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PHYLOGENETIC STUDY OF APOCRITA (HYMENOPTERA) WITH EMPHASIS ON WING VENATION

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May 1995

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfilment of the degree requirements of the degree of
Master of Science.

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Short title: **Phylogeny of Apocrita (Hymenoptera) with emphasis on wing venation**

ABSTRACT:

A phylogenetic character analysis of the wing venation within Apocrita (Hymenoptera) was conducted in order to examine the phylogenetic significance of wing characters. The venational data were then combined with published studies of other character suites to produce a hypothesis of phylogenetic relationships among apocritan superfamilies and families. Whereas the cladograms obtained from the collection of papers on character suites provide strong support for the sister group relationship between Orussidae and Apocrita, the ones derived from wing venation did not establish such a relationship, although they provided more support for relationships within Apocrita. A ground plan is proposed for the wing venation of each taxon examined; for Apocrita, it is close to the groundplan established for Aculeata. The variability of wing venation is higher between and within apocritan taxa than in Symphyta. This research confirms that groupings such as the Symphyta, Siricoidea, Evanioidea and possibly the Proctotrupoidea are artificial.

RÉSUMÉ:

Cette étude compare la nervation alaire des taxons d'Hyménoptères apocrites ainsi que des Symphytes afin d'en établir l'importance phylogénétique. Ces données sur la nervation alaire permirent d'établir différents arbres phylogénétiques qui furent comparés à ceux provenant d'autres groupes de caractères. Ces données, une fois combinées, ont permis d'établir une hypothèse globale basée sur des groupes de caractères. Bien que ces derniers produisent des résultats permettant de supporter la relation groupe soeur entre Orussidae et Apocrita, les cladogrames dérivant des matrices de données sur la nervation alaire possèdent une meilleure résolution parmi les familles d'apocrites. Les caractéristiques de base des ailes des différents groupes sont décrites et celles des Apocrites demeurent très proches de celles des Aculéates. La nervation alaire varie plus chez les Apocrites que chez les Symphytes. Les résultats de cette recherche confirment que les regroupements comme les Symphytes, Siricoidea, les Evanioidea et possiblement les Proctotrupoidea sont artificiels.

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INTRODUCTION:

The Hymenoptera is a large and highly diversified group of insects and its phylogeny remains poorly known; the phylogeny of most taxa and characters is not well substantiated. Even the definitions of some families or superfamilies are uncertain; although the classification used by Huber (1993) is used in this paper, some taxa are of dubious monophyly. The following is a list of the taxa recognized by Huber (1993); the newly described family (in parentheses) was not included in the present analysis. Superfamilies whose monophyly are weakly supported are indicated with an asterisk.

Since the first attempt to establish a family level phylogeny of Hymenoptera, undertaken by Ashmead (1895), the situation has improved. Authors such as Börner (1919), Koenigsmann (1976, 1977, 1978a, 1978b), Malyshev (1968) and Rasnitsyn (1975, 1980, 1988) have made it possible to construct a phylogenetic tree that is based more on empirical data than on personal impressions. These authors have proposed different and competing hypotheses of hymenopteran phylogeny. New studies are resolving more relationships and thus, group by group, hymenopterists are getting closer to unveiling the phylogeny of the Hymenoptera.

The studies cited above were based on a broad spectrum of characters. In-depth research on characters must be conducted in order to determine polarity and character state order. Other authors have produced studies on the comparative morphology of a character suite of some apocritan taxa and have used these data for phylogenetic inferences (see the literature review, analyses of character suites for more details). Non-morphological character suites have also been used; the cleaning behaviour of several hymenopteran taxa was examined by Farish (1972) and more recently, a number of papers have been based on genetic analysis (Deer

Table 1: Taxa recognized by Huber (1993)

Xyeloidea*
- Xyelidae

Megalodontoidea
- Megalodontidae
- Pamphilidae

Tenthredinoidea
- Tenthredinidae
- Blasticotomidae
- Argidae
- Pergidae
- Diprionidae
- Cimbicidae

Siricoidea*
- Siricidae
- Anaxyelidae
- Xiphydriidae

Cephoidea
- Cephidae

Orussoidea
- Orussidae

Symphyta

Chrysidoidea
- Chrysididae
- Dryinidae
- Embolemidae
- Sclerogibbidae
- Scolebythidae
- Plumariidae
- Bethylidae

Vespoidea
- Vespidae
- Scoliidae
- Rhopalosomatidae
- Tiphiidae
- Mutillidae

Bradynobaenidae
Sierolomorphidae
Formicidae
Sapygidae

Aculeata

Apoidea
Apidae
Anthophoridae
Megachilidae
Fideliidae
Andrenidae
Ctenoplectidae
Melittidae
Oxaeidae
Halictidae
Colletidae
Sphecidae
Ampulicidae
Heterogynaidae
Pemphredonidae
Nyssonidae
Mellinidae
Philanthidae
Crabronidae
Astatidae

Ichneumonoidea
Ichneumonidae
Braconidae

Trigonalioidea
Trigonalidae

Megalyroidea
Megalyridae

Stephanoidea
Stephanidae

Evanioidea*
Evaniidae
Aulacidae

Gasteruptiidae

Cynipoidea
    Cynipidae
    Ibaliidae
    Figitidae
    Liopteridae
    Eucoilidae
    Charipidae

Proctotrupoidea*
    Proctotrupidae
    Pelecinidae
    Heloridae
    (Renyxidae)
    Roproniidae
    Monomachidae
    Austroniidae
    Peradeniidae
    Vanhorniidae
    Diapriidae

Ceraphronoidea
    Ceraphronidae
    Megaspilidae

Platygastroidea
    Platygastridae
    Scelionidae

Chalcidoidea
    Chalcididae
    Pteromalidae
    Leucospidae
    Torymidae
    Trichogrammatidae
    Mymaridae
    Signiphoridae
    Encyrtidae
    Aphelinidae
    Eupelmidae
    Tanaostigmatidae

Terebrantia
(Parasitica,
parasitic
wasps)

Apocrita

    Elasmidae
    Rotoitidae
    Agaonidae
    Tetracampidae
    Eucharitidae
    Perilampidae
    Ormyridae
    Eulophidae
    Eurytomidae

Mymarommatoidea
    Mymarommatidae

et al, 1992a and 1992b; Dowton and Austin, 1994). Each of these papers on specific character suites is discussed in the following section. The more general studies presented in the paragraph above are not criticized in the next section because the emphasis is placed on those which treat specific character suites.

Phylogenetic research using a specific character suite does not replace the more general studies, but it does allow us to obtain a better understanding of the phylogeny of particular character suites so that these can in turn be used to test existing hypotheses or added to a large data set in order to contribute to a broader understanding of the phylogeny of the taxa studied.

Wing venation is an easy character suite to study because no extensive dissection is needed and the veins are often better preserved than many other body characters in fossils. The main problem with the use of wing venation has been its assumed lack of reliability in phylogenetic studies for high taxonomic levels (family and superfamily); most scientists assume that it is too variable (showing many convergences) because it is thought to be highly affected by the size of the insect. Furthermore, there is a tendency in phylogenetic analyses to believe that morphology and function can be separated and that only characters which are not affected by the latter should be used for such studies. It is, however, often impossible to separate these two aspects (Bigelow 1954a) and knowledge of the function of a character set can be used to interpret its different evolutionary tendencies in order to avoid erroneous homologies (Louis 1972).

Since venation is more extensive in Symphyta (outgroups) than in Apocrita, there seems to be a tendency for a loss of wing venation. Thus, the majority of apomorphies within the Apocrita may be due to reductions and losses in venation.

The main objective of this research is to add to the body of knowledge of apocritan characters that have stability in phylogenetic analysis, to investigate the trends in wing venation within the Apocrita, and to establish synapomorphies in the wing venation for various taxa of Apocrita.

LITERATURE REVIEW

This study is not the first one to treat a specific character suite, and a review of the others is necessary to understand the history of research on character suites, to compare the validity of venational characters and to present an account of the evidence related to apocritan phylogeny. The data from many of these references are used to create a data matrix (Tonapi 1958; Daly 1963; Robertson 1968; Richards 1972; Farish 1972; Iwata 1976; Johnson 1988; Whitfield et al. 1989; Quicke et al. 1992a, b; Quicke 1994; Heraty et al. 1994). The other references were not used for the data matrix because they did not include enough apocritan taxa in their studies or because their characters were poorly defined. Since this study has an emphasis on wing characters, previous papers treating wing characters are presented in a separate section. Finally, papers dealing with the phylogeny of the Apocrita, based on all characters, are introduced in the third section of the Literature Review.

ANALYSIS OF CHARACTER SUITES:

Baird (1921) presented a review of the literature published on the female reproductive organs of Hymenoptera. Although the number of taxa presented is relatively high for such an early analysis, much information is lacking on most of them and Baird did not attempt to verify the results of any cited author. D'Rozario (1940) examined the male and female internal reproductive organs of some hymenopteran taxa and provided a number of notes on their development. Later, Robertson (1968) described the venom apparatus of several hymenopteran taxa, including Symphyta. This study included few taxa of parasitic Hymenoptera and no phylogenetic conclusions can be drawn. The work of Togashi (1970) could not be obtained and is not included in the present analysis.

Liu (1925) examined the mouthparts in a wide array of taxa with his survey of the submentum and the shape of acroglossal buttons in most hymenopteran families recognized today. Liu found that the submentum is absent in most Apocrita as well as in Orussidae.

Schmieder (1928) investigated the fat bodies of a few Hymenoptera in detail and produced a table of character states for the albuminoid spheres, based on his data and those of other authors. The paucity of hymenopteran taxa included in his study does not allow any conclusions to be made concerning the phylogeny of these taxa, Schmieder however, was able to find a few ground plan characters for Hymenoptera.

Thorough reviews of head characters, especially the face, were undertaken by DuPorte and Bigelow (1953) and Bigelow (1954a, b). Many taxa were studied and the conclusions were relatively similar: most characters of the face are homoplastic and/or continuously variable and little phylogenetic information can be retrieved.

Maxwell (1955) examined the internal larval anatomy of sawfly larvae and produced a tree of Symphyta using her data as well as other morphological characters of adults and larvae. A number of characters, such as the structure of the salivary glands, seem to offer promise and it would be interesting to investigate them in Apocrita.

Tonapi (1958) examined the respiratory system of several Hymenoptera in great detail, but few parasitic groups were included. The thoracic spiracular structures were reexamined by Richards (1972) who included more parasitic taxa and more details about surrounding sclerites than Tonapi.

The thorax is the most intensively studied body part. Daly (1963) made a comprehensive study of the thoracic muscles of the Hymenoptera, but again, included few parasitic taxa. He also discussed the evolutionary trends of muscle structure in insects, but the paper concentrated mainly on comparative morphology and not phylogeny.

Malyshev (1968) compared different hypotheses of the evolution of the biology of the Hymenoptera. A number of theories were discussed in detail, but little consensus was established because too much information was lacking on specific taxa. A comparative study of the biology of Hymenoptera was also undertaken by Iwata (1976); the author placed the emphasis on the Aculeata but presented a substantial number of biological details of parasitic wasps. Whitfield (1992) presented a review of previous research of higher level phylogenetic studies of Hymenoptera, highlighting biological traits such as the type of parasitism (endo or exoparasitic) and the presence of viruses associated with oviposition.

Farish (1972) conducted a behavioral study of the grooming behavior of most families of Hymenoptera. Several branches of the tree suggested by the author are not supported by his data. Cephidae, for example, was shown as the sister group of Apocrita although it was not studied and his hypothesis infers that three characters are convergent between Siricidae and Apocrita thus increasing the number of steps in his tree.

Saini and Dhillon (1979a) surveyed the galea and lacinia in a number of Hymenoptera, but only included Chalcidoidea and Ichneumonoidea as parasitic groups. Their claim to have a representative from all the superfamilies of Apocrita is incorrect and the conclusions of their paper are not supported by their data. Similar comments would apply to their paper on glossal and paraglossal characters (Saini and Dhillon 1979b).

Shcherbakov (1980, 1981) studied the meso and metapleura of Hymenoptera. These works are important because they shed light on the phylogeny of some characters and provide arguments that suggest the phylogenetic relationships of some of the major groups of Hymenoptera. Thoracic characters were reviewed later by Gibson (1985), who settled some controversies regarding some phylogenetic relationships and the nomenclature of thoracic musculature and sclerites. The relationships presented in the text, such as the sister group relationship between Ceraphronidae and Megaspilidae (which was originally suggested by Masner and Dessart, 1967), as well as that between (Xiphydriidae (Orussidae + Apocrita)) are clearly demonstrated, although apocritan taxa are generally unresolved by this character set.

