened, meso-metathoracic suture obliterated dorsally and prepectus fused with mesepisternum = 1. As for State 1 but pro-mesothoracic articulation functional and metathoracic-propodeal suture obliterated dorsally = 2. (C69, V122)
140. Mesosoma of apterous or micropterous female (fourth variable): Similar to that of male or macropterous female (or modified differently from State 1) = 0. As for Variable 139 State 1 but pro-mesothoracic articulation distinct although not functional and metathoracic-propodeal suture indistinct dorsally = 1. (C69, V123)
141. Mesosoma of apterous or micropterous female (fifth variable): Similar to that of male or macropterous female (or modified differently from States 1 and 2) = 0. Proportions different from those of male, with mesopleuron somewhat protuberant, pro-mesothoracic articulation functional, meso-metathoracic suture visible but not functional, mesonotum neither reduced nor enlarged and fused with mesepisternum = 1. As for State 1 but mesonotum very short and transverse = 2. (C69, V124)
142. Mesosoma of apterous or micropterous female (sixth variable): Similar to that of male or macropterous female (or modified differently from State 1) = 0. As forVariable 141 State 1 but mesopleuron protuberant, meso-metathoracic suture indistinct and mesonotum somewhat posteriorly produced = 1. (C69, V125)
143. Mesosoma of apterous or micropterous female (seventh variable): Similar to that of male or macropterous female (or modified differently from States 1 and 2) = 0. Proportions different from those of male, with propleura fused to form a rigid tube and with deep lateral and ventral constriction between meso- and metathorax = 1. Proportions different from those of male, with most mesosomal sutures and subdivisions distinct and metapostnotum much enlarged = 2. NONADDITIVE (C69)
144. Mesosoma of apterous or micropterous female (eighth variable): Similar to that of male or macropterous female (or modified differently from State 1) = 0. Proportions different from those of male, with pronotum much enlarged, pro-meso- and meso-metathoracic articulations functional and propleura free and greatly swollen = 1. Proportions different from those of male and macropterous female, with pronotum enlarged, pro-mesothoracic articulation functional, mesonotal subdivisions distinguishable, meso-metathoracic pleural suture fused

and prepectus fused with pronotum = 2. Proportions different from those of male and macropterous female, with pro-mesonotal suture functional, meso-metanotal and metanotal propodeal sutures indistinct, meso-metapleural suture distinct and metapleural-propodeal suture indistinct = 3. NONADDITIVE

[Variables 137-144: reformulation to refer to the adaptive complex of the mesosoma only when apterous or micropterous rather than being confounded by simultaneous consideration of independent mechanisms governing degree of wing development; addition of states and variable for conditions in *Olixon*, Diamminae, Heterogynaidae, Sclerogibbidae, Embolemidae and Formicidae.]

145. 'Felt lines' (first variable): Absent (or modified differently from State 1) = 0. Lateral longitudinal pubescent depression on metasomal tergumII and sternum II = 1. (C70, V127)
146. 'Felt lines' (second variable): Absent (or modified differently from States 1 and 2) = 0. Pubescent felt line on metasomal tergumII only = 1. Longitudinal cuticular invagination on metasomal tergumII = 2. (C70, V128)
147. Stridulitra (first variable): Absent (or paired) = 0. Single narrow stridulitrum basally on metasomal tergumIII = 1. Single very broad stridulitrum basally on metasomal tergum III = 2. NONADDITIVE (C71) [State added to V129 for condition in *Olixon*.]
148. Stridulitra (second variable): Absent (or one) = 0. Pair of stridulitra basally on metasomal tergum IV = 1. (C71, V130)
149. Junction of metasomal terga I and II: Smoothly continuous = 0. Slightly constricted = 1. Strongly constricted and first segment nodose = 2. (C72, V131)
150. Metasomal petiole: None, segment evenly narrowed anteriorly = 0. Distinct, segment cylindrical anteriorly = 1. (C73, V132)
151. Lateral margin of metasomal tergumI (first variable): Entirely broadly overlying sternumI and articulating with it anteriorly (or very broadly overlying sternumI posteriorly but fused with it anteriorly) = 0. Narrowly overlying sternumI posteriorly, abutting it and not movable anteriorly = 1. Narrowly overlying sternumI posteriorly and fused with it along petiole = 2. (C74, V133)
152. Lateral margin of metasomal tergum I (second variable): Entirely broadly overlying sternum I and articulating with it anteriorly (or narrowly overlying sternum I posteriorly) = 0. Very broadly overlying sternum I posteriorly but strongly narrowed and fused with laterodorsal face of sternum I anteriorly = 1. [Variable added for condition in Chrysidoidea.]
153. Width of metasomal tergum I: Entirely about as wide as or broader than sternum I = 0. Much narrower than sternum I anteriorly = 1. Absent anteriorly, petiole entirely formed by sternum I = 2. (C75, V134)
154. Differentiation of metasomal sternum I: Thin and overlying or abutting sternum II without any marked discontinuity = 0. Depressed posteriorly and differentiated from sternum II by a marked constriction = 1. Thick and abutting sternum I I = 2. Forming posterior lobules = 3. Thick and overlapping sternum II = 4. NONADDITIVE (C76) [States added to V135 for conditions in various Chrysidoidea, see Rasnitsyn (1980) and Carpenter (1986), and for Fedtschenkiinae.]
155. Junction of metasomal terga II and III: Smoothly continuous = 0. Strongly constricted = 1. (C77, V136)
156. Reduction of metasomal terga of female (first variable): Tergum VII partly exposed and evenly sclerotized (or modified differently from States 1 and 2) = 0. Tergum VI exposed and evenly sclerotized, tergum VII hidden and considerably desclerotized with an anterior short sclerotized strip connecting lateral spiracular plates = 1. Tergum VI exposed and evenly sclerotized, tergum VII hidden and very considerably desclerotized with lateral spiracular plates unconnected by any sclerotized strip = 2. (C78, V137)
157. Reduction of metasomal terga of female (second variable): Six or seven terga exposed and evenly sclerotized = 0. Four terga ex-

posed and evenly sclerotized, terga V to VII hidden and desclerotized = 1.

158. Reduction of metasomal terga of female (third variable): Tergum VII exposed and evenly sclerotized (or modified differently from State 1) = 0. Tergum VII hidden under enlarged sternum VI and scarcely desclerotized = 1.

159. Reduction of metasomal terga of female (fourth variable): Tergum VII exposed and evenly sclerotized (or modified differently from State 1) = 0. Tergum VII hidden under tergum VI but scarcely desclerotized = 1. [Variables 157-159: variables added to C78 for conditions in various Chrysidoidea.]

160. Articulation within gonocoxite IX of female: Absent = 0. Present = 1. (C79, V138)

161. Valve comprising paired valvilli on gonapophysis VIII of female: Present = 0. Absent = 1. (C80, V139) [See Quicke, Fitton & Ingram (1992) for further justification of polarity.]

162. GonapophysisIX of female (first variable): Weakly arcuate dorsally (or almost straight) = 0. Strongly arcuate dorsally with apex directed downward = 1. (C81, V140)

163. GonapophysisIX of female (second variable): Weakly (or strongly) arcuate dorsally with apex directed obliquely (or strongly) ventrally = 0. Almost straight or slightly arcuate ventrally with apex directed posteriorly or slightly upward = 1. (C81, V141)

164. Metasomal sternumVII of male: Well-developed and exposed = 0. Reduced and partly exposed = 1. Much reduced and concealed = 2. (C82, V142)

165. Form of male hypopygium (first variable): Simple (or apically lobed or spined) = 0. Peglike and not acute apically = 1. (C83, V143)

166. Form of male hypopygium (second variable): Simple (or modified differently from States 1 and 2) = 0. Elongate with apex trilobed = 1. Elongate with three subequal apical spines about as long as base excluding anterior processes = 2. (C83) [Intermediate state added to V144 for condition in Proscoliinae.]

167. Form of male hypopygium (third variable): Simple (or modified differently from State 1) = 0. Apically forming a single long upcurved spine = 1. (C83, V145)

168. Form of male hypopygium (fourth variable): Simple (or modified differently from States 1 and 2) = 0. Apically trispinose with middle spine upcurved and much longer than laterals which much shorter than base of hypopygium = 1. Apically trispinose with middle spine straight and slightly longer than laterals which much shorter than base of hypopygium = 2. (C83, V146)

169. Concealment of male hypopygium (first variable): Exposed (or more than basal half concealed) = 0. Up to basal half concealed = 1. (C84, V147)

170. Concealment of male hypopygium (second variable): Exposed (or no more than half concealed) = 0. Almost or completely concealed = 1. (C84, V148)

171. Cercus of male: Present = 0. Absent = 1. (C85, V149)

172. Gonapophyses IX of male (first variable): Fused dorsally over much of length (or modified differently from State 1) = 0. Linked dorsally by membrane over most of length = 1. (C86, V150)

173. Gonapophyses IX of male (second variable): Fused dorsally over much of length (or modified differently from State 1) = 0. Free over most of length and linked only basally by membrane = 1. (C86, V151)

174. Gonapophyses IX of male (third variable): Simple and fused dorsally over much of length (or modified differently from State 1) = 0. Forming basal bulge and apical lobe and fused dorsally over most of length = 1. [Variable added to C86 for condition in Thynninae, see Kimsey (1991).]

175. Larval mandibular teeth (first variable): Four (two or one) = 0. Three = 1. (C87, V152)

176. Larval mandibular teeth (second variable): Four (three or one) = 0. Two = 1. (C87, V153)

177. Larval mandibular teeth (third variable): Four (three or two) = 0. One = 1. (C87, V154)

178. Larval spiracles: Ten pairs fully developed, of similar size and complexity = 0. Nine pairs fully developed, second thoracic pair much reduced although still distinguishable = 1. Nine pairs fully developed, first thoracic pair apparently absent = 2. NONADDITIVE (C88) [State added to V155 for condition in Typhoctini (unpublished data).]
179. Number of prey: One = 0. Many = 1. (C89, V156)
180. Nesting (first variable): Prey not relocated, no nest construction (or host cavity closed) = 0. Prey relocated, no nest construction (or nest constructed but not closed, or pre-existing cavity closed off) = 1. Prey relocated, nest constructed and closed = 2. (C90, V157)
181. Nesting (second variable): Prey not relocated, no nest construction (or modified differently from State 1) = 0. Prey relocated, nest constructed but not closed = 1. (C90, V158)
182. Nesting (third variable): Prey not relocated, no nest construction (or modified differently from State 1) = 0. Prey relocated into pre-existing cavity which closed = 1. (C90, V159)
183. Nesting (fourth variable): Prey not relocated and no nest construction (or prey relocated) = 0. Prey not relocated and host cavity closed = 1. (C90, V160)
184. Oviposition sequence: On prey or host = 0. In empty cell before prey location = 1. (C91, V161)
185. Type of provisions: Arthropods = 0. Plant matter = 1. (C92, V162)
186. Third mesosomal phragma of macropterous form (first variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from States 1, 2 or 3) = 0. Forming even narrow flange with muscles *2ph-3ph* attaching on widely separated areas of metapostnotum = 1. Absent medially with muscles *2ph-3ph* attaching on widely separated areas of metapostnotum = 2. Entirely absent with muscles *2ph-3ph* attaching on widely separated areas of metapostnotum = 3.
187. Third mesosomal phragma of macropterous form (second variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from States 1, 2 and 3) = 0. Forming distinct even flange laterally or entirely with muscles *2ph-3ph* large and attaching over medial area of variously developed metapostnotum and phragma = 1. Medially reduced (or expanded as a thin plate, or expanded laterally) with muscles *2ph-3ph* attaching on adjacent (or separated) areas on either side of midline ofmetapostnotum and/or phragma = 2. Much reduced over most of width with muscles *2ph-3ph* lost = 3.
188. Third mesosomal phragma of macropterous form (third variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from State 1) = 0. Expanded medially as a thin plate with muscles *2ph-3ph* attaching on narrow adjacent areas on either side of midline of phragma = 1.
189. Third mesosomal phragma of macropterous form (fourth variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from State 1) = 0. Absent with muscles *2ph-3ph* much reduced and attaching at small separated points = 1.
190. Third mesosomal phragma of macropterous form (fifth variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from State 1) = 0. Weakly expanded laterally with muscles *2ph-3ph* small and attaching on somewhat separated areas of phragma = 1. Strongly expanded laterally with muscles *2ph-3ph* small basally and attaching on broadly separated areas of phragma = 2. Strongly expanded laterally as plates with muscles *2ph-3ph* very large and attaching on

broadly separated areas of phragma = 3. NONADDITIVE

191. Second mesosomal phragma of macropterous form (first variable): Strongly oblique with dorsal posterior extremity of muscles *1ph-2ph* far anterior to ventral extremity and muscles *2ph-3ph* attaching on its anterior half (or modified differently from State 1) = 0. Scarcely oblique posteriorly with dorsal posterior extremity of muscles *1ph-2ph* only slightly anterior to ventral extremity and muscles *2ph-3ph* attaching on its anterior half = 1.
192. Second mesosomal phragma of macropterous form (second variable): Strongly (or scarcely) oblique posteriorly with muscles *2ph-3ph* attaching on its anterior half = 0. Scarcely oblique posteriorly with dorsal posterior extremity of muscles *1ph-2ph* only slightly anterior to ventral extremity and muscles *2ph-3ph* attaching on its posterior half = 1.

[Variables 186-192: new characters modified and extended from Brothers (1976), polarized by reference to non-aculeates, newly scored.]

193. Mesocoxal subdivision and insertion: Mesocoxa subdivided by a broad sulcus into large basicoxite and disticoxite and mesocoxal cavities large and approximated or narrowly separated medially = 0. Mesocoxa subdivided by a broad sulcus into large basicoxite and disticoxite and mesocoxal cavities large and widely separated = 1. Mesocoxa subdivided by a fairly deep sulcus into reduced basicoxite and large disticoxite and mesocoxal cavities moderate and widely separated = 2. Mesocoxa subdivided by a deep narrow sulcus into much-reduced basicoxite and large disticoxite and mesocoxal cavities small and widely separated = 3. [New character from Johnson (1988), modified and checked.]
194. Hypopharynx pubescence: Present = 0. Reduced = 1. [New character from Rasnitsyn (1980, 1988), not checked.]
195. Metasomal sternum I and tergum II: Not articulated, tergum II not touching or freely overlying or underlying lateral extremities of sternumI = 0. Articulated, tergum II overlying lateral extremities of sternum I = 1. Hinged, tergum II underlying lateral extremities of tergum I = 2. [New character modified from Rasnitsyn (1980, 1988), rescored.]
196. Mesotrochantellus: Distinctly present = 0. Reduced but discernible = 1. Absent = 2. [New character from Rasnitsyn (1980, 1988) with state added to describe variation more accurately, rescored.]
197. Mandibles: 'Chewing type' = 0. 'Cutting type' = 1. [New character from Rasnitsyn (1980, 1988), rescored.]
198. Female cerci: Present = 0. Absent = 1. [New character from Rasnitsyn (1980, 1988), scored as by Rasnitsyn (1980, not 1988) and checked.]
199. Metasomal sternum VI of female (first variable): Convex apically with lateral areas not strongly differentiated nor produced; sting aperture formed by sternum VI and tergum VI or VII = 0. Convex apically with lateral areas strongly differentiated and dorsomesally produced; sting aperture formed by sternum VI and narrow = 1. Depressed apically with lateral areas very strongly differentiated and dorsomesally produced; sting aperture formed by sternum VI and broadly slitlike = 2.
200. Metasomal sternum VI of female (second variable): With lateral areas not strongly differentiated and sting aperture formed by sternum VI and tergum VI or VII (or lateral areas strongly differentiated) = 0. With lateral areas not differentiated but dorsomesally produced; sting aperture formed by sternum VI and circular = 1.

[Variables 199-200: new character re-evaluated and modified from Rasnitsyn (1980, 1988), rescored.]

201. Forewing vein S2: Present = 0. Absent = 1. [Polarized as by Carpenter (1986).]
202. Free furcula in female ovipositor: Present, gonapophysis IX without acute anterodorsal process = 0. Absent, probably fused with gonapophysis IX as acute anterodorsal pro-

cess = 1. [Polarized as by Oeser (1961), Carpenter (1986).]

203. Articulation between gonocoxite IX and gonapophysis IX in female: Present = 0. Absent = 1.
204. Larval arthropod food source: Coleoptera larva = 0. Embioptera = 1. Auchenorrhyncha = 2. Tenthredinoidea cocoon or Phasmida egg = 3. Gryllotalpidae only = 4. Aculeata larva or pupa = 5. Araneae = 6. Gryllidae only = 7. Blattodea and/or Orthoptera = 8. Solifugae = 9. NONADDITIVE
205. Larval lifestyle: Freeliving, predatory or ectoparasitic without cyst formation = 0. Endoparasitic initially with external cyst formation after first instar = 1. Entirely ectoparasitic with cyst formation after first instar = 2. NONADDITIVE
206. Anterior pedicels of tentorium: Broad = 0. Rodlike = 1. Rodlike with lamellar processes = 2.
207. Prothoracic furca: Vertical = 1. Proclined = 1. Proclined and 'modified' = 2.
208. Metasomal sternum II anterior margin: Transversely curved = 0. Transversely straight with lateral notches = 1. With expanded lateral desclerotized areas = 2. With median notch = 3. NONADDITIVE
209. Head form (first variable): Not of prognathous 'bethylid type' = 0. Of 'bethylid type' (more or less prognathous with genal and postgenal bridges enlarged and eyes often reduced) = 1.
210. Head form (second variable): Not concave posteriorly and without sharp carina on vertex and gena = 0. Concave posteriorly with sharp carina on vertex and gena = 1.

[Variables 201-210: new characters from Carpenter (1986) and Rasnitsyn (1980, 1988); Variable 204 including unpublished information; Variable 205 including information from Gurney (1953); Variables 206-208 not checked; Variable 210 by DJB, polarized by reference to non-aculeates.]

211. Clypeal form: Without any median longitudinal carina = 0. With median longitudinal carina = 1.
212. Antennal prominence: Absent = 0. Present = 1.
213. Pedicel-flagellum articulation: Movable = 0. Fixed = 1.

[Variables211-213: new characters from Carpenter (1986) and Rasnitsyn (1980, 1988), checked.]

214. Metacoxal cavities: Open, without any posterolateral projection of metasternum = 0. Open but with metasternum posteriorly produced on each side to narrow opening posteromesally = 1. Closed = 2. [New character from Kimsey (1991), extended and modified, rescored.]
215. Forewing vein Cu2: Present, reaching vein E = 0. Much reduced or absent, not reaching vein E = 1.
216. Larval galea: Well-developed = 0. Much reduced = 1. Absent = 2.
217. Larval head parietal bands: Absent or very weak = 0. Strong = 1.
218. Larval antenna: With 3 sensilla = 0. With 2 sensilla = 1. With 4 to 6 sensilla = 2. NONADDITIVE
219. Larval spinneret: A median transverse slit = 0. Paired spigots = 1.