Darling (1988) examined the labrum of some parasitic Hymenoptera in detail and established the ground plan for Apocrita and Chalcidoidea, as well as for the order itself.

Johnson (1988) examined the midcoxal articulations of recognized taxa of Apocrita and concluded that only some groupings could be confirmed by this work. The Evaniomorpha and Ichneumonomorpha (sensu Rasnitsyn 1980) are shown to be monophyletic based on two characters: the shape of the coxal cavity and mesal lobes. Other relationships were not elucidated by Johnson's character set.

Whitfield et al. (1989) studied the metapostnotum of most hymenopteran families and found that it was a useful character suite to elucidate the relationships of Symphyta (including Orussidae), but not for non-aculeate Apocrita because the basal lineages of each family are relatively plesiomorphic.

They found that the medially divided metapostnotum is a synapomorphy of Siricoidea + Cephidae.

Leluk et al. (1989) compared the protein components of hymenopteran venom for several apocritan taxa (especially Aculeata). Few parasitic taxa were studied. The authors concluded that the relationship between ants and parasitic Hymenoptera is closer than that between bees or vespid wasps and the non-aculeate Apocrita, based on the immunological composition of the venom of these insects. Piek (1990) did similar research, but restricted his investigation to the Aculeata, using Braconidae as an outgroup. The suggested relationships of some taxa of Aculeata is interesting, but does not fit the scope of the present study which concentrates on parasitic Hymenoptera.

Quicke et al. (1992a) reviewed sperm structure and ultrastructure in the Hymenoptera. They produced a table of 13 characters which were neither polarized nor used to produce a phylogenetic tree.

The ovipositor valvilli were examined by Quicke et al. (1992b) and since they exist only in Aculeata and Ichneumonoidea, this character supports the monophyly of this assemblage, as first suggested by Rasnitsyn (1980). Quicke et al. (1994) examined ovipositor cross-sections of a large number of taxa and found nine characters of potential phylogenetic importance.

Heraty et al. (1994) studied the mesofurca and produced a data matrix that was used to test Rasnitsyn's (1988) hypothesis. This character set seems to be more informative for the study of Symphyta than Apocrita since most characters are plesiomorphic for most taxa within the latter group. When I tested their data with Hennig86 (Farris 1988), a nelson consensus tree showed a high resolution for most Symphyta, but none for Xiphydriidae + (Orussidae + Apocrita), except for Ceraphronidae and Megaspilidae (resolved as sister groups).

Crozier (1977) was the first to examine the possibility of using genetic information to investigate the phylogeny of the Hymenoptera and he concluded that such a work might be difficult partly because of haplo-diploidy.

Derr et al. (1992a, b) were the first to attempt to investigate the phylogeny of a few hymenopteran taxa using nucleotide sequence data of the 16S mitochondrial rRNA. Dowton and Austin (1994) proposed a phylogenetic hypothesis of the Hymenoptera that was based on the 18S nuclear rRNA. As suggested by Cameron et al. (1992), the inclusion of Diptera as the outgroup for Hymenoptera is questionable. Many groupings in the fully resolved cladogram are not well substantiated: the bootstrap value drops to 31% or less in some clades. Furthermore, the 18S gene region is significant at the tribal level or lower, but decreases rapidly at higher levels in Hymenoptera (M. Engels, personal communication).

WING VENATION:

Wing characters were usually included in large studies such as those of Koenigsmann (1976, 1977, 1978a, 1978b) and Rasnitsyn (1980, 1988). Only a few other papers have included more than one apocritan taxon in their analysis.

Lanham (1951) reviewed the nomenclatural systems of wing venation. He also attempted to infer some phylogenetic speculations and concluded that the ancestral wing venation for Apocrita could be derived from the generalized hymenopterous wing proposed by Ross (1936) with only a slight reduction in the number of veins. According to Lanham (1951) this 'venational pattern persists with little modification [mostly reductions] up to the bees and other stinging wasps and the development of lobes [anal lobe] on the "trailing edge" of the hind wing'. However, the last assumption is erroneous since this anal lobe is found in all Symphyta and is not a synapomorphy for Aculeata. The use of Pelecinidae by Lanham (1951) as a generalized model for Proctotrupoidea is erroneous because this taxon does not have the most complete venation of the superfamily and it is usually recognized as a specialized member of this group.

Danforth and Michener (1988) surveyed the occurrence of longitudinal wing folding in Apocrita; they concluded that it was derived independently in the fore wing of several apocritan taxa, as evidenced by the fact that longitudinal wing folds can be found in parasitic taxa which mimic stinging wasps and have similar characteristics.

RELATIONSHIPS OF APOCRITAN TAXA:

The relationships of apocritan taxa are very unclear, as demonstrated by Koenigsmann (1978a and b). From Ashmead (1895) to the present, many conflicting hypotheses have been presented and although much knowledge on the morphology, genetics and behaviour of Hymenoptera has been gained, progress on their phylogeny has been slow. Authors generally believe that the Apocrita is monophyletic (Farish 1972; Rasnitsyn 1980, 1988; Johnson 1988; Whitfield et al. 1989) based on characters such as the loss of the postspiracular sclerite and the loss of cenchri (Gibson 1985).

Orussidae are generally considered to be the sister group of the Apocrita (Koenigsmann 1977; Rasnitsyn 1980; Gibson 1985; Gibson and Goulet 1988; Johnson 1988; Whitfield et al; 1989; Zessin 1985) and sometimes even included in this taxon (Rasnitsyn 1988; Quicke et al. 1994).

Within Apocrita, relationships are even more uncertain and major variations are seen in the literature. Aculeata are generally viewed as monophyletic, especially since Brothers' (1975) study. Ashmead (1895) believed the Aculeata to be the sister group of Proctotrupoidea, Farish (1972) to either Proctotrupoidea + Evanioidea or to the stem of parasitic Hymenoptera (thus making Terebrantia a monophyletic group), and several others place Aculeata as the sister group of Ichneumonoidea (Rasnitsyn 1980, 1988; Johnson 1988; Whitfield et al. 1989; Dowton and Austin 1994). Saini and Dhillon (1978a, b), hypothesized that Aculeata is paraphyletic, one part derived from Chalcidoidea and the other from Ichneumonoidea.

The monophyly of Ichneumonoidea (sensu Sharkey and Wahl 1992) has never been questioned, only the internal placement of some taxa (Sharkey and Wahl 1992). The superfamily has always been placed in the basal part of the Apocrita, either as the sister group of the other apocritans (Farish 1972) or as the sister group of Aculeata (Rasnitsyn 1988). Rasnitsyn (1980) included the Ichneumonoidea with Aculeata, Proctotrupoidea, Platygastroidea and Ceraphronoidea in one group, the Ichneumonomorpha.

The position of Proctotrupoidea within the Apocrita and even its definition is rather uncertain. Early authors tended either to include Platygastroidea and Ceraphronoidea in the Proctotrupoidea or to leave either or both these taxa outside their study (Tonapi 1958; Farish 1972). Masner and Dessart (1967) were the first to recognize Ceraphronoidea; Huber (1993) recognized these three taxa as separate superfamilies and Rasnitsyn (1988) included the Platygastroidea in Proctotrupoidea excluding Ceraphronoidea. The relationship of Proctotrupoidea (sensu Huber, 1993) with other taxa is problematic; Rasnitsyn (1988) placed this superfamily at the base of his Proctotrupomorpha (= microhymenoptera minus Ceraphronoidea). Farish (1972) indicated a possible sister group relationship with Evanioidea. In essence, the placement of Proctotrupoidea is unresolved within microhymenoptera (Whitfield et al. 1989; Dowton and Austin 1994) and the monophyly of proctotrupoidea has been poorly documented. Macrohymenoptera, by default, includes all non-microhymenoptera, i.e., Aculeata, Ichneumonoidea, Trigonaloidea, and Evanioidea.

The Platygastroidea are placed close to Proctotrupoidea, Cynipoidea and Chalcidoidea by Rasnitsyn (1980, 1988), but their exact position remains uncertain. Dowton and Austin's (1994) data support a sister group relationship with the Chalcidoidea. The definition of Chalcidoidea itself was reviewed by Gibson (1985).

Although they were often placed in Proctotrupoidea, Rasnitsyn (1980, 1988) placed the two families of Ceraphronoidea into a larger concept of Ceraphronoidea (sensu Rasnitsyn 1980) which also includes Trigonalidae and Megalyridae. In turn, this group was hypothesized to be the sister group of Stephanidae by Rasnitsyn (1980). The two were amalgamated by Rasnitsyn (1988), forming the Stephanoidea. In other papers, the position of Ceraphronoidea (sensu Masner and Dessart 1967) is uncertain.

Often, the Trigonalidae have been omitted from analyses, but when present, they are placed as a specialized but basal lineage of Apocrita (Rasnitsyn 1980, 1988). Most authors place this taxon outside superfamilies recognized by Huber (1993), but Rasnitsyn (1980) included it in Ceraphroniodea (with Megalyridae) and then in Stephanoidea, which is the same group with the addition of Stephanidae (Rasnitsyn 1988). Similar comments to those mentioned above for Trigonalidae apply to Stephanidae.

As with Stephanidae and Trigonalidae, the Megalyridae were not usually included in earlier studies (Ashmead 1895; Farish 1972). Rasnitsyn (1980) placed them within Ceraphronoidea and later in Stephanoidea (Rasnitsyn 1988). Rasnitsyn (1980, 1988) proposed this last superfamily as the sister group of Evanioidea.

Gasteruptiidae and Aulacidae are often combined as a single family (Ashmead 1895; Rasnitsyn 1980, 1988); the split was favored by Johnson (1988), Whitfield et al. (1989) and Mason (1993). These, with Evaniidae, form the Evanioidea, but Mason (1993) admitted that there is no strong support for the monophyly of this superfamily.

Chalcidoidea (including Mymarommatidae) are often seen as the sister group of Platygastroidea (Rasnitsyn 1988; Dowton and Austin 1994) and these two appear to be closely related to both Cynipoidea and Proctotrupoidea (Rasnitsyn 1980, 1988; Dowton and Austin 1994). These four superfamilies form the Proctotrupomorpha (sensu Rasnitsyn 1988).

MATERIALS AND METHODS:

Characters of wing veins and hamuli were investigated. The nomenclatural system invented by Redtenbacher (1886) was chosen because it is widely used, simple and can be applied to all hymenopteran taxa. It is now most often referred to as the Comstock-Needham system (1898) because of the popularity it gained after these authors published a revised version. The modifications proposed by Ross (1936) and Mason (1990) have been adopted.

The classification of Huber (1993) is accepted; it is the most recent and complete taxonomic treatment of family and superfamily level hymenopteran taxa. Families of doubtful superfamilies (i.e. Proctotrupoidea, Ceraphronoidea and Platygastroidea) were examined separately in order to verify the monophyly of these superfamilies or to establish their ground plan (e.g. Cynipoidea). The wing venation of the superfamilies of Aculeata was not compared because the study of Brothers (1975), reanalyzed by Brothers and Carpenter (1993) is sufficiently complete to resolve most questions relative to the aculeate families.

Specimens representing at least one genus (among the most basal ones) for each taxon under study were borrowed from the Canadian National Collection (CNC). Wings of the following taxa were examined:

- Xyelidae (outgroup); *Xyela* sp., *Macroxyela* sp.
- Megalodontoidea (outgroup); *Acantholyda* sp., *Neurotoma* sp., *Pamphilius* sp. (Pamphiliidae)
- Tenthredinoidea (outgroup); *Tenthredo* sp. (Tenthredinidae), *Cimbex* sp. (Cimbicidae), *Diprion* sp. (Diprionidae)
- Cephidae (outgroup); *Cephus* sp.
- Siricidae (outgroup); *Tremex* sp., *Sirex* sp., *Urocerus* sp.

- Anaxyelidae (outgroup); *Syntexis lobocedrii* Rohwer
- Xiphydriidae (outgroup); *Xiphydria maculata* Say
- Orussidae (outgroup); *Orussus occidentalis* (Cresson)
- Aculeata; *Rhopalosoma nearcticum* Brues, *Liosphex* sp. (Rhopalosomatidae: Vespoidea), *Anthobosca* sp. (Tiphiidae: Vespoidea)
- Ichneumonidae; *Rhyssa* sp., *Megarhyssa* sp., *Pimpla* sp.
- Braconidae; *Helcon pedalis* Cresson, *Earinus limitaris* Say, *Aliodes* sp., *Disophrys* sp., *Microgaster* sp.
- Trigonalidae; *Trigonalis* sp., *Orthogonalys* sp., *Taeniogonalos* sp.
- Evaniidae; *Evania* sp.
- Megalyridae; *Megalyra* sp., *Dinapsis* sp., *Rigel* sp.
- Stephanidae; *Megiscus* sp., *Schlettererius cinctipes* (Cress.)
- Aulacidae; *Aulacus* sp.,
- Gasteruptiidae; *Gasteruption* sp.
- Chalcidoidea; *Leucospis* sp. (Leucospidae), *Leptochalcis* sp., *Spilochalcis* sp. (Chalcididae)
- Cynipidae; *Cynips folii* Linnaeus, *Cynips kollari* Hartig, *Callirhytis* sp., *Besbicus mirabilis mirabilis* (Kinsey)
- Ibaliidae; *Ibalia* sp.
- Liopteridae; *Oberthurella* sp.; *Liopteron* sp.
- Figitidae; *Figites* sp., *Melanips* sp., *Callaspida* sp., *Aspicera* sp.
- Eucoilidae; *Acanteucoela* sp., *Tribliographa rapae* Westwood
- Charipidae; *Alloxysta* sp., *Dilyta* sp., *Hemicrisis ruficornis* Foerster
- Proctotrupidae; *Austroserphus albofasciatus* Dodd
- Pelecinidae; *Pelecinus polyturator* (Drury)
- Vanhorniidae; *Vanhornia* sp.
- Heloridae; *Helorus anomalipes* Panz.
- Monomachidae; *Monomachus* sp.
- Roproniidae; *Ropronia* sp.

- Peradeniidae; *Peradenia* sp.
- Austronidae; *Austronia* sp.
- Diapriidae; *Cinetus* sp., *Aclista* sp., *Diapria* sp.
- Platygastridae; *Metactisis* sp.
- Scelionidae; *Archaeotelei* sp., *Sparasion* sp., *Trimorus* sp., *Telenomus* sp.
- Ceraphronidae; *Ceraphron* sp.
- Megaspilidae; *Megaspilus* sp.

The family Renyxidae (Proctotrupoidea) was not included in the present research because it was only recently described (Kozlov 1994; Lelej 1994) and no specimens could be obtained for examination.

Fore and hind wings of each taxon cited above (except for the rare taxa) were slide-mounted. Wings were pulled from the thorax and placed in 70% alcohol to relax. The wings were placed in a drop of glycerin on a slide and covered with a cover slip for drawing.

The wings were drawn using a camera lucida mounted on a stereoscope. Observations were completed with examinations from specimens of a wide array of genera (not only the most plesiomorphic ones) from CNC and the Lyman Entomological Museum and Research Laboratory (McGill University). A first drawing was made from a specimen with relatively complete venation. The drawings were then scanned and imported into CorelDraw to do the final corrections; these changes were completed after the examination of at least a few other genera for each taxon. Because character losses can occur frequently and independently, the presence of a vein in symphytan outgroups is usually considered plesiomorphic (ancestral). Within each taxon, if more than one character state was present, the one which was closer to the ancestral condition was chosen to be the ground plan for this same group. The combination of all these plesiomorphic characters generated a ground plan for each taxon.

The CorelDraw program allows one to create codes to show the different wing characters used by Mason (1986). According to Mason (1986), wing veins can be classified into three types: tubular veins are hollow tubes; nebulous ones are semi-circular and chitinized; and the spectral type can be seen only by a slight inflection of the membrane but is not chitinized or pigmented. The codes used in the wing drawings are explained in the legend of Fig.1 (Appendix 1).

Two data matrices were generated: one which incorporates the state of the veins (Table 2) and one which takes into account their presence or absence only (Table 3). The second data matrix was generated in order to offset the high number of nebulous veins that can be found in some relatively ancestral taxa (Orussidae and Pelecinidae, for example). These taxa would be displaced distally in the cladograms derived from the first data matrix because of the high number of derived character states whereas the cladograms derived from the second data matrix would not be affected by a high number of nebulous veins. These matrices were analyzed using Hennig86 (Farris 1988).

The analysis of each data matrix was done twice, once using unweighted characters, and a second time with non-loss characters (or those which were not affected by the size of the insect) weighted at 39; this weight is equal to the total number of loss characters. This weighting was done to offset the number of losses of veins which may occur simultaneously. *Mesocoelus* sp., for example, has lost about ten vein abscissae (compared to the other Agathinae) in one apparent cladogenetic event (Sharkey, personnal communication). In all cases of the analyses, character 19 was coded as non-additive because no state could be logically derived a priori from another. Clados (Nixon 1992) was used to generate cladograms for the final output.

In order to incorporate the results presented in the other papers dealing with character suites, the data were extracted from each of them and each character is listed in Appendix 2. Only Heraty et al. (1994) published a data matrix and it was used with minor modifications. Farish (1972), Iwata (1972), Quicke et al. (1992a, 1994) provided a table of character states (presence or absence of the characters) which was included in the data matrix provided in Appendix 3. The ovipositor valvilli, studied by Quicke et al. (1992b), were included in the character list of Quicke et al. (1994). The data obtained from Tonapi (1958), Daly (1963), Robertson (1968), Richards (1972), Gibson (1985), Johnson (1988), Whitfield et al. (1989) and Whitfield (1992) were extracted from the text of these papers since no data matrix was provided in any of these. The information gathered from the other references listed in the historical review was not added to the data matrix either because the characters were not well defined or because the number of taxa was too small. Question marks in the data matrix represent unknown character states. A full row of question marks indicates that the taxon was not studied by the author. Some characters (2 with 59, 3 with 50, 13 with 58, 14 with 60, 15 with 79, 17 with 71, and 54 with 80) were examined by two authors and sometimes, different results were presented. These characters were assigned half the weight of the other non-wing characters in order to offset this overlap.

A data matrix was constructed incorporating the venational data and characters from all of the character suites listed in Appendix 2. Since weighted data from the second matrix were preferred (for the reason explained above), the data from the combined characters were also weighted in a similar manner; all non-wing characters were given the same weight as wing characters which did not involve a loss (those involving a loss are interrelated and were downweighted accordingly). Only the consensus cladograms are presented in the figures because the other alternative, including one of the most parsimonious tree (to show the shortest length tree) with the consensus tree (to show which branches are not well supported in the most parsimonious tree), would be too cumbersome and such a procedure would present hypotheses that are weakly supported since all most parsimonious cladograms are equally appropriate (Anderberg and Tehler 1995).

RESULTS and DISCUSSION:

A total of 55 characters was analyzed from both wings and when present, veins were coded as being tubular, nebulous or spectral. Tubular veins are the only ones to be tracheated. Since the state of the vein may change along its length, passing from tubular to nebulous or spectral, the character state coded is the one which represents the longest section. It should be noted that only a small minority of characters did not involve a reduction (from tubular to nebulous or spectral) or a loss. Character 1 involves the loss of the costal vein in the fore wing but since this vein does not undergo reduction to a nebulous state, even in very small specimens (especially Diapriidae), its presence or absence is believed to be more significant than that of the distal abscissae of M or Cu for example. The following is the list of characters and codes used with a brief discussion of the significance of the character on the phylogeny.

CHARACTER ANALYSIS, FORE WING:

1. Costal vein (C):

0, present; 1, absent.

The costa is a stable character within most families studied. In Megalyridae, however, it is present in some genera and absent in more derived ones. This vein is absent, as a ground plan, in Stephanidae, Platygastroidea, Chalcidoidea and Cynipoidea, but present in all other taxa.

2. Radial vein, distal to the stigma (R1):

0, tubular; 1, nebulous; 2, absent.

This abscissa of the radius (R1) is markedly reduced or absent only in Ceraphronoidea, Platygastroidea, most Chalcidoidea and some Cynipoidea. In the absence of a stigma, the observed R1 goes from the distal end of the costal cell to the point of fusion with Rs. In most microhymenoptera where the stigma is absent, R1 rarely goes distal to Rs.

3. Radial sector vein (Rs), abscissa distal to 2r:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

In most families, this abscissa of Rs goes from 2r to R1, but in Pelecinidae and Chalcidoidea, it is oriented toward the tip of the wing. Rs tends to reach R1 at a more proximal location in some derived groups such as many microhymenoptera, but the condition seems to be highly variable within many taxa. In Ceraphronoidea, it is rather difficult to distinguish 3-Rs (4-Rs in Symphyta) and 2r because they have fused into a r&Rs vein.

4. Median vein (M), abscissa distal to Rs+M:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

In Evaniidae, this abscissa of M becomes much thinner shortly after the split from Rs+M (about half the thickness of the preceding abscissa) and it narrows rapidly rather than gradually. This vein is absent as a ground plan only in Ceraphronoidea, but it has been lost secondarily in other Hymenoptera with reduced wing venation (Platygastroidea, Chalcidoidea, Cynipoidea and Diapriidae).

5. Cubital vein (Cu), abscissa between 1-M and 2cu-a:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

This abscissa of Cu is usually stronger than another abscissa (M+Cu or Cu distal to 2cu-a) in some taxa. In Vanhorniidae and some Cynipoidea, it is stronger than M+Cu, whereas, in Peradeniidae, Stephanidae and Evaniidae, it is stronger than the distal section of Cu. The plesiomorphic (tubular) condition has been preserved in most taxa and some microhymenoptera. It is nebulous in Cynipoidea, Chalcidoidea, Platygastroidea, Megaspilidae and Diapriidae. As a ground plan, this abscissa of Cu is absent only in Ceraphronidae (as it is for the rest of Cu) and this should be considered an autapomorphy for this family.

6. Cubital vein (Cu), abscissa distal to 2cu-a:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

In Evaniidae and Gasteruptiidae, this section becomes thinner shortly distal to 2cu-a in a similar manner to M. This abscissa of Cu is tubular only in Ichneumonoidea, Aculeata, Trigonalidae and Aulacidae.

7. vein Rs+M:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

Rs+M is tubular in all Symphyta and macrohymenoptera (except Ichneumonidae), in Ibaliidae, and in some Proctotrupoidea (Heloridae, Roproniidae). It is nebulous in Pelecinidae, Vanhorniidae, Chalcidoidea and most Cynipoidea, and spectral in Proctotrupidae. This vein (or the first abscissa of this vein) is absent in all other taxa, even in groups where the venation is relatively complete and tubular (Monomachidae and Austroniidae). In basal genera of Ichneumonidae (*Megarhyssa* sp., *Pimpla* sp.), a stump of this vein is present, joining with 1m-cu.

8. vein M+Cu:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

The plesiomorphic condition can be found in most macrohymenoptera (except Megalyridae) and most Proctotrupoidea (Monomachidae, Austroniidae, Heloridae, Roproniidae and Proctotrupidae). The M+Cu vein is nebulous in Megalyridae, Vanhorniidae, Diapriidae, Platygastroidea, Megaspilidae, Chalcidoidea, and many Cynipoidea. M+Cu is absent only in Ceraphronidae.

9. vein 1A, abscissa proximal to 1m-cu:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

This vein is tubular in all macrohymenoptera as well as in Proctotrupoidea (except Pelecinidae). It becomes nebulous in Chalcidoidea, Platygastridae and Ceraphronoidea and spectral in Diapriidae, Pelecinidae, and Scelionidae. It is absent in most Cynipoidea (Ibaliidae and some Cynipidae excepted). In Ceraphronidae, it is difficult to identify this vein because it is easily confused with M+Cu. The axillary sclerites show that this is the anal vein and, therefore, that M+Cu is lost.

10. vein 1A, distal abscissa:

0, present; 1, absent.

This abscissa is present in all macrohymenoptera, but it is weak or absent in most taxa of microhymenoptera (tubular in Roproniidae and Monomachidae, and mostly tubular in Heloridae). Megalyridae is an exception among Apocrita in having a large body size and a weakened (nebulous) distal abscissa of A.

11. 2A:

0, present; 1, absent.

Only Symphyta have this vein and even then it is reduced in Orussidae, being fused to 1A for more than half its length; its presence in some Braconidae is secondary.

12. Anal crossvein:

0, present; 1, absent.

Present only in Symphyta, except Orussidae, and regained secondarily by some Braconidae.