[Variables 215-219: new characters by DJB, polarized by reference to non-aculeates.]

APPENDIX VII

Distribution of derived character states on preferred cladogram (see text) of 34 taxa of Aculeata (Fig. 9b) resulting from analysis of data in Table IV; optimization by accelerated transformation, except delayed transformation for variables considered unlikely to show reversals and manual for Variables 80, 95, 105, 201 and 216. Unnamed internodes are referred to by listing the subtended terminal superfamilies, families or lower taxa. Character numbers refer to the variables in Appendix VI; transformations are denoted by listing the ancestral and derived states separated by a '>'.

Final weights of variables (10 is maximum):

Weight = 10: 3, 8, 9, 17, 18, 19, 20, 25, 28, 31, 32, 35, 36, 39, 42, 45, 47, 49, 51, 52, 53, 59, 60, 64, 65, 69, 72, 74, 76, 78, 79, 87, 88, 89, 90, 91, 92, 97, 98, 99, 100, 101, 103, 108, 111, 112, 114, 116, 117, 119, 120, 122, 123,

125, 127, 128, 129, 131, 134, 135, 136, 137, 138, 139, 140, 141, 142, 143, 144, 146, 147, 150, 151, 152, 153, 155, 157, 158, 159, 160, 165, 166, 167, 168, 172, 173, 174, 181, 182, 185, 186, 189, 190, 191, 192, 198, 202, 203, 204, 205, 206, 207, 209, 210, 211, 212, 213, 215, 219

Weight = 6: 85

Weight = 5: 48, 156, 178, 216

Weight = 4: 57, 75, 149, 154, 187

Weight = 3: 15, 23, 34, 70, 73, 86, 132, 196

Weight = 2: 4, 6, 16, 22, 29, 40, 44, 55, 62, 63, 77, 104, 105, 113, 118, 121, 148, 175, 183, 194, 195, 197, 199, 208, 217

Weight = 1: 7, 11, 13, 21, 30, 38, 46, 54, 56, 58, 61, 71, 84, 93, 94, 102, 106, 107, 109, 110, 126, 130, 163, 180, 188

Weight = 0: 1, 2, 5, 10, 12, 14, 24, 26, 27, 33, 37, 41, 43, 50, 66, 67, 68, 80, 81, 82, 83, 95, 96, 115, 124, 133, 145, 161, 162, 164, 169, 170, 171, 176, 177, 179, 184, 193, 200, 201, 214, 218

(Aculeata): 43:0>1, 80:0>1, 84:0>1, 102:0>2, 118:0>1, 121:0>1, 164:0>1, 193:0>1, 197:0>1, 198:0>1

(Chrysidoidea): 33:0>1, 81:0>1, 85:0>1, 109:0>1, 111:0>1, 152:0>1, 160:0>1, 186:0>1, 193:1>3, 196:0>1, 207:0>1, 215:0>1

Plumariidae: 2:0>1, 16:0>1, 29:0>1, 41:0>1, 143:0>1, 159:0>1, 161:0>1, 214:0>2

(Scolebythidae, Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 11:0>1, 13:0>1, 85:1>2, 95:0>1, 98:0>1, 118:1>0, 121:1>0, 186:1>2, 191:0>1, 197:1>0, 201:0>1, 206:0>1

Scolebythidae: 42:0>1, 43:1>0, 45:0>1, 95:1>2, 98:1>2, 120:0>1, 123:0>1, 164:1>0, 193:3>2

(Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 29:0>1, 33:1>0, 56:0>1, 64:0>1, 66:0>1, 136:0>1, 175:0>1, 186:2>3, 208:0>3, 216:0>1

(Bethylidae, Chrysididae): 13:1>0, 64:1>2, 80:1>2, 101:0>1, 154:0>3, 203:0>1, 208:3>2

Bethylidae: 6:0>1, 21:0>1, 22:0>1, 75:0>1, 83:0>1, 95:1>2, 101:1>2, 154:3>2, 164:1>0, 208:2>1, 209:0>1, 211:0>1, 216:1>2, 218:0>1

Chrysididae: 12:0>1, 27:0>1, 43:1>0, 48:0>1, 54:0>1, 56:1>0, 86:0>1, 157:0>1, 170:0>1, 171:0>1, 193:3>0, 204:0>1

(Sclerogibbidae, Dryinidae, Embolemidae): 11:1>0, 40:0>1, 44:0>1, 80:1>0, 93:0>1, 102:2>3, 177:0>1, 202:0>1, 214:0>1

Sclerogibbidae: 2:0>1, 8:0>1, 13:1>2, 19:0>1, 21:0>1, 33:0>1, 41:0>1, 53:0>1, 73:0>1, 81:1>2, 87:0>1, 95:1>2, 100:0>1, 111:1>2, 114:0>1, 144:0>1, 158:0>1, 161:0>1, 204:0>1, 207:1>2, 214:1>2

(Dryinidae, Embolemidae): 20:0>1, 38:0>1, 86:0>1, 99:0>1, 164:1>2, 170:0>1, 171:0>1, 196:1>2, 204:0>2, 205:0>1, 216:1>2

Dryinidae: 30:0>1, 40:1>0, 43:1>0, 44:1>0, 46:0>1, 56:1>0, 81:1>2, 86:1>2, 93:1>0, 124:0>1, 214:1>0, 218:0>1

Embolemidae: 26:0>1, 27:0>1, 32:0>2, 53:0>2, 57:0>2, 61:0>2, 66:1>2, 115:0>1, 144:0>2, 177:1>0, 197:0>1, 206:1>2, 208:3>1, 212:0>1, 213:0>1

(Aculeata s.s.): 18:0>1, 37:0>1, 44:0>1, 66:0>1, 96:0>1, 156:0>1, 187:0>1, 201:0>1

(Apoidea): 35:0>1, 39:0>1, 46:0>1, 52:0>1, 57:0>2, 61:0>1, 65:0>1, 70:0>1, 77:0>1, 93:0>1, 126:0>2>, 163:0>1, 180:0>1, 192:0>1

apids: 4:0>1, 23:0>1, 39:1>2, 55:0>1, 67:0>1, 124:0>1, 156:1>2, 164:1>2, 170:0>1, 171:0>1, 176:0>1, 180:1>2, 185:0>1, 193:1>0, 196:0>2, 208:0>3

(sphecids, Heterogynaidae): 118:1>2, 121:1>2, 164:1>0

sphecids: 46:1>0, 84:1>0, 96:1>0, 102:2>0, 193:1>0, 200:0>1, 204:0>8

Heterogynaidae: 2:0>1, 37:1>0, 81:0>2, 90:0>2, 95:0>1, 109:0>1, 115:0>1, 126:2>1, 130:0>1, 133:0>2, 143:0>2, 171:0>1, 187:1>0, 189:0>1, 193:1>2,

(Vespoidea): 13:0>1, 40:0>1, 48:0>1, 56:0>1, 73:0>1, 107:0>1, 187:1>2, 194:0>1

Sierolomorphidae: 68:0>1, 81:0>1, 88:0>1, 95:0>1, 109:0>1, 130:0>1, 164:1>0, 165:0>l, 170:0>1, 190:0>1, 193:l>2, 200:0>1

(Rhopalosomatidae, Vespidae, Scoliidae, Formicidae, Bradynobaenidae, Pompilidae, Mutillidae, Sapygidae, Tiphiidae): 63:0>1, 80:1>0, 84:1>0, 108:0>1

(Rhopalosomatidae, Vespidae, Scoliidae, Formicidae, Bradynobaenidae): 30:0>1, 38:0>1, 46:0>1, 48:1>2, 93:0>1, 94:0>2, 105:0>1, 149:0>1, 163:0>1, 195:0>1

(Rhopalosomatidae): 56:1>2, 58:0>1, 92:0>1, 95:0>1, 112:0>1, 132:0>1, 194:1>0, 200:0>1, 204:0>7, 205:0>2

rhopalosomatids: 10:0>1, 63:1>0, 68:0>2, 70:0>1, 107:1>0, 177:0>1, 190:0>2, 219:0>1

Olixon: 33:0>1,37:1>0,38:1>0,50:0>1,55:0>1,61:0>1, 80:0>2, 81:0>1, 83:0>1, 92:1>2, 93:1>2, 100:0>2, 118:1>0, 121:1>0, 132:1>2, 147:0>2, 210:0>1

(Vespidae, Scoliidae, Formicidae, Bradynobaenidae): 34:0>1, 57:0>1, 61:0>1, 63:1>2, 154:0>1, 175:0>1, 180:0>1

(Vespidae, Scoliidae): 5:0>1, 10:0>1, 13:1>0, 24:0>1, 34:1>2, 38:1>2, 43:1>2, 96:1>0, 106:0>1, 115:0>1, 163:1>0, 171:0>1, 180:1>2, 190:0>3, 217:0>1

Vespidae: 32:0>1, 34:2>3, 48:2>3, 56:1>0, 58:0>1, 82:0>1, 133:0>1, 149:1>0, 161:0>1, 179:0>1, 184:0>1, 193:1>0, 195:1>2

(Scoliidae): 15:0>1, 31:0>1, 49:0>1, 54:0>1, 59:0>1, 73:1>0, 76:0>1, 79:0>1, 83:0>1, 84:0>1, 95:0>1, 107:1>2, 110:0>1, 117:0>1, 119:0>1, 122:0>1, 126:0>1, 164:1>0, 166:0>1, 172:0>1, 199:1>2

Scoliinae: 67:0>1, 69:0>1, 77:0>1, 117:1>2, 124:0>1, 166:1>2, 170:0>1, 218:0>2

Proscoliinae: 5:1>0, 10:1>0, 24:1>0, 27:0>1, 38:2>1, 43:2>1, 66:1>0, 80:0>1, 81:0>1, 89:0>2, 94:2>1, 154:1>0, 169:0>1, 195:1>0

(Formicidae, Bradynobaenidae): 55:0>1, 56:1>0, 94:2>0, 118:1>2, 121:1>3, 150:0>1, 193:1>3, 214:0>1

Formicidae: 3:0>1, 38:1>2, 50:0>1, 61:1>2, 72:0>1, 85:0>1, 106:0>1, 118:2>3, 128:0>1, 134:0>1, 144:0>3, 164:1>0, 179:0>1, 181:0>1, 184:0>1, 187:2>3, 214:1>2

(Bradynobaenidae): 2:0>1, 16:0>1, 30:1>0, 34:1>0, 46:1>0, 73:1>0, 75:0>1, 77:0>1, 78:0>1, 80:0>2, 84:0>1,95:0>1,107:1>2,141:0>1,146:0>1,148:0>1, 151:0>1, 161:0>1, 180:1>0, 199:0>1

(Typhoctinae): 4:0>1,37:1>0,38:1>0,66:1>0,121:3>2, 130:0>1, 141:1>2

Eotillini: 71:0>1, 93:1>0, 107:2>0, 113:0>1, 118:2>1, 121:2>1

Typhoctini: 96:1>0, 109:0>1, 178:0>2, 188:0>1, 204:0>9

(Chyphotinae, Apterogyninae, Bradynobaeninae): 6:0>1, 9:0>1, 12:0>1, 13:1>0, 21:0>1, 110:0>1, 142:0>1, 151:1>2, 153:0>1, 168:0>1, 195:1>2

Chyphotinae: 61:1>2,66:1>0,81:0>1,93:1>0,153:1>2, 169:0>1

(Apterogyninae, Bradynobaeninae): 15:0>1, 17:0>1, 47:0>1, 62:0>1, 78:1>2, 84:1>2, 91:0>1, 93:1>2, 95:1>2, 96:1>0, 106:0>1, 113:0>1, 116:0>1, 118:2>3, 126:0>1, 127:0>1, 148:1>0, 171:0>1

Apterogyninae: 130:0>1, 149:1>2, 155:0>1, 161:1>0, 193:3>1

Bradynobaeninae: 7:0>1, 12:1>0, 26:0>1, 28:0>1, 29:0>1, 36:0>1, 47:1>2, 60:0>1, 82:0>1, 83:0>1, 91:1>2,97:0>1,115:0>1,116:1>2,118:3>4,121:3>4, 125:0>1, 127:1>2, 146:1>2, 162:0>1, 163:1>0, 168:1>2, 187:2>3, 195:2>1

(Pompilidae,Mutillidae,Sapygidae,Tiphiidae): 13:1>0, 118:1>2, 121:1>2, 178:0>1, 199:0>1

(Pompilidae, Mutillidae, Sapygidae): 51:0>1, 58:0>1, 214:0>1

Pompilidae: 61:0>1,63:1>0,68:0>1,94:0>2,105:0>1, 126:0>1, 132:0>1, 161:0>1, 164:1>2, 175:0>1, 180:0>1, 182:0>1, 187:2>1, 194:1>0, 204:0>6, 217:0>1

(Mutillidae,Sapygidae): 6:0>1,21:0>1,37:1>0,108:1>2, 130:0>1, 162:0>1, 173:0>1, 204:0>5

(Mutillidae): 2:0>1, 22:0>1, 51:1>2, 57:0>1, 81:0>2, 105:0>1, 139:0>1, 147:0>1, 154:0>1, 183:0>1, 193:1>3, 195:0>1

Myrmosinae: 14:0>1, 104:0>1, 130:1>2, 139:1>2, 164:1>0, 170:0>1

mutillids: 30:0>1, 34:0>1, 54:0>1, 62:0>1, 73:1>2, 80:0>1,84:0>1,95:0>1,140:0>1,145:0>1,214:1>2

(Sapygidae): 23:0>1,58:1>0,104:0>1,161:0>1,214:1>0

Fedtschenkiinae: 23:1>2, 80:0>1, 81:0>1, 126:0>1, 154:0>4, 162:1>0

Sapyginae: 10:0>1,25:0>1,66:1>0,118:2>0,121:2>0, 164:1>2, 171:0>1, 176:0>1, 178:1>0, 199:1>0, 200:0>1, 218:0>1

(Tiphiidae): 37:1>0, 56:1>2, 66:1>0, 96:1>0, 102:2>1, 103:0>1, 110:0>1, 199:1>2

Anthoboscinae: 107:1>0, 169:0>1, 193:1>0

(Diamminae, Thynninae, Myzininae, Methochinae, Tiphiinae,Brachycistidinae): 2:0>1,71:0>1,74:0>1, 80:0>1, 130:0>1, 137:0>1, 154:0>1

Diamminae: 138:0>1, 180:0>1, 204:0>4

(Thynninae, Myzininae, Methochinae, Tiphiinae, Brachycistidinae): 7:0>1, 162:0>1, 214:0>1

Thynninae: 156:1>2, 174:0>1

(Myzininae,Methochinae,Tiphiinae,Brachycistidinae): 1:0>1,81:0>1,102:1>2,107:1>0,130:1>0,167:0>1, 188:0>1, 195:0>1, 214:1>2

Myzininae: 2:1>0,63:1>2,133:0>1,145:0>1,162:1>0, 164:1>0

(Methochinae, Tiphiinae, Brachycistidinae): 37:0>1, 71:1>0, 137:1>2

Methochinae: 11:0>1,14:0>1,56:2>1,80:1>2,89:0>1, 96:0>1, 110:1>0, 118:2>1, 121:2>1, 129:0>1, 131:0>1, 135:0>1, 164:1>0, 183:0>1, 193:1>3

(Tiphiinae, Brachycistidinae): 1:1>0, 7:1>0, 34:0>1, 61:0>1, 66:0>1, 83:0>1, 84:0>1, 95:0>1, 130:0>1, 149:0>1, 164:1>2, 170:0>1, 171:0>1

Tiphiinae: 2:1>0, 63:1>2, 74:1>2, 90:0>1

Brachycistidinae: 12:0>1, 16:0>1, 48:1>2, 106:0>1, 115:0>1, 124:0>1, 137:2>3, 188:1>0

APPENDIX VIII

Distribution of derived character states on preferred cladogram (see text) of family ground plans of Aculeata (Fig.10b) resulting from analysis of data in Tables IV and V; optimization by accelerated transformation, except delayed transformation for variables considered unlikely to show reversals and manual for Variables 80, 95, 105, 201 and 216. Unnamed internodes are referred to by listing the subtended superfamilies or families. Character numbers refer to the variables in Appendix VI; transformations are denoted by listing the ancestral and derived states separated by a '>'. Placements which agree with those on Fig. 9b are indicated in boldface. Variables invariant between family ground plans and thus excluded from this analysis: 1, 7, 9, 14, 17, 25, 28, 36, 47, 60, 62, 69, 71, 74, 89, 91, 97, 113, 116, 125, 127, 129, 131, 135, 137, 138, 140, 142, 145, 148, 153, 155, 167, 168, 174, 188, 210

Final weights of variables (10 is maximum):

Weight = 10: 3, 4, 5, 8, 10, 12, 15, 18, 19, 20, 24, 26, 31, 32, 34, 35, 39, 42, 45, 49, 50, 51, 52, 53, 59, 64, 65, 67, 72, 76, 78, 79, 82, 87, 88, 90, 92, 98, 99, 100, 101, 103, 104, 106, 108, 111, 112, 114, 117, 119, 120, 122, 123, 128, 133, 134, 136, 139, 141, 143, 144, 146, 147, 151, 152, 156, 157, 158, 159, 160, 162, 165, 166, 169, 172, 173, 181, 182, 183, 185, 186, 189, 190, 191, 192, 198, 202, 203, 204, 205, 206, 207, 209, 211, 212, 213, 215, 219

Weight = 6: 48, 85

Weight = 5: 187, 216

Weight = 4: 29, 85

Weight = 3: 38, 57, 63, 70, 77, 86, 107, 126, 149, 178, 196

Weight = 2: 6, 11, 40, 44, 80, 102, 105, 109, 118, 121, 154, 163, 175, 180, 194, 195, 197, 199, 208, 217

Weight = 1: 13, 21, 30, 37, 56, 61, 73, 81, 84, 93, 94, 115, 130

Weight = 0: 2, 16, 22, 23, 27, 33, 41, 43, 46, 54, 55, 58, 66, 68, 75, 83, 95, 96, 110, 124, 132, 150, 161, 164, 170, 171, 176, 177, 179, 184, 193, 200, 201, 214, 218

(Aculeata): **43:0>1, 80:0>1, 84:0>1, 102:0>2, 118:0>1, 121:0>1,** 193:0>2, **197:0>1, 198:0>1**

(Chrysidoidea): **33:0>1, 81:0>1, 85:0>1, 109:0>1, 111:0>1, 152:0>1, 160:0>1,** 164:0>1, **186:0>1,** 193:2>3, **196:0>1, 207:0>1, 215:0>1**

Plumariidae: **2:0>1, 16:0>1, 29:0>1, 41:0>1, 143:0>1, 159:0>1, 161:0>1, 214:0>2**

(Scolebythidae, Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): **11:0>1, 13:0>1, 85:1>2, 95:0>1, 98:0>1, 118:1>0, 121:1>0, 186:1>2, 191:0>1, 197:1>0, 201:0>1, 206:0>1**