13. Subcostal vein (Sc), distal (free) section:

0, present; 1, absent.

The sc crossvein is nearly continuous with the abscissa of Sc that bends at 90 degrees toward C, before it reaches the latter. When Sc is fused with R (resulting in Sc+R), only the free section of Sc between C and R remains visible and looks like a crossvein. In Tenthredinoidea and Xiphydriidae, only this section of Sc remains present and in the other taxa Sc and its bent abscissa are lost.

14. 2rs-m:

0, tubular; 1, nebulous/partial; 2, absent.

For the terminology of rs-m crossveins, this paper agrees with Rasnitsyn (1980, 1988) and Sharkey (1988) in that 1rs-m is absent in all Hymenoptera and that only 2rs-m and 3rs-m are present. In Apocrita 2rs-m can only be found in Aculeata, Trigonalidae, and Aulacidae (as a stump).

15. 3rs-m:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

3rs-m is more common in Apocrita than 2rs-m; it is tubular in Ichneumonoidea, Aulacidae, Aculeata, and even in Cynipoidea, where venation is reduced and weakened (most veins being nebulous). However, it is generally reduced to a spectral state in Evaniidae and Megalyridae, and lost in other groups with strong venation (Proctotrupoidea, Stephanidae and Gasteruptiidae). It is also absent in Chalcidoidea, Platygastroidea, and Ceraphronoidea.

16. 1r:

0, present; 1, absent.

This vein seems to be characteristic of all Symphyta, except Orussidae and reduced in a few Cephidae. The inclusion of *Stephanogaster magna* Rasnitsyn in Ephialtitidae (Rasnitsyn 1975), an extinct family of Apocrita, should be investigated further since it was described as having 1r present.

17. Length of vein 2-Rs+M and 2-Rs:

0, shorter than the abscissa of Cu between 1-M and 2cu-a;

1, at least 1.25 the length of 1-Cu and 1-M present;

2, at least 1.5 the length of 1-Cu and 1-M absent.

In most Hymenoptera, these two abscissae are, when present, shorter than 1-Cu but in Proctotrupoidea, 1-Rs+M is sloped downward (toward the hind wing). Thus, in this superfamily (except Pelecinidae), 2-Rs+M is relatively long and so is 2-Rs. A similar condition is found only in Gasteruptiidae, but in this family, 1-Rs+M is not tilted (it is placed on the same line as M+Cu and thus, 1-M is absent) and 1-Cu is very short. Therefore, character state 1 is considered a potential synapomorphy for Proctotrupoidea whereas character state 2 is an autapomorphy for Gasteruptiidae.

18. 1m-cu:

0, tubular; 1, nebulous; 2, absent.

This crossvein is tubular in macrohymenoptera (except Megalyridae) and Proctotrupoidea (except Pelecinidae), nebulous in Megalyridae and Pelecinidae, and absent in Ceraphronoidea, Platygastroidea, Cynipoidea and Diapriidae.

19. 2m-cu:

0, present; 1, absent.

This vein is present only in a few Apocrita (some Braconidae, Ichneumonidae, Trigonalidae, Aculeata and Aulacidae).

20. 1cu-a:

0, tubular; 1, nebulous; 2, absent.

This crossvein is tubular in macrohymenoptera, Proctotrupoidea (except Pelecinidae) and some basal Cynipoidea, nebulous in most other Apocrita, and absent only in Ceraphronoidea, Platygastroidea and Diapriidae.

21. 2cu-a:

0, tubular; 1, nebulous; 2, absent.

This crossvein is tubular in macrohymenoptera and Proctotrupoidea (except Megalyridae, Stephanidae and Pelecinidae), nebulous in most other Apocrita, and absent in the same taxa as 1cu-a. Although nebulous, it is surprising to see this crossvein in most Cynipoidea despite the absence of an anal vein.

22. Junction of 1cu-a with Cu vein:

0, 1cu-a closer to the middle of cell 1M than to vein 1-M;

1, 1cu-a closer to vein 1-M.

Only some taxa of Symphyta possess the plesiomorphic condition: Xyelidae, Megalodontoidea, Tenthredinoidea, Anaxyelidae and Siricidae. In these groups, 1cu-a is situated at the middle of the cell, except in Anaxyelidae where it meets Cu closer to the first third of cell 1M (but even here, the crossvein is closer to the middle of the cell than to vein 1-M). This crossvein has migrated closer to 1-M in Cephidae, where it is still not continuous with this abscissa, and Xyphydriidae, Orussidae and Apocrita, where it is usually continuous with 1-M. In the Apocrita, variations may occur: 1cu-a may be proximal or distal to 1-M in Ichneumonoidea and Aculeata, but if distal, it is usually closer to the first abscissa of M.

23. Costal cell:

0, wider than Radius;

1, narrower than Radius or absent.

The costal cell is usually large in Hymenoptera (even if the costal vein is absent) but it becomes reduced or absent in Ichneumonoidea and absent in

Ceraphronoidea.

24. Stigma:

0, present; 1, absent.

The stigma is present in most hymenopteran taxa, but has been reduced in a number of families. It is reduced in some Diapriidae but absent in others. It is absent in Cynipoidea, Chalcidoidea and Platygastroidea, taxa which have also lost the costal vein.

25. Cubital vein (Cu), abscissa distal to 2cu-a:

0, lower than the abscissa between the two cu-a crossveins (part of Cu runs in the same axis as 2cu-a);

1, at the same level or higher than the section between the two cu-a crossveins (2cu-a longer than 1cu-a).

In almost all Hymenoptera, Cu follows a course where the abscissa between 1m-cu and 2cu-a follows the same axis as 2cu-a before bending toward the tip of the wing. Then, 2cu-a is usually shorter than 1cu-a, except in Gasteruptiidae because A, distal to 1cu-a, is also bent toward the hind wing, but even then, the distal abscissa of Cu is still posterior to the other (more proximal) sections. The derived condition can be found in all microhymenoptera, although Cu is absent in Ceraphronidae. The absence of 2cu-a in Platygastroidea, Megaspilidae and Diapriidae may also influence this character because there is no pull exerted by this crossvein; it is thus difficult to say if the condition is similar to the one found in Proctotrupoidea, Chalcidoidea and Cynipoidea (where it is present).

26. 2-Rs vein:

0, tubular; 1, nebulous; 2, absent.

This abscissa of Rs is tubular in all macrohymenoptera and Proctotrupoidea, nebulous in Scelionidae, Chalcidoidea and Diapriidae, and absent only in groups with very reduced venation (Ceraphronoidea and Platygastridae). When present, its length varies from about half that of r (Cynipoidea and Ichneumonidae), to much more than half.

27. Position of the 3r-rs crossvein:

0, not continuous with 2r;

1, continuous with 2r and cell 3Rs triangular but less than twice as long as high;

2, continuous with 2r, cell 3Rs triangular and more than twice as long as high.

In most Hymenoptera, 2-Rs and 3r-rs are not as shortened so that the cell 3Rs is not triangular and the last vein does not follow the path of the 2r crossvein. The highly shortened 2-Rs and 3r-rs are found only in Ichneumonidae and Cynipoidea (when they are present). However, the veins are displaced apically in Ichneumonidae and the cell 3Rs is shorter than in Cynipoidea where these veins are not displaced apically.

28. Rs_2 vein:

0, absent; 1, present.

This vein is found only in Xyelidae, Pelecinidae and some Chalcidoidea (Chalcididae and Leucospidae). In opposition to most authors (Burks 1938; Lanham 1951; Bradley 1955, 1958; Rasnitsyn 1988), this vein was homologized with Rs_2 instead of 3rs-m because it follows the path of the former, not the latter. It was considered ground plan for the last taxon because, even though these two families are the only ones to have this vein, they have the most complete venation of the whole superfamily and are among the most ancestral families of this taxon. The second problem with this character was to establish which state is the plesiomorphic condition for the order or at least for Apocrita. Since Xyelidae is usually seen as the most ancestral taxon of Hymenoptera, it would thus be tempting to consider it to be a ground plan character for the order, especially since this is a common belief. However, in the absence of other comparisons outside Hymenoptera, the most parsimonious hypothesis would be an independent origin of this character in all these taxa.

29. 2-Rs+M:

0, absent; 1, present.

The second Rs+M is only present in some Apocrita: Ichneumonoidea, Gasteruptiidae, Aulacidae, Trigonalidae, Stephanidae, and Proctotrupoidea (minus Pelecinidae and Diapriidae). However, 2-Rs+M is usually short or even absent in Braconidae, Aulacidae, Trigonalidae and Stephanidae. In Trigonalidae at least, the presence of this abscissa may be a ground plan character for the family (Carmean, personal communication). In Symphyta and Aculeata, 2-Rs connects with 1r close to the middle of cell 1R, and the second abscissa is absent. In the other taxa, 2-Rs and 1m-cu meet at the same point on M, thus leaving no 2-Rs+M abscissa. In groups with reduced venation, one of the crossveins is missing and it is impossible to recognize the character.

30. Sc vein:

0, present; 1, absent.

A separate Subcosta is found only in a few Symphyta: Xyelidae, Megalodontoidea and Siricidae.

31. Angle of 1-Rs vein with the radial vein (R):

0, more than 100° with R;

1, 90° or less with R.

This character is found only in some Symphyta: Xyelidae, Anaxyelidae and Xiphydriidae and it is thus considered to be a ground plan character for Hymenoptera.

32. Supplementary cu-a crossvein (basal to 1cu-a):

0, absent; 1, present.

This crossvein joins the M vein before the bifurcation of M+Cu and 1-M. This character, present in Megalodontoidea and Siricidae, is seen as a ground plan even though it is found only in a few taxa of Symphyta. Alternatively, it is also possible that it was developed after the separation of Xyelidae from the common stem of Hymenoptera; in either case, its absence in the common stem of Xiphydriidae (Orussidae + Apocrita) is apomorphic.

CHARACTER ANALYSIS, HIND WING:

33. orientation of vein Rs:

0, toward and touching R1;

1, toward wing tip.

The derived condition is found only in Anaxyelidae, Siricidae, Orussidae and all apocritan taxa where Rs is present.

34. Rs vein:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

This vein is tubular in all Symphyta (except Orussidae) and in Aculeata, Ichneumonoidea, Megalyridae and Trigonalidae; nebulous in Orussidae, Stephanidae and Chalcidoidea; and spectral in Evaniidae and Ceraphronoidea. It is absent in Aulacidae, Gasteruptiidae, Proctotrupoidea, Cynipoidea and Platygastroidea.

35. M vein:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

This vein is tubular in Symphyta (except Orussidae), Ichneumonoidea, Aculeata, Trigonalidae, Monomachidae and Austroniidae. It becomes nebulous in Aulacidae, Stephanidae, Gasteruptiidae and Roproniidae, and spectral in Heloridae, Proctotrupidae, Vanhorniidae, Peradeniidae and Ceraphronoidea. It is absent in Diapriidae, Megalyridae, Evaniidae, Platygastridae, Chalcidoidea and some members of the superfamily Cynipoidea. When present in any member of the last superfamily, M can be seen as a short nebulous or spectral vein.

36. Cu vein:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

This vein is present and tubular in Symphyta (except Orussidae), Ichneumonoidea, Aculeata, Trigonalidae, Megalyridae, Evaniidae, Roproniidae, Peradeniidae, Monomachidae, Heloridae and Austroniidae. In Stephanidae, Aulacidae, Gasteruptiidae, Proctotrupidae, Vanhorniidae, Diapriidae, Chalcidoidea, Platygastroidea and most Cynipoidea it is nebulous, and it is spectral in Ceraphronoidea, Pelecinidae and some Cynipoidea. This vein is absent only in Megalyridae. It has a similar shape and location in some Braconidae and most Proctotrupoidea. The cu-a crossvein tends either to disappear, thus leaving a bent Cu (as in Heloridae), or to fuse with the first abscissa of Cu into a Cu&cu-a vein (as in many small Hymenoptera such as Platygastroidea).

37. 1A vein:

0, tubular; 1, nebulous; 2, absent.

1A is the only anal vein present in most parasitic macrohymenoptera; it is tubular in Ichneumonoidea, Aculeata and Trigonalidae, and nebulous in Aulacidae and Stephanidae. It is absent in all other taxa.

38. 2A vein:

0, tubular; 1, nebulous; 2, absent.