Scolebythidae: 42:0>1, 43:1>0, 45:0>1, 95:1>2, 98:1>2, 120:0>1, 123:0>1, 164:1>0, 193:3>2

(Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): **29:0>1, 33:1>0, 56:0>1, 64:0>1, 66:0>1, 136:0>1, 175:0>1, 186:2>3, 208:0>3, 216:0>1**

(Bethylidae, Chrysididae): **13:1>0, 64:1>2, 80:1>2, 101:0>1, 154:0>3, 203:0>1, 208:3>2**

Bethylidae: 6:0>1, 21:0>1, 22:0>1, 75:0>1, 83:0>1, 95:1>2, 101:1>2, 154:3>2, 164:1>0, 208:2>1, 209:0>1, 211:0>1, 216:1>2, 218:0>1

Chrysididae: 12:0>1, 27:0>1, 43:1>0, 48:0>1, 54:0>1, 56:1>0, 86:0>1, 157:0>1, 170:0>1, 171:0>1, 193:3>0, 204:0>3

(Sclerogibbidae, Dryinidae, Embolemidae): **11:1>0, 40:0>1, 44:0>1, 80:1>0, 93:0>1, 102:2>3, 177:0>1, 202:0>1, 214:0>1**

Sclerogibbidae: **2:0>1, 8:0>1, 13:1>2, 19:0>1, 21:0>1, 33:0>1, 41:0>1, 53:0>1, 73:0>1, 81:1>2, 87:0>1, 95:1>2, 100:0>1, 111:1>2, 114:0>1, 144:0>1, 158:0>1, 161:0>1, 204:0>1, 207:1>2, 214:1>2**

(Dryinidae, Embolemidae): **20:0>1, 38:0>1, 86:0>1, 99:0>1, 164:1>2, 170:0>1, 171:0>1, 196:1>2, 204:0>2, 205:0>1, 216:1>2**

Dryinidae: 30:0>1, 40:1>0, 43:1>0, 44:1>0, 46:0>1, 56:1>0, 81:1>2, 86:1>2, 93:1>0, 124:0>1, 214:1>0, 218:0>1

Embolemidae: 26:0>1, 27:0>1, 32:0>2, 53:0>2, 57:0>2, 61:0>2, 66:1>2, 115:0>1, 144:0>2, 177:1>0, 197:0>1, 206:1>2, 208:3>1, 212:0>1, 213:0>1

(Aculeata s.s.): **18:0>1, 44:0>1, 66:0>1, 96:0>1, 156:0>1, 187:0>1, 201:0>1**

(Apoidea): **35:0>1, 39:0>1, 46:0>1, 52:0>1, 57:0>2, 61:0>1, 65:0>1, 70:0>1, 77:0>1, 93:0>1,** 118:1>2, 121:1>2, 126:0>1, **163:0>1, 192:0>1**

Heterogynaidae: 2:0>1, 81:0>2, 90:0>2, 95:0>1, 109:0>1, 115:0>1, 130:0>1, 133:0>2, 143:0>2, 171:0>1, 187:1>0, 189:0>1

(sphecids, apids): 37:0>1, 126:1>2, 180:0>1, 193:2>0

sphecids: 46:1>0, 84:1>0, 96:1>0, 102:2>0, **200:0>1, 204:0>8**

apids: 4:0>1, 23:0>1, 39:1>2, 55:0>1, 67:0>1, 118:2>1, 121:2>1, **124:0>1, 156:1>2,** 164:0>2, **170:0>1, 171:0>1, 176:0>1, 180:1>2, 185:0>1, 196:0>2, 208:0>3**

(Vespoidea): **40:0>1, 48:0>1, 56:0>1, 73:0>1, 107:0>1, 187:1>2, 194:0>1**

Sierolomorphidae: 13:0>1, 37:0>1, **68:0>1, 81:0>1, 88:0>1, 95:0>1, 109:0>1, 130:0>1, 165:0>1, 170:0>1, 190:0>1, 200:>1**

(Tiphiidae, Pompilidae, Sapygidae, Mutillidae, Rhopalosomatidae, Bradynobaenidae, Formicidae, Scoliidae, Vespidae): **63:0>1, 80:1>0, 84:1>0, 108:0>1,** 164:0>1

(Tiphiidae, Pompilidae, Sapygidae, Mutillidae): **118:1>2, 121:1>2, 178:0>1,** 193:2>1, **199:0>1**

Tiphiidae: 56:1>2, 66:1>0, 96:1>0, 102:2>1, 103:0>1, 107:1>0, **110:0>1,** 169:0>1, 193:1>0, **199:1>2**

(Pompilidae, Sapygidae, Mutillidae): **51:0>1, 58:0>1, 214:0>1**

Pompilidae: 37:0>1, **61:0>1, 63:1>0, 68:0>1, 94:0>2, 105:0>1, 126:0>1, 132:0>1, 161:0>1, 164:1>2, 175:0>1, 180:0>1, 182:0>1, 187:2>1, 194:1>0, 204:0>6, 217:0>1**

(Sapygidae, Mutillidae): **6:0>1, 21:0>1, 108:1>2, 130:0>1, 173:0>1, 204:0>5**

Sapygidae: 23:0>1, 58:1>0, 66:1>0, **104:0>1,** 118:2>1, 121:2>1, **161:0>1,** 176:0>1, 178:1>0, **214:1>0,** 218:0>1

Mutillidae: 2:0>1, 22:0>1, 51:1>2, 57:0>1, 81:0>2, 105:0>1, 139:0>1, 147:0>1, 154:0>1, 162:0>1, 164:1>0, **183:0>1, 193:1>3, 195:0>1**

(Rhopalosomatidae, Bradynobaenidae, Formicidae, Scoliidae, Vespidae): **30:0>1, 46:0>1, 48:1>2, 93:0>1, 105:0>1, 149:0>1, 163:0>1, 195:0>1**

Rhopalosomatidae: 13:0>1, **56:1>2, 58:0>1,** 63:1>0, 68:0>2, 70:0>1, **92:0>1,** 94:0>1, **95:0>1,** 107:1>0, **112:0>1, 132:0>1,** 177:0>1, 190:0>2, 193:2>1, **194:1>0, 200:0>1, 204:0>7, 205:0>2,** 219:0>1

(Bradynobaenidae, Formicidae, Scoliidae, Vespidae): 55:0>1, 56:1>0, **57:0>1, 61:0>1, 63:1>2,** 96:1>0, 150:0>1, 154:0>1, **175:0>1,** 214:0>1

Bradynobaenidae: 2:0>1, 16:0>1, 30:1>0, 46:1>0, 66:1>0, **73:1>0, 75:0>1, 77:0>1, 78:0>1, 80:0>2, 84:0>1,** 93:1>0, **95:0>1, 141:0>1, 146:0>1, 151:0>1,** 178:0>2, **199:0>1,** 204:0>9

(Formicidae, Scoliidae, Vespidae): 34:0>1, 37:0>1, 38:0>2, 106:0>1, 179:0>1, 180:0>1, 184:0>1

Formicidae: 3:0>1, 13:0>1, **50:0>1, 61:1>2, 72:0>1, 85:0>1,** 96:0>1, 118:1>3, 121:1>3, **128:0>1, 134:0>1, 144:0>3, 164:1>0, 181:0>1, 187:2>3,** 193:2>3, **214:1>2**

(Scoliidae, Vespidae): **34:1>2,** 55:1>0, 94:0>1, **115:0>1,** 150:1>0, **163:1>0, 171:0>1, 180:1>2, 190:0>3,** 193:2>1, 214:1>0, **217:0>1**

Scoliidae: 15:0>1, 31:0>1, 38:2>1, **49:0>1, 54:0>1,** 56:0>1, **59:0>1,** 66:1>0, **73:1>0, 76:0>1, 79:0>1, 83:0>1, 84:0>1, 95:0>1, 107:1>2, 110:0>1, 117:0>1, 119:0>1, 122:0>1, 126:0>1,** 154:1>0, **164:1>0, 166:0>1, 172:0>1,** 179:1>0, 184:1>0, 195:1>0, **199:0>2,** 218:0>2

Vespidae: 5:0>1, 10:0>1, 24:0>1, **32:0>1, 34:2>3,** 43:1>2, **48:2>3, 58:0>1, 82:0>1,** 94:1>2, **133:0>1, 149:1>0, 161:0>1, 193:1>0, 195:1>2**

APPENDIX IX

Distribution of derived character states on composite cladogram based on preferred results (see text) of all analyses of Aculeata (Fig. 11); optimization by accelerated transformation, except delayed transformation for variables considered unlikely to show reversals and manual for Variables 80, 95, 105, 109, 161, 201 and 216. Unnamed internodes are referred to by listing the subtended superfamilies, families or lower taxa. Character numbers refer to the variables in Appendix VI; transformations are denoted by listing the ancestral and derived states separated by a '>'. Placements which differ from those on Figs. 9b and/or 10b are in italics.

Weights of variables (10 is maximum):

Weight = 10: 1, 3, 8, 9, 17, 18, 19, 20, 25, 28, 31, 32, 35, 36, 39, 42, 45, 47, 49, 51, 52, 53, 59, 60, 64, 65, 69, 72, 74, 76, 78, 79, 87, 88, 89, 90, 91, 92, 97, 98, 99, 100, 101, 103, 108, 111, 112, 114, 116, 117, 119, 120, 122, 123, 125, 127, 128, 129, 131, 134, 135, 136, 138, 139, 140, 141, 142, 143, 144, 146, 147, 151, 152, 153, 155, 157, 158, 159, 160, 165, 166, 167, 168, 172, 173, 174, 181, 182, 185, 186, 189, 190, 191, 192, 198, 202, 203, 204, 205, 206, 207, 209, 210, 211, 212, 213, 215, 219

Weight = 6: 85, 137

Weight = 5: 48, 156, 178, 216

Weight = 4: 34, 57, 75, 149, 150, 154, 187

Weight = 3: 15, 23, 70, 73, 86, 132, 196
Weight = 2: 4, 6, 16, 22, 29, 38, 40, 44, 62, 63, 77, 104, 105, 106, 113, 121, 148, 175, 183, 194, 195, 197, 199, 208, 217
Weight = 1: 7, 11, 13, 21, 30, 46, 54, 55, 56, 58, 61, 84, 93, 94, 102, 107, 109, 110, 118, 126, 130, 163, 180, 188
Weight = 0: 2, 5, 10, 12, 14, 24, 26, 27, 33, 37, 41, 43, 50, 66, 67, 68, 71, 80, 81, 82, 83, 95, 96, 115, 124, 133, 145, 161, 162, 164, 169, 170, 171, 176, 177, 179, 184, 193, 200, 201, 214, 218

(Aculeata): 43:0>1, 80:0>1, 84:0>1, 102:0>2, 118:0>1, 121:0>1, 193:0>2, 197:0>1, 198:0>1

(Chrysidoidea): 33:0>1, 81:0>1, 85:0>1, 109:0>1, 111:0>1, 152:0>1, 160:0>1, 164:0>1, 186:0>1, 193:2>3, 196:0>1, 207:0>1, 215:0>1

Plumariidae: 2:0>1, 16:0>1, 29:0>1, 41:0>1, 143:0>1, 159:0>1, 161:0>1, 214:0>2

(Scolebythidae, Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 11:0>1, 13:0>1, 85:1>2, 95:0>1, 98:0>1, 118:1>0, 121:1>0, 186:1>2, 191:0>1, 197:1>0, 201:0>1, 206:0>1

Scolebythidae: 42:0>1, 43:1>0, 45:0>1, 95:1>2, 98:1>2, 120:0>1, 123:0>1, 164:1>0, 193:3>2

(Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 29:0>1, 33:1>0, 56:0>1, 64:0>1, 66:0>1, 136:0>1, 175:0>1, 186:2>3, 208:0>3, 216:0>1

(Bethylidae, Chrysididae): 13:1>0, 64:1>2, 80:1>2, 101:0>1, 154:0>3, 203:0>1, 208:3>2

Bethylidae: 6:0>1, 21:0>1, 22:0>1, 75:0>1, 83:0>1, 95:1>2, 101:1>2, 154:3>2, 164:1>0, 208:2>1, 209:0>1, 211:0>1, 216:1>2, 218:0>1

Chrysididae: 12:0>1, 27:0>1, 43:1>0, 48:0>1, 54:0>1, 56:1>0, 86:0>1, 157:0>1, 170:0>1, 171:0>1, 193:3>0, 204:0>3

(Sclerogibbidae, Dryinidae, Embolemidae): 11:1>0, 40:0>1, 44:0>1, 80:1>0, 93:0>1, 102:2>3, 177:0>1, 202:0>1, 214:0>1

Sclerogibbidae: 2:0>1, 8:0>1, 13:1>2, 19:0>1, 21:0>1, 33:0>1, 41:0>1, 53:0>1, 73:0>1, 81:1>2, 87:0>1, 95:1>2, 100:0>1, 111:1>2, 114:0>1, 144:0>1, 158:0>1, 161:0>1, 204:0>1, 207:1>2, 214:1>2

(Dryinidae, Embolemidae): 20:0>1, 38:0>1, 86:0>1, 99:0>1, 164:1>2, 170:0>1, 171:0>1, 196:1>2, 204:0>2, 205:0>1, 216:1>2

Dryinidae: 30:0>1, 40:1>0, 43:1>0, 44:1>0, 46:0>1, 56:1>0, 81:1>2, 86:1>2, 93:1>0, 124:0>1, 214:1>0, 218:0>1

Embolemidae: 26:0>1, 27:0>1, 32:0>2, 53:0>2, 57:0>2, 61:0>2, 66:1>2, 115:0>1, 144:0>2, 177:1>0, 197:0>1, 206:1>2, 208:3>1, 212:0>1, 213:0>1

(Aculeata s.s.): 18:0>1, 37:0>1, 44:0>1, 66:0>1, 96:0>1, *118:1>2, 121:1>2,* 156:0>1, 187:0>1, 201:0>1

(Apoidea): 35:0>1, 39:0>1, 46:0>1, 52:0>1, 57:0>2, 61:0>1, 65:0>1, 70:0>1, 77:0>1, 93:0>1, 126:0>1, 163:0>1, 192:0>1

Heterogynaidae: 2:0>1, 37:1>0, 81:0>2, 90:0>2, 95:0>1, 109:0>1, 115:0>1, 130:0>1, 133:0>2, 143:0>2, 171:0>1, 187:1>0, 189:0>1

(sphecids, apids): 126:1>2, 180:0>1, 193:2>0

sphecids: 46:1>0, 84:1>0, 96:1>0, 102:2>0, 200:0>1, 204:0>8

apids: 4:0>1, 23:0>1, 39:1>2, 55:0>1, 67:0>1, 118:2>1, 121:2>1, 124:0>1, 156:1>2, 164:0>2, 170:0>1, 171:0>1, 176:0>1, 180:1>2, 185:0>1, 196:0>2, 208:0>3

(Vespoidea): 13:0>1, 40:0>1, 48:0>1, 56:0>1, 73:0>1, 107:0>1, 187:1>2, 194:0>1

Sierolomorphidae: 68:0>1, 81:0>1, 88:0>1, 95:0>1, 109:0>1, *118:2>1, 121:2>1,* 130:0>1, 165:0>1, 170:0>1, 190:0>1, 200:>1

(Rhopalosomatidae, Formicidae, Vespidae, Scoliidae, Bradynobaenidae, Pompilidae, Mutillidae, Sapygidae, Tiphiidae): 63:0>1, 80:1>0, 84:1>0, 108:0>1, 164:0>1

(Rhopalosomatidae, Formicidae, Vespidae, Scoliidae, Bradynobaenidae): 30:0>1, 38:0>1, 46:0>1, 48:1>2, *55:0>1,* 93:0>1, 105:0>1, 149:0>1, 163:0>1, 195:0>1

(Rhopalosomatidae): 56:1>2, 58:0>1, 92:0>1, *94:0>2,* 95:0>1, 112:0>1, *118:2>1, 121:2>1,* 132:0>1, 193:2>1, 194:1>0, 200:0>1, 204:0>7, 205:0>2

rhopalosomatids: 10:0>1, *55:1>0,* 63:1>0, 68:0>2, 70:0>1, 107:1>0, 177:0>1, 190:0>2, 219:0>1

Olixon: 33:0>1, 37:1>0, 38:1>0, 50:0>1, 61:0>1, 80:0>2, 81:0>1, 83:0>1, 92:1>2, 93:1>2, 100:0>2, 118:1>0, 121:1>0, 132:1>2, 147:0>2, 210:0>1

(Formicidae, Vespidae, Scoliidae, Bradynobaenidae): 56:1>0, 57:0>1, 61:0>1, 63:1>2, 150:0>1, 154:0>1, 175:0>1, 214:0>1

(Formicidae, Vespidae, Scoliidae): 34:0>1, *38:1>2,* 106:0>1, 179:0>1, 180:0>1, 184:0>1

Formicidae: 3:0>1, 50:0>1, 61:1>2, 72:0>1, 85:0>1, 118:2>3, *121:2>3,* 128:0>1, 134:0>1, 144:0>3, 164:1>0, 181:0>1, 187:2>3, 193:2>3, 214:1>2

(Vespidae, Scoliidae): 5:0>1, 10:0>1, 13:1>0, 24:0>1, 34:1>2, 43:1>2, 55:1>0, *94:0>2,* 96:1>0, 115:0>1, 118:2>1, 121:2>1, 150:1>0, 163:1>0, 171:0>1, 180:1>2, 190:0>3, 193:2>1, 214:1>0, 217:0>1

Vespidae: 32:0>1, 34:2>3, 48:2>3, 58:0>1, 82:0>1, 133:0>1, 149:1>0, 161:0>1, 193:1>0, 195:1>2

(Scoliidae): 15:0>1, 31:0>1, 49:0>1, 54:0>1, 56:0>1, 59:0>1, 73:1>0, 76:0>1, 79:0>1, 83:0>1, 84:0>1, 95:0>1, 107:1>2, 110:0>1, 117:0>1, 119:0>1, 122:0>1, 126:0>1, 164:1>0, 166:0>1, 172:0>1, 199:0>2

Scoliinae: 67:0>1, 69:0>1, 77:0>1, 117:1>2, 124:0>1, 166:1>2, 170:0>1, *179:1>0, 184:1>0*, 218:0>2

Proscoliinae: 5:1>0, 10:1>0, 24:1>0, 27:0>1, 38:2>1, 43:2>1, 66:1>0, 80:0>1, 81:0>1, 89:0>2, 94:2>1, 154:1>0, 169:0>1, 195:1>0

(Bradynobaenidae): 2:0>1, 16:0>1, 30:1>0, 46:1>0, 73:1>0, 75:0>1, 77:0>1, 78:0>1, 80:0>2, 84:0>1, 95:0>1, 107:1>2, 141:0>1, 146:0>1, 148:0>1, 151:0>1, 161:0>1, *193:2>3,* 199:0>1,