This vein is tubular in Symphyta and Aculeata, nebulous in Orussidae and Ichneumonidae, but absent in all other extant Apocrita. It can be distinguished from the other anal veins by the absence of an adjacent cu-a and by its location (in the claval lobe). It seems possible that it is a ground plan character for Ichneumonoidea, but that it was secondarily lost by the ancestor of Braconidae.

39. 3A vein:

0, tubular; 1, nebulous; 2, absent.

The third anal vein can be identified by its location in the anal lobe. It is present in only two apocritan taxa, Aculeata and Evaniidae, but the anal lobe of the latter may not be homologous with that of the former.

40. 1rs-m crossvein:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

1rs-m is the only crossvein remaining in the hind wing of most Apocrita. This crossvein is tubular in Symphyta (except Orussidae), Aculeata, Ichneumonoidea and Trigonalidae. It becomes nebulous in Stephanidae, Aulacidae, Gasteruptiidae, many Cynipoidea and Chalcidoidea. It is absent from Vanhorniidae, Megalyridae and Evaniidae; its presence in minute taxa (such as Platygastridae), although fused with the cubitus (rs-m&Cu&cu-a), may suggest that it is a relatively stable character.

41. 3rs-m crossvein:

0, present; 1, absent.

The name follows the one given by Rasnitsyn (1969, 1988) because a third crossvein is found between 1rs-m and 3rs-m in Macroxyelinae (but only in this subfamily, not in Xyelinae). Thus the name 2rs-m should be changed to 3rs-m.

42. cu-a crossvein:

0, present; 1, absent.

This crossvein is usually short in Apocrita. It is present and separate from Cu in Aculeata, Ichneumonoidea, Stephanidae, Trigonalidae, Monomachidae and Austroniidae. It is an important character because it divides Cu into two abscissae; in Platygastroidea, it is most probably fused with the first free section of Cu.

43. Costal vein:

0, complete; 1, partial; 2, absent.

The costa is usually absent in parasitic Hymenoptera (as well as in Anaxyelidae and Orussidae); a small stump can be seen in Cephidae, Ichneumonoidea and Trigonalidae, and it is complete in Aculeata. The costa is never nebulous or spectral, whether on the fore or hind wing.

44. m-cu crossvein:

0, present; 1, absent.

This crossvein is present only in Symphyta, but absent in Anaxyelidae and Orussidae.

45. R1 vein:

0, tubular; 1, nebulous; 2, absent.

R1 is tubular in most Hymenoptera, nebulous in Cynipoidea, Chalcidoidea, Diapriidae, Vanhorniidae, Peradeniidae, Stephanidae and Orussidae, and absent only in minute forms (Platygastroidea and Ceraphronidae); its length varies greatly because of the basal displacement of the hamuli in microhymenoptera.

46. M+Cu vein:

0, tubular; 1, nebulous; 2, spectral; 3, absent.

This vein is tubular in Symphyta, Aculeata, Ichneumonoidea, Trigonalidae and Monomachidae, nebulous in Stephanidae, Aulacidae, Gasteruptiidae, Chalcidoidea and basal cynipoid taxa. It is spectral in most other Proctotrupoidea, Ceraphronoidea, and is absent in Platygastroidea only. In some proctotrupoid families, it has a strong bend.

47. Basal hamuli:

0, present; 1, absent.

The basal group of hamuli is present only in Symphyta and in the basal apocritan lineages (Ichneumonidae, Aculeata and Trigonalidae). In Anaxyelidae, Orussidae and Braconidae, a single hamulus can be found and it is non-functional in Braconidae.

48. Junction of 1rs-m on vein Rs or R:

0, at or distal to the first distal hamuli;

1, basal to the hamuli.

The point of insertion of 1rs-m on R or Rs is displaced basally in the more derived groups of Apocrita (most of the microhymenoptera); in Symphyta, it is usually distal to the first distal hamulus, but in many Apocrita, it is basal to the latter.

49. Junction of 1rs-m on M vein:

0, on M;

1, on M+Cu.

This character measures the presence or absence of a basal abscissa of the

M vein. When the 1rs-m crossvein unites with M, the free section of M develops a second abscissa. This character is present in Symphyta and most basal Apocrita (Aculeata, Ichneumonoidea, Aulacidae, some Stephanidae, Ceraphronoidea, Monomachidae and Austroniidae); when 1rs-m makes contact with M+Cu, there is only one abscissa of M.

50. Sc vein:

0, present; 1, absent.

A separate subcosta is present in Pamphiliidae and to a lesser degree, in Xyelidae where it is not as strong as in the former taxon. This character was thus lost after the ancestor of Megalodontoidea had split from the common stem of Hymenoptera.

51. free basal segment of Cu and M veins:

0, present; 1, absent.

The split of these two veins at the base of the hind wing is present only in Xyelidae. It is as parsimonious to view this segment as a ground plan of Hymenoptera as the possibility that it is an apomorphy of Xyelidae; this is in accordance with Ross (1936).

52. supplementary rs-m crossvein:

0, present; 1, absent.

This supplementary rs-m crossvein should be called 2rs-m because it is situated between 1rs-m and 3rs-m. This crossvein was found only in Xyelidae and it is considered a ground plan for Hymenoptera.

53. Anal cell (A):

0, closed; 1, open.

This cell is bordered by the veins 1A and 2A and is closed only in

Symphyta and open in Orussidae and Apocrita.

54. orientation of the Median (M) vein:

0, anterior to M+Cu;

1, continuous with M+Cu.

In all Symphyta, M is elevated anterior to M+Cu whereas in Apocrita, it is continuous. In taxa where M is elevated, its basal abscissa is oriented toward the anterior part of the wing.

55. orientation of the Cubital (Cu) vein:

0, continuous with M+Cu;

1, posterior to M+Cu.

In Symphyta, excluding Orussidae, the Cu vein is continuous with M+Cu whereas it is posterior to M+Cu in Orussidae and Apocrita. In the latter taxa, the first abscissa of Cu is oriented toward the posterior side of the wing.

CLADISTIC ANALYSIS:

Wing venation is comprised of a suite of characters and, like the other ones described in the literature review, it has limitations and should not be used alone to establish a hypothesis for the phylogeny of Hymenoptera. Rather, it should be combined with other studies in order to obtain a consensus of all of the evidence. The venational data are here analyzed independently of other evidence to help show the reliability, or lack thereof, of the characters. These data are then combined with other characters to establish a cladogram of total evidence. Two data matrices were generated, one which included all the character states (tubular, nebulous, spectral or absent) presented above (Table 2), and a second matrix that was derived from the first one, taking into account the presence or absence of the veins only (Table 3).

In the following text, only those clades resolved in the consensus trees are discussed because these are the clades that are unambiguously supported in all of the minimum length trees. The consensus trees are not meant to infer the phylogeny of the entire Hymenoptera, rather they are meant to show the phylogeny of those clades that are resolved.

The data matrix resulting from the character list presented above with all states (tubular, nebulous, spectral) is shown in Table 2. The 20 most parsimonious trees, obtained by using unweighted data and the m* and bb* functions of Hennig86 (Farris 1988), have a length of 230 steps, a consistency index of 0.41 and a retention index of 0.82. The nelson consensus tree (Fig.1) was generated using the nelson command of Hennig86. Weighted data from the same matrix led to very different results; the 96 most parsimonious trees have the following statistics: L= 242, CI= 0.39, RI= 0.80. The nelson consensus tree is shown in Fig.2. The cladograms have a similar topology, but the weighting procedure affects the basal and distal parts. The basal clades of the weighted cladogram (the outgroups) are collapsed because some weighted characters are in conflict. However, the proctotrupoid families are more highly resolved on the same cladogram (Fig.2).

The unweighted analysis of the second data matrix (Table 3), where only the presence or absence of the veins was recorded, resulted in 100 equally parsimonous trees with the following statistics: L=104, CI=0.53, RI=0.85. The nelson consensus tree is shown in Fig.3. The weighted trees (501 equally parsimonous cladograms) have L= 105, CI= 0.53, and RI= 0.85. The nelson consensus tree is shown in Fig.4.

The trees derived from the second data matrix show similar trends to those obtained from the first data matrix in that the basal part of Fig.4 is collapsed but the resolution is higher for microhymenoptera compared to Fig.3. The retention index favours the second data matrix since it is much higher.

The decision to weight data was more difficult. Although the length is slightly lower in Fig.3 than Fig.4, the basic principle of character independance was judged to be more important and since the analysis of unweighted cladograms (Figs 1, 3) shows that abscissa are not lost in a step-wise fashion. Rather, whole vein systems can be lost at one node. This phenomenon is repeatedly supported in investigations within many members of the Apocrita where sister species or sister genera can have great discrepancies in the amount of venation. It is well illustrated by a comparison between *Mansonia prognata* Achterberg (Braconidae) which has no vein in the hind wing and only the Costa in the fore wing, whereas its sister species, *Mansonia bulbofemoralis* Achterberg, which has almost all veins present in the ground plan of the Braconidae (Achterberg 1995). The need to give a lower weight to those characters was demonstrated by Swofford (1991) "if you break a ten-state character into nine binary characters, it is indeed true that each of the resulting binary characters has the same weight as does a truly binary (e.g., presence-absence) character, but there are nine of them". However, Hennig86 (Farris 1988) does not offer this option. To effect the same result, one must increase the weight of the non-multistate (binary) characters.

To compare the validity of wing characters, non-wing character suites were compiled (Appendix 2), polarized according to the authors (Table 4) and analyzed. Characters 2, 30, 31, 49, 62, 78 were coded as non-additive. The 2500 most parsimonious trees have the following statistics: L= 292, CI= 0.54, RI= 0.70. The lack of resolution of the nelson consensus tree (Fig.41) is due to the high number of conflicts between topologies of the parsimonious trees.

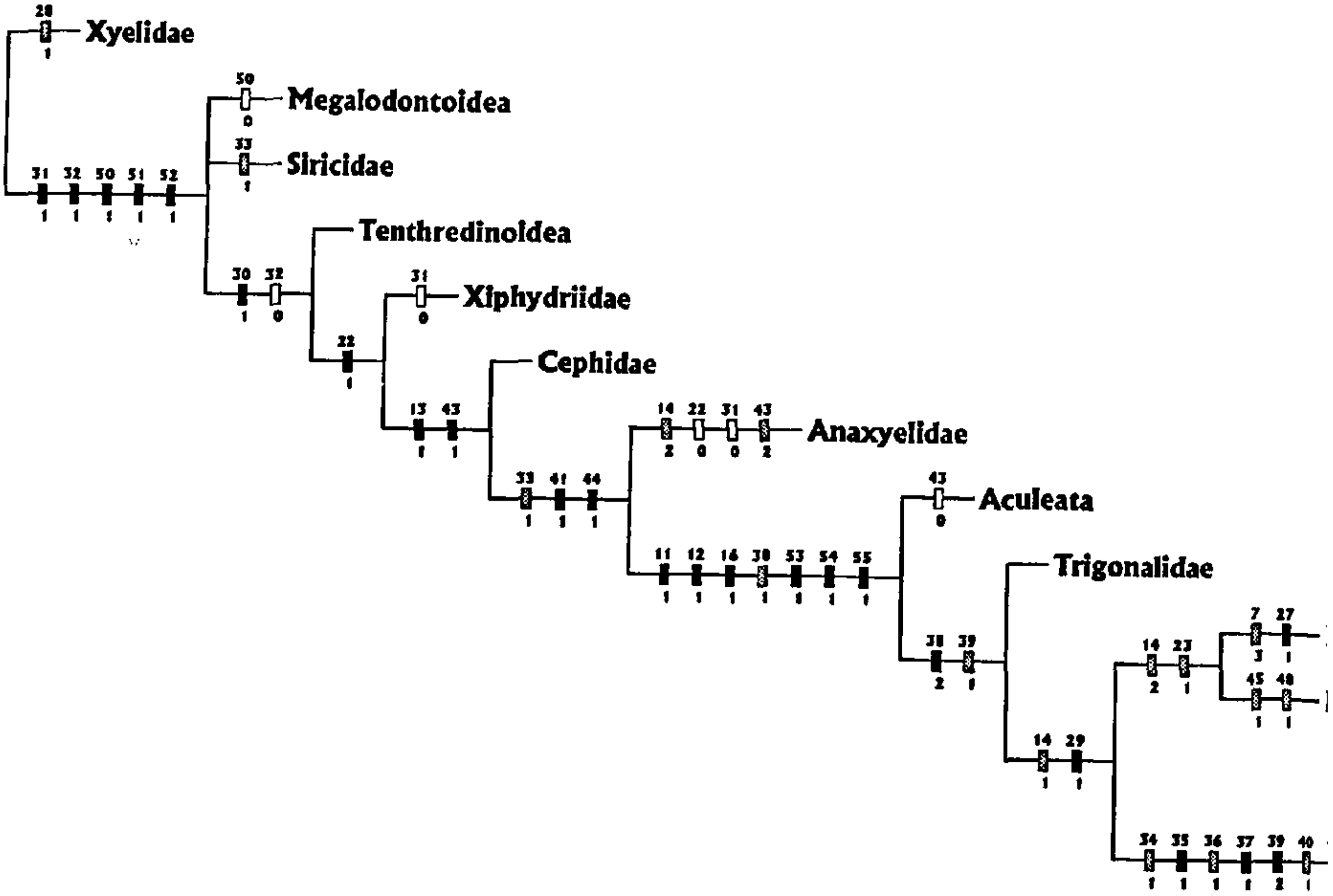
Table 2: Wing characters of Apocrita (with state of the veins indicated)