(Typhoctinae): 4:0>1, 37:1>0, 38:1>0, 66:1>0, 130:0>1, 141:1>2

Eotillini: 71:0>1, 93:1>0, 107:2>0, 113:0>1, 118:2>1, 121:2>1

Typhoctini: 96:1>0, 109:0>1, 178:0>2, 188:0>1, 204:0>9

(Chyphotinae, Apterogyninae, Bradynobaeninae): 6:0>1, 9:0>1, 12:0>1, 13:1>0, 21:0>1, 110:0>1, *121:2>3,* 142:0>1, 151:1>2, 153:0>1, 168:0>1, 195:1>2

Chyphotinae: 61:1>2, 66:1>0, 81:0>1, 93:1>0, 153:1>2, 169:0>1

(Apterogyninae, Bradynobaeninae): 15:0>1, 17:0>1, 47:0>1, 62:0>1, 78:1>2, 84:1>2, 91:0>1, 93:1>2, 95:1>2, 96:1>0, 106:0>1, 113:0>1, 116:0>1, 118:2>3, 126:0>1, 127:0>1, 148:1>0, 171:0>1

Apterogyninae: 130:0>1, 149:1>2, 155:0>1, 161:1>0, 193:3>1

Bradynobaeninae: 7:0>1, 12:1>0, 26:0>1, 28:0>1, 29:0>1, 36:0>1, 47:1>2, 60:0>1, 82:0>1, 83:0>1, 91:1>2, 97:0>1, 115:0>1, 116:1>2, 118:3>4, 121:3>4, 125:0>1, 127:1>2, 146:1>2, 162:0>1, 163:1>0, 168:1>2, 187:2>3, 195:2>1

(Pompilidae, Mutillidae, Sapygidae, Tiphiidae): 13:1>0, 178:0>1, 193:2>1, 199:0>1

(Pompilidae, Mutillidae, Sapygidae): 51:0>1, 58:0>1, 214:0>1

Pompilidae: 61:0>1, 63:1>0, 68:0>1, 94:0>2, 105:0>1, 126:0>1, 132:0>1, 161:0>1, 164:1>2, 175:0>1, 180:0>1, 182:0>1, 187:2>1, 194:1>0, 204:0>6, 217:0>1

(Mutillidae, Sapygidae): 6:0>1, 21:0>1, 37:1>0, 108:1>2, 130:0>1, 162:0>1, 173:0>1, 204:0>5

(Mutillidae): 2:0>1, 22:0>1, 51:1>2, 57:0>1, 81:0>2, 105:0>1, 139:0>1, 147:0>1, 154:0>1, 183:0>1, 193:1>3, 195:0>1

Myrmosinae: 14:0>1, 104:0>1, 130:1>2, 139:1>2, 164:1>0, 170:0>1

mutillids: 30:0>1, 34:0>1, 54:0>1, 62:0>1, 73:1>2, 80:0>1, 84:0>1, 95:0>1, 140:0>1, 145:0>1, 214:1>2

(Sapygidae): 23:0>1, 58:1>0, 104:0>1, 161:0>1, 214:1>0

Fedtschenkiinae: 23:1>2, 80:0>1, 81:0>1, 126:0>1, 154:0>4, 162:1>0

Sapyginae: 10:0>1, 25:0>1, 66:1>0, 118:2>0, 121:2>0, 164:1>2, 171:0>1, 176:0>1, 178:1>0, 199:1>0, 200:0>1, 218:0>1

(Tiphiidae): 37:1>0, 56:1>2, 66:1>0, 96:1>0, 102:2>1, 103:0>1, 110:0>1, 199:1>2

Anthoboscinae: 107:1>0, 169:0>1, 193:1>0

(Diamminae, Thynninae, Myzininae, Methochinae, Tiphiinae, Brachycistidinae): 2:0>1, 71:0>1, 74:0>1, 80:0>1, 130:0>1, 137:0>1, 154:0>1

Diamminae: 138:0>1, 180:0>1, 204:0>4

(Thynninae, Tiphiinae, Brachycistidinae, Myzininae, Methochinae): 7:0>1, 162:0>1, 214:0>1

Thynninae: 156:1>2, 174:0>1

(Tiphiinae, Brachycistidinae, Myzininae, Methochinae): *37:0>1, 71:1>0,* 81:0>1, 102:1>2, 107:1>0, 167:0>1, 188:0>1, 195:0>1, 214:1>2

(Tiphiinae, Brachycistidinae): 7:1>0, 34:0>1, 61:0>1, 66:0>1, 83:0>1, 84:0>1, 95:0>1, 149:0>1, 164:1>2, 170:0>1, 171:0>1

Tiphiinae: 2:1>0, 63:1>2, 74:1>2, 90:0>1

Brachycistidinae: 12:0>1, 16:0>1, 48:1>2, 106:0>1, 115:0>1, 124:0>1, *137:1>3,* 188:1>0

(Myzininae, Methochinae): *1:0>1, 130:1>0, 164:1>0*

Myzininae: 2:1>0, *37:1>0,* 63:1>2, *71:0>1*, 133:0>1, 145:0>1, 162:1>0

Methochinae: 11:0>1, 14:0>1, 56:2>1, 80:1>2, 89:0>1, 96:0>1, 110:1>0, 118:2>1, 121:2>1, 129:0>1, 131:0>1, 135:0>1, *137:1>2*, 183:0>1, 193:1>3

Table I. Data matrix for Aculeata derived from Rasnitsyn (1980), as in Appendix II. Variables7, 9, 12-15, 20-21 and 36 are nonadditive. A corrected score is indicated in the Note. A question mark denotes missing data (state unknown in the taxon).

Plumariidae	10111000??	?000000000	0000000010 00000000
Scolebythidae	101110000?	?000000000	0000000010 00000000
Sclerogibbidae	1012103011	0103000001	0000000010 00000000
Embolemidae	1021102120	1201100001	0000000010 00000000
Dryinidae	1011102021	1103000001	0000000010 00000000
Bethylidae	1011120000	0011300001	0000000010 00000000
Chrysididae	1011110030	0022200001	0000000010 00000000
Sphecidae	0100001000	0000011012	1000010000 00000100
Apidae	010000104?	0000011012	2000010000 00100000
Tiphiidae	0100001000	0010311103	0111101011 11100120
Sapygidae	0200001050	0010011103	0100101111 11100111
Mutillidae	0200001050	0010011103	0111101211 11100111
Sierolomorphidae	0000001???	?010011100	0100101011 11100010
Pompilidae	0100001061	0000011010	3000101111 11100110
Rhopalosomatidae	0100001071	0000011010	3000102011 11101020
Formicidae	0100001081	0010011104	4111102011 11101200
Scoliidae	0100001000	0010311104	0111102011 11112300
Vespidae	0100001001	0010011104	5111102011 11113000
Bradynobaenidae	0100001091	0010311104	0111102011 11100100

Note:
Variable 13 = 0 in Embolemidae; State1 is not general in that taxon.

Table II. Data matrix for Aculeata derived from Rasnitsyn (1988), as in Appendix III. Variables 7, 9, 12-15, 20-21, 23 and 35 are nonadditive. Corrected scores are indicated in the Notes. A question mark denotes missing data (state unknown in the taxon).

Plumariidae	10111000??	?000000000	0000000100	0000000001	00101?0
Scolebythidae	101110000?	?000000000	0000000100	0000000100	0010100
Sclerogibbidae	1012103011	0103000001	0000000100	0000000112	0010100
Embolemidae	1021102120	1201100001	0000000100	0000000113	1010100
Dryinidae	1011102021	1103000001	0000000100	0000000110	0010100
Bethylidae	1011120000	0011300001	0000000100	0000000110	1010100
Chrysididae	1011110030	0022200001	0000000100	0000000110	1010100
Sphecidae	0100001000	0000011012	1000100000	0000100000	0110000
Apidae	010000104?	0000011012	2000100000	0100000000	0110000
Tiphiidae	0100001000	0010311103	0101010111	1100120000	0110101
Sapygidae	0200001050	0010011103	0101011111	1100011000	0110100
Mutillidae	0200001050	0010011103	0101012111	1100001000	0110101
Sierolomorphidae	0000001???	?010011100	0111010111	1100010000	01111?0
Pompilidae	0100001061	0000010010	3001011111	1100110000	0111000
Rhopalosomatidae	0100001071	0000011010	3001020111	1101020000	0111000
Formicidae	0100001081	0010011104	4111020111	1101200000	0111110
Scoliidae	0100001000	0010311104	0101020111	1112300000	0110101
Vespidae	0100001001	0010010104	5121020111	1113000000	0110110
Bradynobaenidae	0100001091	0010311104	0101020111	1100100000	0110101

Notes:
Variable 13 = 0 in Embolemidae; State 1 is not general in that taxon.
Variable 43 = 1 in all, see Brothers (1975: Character 85), Rasnitsyn (1980).

Table III. Data matrix for Aculeata derived from Brothers (1975). The character state trees have been coded using nonredundant linear coding (Appendix IV); spaces separate the variables representing each of the original 92 characters. Where a character is sometimes sexually dimorphic, scoring is as explained in the text. A question mark denotes missing data (state unknown in the taxon, except as explained in the Notes).

Plumariidae	0 1 0 0 00 00 000 0 000 1 0 0 0 0 0000 00 0 00 0 0 000 0 00 01 1 00 0 0 00000 00 00 00 0 00 000 0000 0 10 0 0 0 1 0 0 1 10000 0 0 0 000 01 0 0 00 0 01 100 0 0 00 100 100 00 00 00 0 0 0000 000001 00 00 0 0 0 0 0 0 0 1 1 00 1 0000 00 0 00 ??? ? ? ???? ? ?
bethylids	0 0 0 0 00 00 000 0 000 0 0 0 0 0 0000 00 1 00 0 0 000 0 00 00 0 00 0 0 00000 00 00 00 0 00 010 0000 0 00 0 0 0 1 0 0 1 20000 0 0 1 001 01 0 0 00 0 01 000 0 0 00 000 000 00 00 00 0 0 0000 000000 00 00 0 0 0 0 0 0 0 1 0 00 0 0000 00 0 00 000 0 0 0000 0 0
Scolebythidae	0 0 0 0 10 00 001 0 100 0 0 0 0 0 0000 00 0 00 0 1 000 0 00 00 0 01 0 0 00000 00 00 00 0 01 010 0000 0 00 0 0 0 1 0 0 1 30000 0 0 2 002 01 0 0 00 0 01 010 0 0 00 001 001 00 00 00 0 0 0000 000000 00 00 0 0 0 0 0 0 1 0 00 0 0000 00 0 00 ??? ? ? ???? ? ?
sphecids	0 0 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 01 0 0 020 1 01 00 1 10 1 0 00001 00 01 00 1 00 001 0001 0 00 1 0 0 0 0 0 0 00000 1 0 0 000 00 0 0 00 0 00 000 0 0 00 200 200 00 20 00 0 0 0000 000000 00 00 0 0 0 0 0 0 1 0 0 01 0 0000 00 0 00 000 0 0 1000 0 0
apids	0 0 0 1 00 00 000 0 000 0 0 1 0 0 1000 00 0 01 0 0 010 1 01 00 1 10 1 0 00001 01 01 00 1 00 001 0001 0 00 1 0 0 1 0 0 1 00000 1 0 0 100 10 0 0 00 0 00 000 0 0 00 100 100 10 20 00 0 0 0000 000000 00 00 0 0 0 0 0 0 2 0 0 01 2 0000 01 1 00 010 0 1 2000 0 1
Anthoboscinae	0 0 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 10000 00 20 00 0 00 100 0000 0 10 0 0 0 0 0 0 0 00000 0 0 0 000 01 1 0 00 0 10 100 0 0 00 200 200 00 00 00 0 0 0000 000000 00 00 0 0 0 0 0 0 1 0 0 00 1 0000 10 0 00 000 1 0 0000 0 0

Table III (cont.)

Thynninae	0 1 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 10000 00 20 00 0 00 100 0000 0 10 0 0 0 0 0 0 0 00000 0 0 0 000 01 1 0 00 1 10 100 0 0 00 200 200 00 00 00 1 0 0000 100000 00 00 0 0 0 0 0 0 1 0 0 00 1 0000 00 0 00 000 1 0 0000 0 0
Myzininae	1 0 0 0 00 01 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 10000 00 20 00 0 00 200 0000 0 10 0 0 0 0 0 0 0 00000 0 0 0 000 01 1 0 00 0 10 100 0 0 00 200 200 00 00 00 0 0 0000 000000 00 00 0 0 0 0 1 0 1 0 0 00 0 0010 00 0 00 000 1 0 0000 0 0
Methochinae	1 1 0 0 00 01 001 0 010 0 0 1 0 0 0000 00 0 00 0 0 000 1 00 10 1 10 0 0 10000 00 10 00 0 00 100 0000 0 10 0 0 0 1 0 0 0 00100 0 0 0 100 01 1 0 00 0 10 000 0 0 00 100 100 00 00 01 0 1 0001 200000 00 00 0 0 0 0 1 0 1 0 0 10 0 0010 00 0 00 000 1 0 0001 0 0
Tiphiinae	0 0 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 100 1 00 10 1 10 0 0 10000 00 20 00 1 00 200 2000 0 10 0 0 0 2 0 1 1 00010 0 0 1 000 01 1 0 00 0 10 100 0 0 00 200 200 00 00 00 1 0 0000 000000 00 00 1 0 0 0 1 0 1 0 0 10 2 0010 01 1 00 000 1 0 0000 0 0
Brachycistidinae	0 1 0 0 00 00 000 1 000 1 0 1 0 0 0000 00 0 00 0 0 100 1 00 10 1 10 0 0 20000 00 20 00 1 00 100 2000 0 10 0 0 0 1 0 1 1 00000 0 0 1 000 01 1 0 01 0 10 100 0 1 00 200 200 10 00 00 1 0 0000 300000 00 00 1 0 0 0 1 0 1 0 0 10 2 0010 01 1 00 ??? ? ? ???? ? ?
Sapygidae	0 0 0 0 00 10 000 0 000 0 0 1 0 0 0010 00 0 00 0 0 000 0 00 10 1 10 0 0 10010 00 10 00 0 00 100 0000 0 20 0 0 0 0 0 0 0 00000 0 0 0 100 01 1 1 00 1 20 000 0 0 00 200 200 00 00 00 1 0 0000 000000 00 00 0 0 0 0 0 0 1 0 1 00 1 0000 00 0 01 010 0 0 000? 0 0
Myrmosinae	0 1 0 0 00 10 000 0 010 0 0 1 1 1 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 10020 00 10 10 0 00 100 1000 0 20 0 0 0 2 0 0 0 00000 0 0 0 100 01 1 1 10 1 20 000 0 0 00 200 200 00 00 00 2 0 0000 020000 00 10 0 0 0 0 1 0 1 0 0 10 0 0000 01 0 01 000 1 0 0001 0 0

Table III (cont.)

mutillids	0 1 0 0 00 10 000 0 000 0 0 1 1 1 0000 00 0 10 0 0 100 0 00 10 1 10 0 0 10020 10 10 10 0 10 100 1000 0 30 0 0 0 2 0 0 1 00000 0 0 1 100 01 1 1 10 1 20 000 0 0 00 200 200 00 00 00 1 0 0000 011000 10 10 0 0 0 0 1 0 1 0 0 10 1 0000 00 0 01 000 1 0 0001 0 0
Sierolomorphidae	0 0 0 0 00 00 000 0 100 0 0 1 0 0 0000 00 0 00 0 0 000 1 00 10 1 0 0 0 10000 00 10 00 0 00 000 0010 0 20 0 0 0 1 0 0 1 01000 0 0 1 100 01 0 0 00 1 01 000 0 0 00 100 100 00 00 00 1 0 0000 000000 00 00 0 0 0 0 0 0 1 0 0 00 0 1000 01 0 00 ??? ? ? ???? ? ?
Pompilidae	0 0 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 000 1 00 10 1 10 0 0 10010 00 10 10 1 00 000 0010 0 20 0 0 0 0 0 0 0 00000 1 1 0 100 01 0 0 10 1 10 000 0 0 00 200 200 00 10 00 0 0 1000 000000 00 00 0 0 0 0 0 0 1 0 1 00 1 0000 00 0 00 100 1 0 0010 0 0
Rhopalosomatidae	0 0 0 0 00 00 000 0 100 0 0 1 0 0 0000 00 0 10 0 0 100 1 00 10 1 10 1 0 20000 00 20 10 0 00 000 0010 0 20 0 0 0 0 0 0 1 10000 1 1 1 100 01 0 0 10 0 10 001 0 0 00 100 100 00 00 00 0 0 1000 000000 00 00 1 0 0 0 0 0 1 0 0 01 1 0000 00 0 00 001 0 0 0000 0 0
Formicidae	0 0 1 0 00 00 000 0 100 0 0 1 0 0 0000 00 0 10 0 0 100 1 10 10 1 10 1 0 20100 01 00 00 2 00 200 1000 1 20 0 0 0 0 0 0 0 10000 1 0 0 100 01 0 0 01 1 10 000 0 0 00 300 300 00 00 10 0 0 0010 000000 00 00 1 1 0 0 1 0 1 0 0 01 0 0000 00 0 00 100 0 1 1100 1 0
Scoliidae	0 0 0 0 01 00 010 0 001 0 0 1 0 0 0100 00 0 10 1 0 200 1 10 10 2 10 1 0 21000 10 01 01 1 00 200 1100 0 21 1 0 1 0 0 1 1 00000 1 1 1 000 01 0 0 01 2 10 100 0 1 01 110 110 10 10 00 0 0 0000 000000 00 00 1 0 0 0 1 0 1 0 0 00 0 0100 01 1 10 100 0 0 ?000 0 0
Vespidae	0 0 0 0 01 00 010 0 000 0 0 1 0 0 0100 00 0 10 1 0 300 1 10 10 2 10 1 0 30000 00 01 10 1 00 200 1000 0 20 0 0 0 0 1 0 0 00000 1 1 0 000 01 0 0 01 1 10 000 0 0 00 100 100 00 00 00 0 0 0100 000000 00 00 0 0 0 0 1 0 1 0 1 00 1 0000 00 1 00 100 0 1 2000 1 0
Eotillini	0 1 0 1 00 00 000 0 100 1 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 00000 01 00 00 1 00 200 0010 0 00 1 1 0 1 0 0 1 00000 0 0 1 100 01 0 0 10 0 10 000 1 0 00 100 100 00 00 00 1 0 0000 000200 01 01 1 1 1 0 1 0 1 0 ? 01 1 0000 00 0 00 ??? ? ? ???? ? ?

Table III (cont.)