	0	1	2	3	4	5
	0123456789	0123456789	0123456789	0123456789	0123456789	012345
Xyelidae	0000000000	0000000000	0000000010	0000000000	0000000000	000000
Megalodontcidea	0000000000	0000000000	0000000000	0110000000	0000000000	011000
Tenthredinoidea	0000000000	0000000000	0000000000	1100000000	0000000000	111000
Xiphydriidae	0000000000	0000000000	0010000000	1000000000	0000000000	111000
Anaxyelidae	0000000000	0001200000	0000000000	1001000000	0102100000	111000
Siricidae	0000000000	0000000000	0000000000	0111000000	0000000000	111000
Cephidae	0000000000	0001000000	0010000000	1100000000	0002000000	111000
Orussidae	0001111100	0011131011	111000200?	1101111011	1102110000	111101
Ichneumonidae	0000000300	0111201000	0011000101	1101000021	0101100000	111111
Braconidae	0000000000	0111201000	001100000?	1101000021	0101110010	111111
Trigonalidae	0000000000	0111001000	001000000?	1101000021	0101100000	111111
Aculeata	0000000000	0111001000	0010000000	1101000010	0100100000	111111
Evaniidae	0000101000	0111221001	0010000000	1101230321	31121101??	1111??
Megalyridae	0000011010	1111221011	0110000000	1101033323	31121131??	1111??
Aulacidae	0000000000	0111101000	0010000001	1101311123	1102101100	111111
Stephanidae	0100001000	1111231001	011000000?	1101111123	110211l?0	111111
Gasteruptiidae	0000000000	0111231201	0110000001	1101311?23	1112102101	111111
Chalcidoidea	0101111311	3111231021	111011201?	1101131323	1112112111	1111?1
Cynipidae	0100111112	3111201021	0110110200	1101332323	0112111111	111111
Ibaliidae	0100111011	1111201021	0110110200	1101331323	1112112111	111111
Liopteridae	0100111123	3111201021	1110111200	1101332323	2112112111	111111
Figitidae	0100111113	3111201021	0110110200	1101331323	0112112111	111111
Eucoilidae	0100111123	3111201021	1210111200	1101333323	0112122111	111111
Charipidae	0100111123	3111201021	1110111200	1101333323	0112122111	111111
Proctotrupidae	0000000200	1111231101	0010010001	1101321323	2112112111	111111
Pelecinidae	0001111112	1111231111	111001101?	1101322323	?1121231?1	111111
Vanhorniidae	0000000110	2111231101	0110010001	1101321323	?112112101	111111
Heloridae	0000000000	0111231101	0010010001	1101320323	2112102101	111111
Monomachidae	0000000300	0111231?01	0010010001	1101300323	0102100110	111111
Roproniidae	0000000000	0111231101	0010010001	1101310323	2112100101	111111
Peradeniidae	0000101300	2111231??1	001001?001	1101320323	?1121?01?1	111111
Austroniidae	0000000300	1111231?01	0010010001	1101300323	01121?2110	111111
Diapriidae	0010111312	3111231?21	221001100?	1101331323	1112111111	1111?1
Platygastridae	0112211312	3111231?21	221011200?	1101331323	1112123111	1111?1
Scelionidae	0101111312	3111211?21	221011100?	1101332323	1112123111	1111?1
Ceraphronidae	0021333332	2111231?21	22110?200?	1101222323	2112122211	111111
Megaspilidae	0021311311	1111231?21	221101200?	1101122323	1112121110	111111

Fig.1. Consensus cladogram of unweighted characters (taking account of the state of the veins)

numbers on top of the rectangles refer to the character,
those below the rectangle refer to the character state

- ■ Non-homoplastic apomorphy
- ▨ Homoplastic convergent apomorphy
- ☐ Homoplastic reversal apomorphy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Xyelidae
50
0
Megalodontoidea
33
1
Siricidae
31 32 50 51 52
1 1 1 1 1
Tenthredinoidea
30 32
1 0
31
0
Xiphydriidae
22
1
Cephidae
13 43
1 1
14 22 31 43
2 0 0 2
Anaxyelidae
33 41 44
1 1 1
43
0
Aculeata
11 12 16 38 53 54 55
1 1 1 1 1 1 1
Trigonalidae
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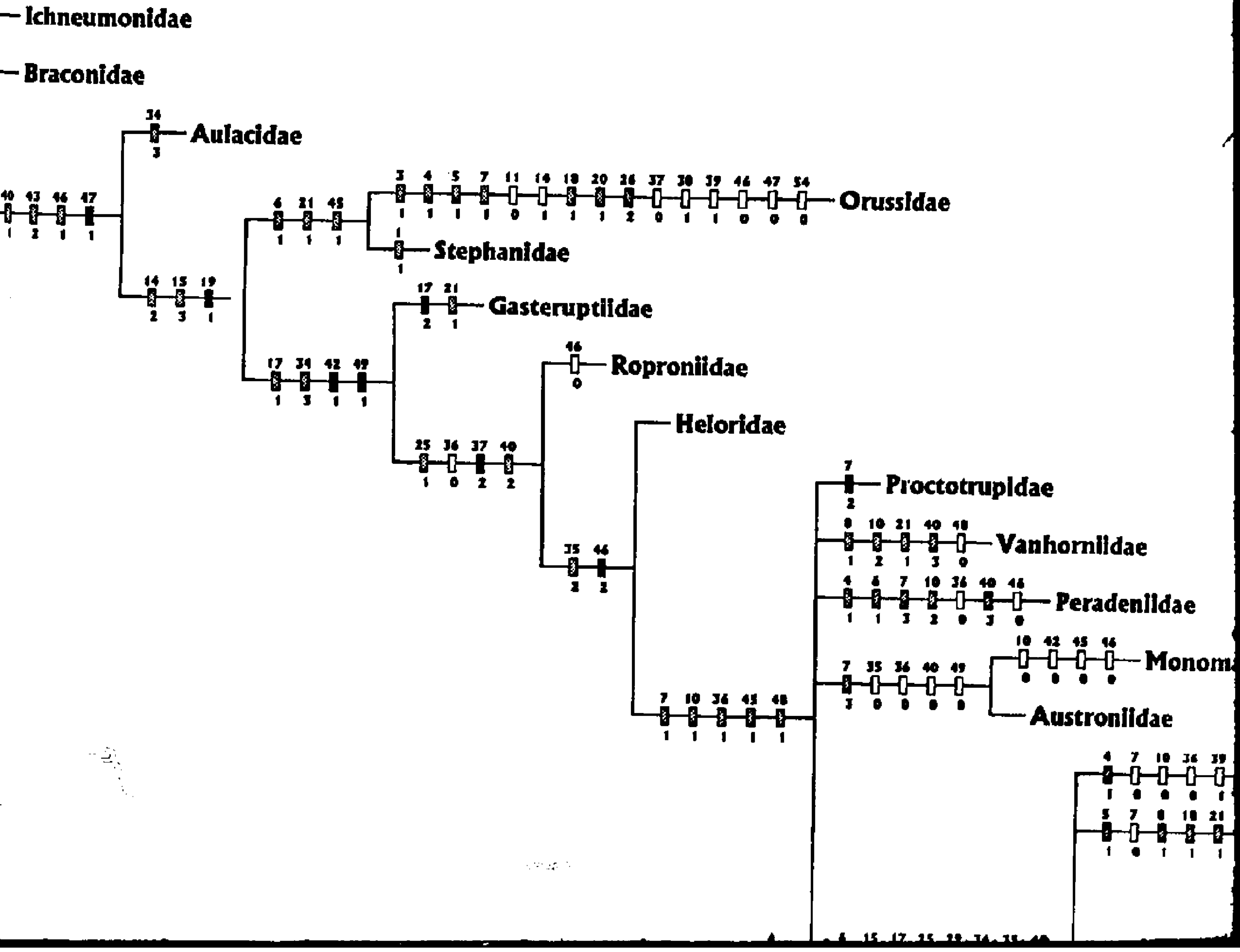
2 1
7 27
3 1
14 23
2 1
45 48
1 1
14 29
1 1
34 35 36 37 39 40
1 1 1 1 2 1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Braconidae
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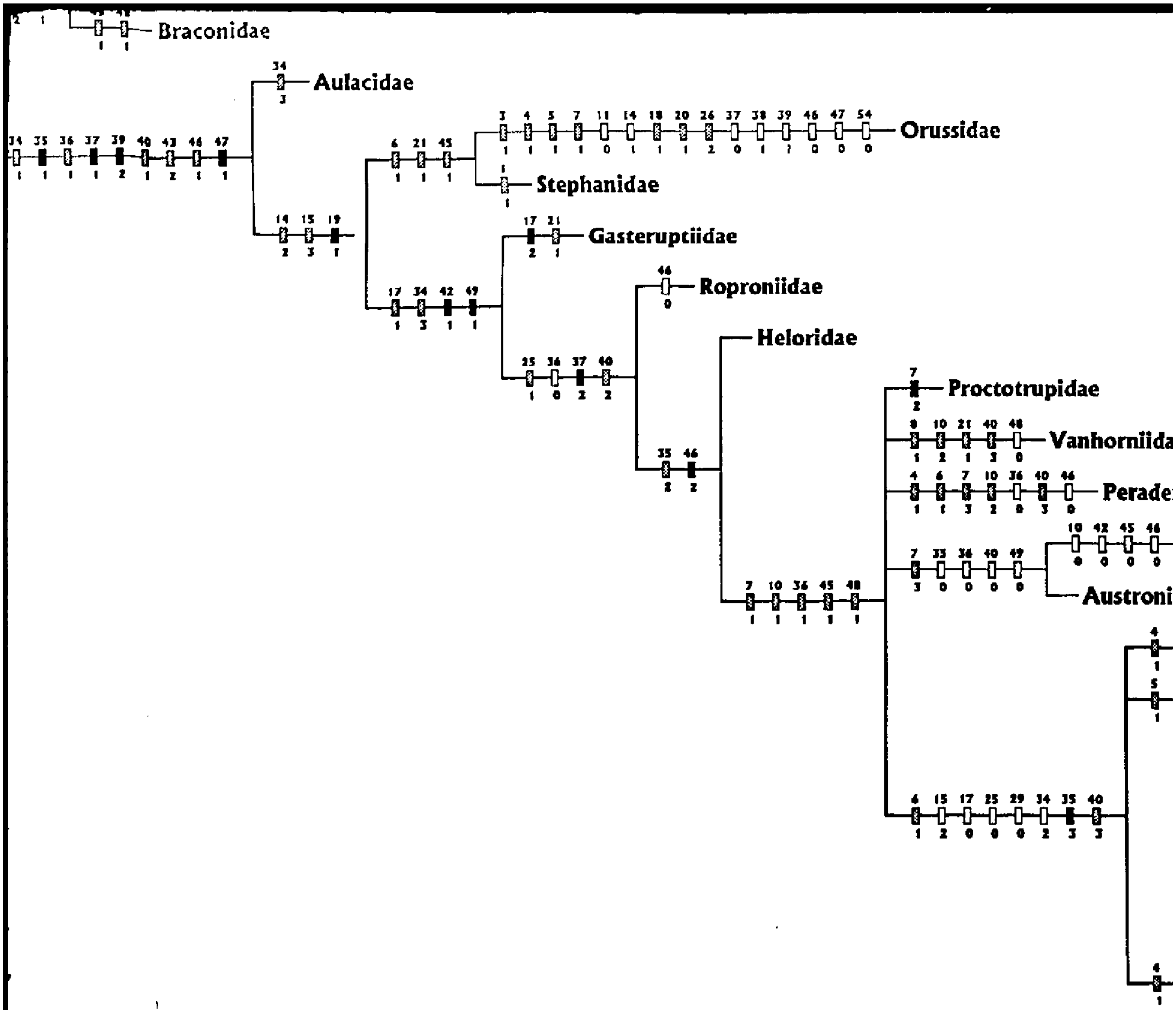
1 2 1 1
34
3
Aulacidae
14 15 19
2 3 1
6 21 45
1 1 1
3 4 5 7 11 14 18 20 26 37 38 39 46 47 54
1 1 1 1 0 1 1 1 2 0 1 1 0 0 0
Orussidae
1
1
Stephanidae
17 34 42 49
1 3 1 1
17 21
2 1
Gasteruptiidae
25 36 37 40
1 0 2 2
46
0
Roproniidae
35 44
2 2
Heloridae
7 10 36 45 48
1 1 1 1 1
7
2
Proctotrupidae
8 10 21 40 48
1 2 1 3 0
Vanhorniidae
4 6 7 10 36 40 46
1 1 3 2 0 3 0
Peradeniidae
7 35 36 40 49
3 0 0 0 0
10 42 45 46
0 0 0 0
Monom
Austroniidae
4 7 10 36 39
1 0 0 0 1
5 7 8 10 21
1 0 1 1 1