Typhoctini	0 1 0 1 00 00 000 0 100 1 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 20000 01 00 00 1 00 200 0010 0 00 1 1 0 1 0 0 1 00000 1 0 1 000 01 0 0 10 2 01 000 0 0 00 200 200 00 00 00 1 0 0000 000200 01 01 1 1 1 0 1 0 1 0 1 01 1 0000 00 0 00 ??? ? ? ???? ? ?
Chyphotinae	0 1 0 0 00 10 100 1 000 1 0 1 1 0 0000 00 0 00 0 0 000 1 10 10 1 10 0 0 20000 01 00 00 2 00 200 1000 0 00 1 1 0 1 0 0 1 00000 0 0 1 100 01 0 0 10 2 10 100 0 0 00 200 300 00 00 00 0 0 0000 000110 01 01 1 1 2 2 1 0 1 0 1 01 1 0001 10 0 00 ??? ? ? ???? ? ?
Apterogyninae	0 1 0 0 00 10 100 1 001 1 1 1 1 0 0000 00 0 00 0 0 000 1 10 10 1 10 0 1 20000 01 00 00 1 10 200 1000 0 00 1 2 0 1 0 0 2 00001 2 0 2 000 01 0 0 01 2 10 100 1 0 10 300 300 00 11 00 1 0 0000 000110 01 00 2 1 2 1 1 1 1 0 0 01 1 0001 00 1 00 ??? ? ? ???? ? ?
Bradynobaeninae	0 1 0 0 00 11 100 0 001 1 1 1 1 0 0001 01 1 00 0 0 001 1 10 10 1 10 0 2 20000 01 00 00 1 10 200 2000 0 00 1 2 0 1 1 1 2 00002 2 0 2 010 01 0 0 01 2 10 100 1 1 20 400 400 01 13 00 0 0 0000 000110 02 00 1 1 2 1 1 0 1 0 1 10 1 0002 00 1 00 ??? ? ? ???? ? ?

Notes:
Sapygidae:
Character 90 (Variables 157 - 160), uncertainty as to whether female closes off cavity containing prey.
Scoliidae:
Character 90 (Variables 157 - 160), uncertainty about transport of prey.
Bradynobaeninae:
Variables 7 & 8 coded to indicate derivation of 8:1 from 7:1.

Table IV (cont.)

Table IV. Data matrix for final analysis of Aculeata using characters of Appendix VI. Variables 32, 53, 57, 80, 81, 89, 90, 100, 133, 143, 144, 147, 154, 178, 190, 204, 205, 208 and 218 are nonadditive. Comments on changes in scoring from those in Table III (from Brothers, 1975) appear in the Notes. Scores for other taxa and variables not included in Table III are taken from later authors or they are newly scored, as indicated in the Notes and Appendix VI. A question mark (?) denotes missing data (state unknown in the taxon); a dash (-) denotes a taxon for which the variable is inapplicable.

Plumariidae	0100000000	0000010000	0000000010	0010000000	1010000000	0000000000
	0000000000	0000000001	1001100000	0000000000	0200000010	1000000100
	1000000000	0000000000	0010000000	0100000011	1001000000	0000????00
	00?0010000	0030011100	000??01000	00021????		
Bethylidae	0000010000	1000000000	1100000010	0000000000	0010000000	0000010000
	0002010000	0000100002	1011200000	0000200100	22- -000010	1000000000
	0000000000	0000010000	0000000000	0102000001	0000000000	0000100000
	0000030000	1030010100	1010011110	100012010		
Chrysididae	0000000000	1100000000	0000001010	0000000000	0000000100	0001000000
	0002010000	0000000002	1001210000	0000100100	12- -000010	1000000000
	0000000000	0000010000	0000000000	0103001001	0001000001	1000100000
	0000030000	1000010100	1013011200	000011000		
Sclerogibbidae	0100000100	0020000010	1000000010	0010000001	1011000000	0010010000
	0001010000	0010000000	2001201000	0010200101	03- -000010	2001000000
	0000000000	0000010000	0001000000	0100000101	1001000000	0000101000
	0000030000	1030010100	1101012300	00021????		
Dryinidae	0000000000	0010000001	0000000011	0000000100	0000010000	0000000000
	0001010000	0000000000	2001220000	0000100110	03- -000010	1000000000
	0001000000	0000010000	0000000000	0100000001	0002000001	1000101000
	0000030000	1030020100	1102111300	000012010		
Embolemidae	0000000000	0010000001	0000011010	0200000101	0011000000	0020012000
	2001020000	0000000000	1001210000	0010100110	03- -000010	1000100000
	0000000000	0000010000	0002000000	0100000001	0002000001	1000100000
	0000030000	1030021100	1102121100	011112000		

Table IV (cont.)

Scolebythidae	0000000000	1010000000	0000000000	0010000000	0100100000	0000000000
	0000000000	0000000001	1001200000	0000200200	02- - 000010	1000000001
	0010000000	000000- - - -	- - - -000000	0100000001	0000000000	0000????00
	0000020000	1020010100	1000011000	00001????		
sphecids	0000000000	0000000100	0000000000	0000101010	0011000000	0100002000
	1000110001	0000001001	0000000000	0010000000	0000000000	0000000200
	2000020000	000000- - - -	- - - -000000	0000010000	0010000000	0000000001
	0000001000	0100001101	1008000000	000000000		
Heterogynaidae	0100000000	0000000100	0000000000	0000100010	0011010000	0100002000
	1000110001	0000001001	2001000002	0010110000	0200000010	0000100200
	2000010001	0020000000	0020000000	0000010000	?010000000	1000????0?
	???0000010	0120001100	100??00000			
apids	0001000000	0000000100	0010000000	0000101020	0011010000	0100102000
	1000111001	0000001001	0001000000	0010010000	0200000000	0000000100
	1001020000	0000000000	0000000000	0000020000	0012000001	10000100-2
	0000101000	0100021100	100-000300	000000000		
Anthoboscinae	0000000000	0000000100	0000000000	0000000001	0011000100	0000020000
	0010000000	0010000000	0000000000	0000000000	0110000101	0000000200
	2000000000	000000- - - -	- - - -000000	0000010000	0001000010	0000000100
	0000002000	0001001120	1000000000	000000000		
Thynninae	0100001000	0000000100	0000000000	0000000001	0011000100	0000020000
	0010000000	1011000001	0000000000	0000000000	0110001101	0000000200
	2000000001	0000001000	0000000000	0001020000	0101000000	0001000100
	0000002000	0011001120	1000000000	000100000		
Diamminae	0100000000	0000000100	0000000000	0000000001	0011000100	0000020000
	0010000000	1011000001	0000000000	0000000000	0110001101	0000000200
	2000000001	0000001100	0000000000	0001010000	0001000000	0000????01
	0000002000	0011001120	1004000000	00000????		

Table IV (cont.)

Myzininae	1000001000	0000000100	0000000000	0000000001	0011000100	0000020000
	0020000000	1011000001	1000000000	0000000000	0210000101	0000000200
	2000000000	0010001000	0000100000	0001010000	0000001000	0000000100
	0000002100	0011101120	1000000000	000200000		
Methochinae	1100001000	1001000100	0000000000	0000001001	0011000100	0000010000
	0010000000	0011000002	1000000010	0000000000	0210000100	0000000100
	1000000010	1000102000	0000000000	0001010000	0100001000	0000000100
	0010002100	0031101120	1000000000	000200000		
Tiphiinae	0000000000	0000000100	0000000000	0001001001	0011000100	0000020000
	1020010000	0012000001	1011000001	0000100000	0210000101	0000000200
	2000000001	000000- - - -	- - - -000010	0001010000	0102001001	1000000100
	0000002100	0011101120	1000000000	000200000		
Brachycistidinae	0100000000	0100010100	0000000000	0001001001	0011000200	0000020000
	1010010000	0011000001	1011000000	0000100000	0210010101	0000100200
	2001000001	0000003000	0000000010	0001010000	0102001001	1000????00
	00?0002000	0011101120	100??00000	00020????		
Fedtschenkiinae	0000010000	0000000100	1020000000	0000000001	0011000100	1000010000
	0010010000	0010000001	1000000000	0000010000	02-1001200	0000000200
	2000010001	000000- - - -	- - - -000000	0004010000	1001000000	0010????00
	00?0002000	0011001110	1005?00000	00000????		
Sapyginae	0000010001	0000000100	1010100000	0000000001	0011000100	1000010000
	0010000000	0010000000	0000000000	0000010000	02-1001200	0000000000
	0000000001	000000- - - -	- - - -000000	0000010000	1102000000	1010010000
	0000002000	0011001101	1005000000	000000010		
Myrmosinae	0100010000	0001000100	1100000000	0000000001	0011000100	2000011100
	0010010000	0010000000	2000000000	0000010000	02-1101200	0000000200
	2000000002	0000000020	0000001000	0001010000	0100000001	0010000100
	0010002000	0031101110	1005000000	000100000		

Table IV (cont.)

mutillids	0100010000	0000000100	1100000001	0001000001	0011000100	2001011100
	0110010000	0020000001	2001000000	0000110000	0200101200	0000000200
	2000000001	0000000011	0000101000	0001010000	0101000000	0010000100
	0010002000	0031101110	1005000000	000200000		
Sierolomorphidae	0000000000	0010000100	0000000000	0000001001	0011000100	0000010000
	0000010100	0010000001	1001000100	0000110000	0200001010	0000000100
	1000000001	0000000000	0000000000	0000010000	0000100001	0000????00
	00?0002001	0021001101	100??00000	00000????		
Pompilidae	0000000000	0000000100	0000000000	0000001001	0011000100	1000010100
	1000010100	0010000000	0000000000	0002010000	0200101100	0000000200
	2000010000	0100000000	0000000000	0000010000	1002000000	0000100101
	0100001000	0010001110	1006000000	000100100		
rhopalosomatids	0000000001	0010000100	0000000001	0000001101	0011010200	0000020100
	0000010201	0010000000	0000000000	0112110000	0200100100	0100000100
	1000000000	010000- - - -	- - - -000010	0000010000	0011000000	0000001000
	0000002002	0010101101	1007200000	000000001		
Olixon	0000000000	0010000100	0000000001	0010000001	0011010201	0000120100
	10100- - - -	- 010000002	1010000000	0222110002	02- - - - - - 0	0100000000
	0000000000	0200000000	0000002010	0000010000	0011000000	0000????00
	00000- - - -	- - 10101101	1007200001	0000-????		
Formicidae	0010000000	0010000100	0000000001	0001001201	0011010201	0000101000
	2020010000	0110000000	0000100000	0010010000	0200111100	0000000300
	3000000100	0001000000	0003000011	0001010000	0010000000	0000100011
	1001003000	0031101100	100?000000	000200000		
Scoliinae	0000100001	0000100100	0001000001	1002001201	0021010210	0001011010
	1020011010	0000011010	0011000000	0012100000	0200112101	0000102110
	1101010000	000000- - - -	- - - -000010	0001010000	0000020001	1100100002
	0000002003	0011101120	1000000000	000000120		

Table IV (cont.)

Proscoliinae	0000000000	0000100100	0000001001	1002001101	0011010210	0001011010
	1020000000	0000010011	1011000020	0011100000	0200112101	0000101110
	1100010000	000000- - - -	- - - -000010	0000010000	0000010010	1100??????
	?????02003	0011001120	1000000000	00000????		
Vespidae	0000100001	0000000100	0001000001	0103001201	0021010300	0000001100
	1020010000	0010000000	0100000000	0012000000	0200111100	0000100100
	1000000000	001000- - - -	- - - -000000	0001010000	1001000000	1000100012
	0001002003	0001201100	1000000000	000000100		
Eotillini	0101000000	0010010100	0000000000	0000000001	0011000200	0000101000
	1020000000	1000101102	0001000000	0000110000	0200100100	0010000100
	1000000001	0000000000	2000010111	1001010000	?011000000	0000????00
	00?00?????	??31101110	100??00000	00010????		
Typhoctini	0101000000	0010010100	0000000000	0000000001	0011000200	0000101000
	1020000000	0000101102	0001000000	0010100000	0200102110	0000000200
	2000000001	0000000000	2000010111	1001010000	1011000000	0000100200
	0000002100	0031101110	1009000000	00010?0?0		
Chyphotinae	0100010010	0100010100	1000000000	0000001101	0011000200	0000101000
	2020000000	0000101102	1001000000	0000110000	0200102101	0000000200
	3000000000	0000000000	1100010111	2021010000	1011000110	0000????00
	00?0002000	0031201110	100??00000	00010????		
Apterogyninae	0100010010	0100111100	1000000000	0000001101	0011001200	0000101000
	1120010000	0000101202	0002000000	1020200000	0200112101	0010010300
	3000011001	0000000000	1100010021	2011110000	0011000100	1000????00
	00?0002000	0011201110	100??00000	00010????		
Bradynobaeninae	0100011010	0000111100	1000010110	0000011101	0011002200	0000101001
	1120010000	0000101202	0112000000	2020201000	0200112101	0010120400
	4000112000	0000000000	1100020011	2011010000	1101000200	1000????00
	00?0003000	0031101110				
	100??00000	0001-????				

Table IV (cont.)

Notes:
Variable 7: Thynninae & Methochinae see Kimsey (1991); doubtfully correct (see above discussion of her paper).
Variable 10: Myzininae, Kimsey (1991) corrected.
Variable 11, 13: Scolebythidae corrected based on *Ycaploca*.
Variables 19-20: newly scored.
Variable 21: Fedtschenkiinae, Sapyginae, Brothers (1975) corrected.
Variables 23, 25: newly scored.
Variable 27: Sclerogibbidae, Embolemidae, Carpenter (1986) corrected.
Variable 29: Plumariidae see Carpenter (1986), Brothers (1975) corrected.
Variables 31, 32: newly scored.
Variable 33: newly scored; Plumariidae, Scolebythidae, Brothers (1975) corrected.
Variable 34: rhopalosomatids corrected based on *Liosphex*.
Variable 35: sphecids corrected based on Dolichurini.
Variables 38, 39, 41, 42: newly scored.
Variable 43: Bethylidae, Sclerogibbidae, Embolemidae, Carpenter (1986) corrected.
Variable 46: sphecids corrected based on Dolichurini.
Variable 53: newly scored.
Variable 56: Scoliinae, Brothers (1975) corrected.
Variables 57, 59: newly scored.
Variable 60: newly scored; Bradynobaeninae, Brothers (1975) corrected.
Variable 64: newly scored; Carpenter (1986) corrected.
Variables 66-71: newly scored; Brothers (1975) corrected.
Variables 73-76: newly scored; Brothers (1975) corrected.
Variables 80, 81: newly scored.
Variable 84: rhopalosomatids corrected based on *Liosphex*.
Variable 85: Scolebythidae see Carpenter (1986); *Olixon* postulated condition from which State 1 of Variable 92 derived.
Variables 87, 89, 90, 92: newly scored.
Variable 93: Pompilidae see Rasnitsyn (1980).
Variable 94: newly scored.
Variable 96: Olixon postulated condition from which State 2 of Variable 98 derived.
Variables 98-102: newly scored; Brothers (1975) and Carpenter (1986) corrected.
Variables 103, 104: mutillids, Myrmosinae, Brothers (1975) corrected.
Variable 105: Formicidae, Scoliinae, Proscoliinae, Vespidae, Apterogyninae, Bradynobaeninae postulated condition from which State 1 of Variable 106 derived in these taxa.
Variable 108: Typhoctini postulated condition from which State 1 of Variable 109 derived.
Variables 110-112, 114: newly scored.
Variable 115: Vespidae see Carpenter (1981).
Variable 117: newly scored.
Variable 124: Embolemidae corrected, see Carpenter (1990a).
Variables 131-138, 143, 144, 147, 152, 154, 157-159: newly scored, and Brothers (1975) corrected.
Variable 161: Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae see Rasnitsyn (1980); Thynninae, *Olixon*, Proscoliinae newly scored; also see Quicke, Fitton & Ingram (1992).
Variable 164: Pompilidae, Brothers (1975) corrected.
Variables 166, 174: newly scored.
Variables 175-177: Bethylidae, Chrysididae, Dryinidae, Sclerogibbidae (derived state of Variable 175 assumed as precursor to derived state of Variable 177) see Evans (1987) and Stefani (1956); Embolemidae see Wharton (1989); Typhoctini unpublished information.
Variable 178: newly scored; Typhoctini unpublished information.

Table IV (cont.)

Variable 179: Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Typhoctini unpublished information; Plumariidae, Heterogynaidae, Sierolomorphidae (some females apterous, unpublished), Brachycistidinae, Eotillini, Chyphotinae, Apterogyninae and Bradynobaeninae apterous or brachypterous females highly unlikely to provision with more than one prey.

Variable 180: Diamminae, Scoliinae see Clausen (1940).

Variables 180-183: Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Typhoctini unpublished information; Plumariidae, Sierolomorphidae (some females apterous, unpublished), Brachycistidinae, Eotillini, Chyphotinae, Apterogyninae and Bradynobaeninae apterous females highly unlikely to relocate prey but Heterogynaidae (see Day 1984) may do so.

Variable 184: Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Typhoctini unpublished information; Plumariidae, Heterogynaidae, Sierolomorphidae (some females apterous, unpublished), Brachycistidinae, Eotillini, Chyphotinae, Apterogyninae and Bradynobaeninae apterous or brachypterous females highly unlikely to oviposit before prey located.

Variable 185: Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Typhoctini unpublished information; Plumariidae, Heterogynaidae, Sierolomorphidae (some females apterous, unpublished), Brachycistidinae, Eotillini, Chyphotinae, Apterogyninae and Bradynobaeninae apterous or brachypterous females highly unlikely to provision with plant material.

Variables 186-193: newly scored.

Variable 194: scored following Rasnitsyn (1980, 1988).

Variables 195-197: newly scored.

Variable 198: scored following Brothers (1975) and Rasnitsyn (1980) (not Rasnitsyn 1988).

Variables 199-202: newly scored.

Variable 203: newly scored, and see Carpenter (1986) and Rasnitsyn (1988).

Variable 204: newly scored; Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Chrysididae see Kimsey & Bohart (1990); Diamminae see Clausen (1940); sphecids see Iwata (1976); Typhoctini unpublished information; and see Carpenter (1986) and Rasnitsyn (1980, 1988).

Variable 205: newly scored; Dryinidae see Olmi (1984); Embolemidae see Wharton (1989); rhopalosomatids, *Olixon* see Townes (1977); and see Carpenter (1986).

Variables 206, 207: scored following Rasnitsyn (1980, 1988).

Variables 208-216: newly scored.

Variables 217-219: newly scored and see Evans (1987), Stefani (1956), Wharton (1989); Typhoctini unpublished information.

TableV. Data matrix for ground plans of families of Vespoidea other than those included as such in Table IV, using characters of Appendix VI. The ground-plan state of each variable is the relatively most plesiomorphic state found in any of the component taxa of the family, or the known state where states are unknown in some component taxa, unless otherwise specified in the Notes. Variables 32, 53, 57, 80, 81, 89, 90, 100, 133, 143, 144, 147, 154, 178, 190, 204, 205, 208 and 218 are nonadditive. A question mark (?) denotes missing data (state unknown in the taxon); a dash (-) denotes a taxon for which the variable is inapplicable.