Braconidae
Aulacidae
Orussidae
Stephanidae
Gasteruptiidae
Roproniidae
Heloridae
Proctotrupidae
Vanhorniida
Perade
Austroni
34 35 36 37 39 40 43 46 47
1 1 1 1 2 1 2 1 1
34
3
14 15 19
2 3 1
6 21 45
1 1 1
3 4 5 7 11 14 18 20 26 37 38 39 46 47 54
1 1 1 1 0 1 1 1 2 0 1 ? 0 0 0
17 34 42 49
1 3 1 1
17 21
2 1
46
0
25 36 37 40
1 0 2 2
35 46
2 2
7 10 36 45 48
1 1 1 1 1
7
2
8 10 21 40 48
1 2 1 3 0
4 6 7 10 36 40 46
1 1 3 2 0 3 0
7 35 36 40 49
3 0 0 0 0
10 42 45 46
0 0 0 0
6 15 17 25 29 34 35 40
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4
1
5
1
4
1

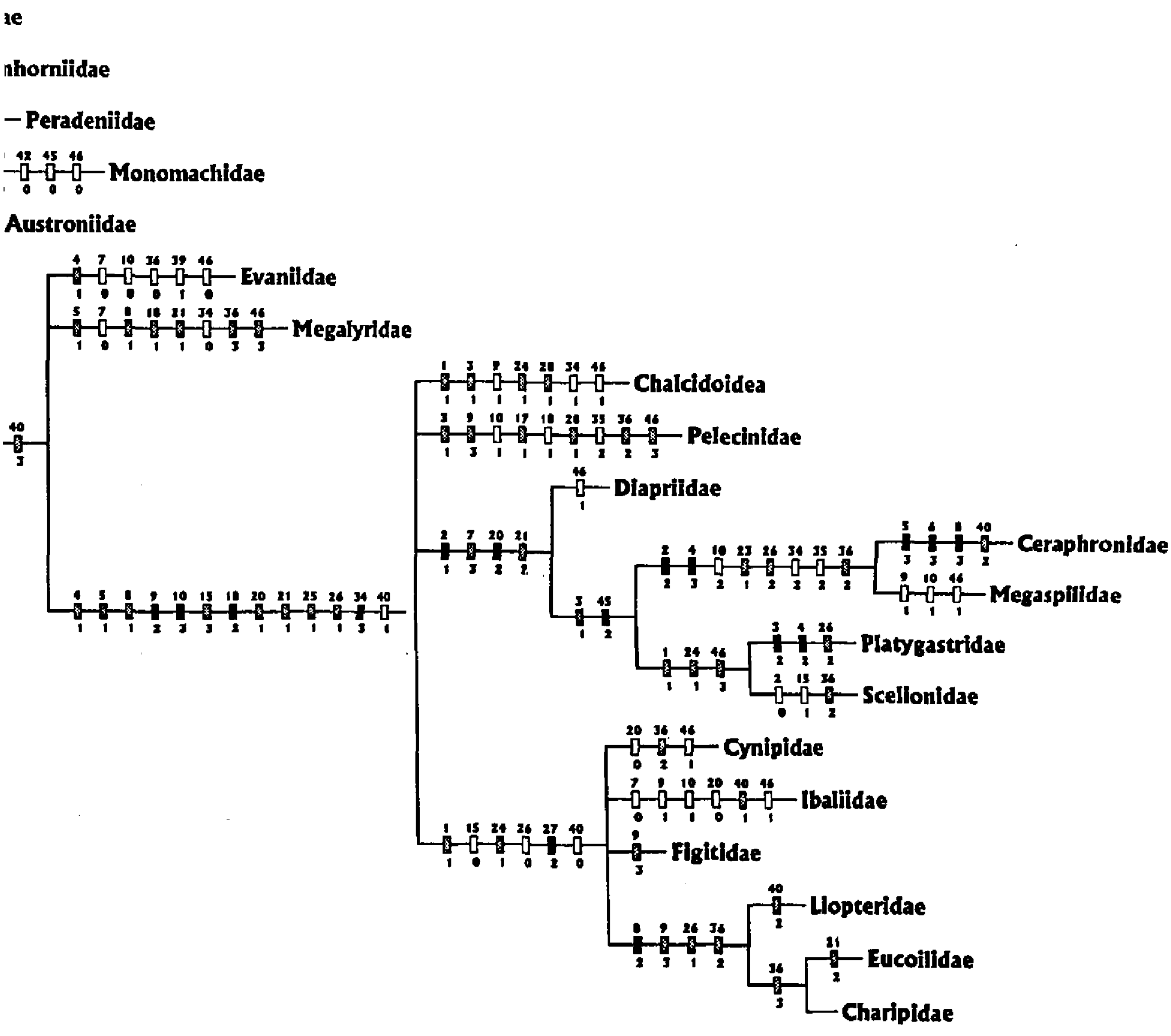
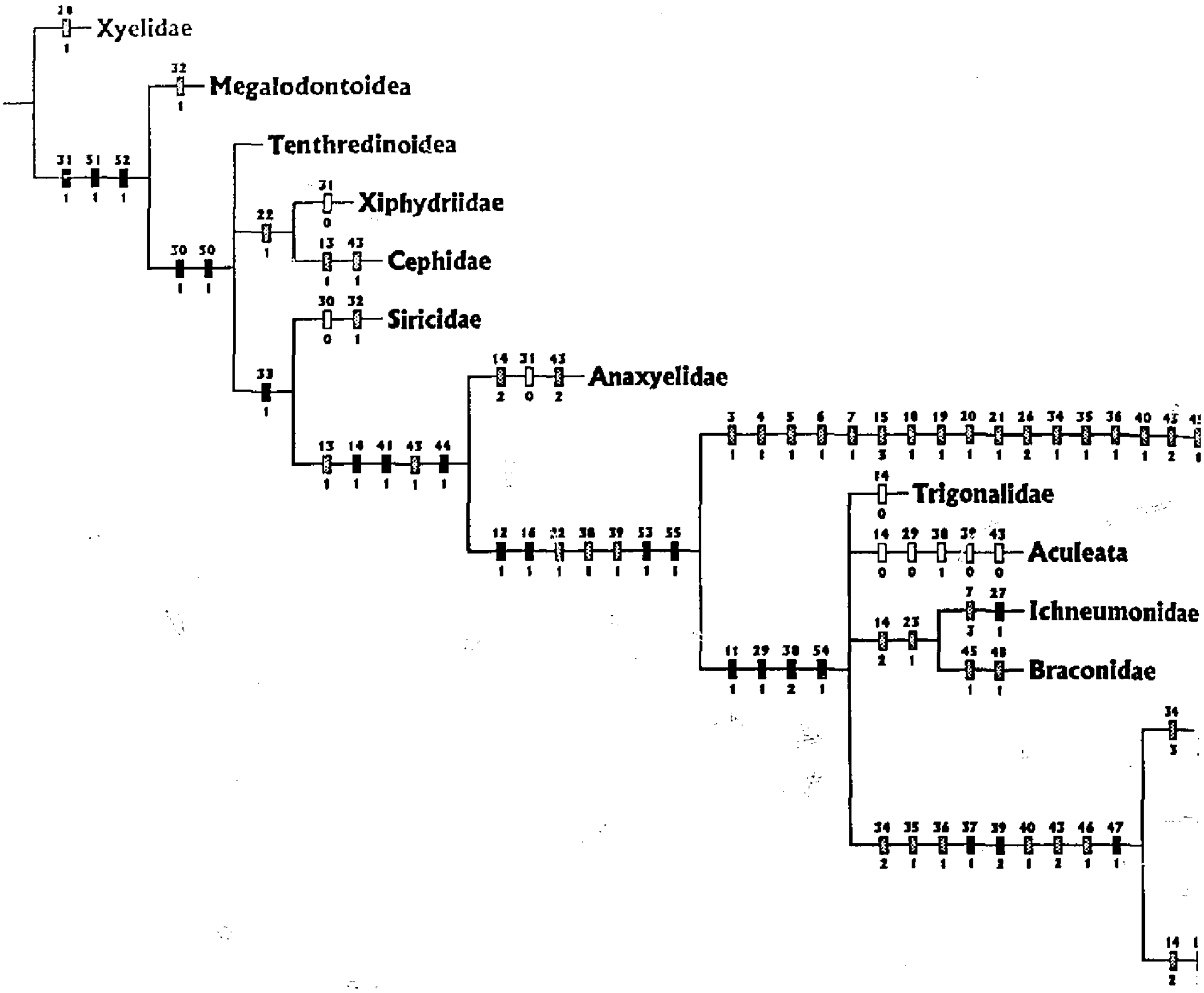
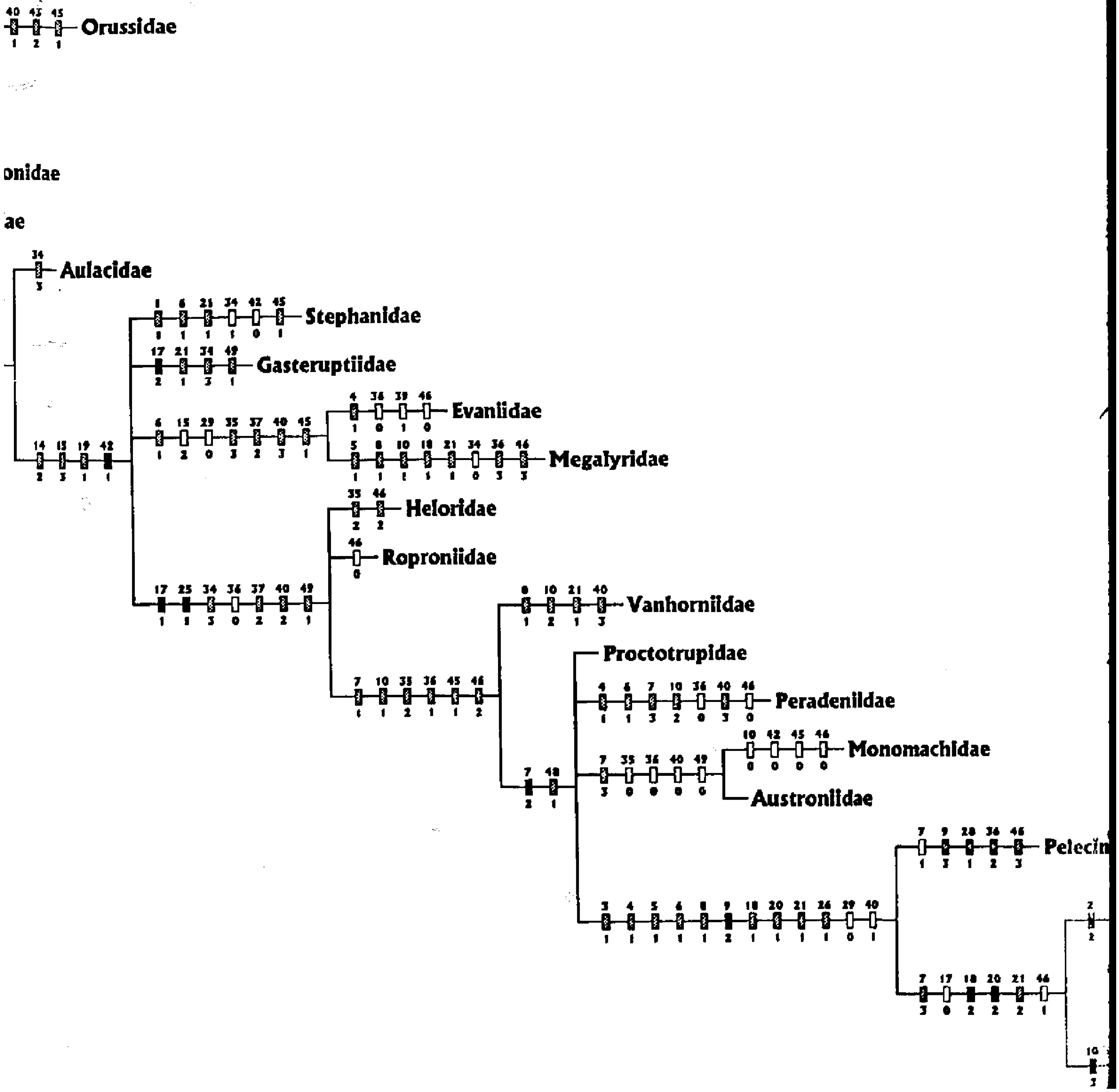

ae
nhorniidae
Peradeniidae
Monomachidae
Austroniidae
Evaniidae
Megalyridae
Chalcidoidea
Pelecinidae
Diapriidae
Ceraphronidae
Megaspilidae
Platygastridae
Scelionidae
Cynipidae
Ibaliidae
Figitidae
Liopteridae
Eucoilidae
Charipidae

Fig.2. Consensus cladogram of weighted characters (taking account of the state of the veins)

numbers on top of the rectangles refer to the character, those below the rectangle refer to the character state

- ■ Non-homoplastic apomorphy
- ▨ Homoplastic convergent apomorphy
- □ Homoplastic reversal apomorphy


Xyelidae
Megalodontoidea
Tenthredinoidea
Xiphydriidae
Cephidae
Siricidae
Anaxyelidae
Trigonalidae
Aculeata
Ichneumonidae
Braconidae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Orussidae
onidae
ae
34
3
Aulacidae
1 6 21 34 42 45
1 1 1 1 0 1
Stephanidae
17 21 34 49
2 1 3 1
Gasteruptiidae
4 36 39 46
1 0 1 0
Evaniidae
6 15 29 35 37 40 45
1 2 0 3 2 3 1
5 8 10 18 21 34 36 46
1 1 1 1 1 0 3 3
Megalyridae
14 15 19 42
2 3 1 1
35 46
2 2
Heloridae
46
0
Roproniidae
17 25 34 36 37 40 49
1 1 3 0 2 2 1
8 10 21 40
1 2 1 3
Vanhorniidae
Proctotrupidae
7 10 35 36 45 46
1 1 2 1 1 2
4 6 7 10 36 40 46
1 1 3 2 0 3 0
Peradeniidae
10 42 45 46
0 0 0 0
Monomachidae
7 35 36 40 49
3 0 0 0 0
7 48
2 1
Austroniidae
7 9 28 36 46
1 2 1 2 3
Pelecin
3 4 5 6 8 9 18 20 21 26 29 40
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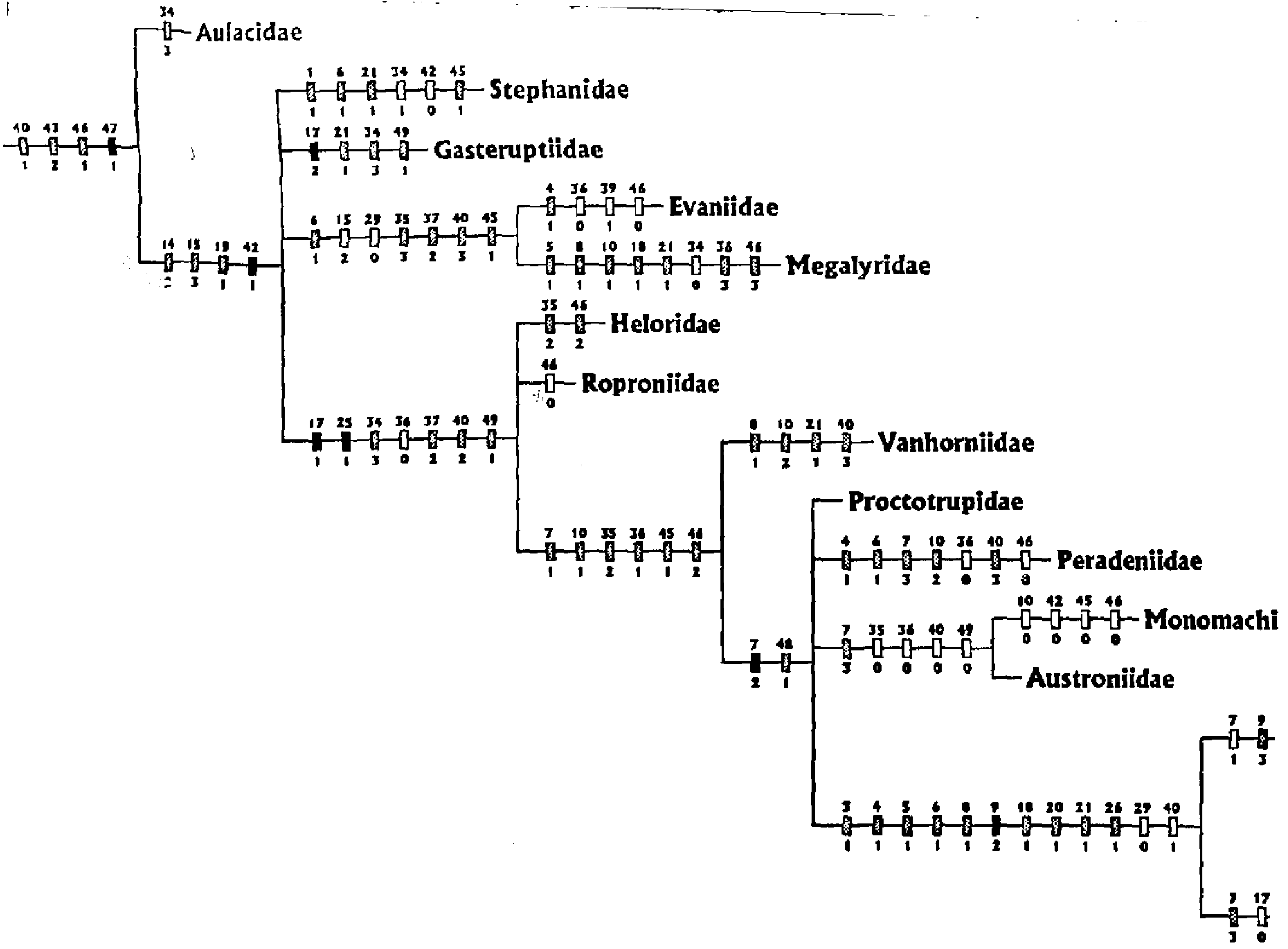
3 0 2 2 2 1
10
2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1 2 1 1
34
3
Aulacidae
14 15 19 42
2 3 1 1
1 6 21 34 42 45
1 1 1 1 0 1
Stephanidae
17 21 34 49
2 1 3 1
Gasteruptiidae
6 15 29 35 37 40 45
1 2 0 3 2 3 1
4 36 39 46
1 0 1 0
Evaniidae
5 8 10 18 21 34 36 46
1 1 1 1 1 0 3 3
Megalyridae
17 25 34 36 37 40 49
1 1 3 0 2 2 1
35 46
2 2
Heloridae
46
0
Roproniidae
7 10 35 36 45 46
1 1 2 1 1 2
8 10 21 40
1 2 1 3
Vanhorniidae
7 48
2 1
Proctotrupidae
4 6 7 10 36 40 46
1 1 3 2 0 3 0
Peradeniidae
7 35 36 40 49
3 0 0 0 0
10 42 45 46
0 0 0 0
Monomachi
Austroniidae
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1 1 1 1 1 2 1 1 1 1 0 1
7 9
1 3
7 17
3 0

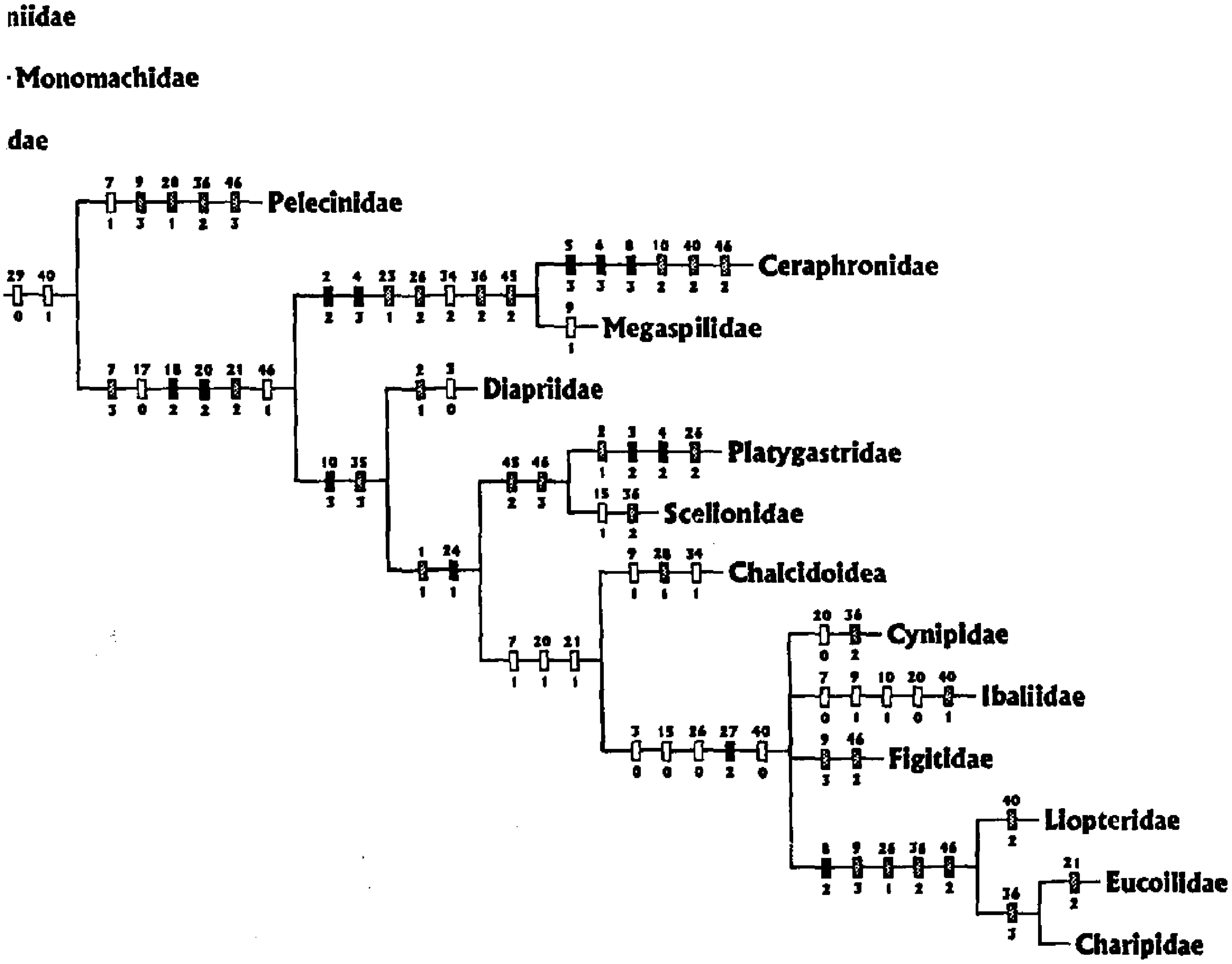

niidae
Monomachidae
dae
29 40
0 1
7 9 28 36 46
1 3 1 2 3
Pelecinidae
7 17 18 20 21 46
3 0 2 2 2 1
2 4 23 26 34 36 45
2 3 1 2 2 2 2
5 4 8 10 40 46
3 3 3 2 2 2
Ceraphronidae
9
1
Megaspilidae
10 35
3 3
2 3
1 0