Tiphiidae	0000000000	0000000100	0000000000	0000000001	0011000100	0000020000
	0010000000	0010000000	0000000000	0000000000	0110000101	0000000200
	2000000000	000000- - - -	- - - -000000	0000010000	0001000010	0000000100
	0000002000	0001001120	1000000000	000000000		
Sapygidae	0000010000	0000000100	1010000000	0000000001	0011000100	1000010000
	0010000000	0010000000	0000000000	0000010000	02-1001200	0000000100
	1000000001	000000- - - -	- - - -000000	0000010000	1001000000	0010010000
	0000002000	0011001110	1005000000	000000010		
Mutillidae	0100010000	0000000100	1100000000	0000000001	0011000100	2000011100
	0010010000	0010000000	2000000000	0000010000	0200101200	0000000200
	2000000001	0000000010	0000001000	0001010000	0100000000	0010000100
	0010002000	0031101110	1005000000	000100000		
Rhopalosomatidae	0000000000	0010000100	0000000001	0000000001	0011010200	0000020100
	0000010201	0010000000	0000000000	0111110000	0200100100	0100000100
	1000000000	010000- - - -	- - - -000010	0000010000	0011000000	0000001000
	0000002002	0010101101	1007200000	000000001		
Scoliidae	0000000000	0000100100	0000000001	1002001101	0011010210	0001011010
	1020000000	0000010010	0011000000	0011100000	0200112101	0000101110
	1100010000	000000- - - -	- - - -000010	0000010000	0000010000	1100100002
	0000002003	0011001120	1000000000	000000120		
Bradynobaenidae	0100000000	0000010100	0000000000	0000000001	0011000200	0000101000
	1020000000	0000101102	0001000000	0000100000	0200101100	0000000100
	1000000000	0000000000	1000010011	1001010000	0011000000	0000100200
	0000002000	0021101110	1009000000	00010?0?0		

Notes:

Tiphiidae: Variables 56, 110, 118, 121: states in Methochinae considered reversals.

Sapygidae: Variables 118, 121: ground plan states considered intermediate between states in subfamilies. Variable 199: state in Sapyginae considered reversal.

Rhopalosomatidae: Variables 118, 121: states in *Olixon* considered reversals.

Bradynobaenidae: Variable 107: ground-plan state considered intermediate between states in components. Variable 163: state in Bradynobaeninae considered reversal. Variable 193: ground-plan state considered intermediate between states in components.

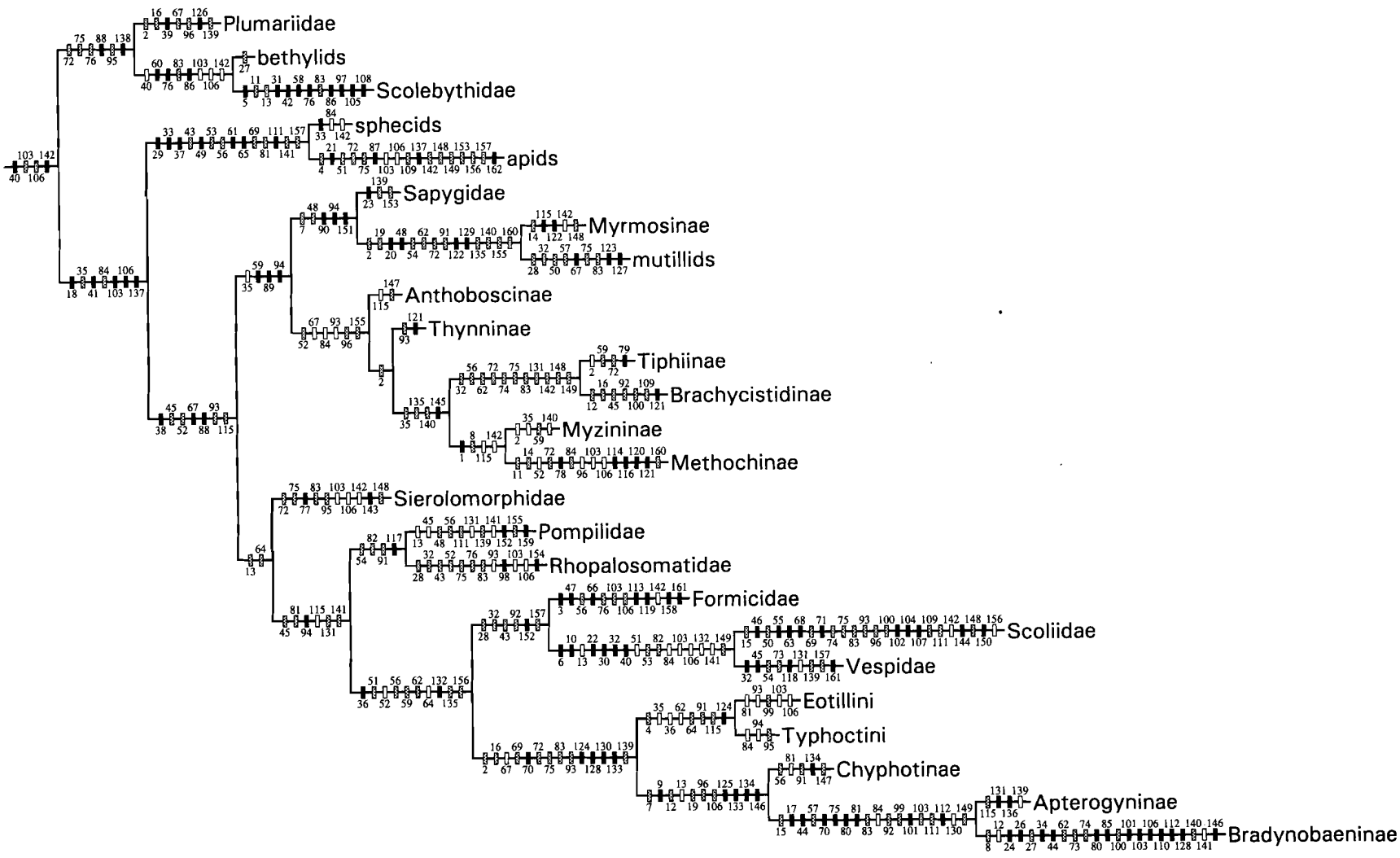


Fig. 1. Cladogram of Aculeata from Brothers (1975: Fig. 2), with distribution of variables based on scoring in Table III plotted using accelerated transformation option of Clados (Nixon 1992), except using delayed transformation for variables considered unlikely to show reversals (length 408, consistency index 0.51, retention index 0.62); state changes determined by Brothers (1975) and those plotted by Clados (translated into codes originally used by Brothers) given in

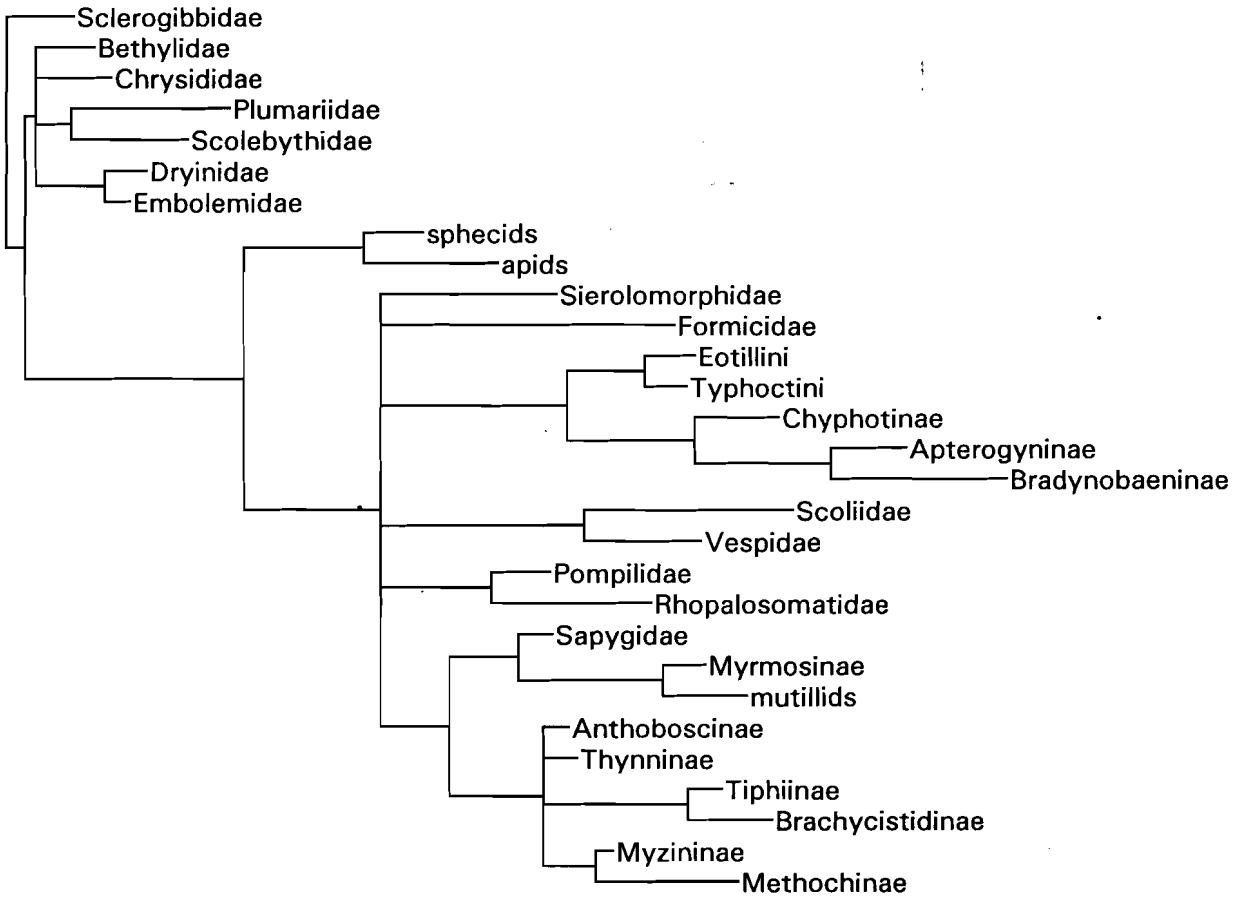


Fig. 2. Phylogeny of Aculeata after Königsmann (1978: Figs. 4, 13).

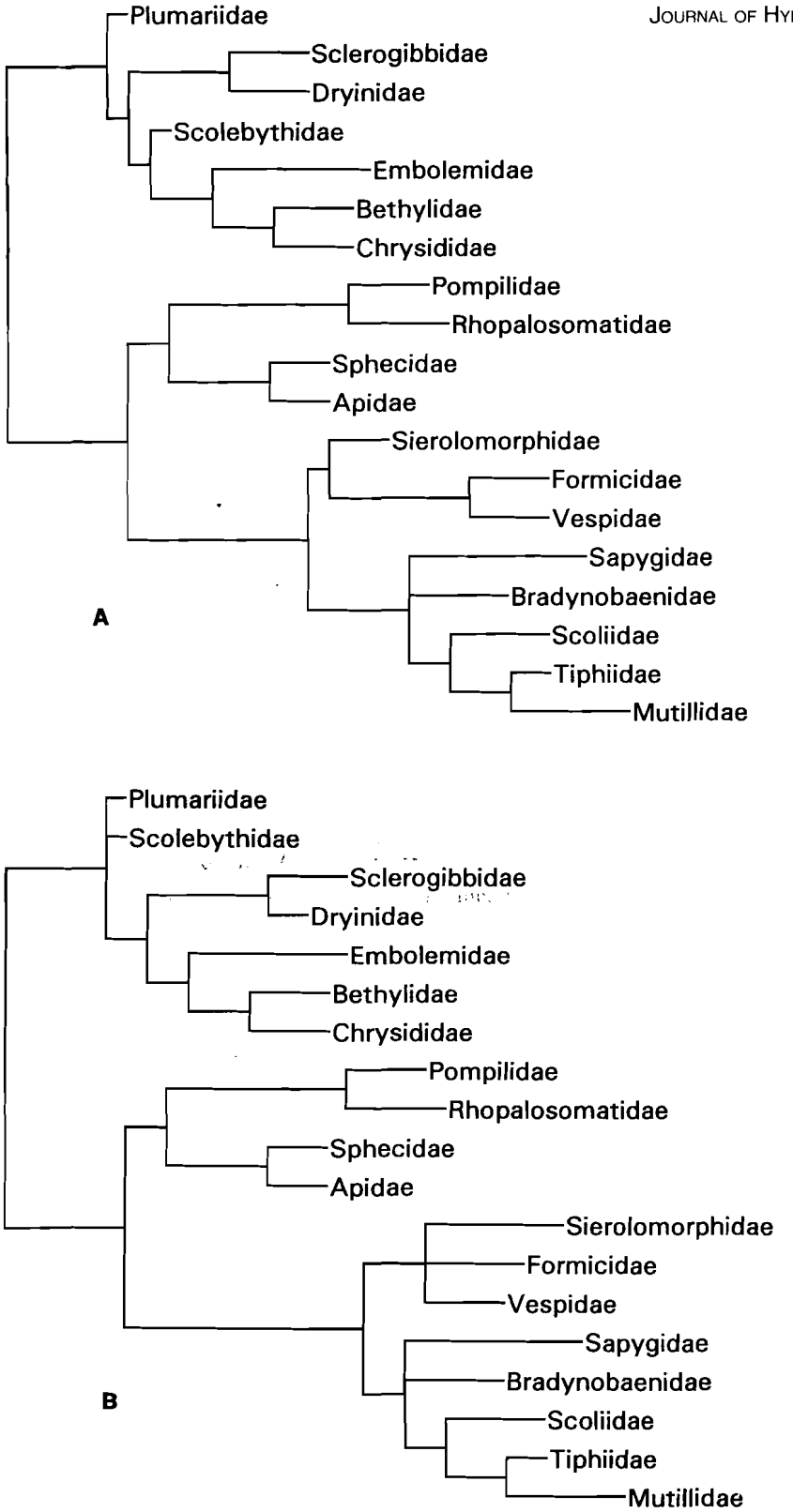


Fig. 3. Phylogenies of Aculeata from Rasnitsyn (1980) (consistency index 0.62, retention index 0.77 based on scoring in Table I). 3a. After his Fig. 38 (length 115). 3b. Based on discussion in text which implied less resolution than shown in his figure (length 116). Character hashmark shading: black=unique derivation; grey=convergent derivation; open=reversal (unique or convergent).

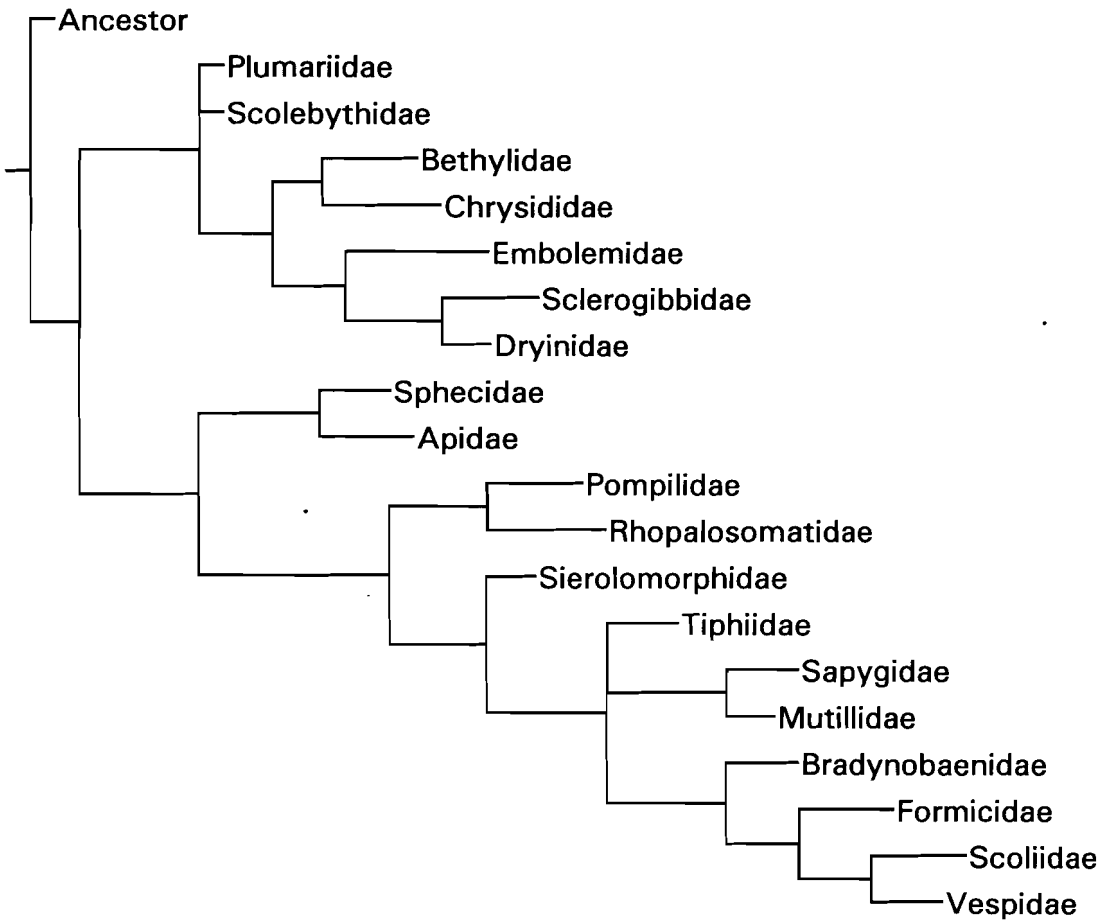


Fig. 4. Strict consensus tree for three cladograms of Aculeata based on characters and states from Rasnitsyn (1980) (as coded in Appendix II and scored in Table I) resulting from exact analysis by implicit enumeration (length 94, consistency index 0.76, retention index 0.88) and stable to successive approximations character weighting as implemented in Hennig86.

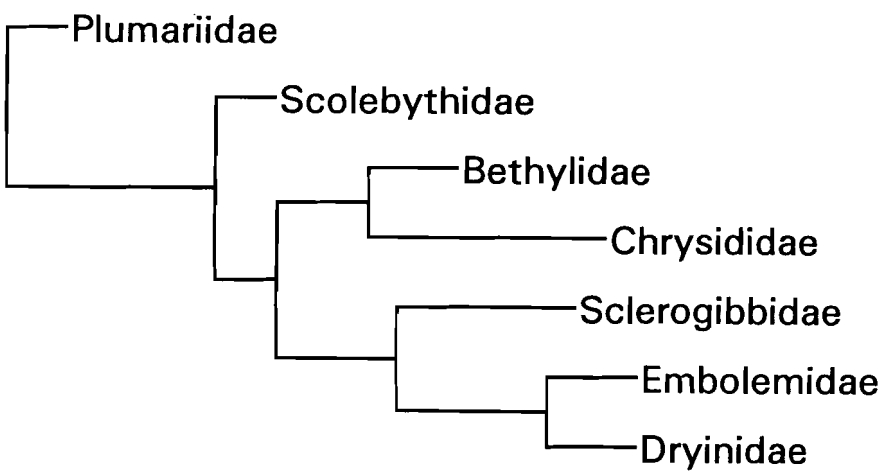


Fig. 5. Cladogram of Chrysidoidea from Carpenter (1986: Fig. 4).

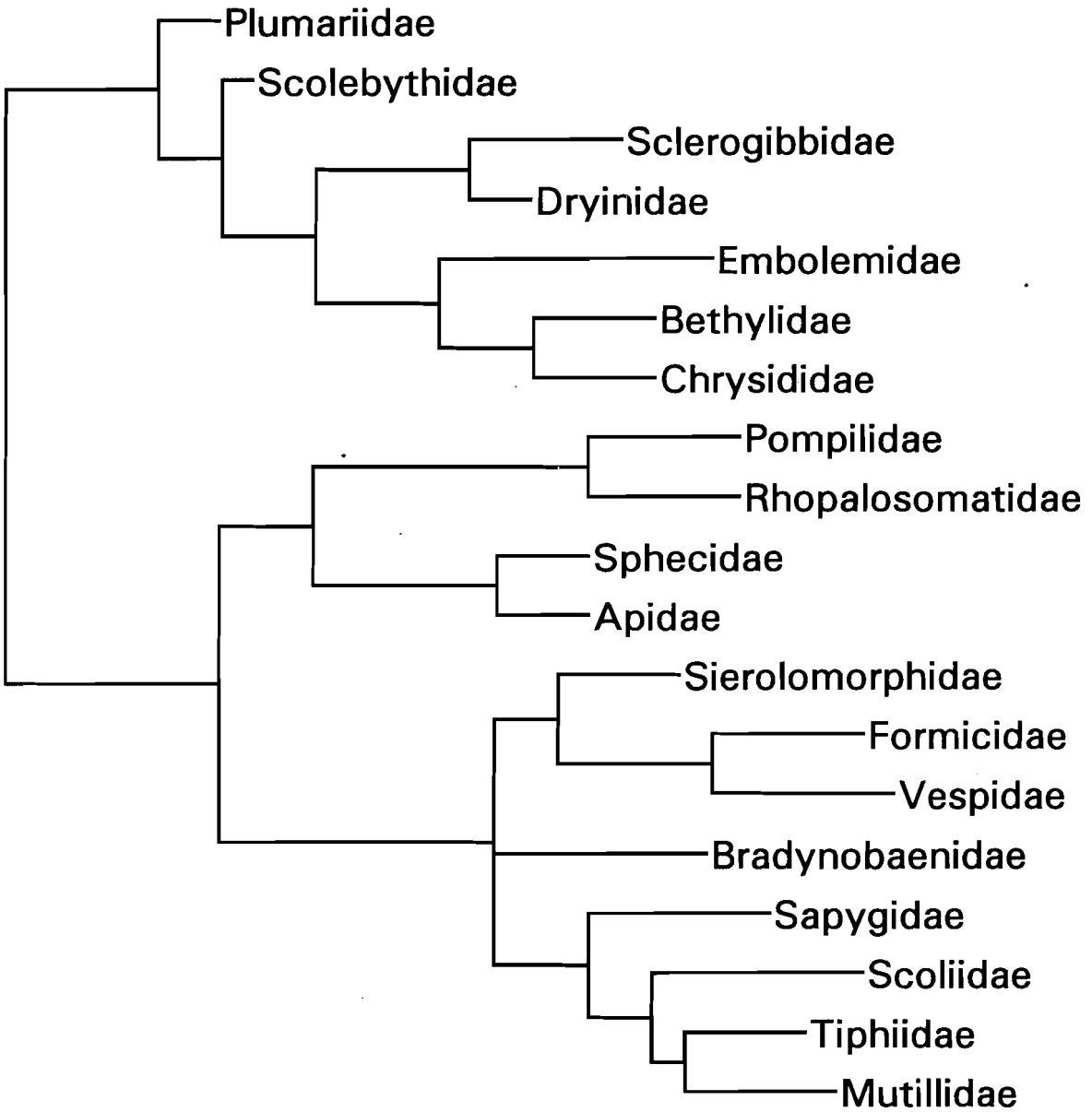


Fig. 6. Phylogeny of Aculeata from Rasnitsyn (1988: Fig. 4); ambiguous position of Bradynobaenidae indicated as a trifurcation (length 132, consistency index 0.63, retention index 0.78 based on scoring in Table II).

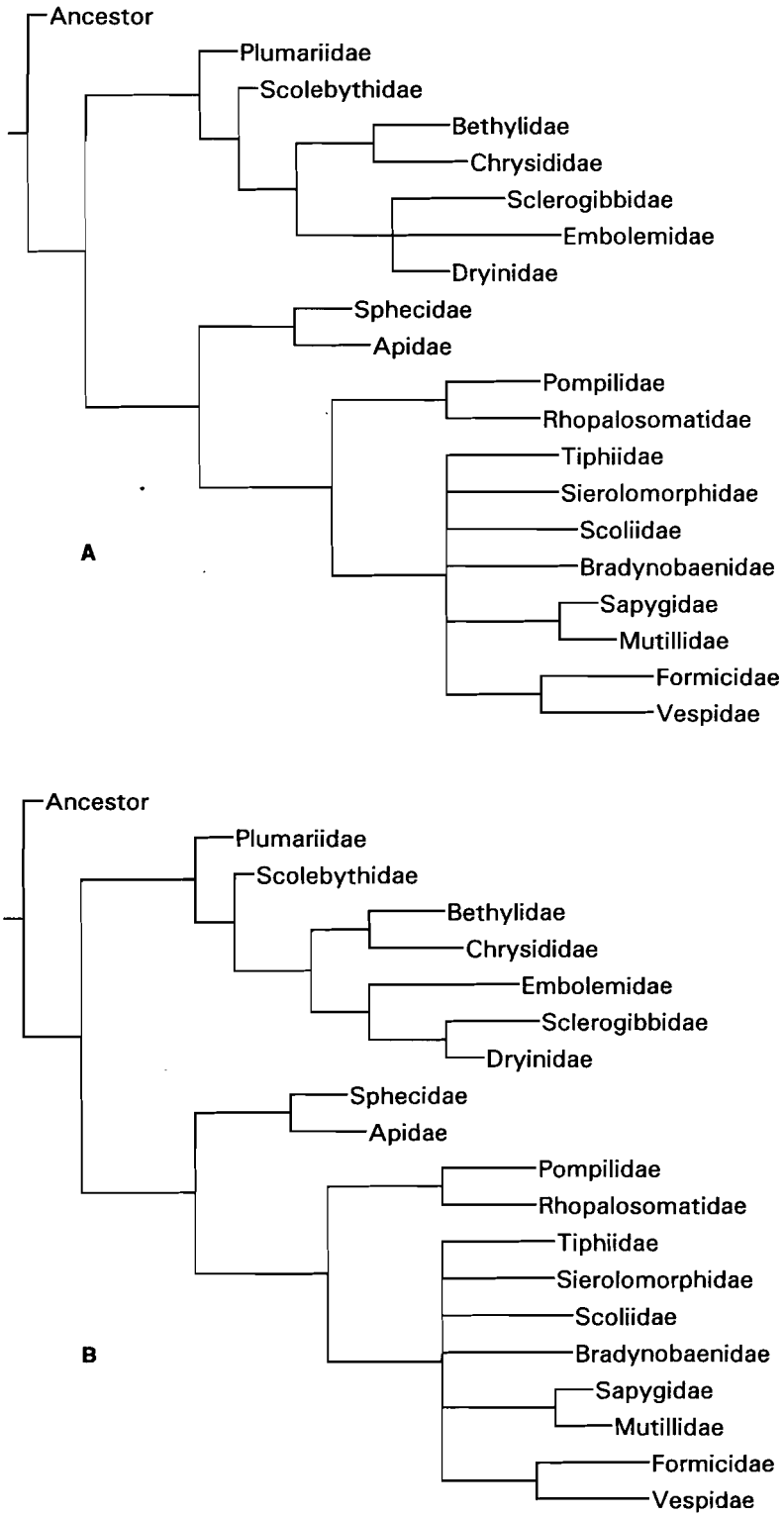
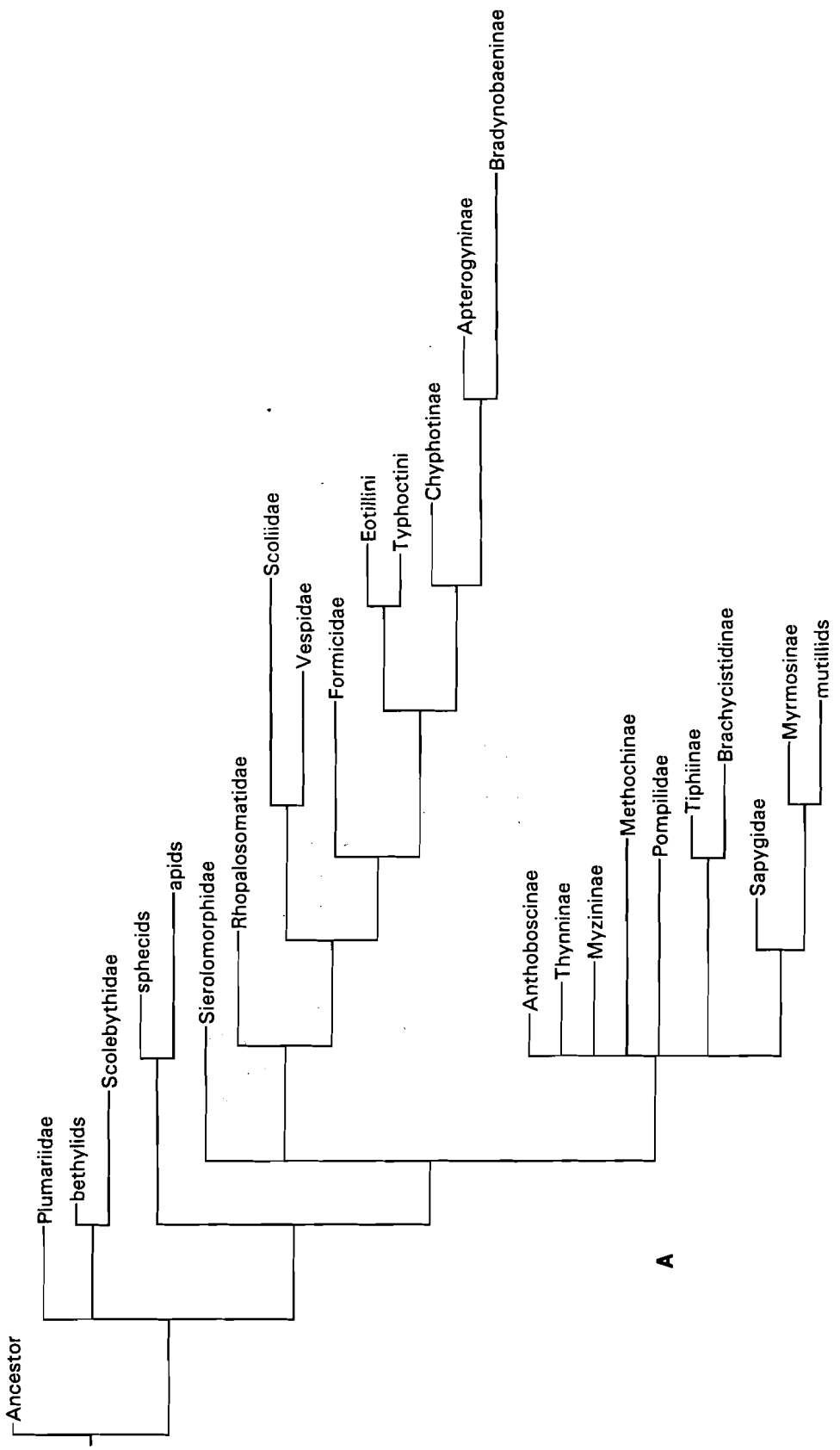


Fig. 7. Results of analysis of characters and states for Aculeata from Rasnitsyn (1988), as coded in Appendix III and scored in Table II. 7a. Strict consensus tree for six cladograms resulting from exact analysis by implicit enumeration (length 118, consistency index 0.71, retention index 0.84). 7b. Strict consensus tree for two cladograms resulting from successive approximations character weighting (weighted length 684); these two cladograms are among the initial six.


Ancestor
Plumariidae
bethylids
Scolebythidae
sphecids
apids
Sierolomorphidae
Rhopalosomatidae
Scoliidae
Vespidae
Formicidae
Eotillini
Typhoctini
Chyphotinae
Apterogyninae
Bradynobaeninae
Anthoboscinae
Thynninae
Myzininae
Methochinae
Pompilidae
Tiphiinae
Brachycistidinae
Sapygidae
Myrmosinae
mutillids
A

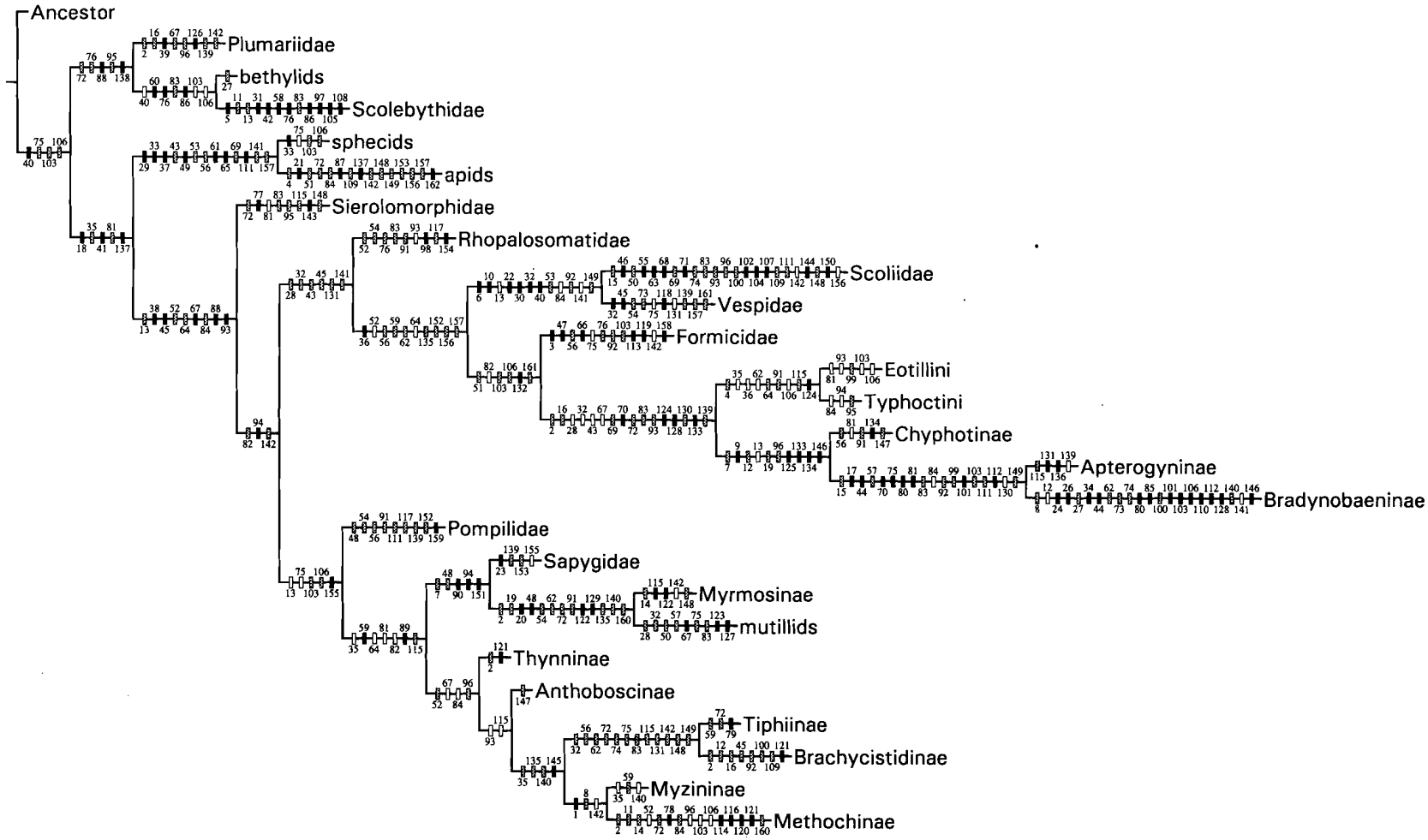
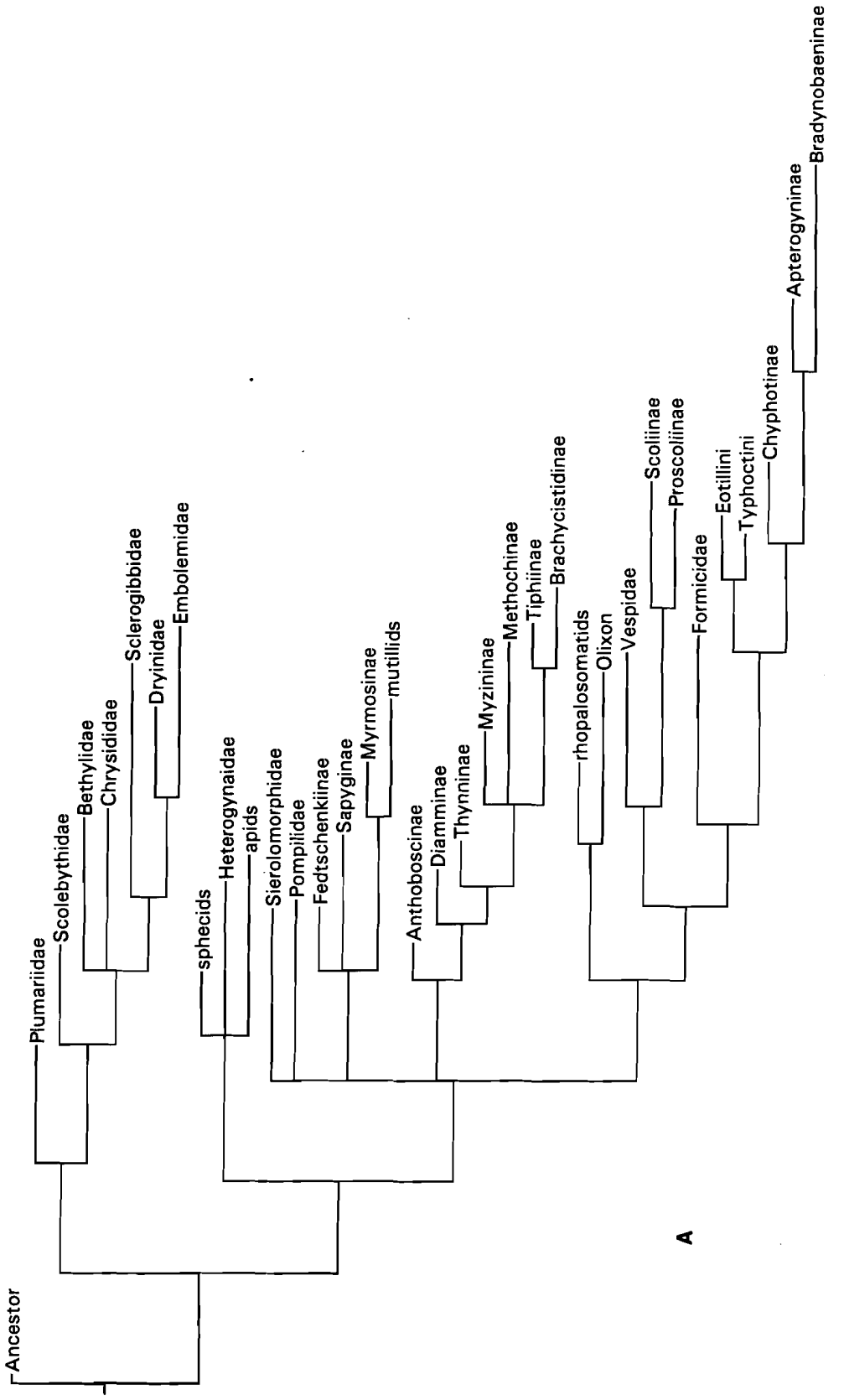


Fig. 8. Results of analysis of characters and states for 25 taxa of Aculeata from Brothers (1975), as coded in Appendix IV and scored in Table III. 8a. Strict consensus tree for eight cladograms resulting from approximate analysis by multiple tree searching with extended branch swapping (length 401, consistency index 0.52, retention index 0.64). 8b. Preferred cladogram (see text) of two produced by successive approximations character weighting (both are among the initial eight; weighted length 1463); state changes given in Appendix V. Character hashmark shading: black = unique derivation; grey = convergent derivation; open = reversal


Ancestor
Plumariidae
Scolebythidae
Bethylidae
Chrysididae
Sclerogibbidae
Dryinidae
Embolemidae
sphecids
Heterogynaidae
apids
Sierolomorphidae
Pompilidae
Fedtschenkiinae
Sapyginae
Myrmosinae
mutillids
Anthoboscinae
Diamminae
Thynninae
Myzininae
Methochinae
Tiphiinae
Brachycistidinae
rhopalosomatids
Olixon
Vespidae
Scoliinae
Proscoliinae
Formicidae
Eotillini
Typhoctini
Chyphotinae
Apterogyninae
Bradynobaeninae
A

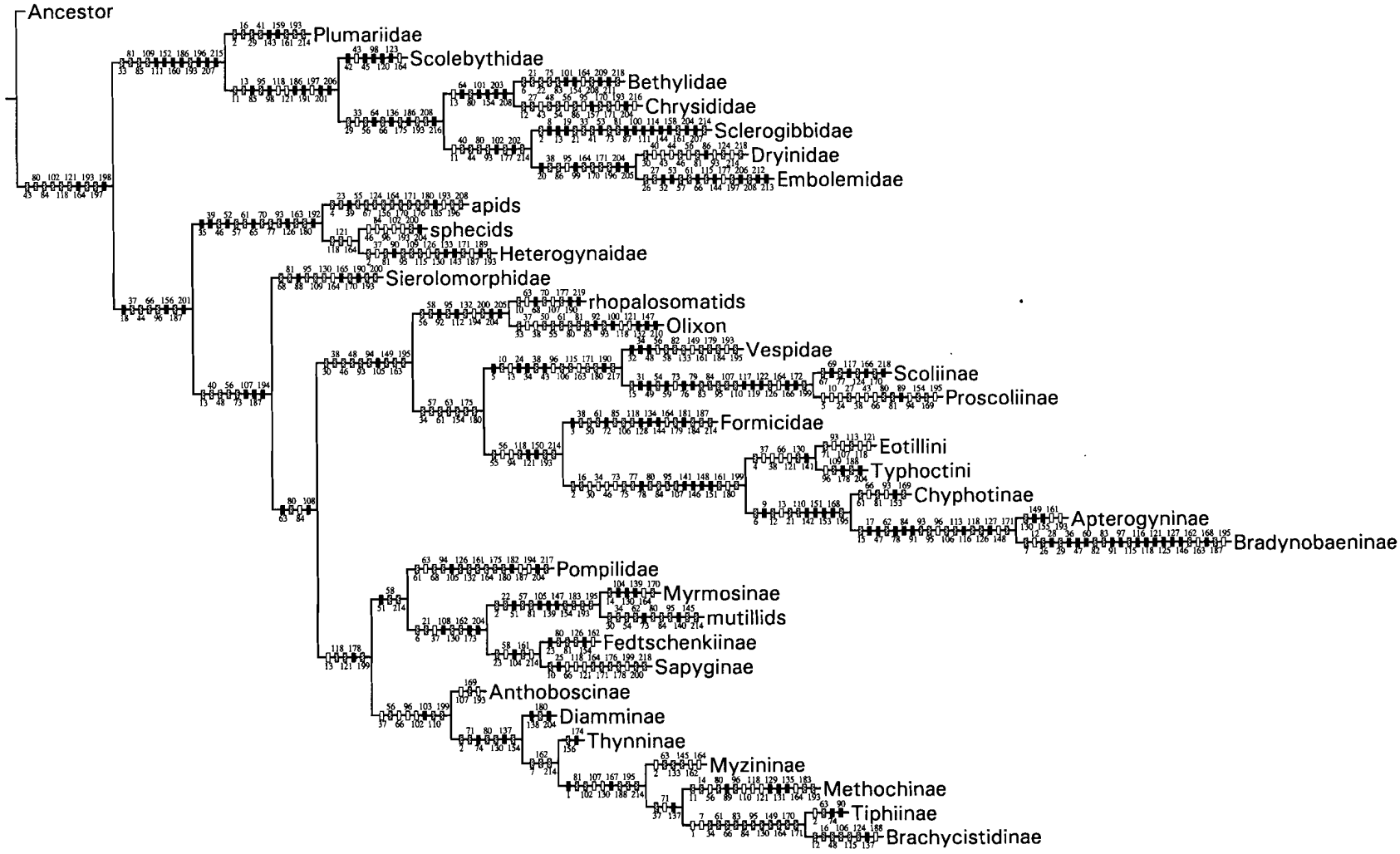
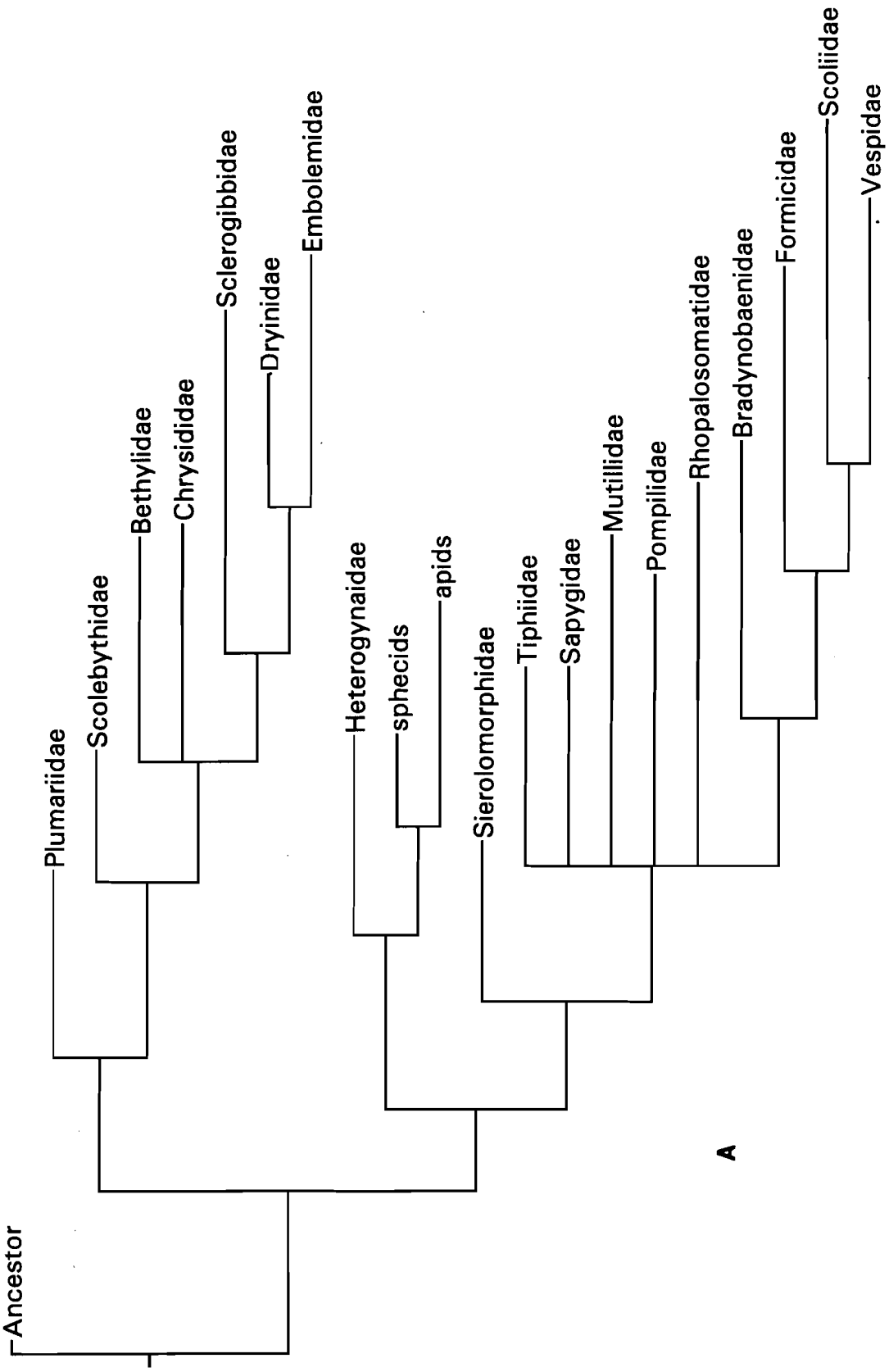


Fig. 9. Results of analysis of characters and states for 34 taxa of Aculeata, as coded in Appendix VI and scored in Table IV. 9a. Strict consensus tree for 64 cladograms resulting from approximate analysis by multiple tree searching with extended branch swapping (length 689, consistency index 0.46, retention index 0.66). 9b. Preferred cladogram (see text) of two produced by successive approximations character weighting (only this one is among the initial 64; weighted length 2173); state changes given in Appendix VII. Character hashmark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent).


Ancestor
Plumariidae
Scolebythidae
Bethylidae
Chrysididae
Sclerogibbidae
Dryinidae
Embolemidae
Heterogynaidae
sphecids
apids
Sierolomorphidae
Tiphiidae
Sapygidae
Mutillidae
Pompilidae
Rhopalosomatidae
Bradynobaenidae
Formicidae
Scoliidae
Vespidae
A

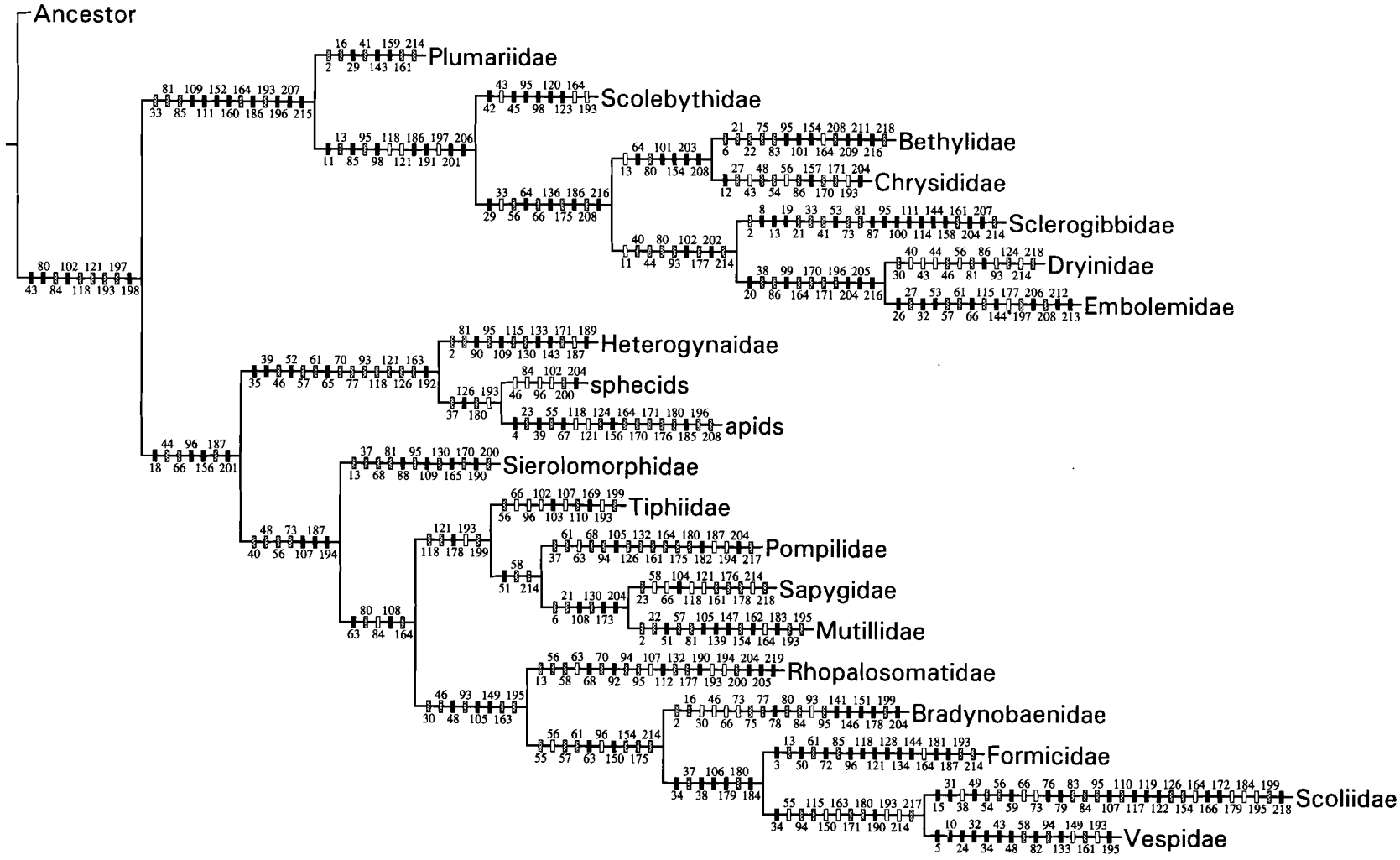


Fig.10. Results of analysis of characters and states for 20 family groundplans of Aculeata, as coded in Appendix VI and scored in Tables IV and V. 10a. Strict consensus tree for four cladograms resulting from approximate analysis by multiple tree searching with extended branch swapping (length 467, consistency index 0.54, retention index 0.63). 10b. Preferred cladogram (see text) of two produced by successive approximations character weighting (only this one is among the initial four; weighted length 1701);state changes given in Appendix VIII. Character hashmark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent).

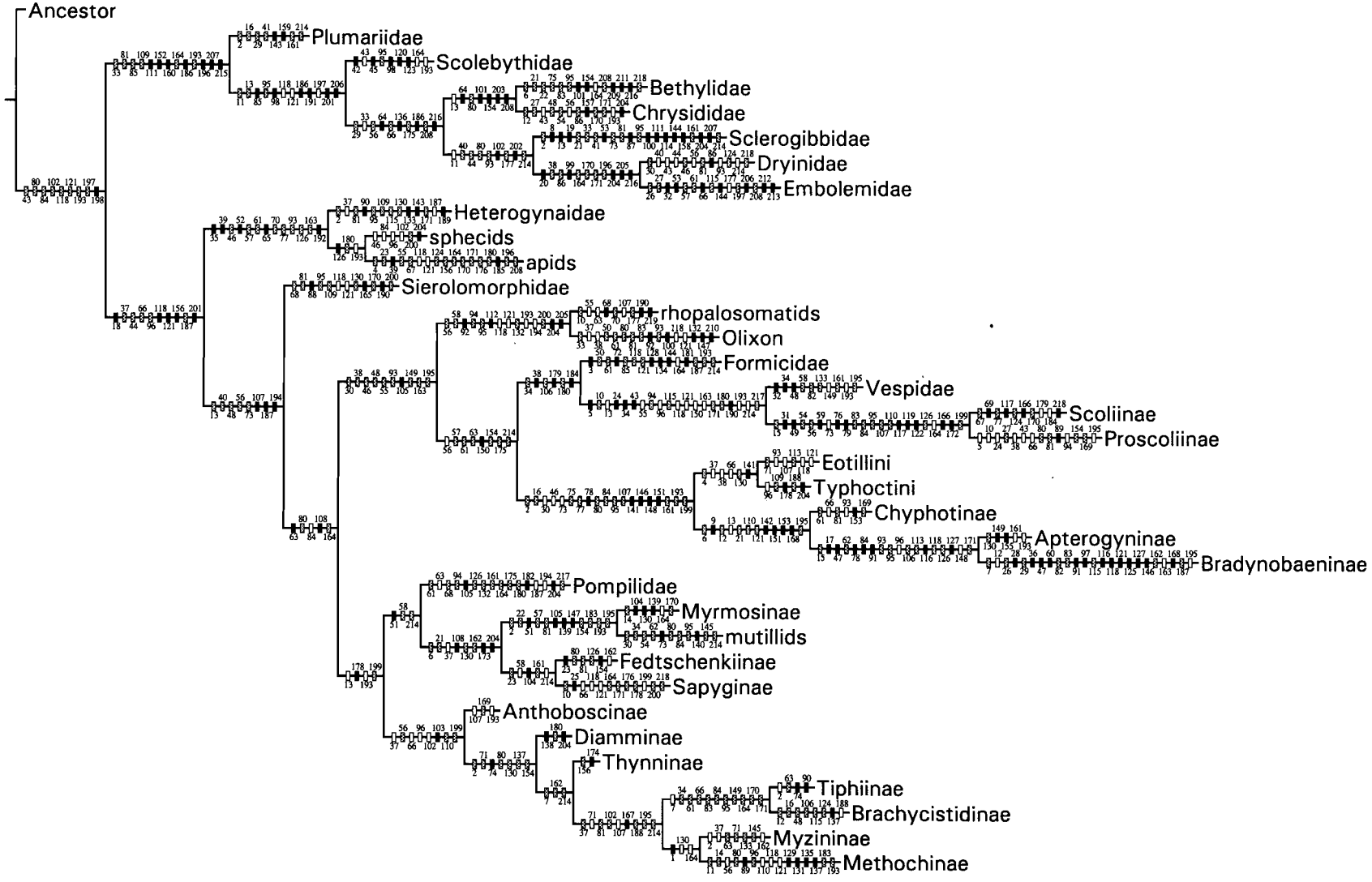


Fig. 11. Composite cladogram based on preferred results (see text) of all analyses of Aculeata (length 692, consistency index 0.46, retention index 0.65); state changes given in Appendix IX. Character hashmark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent).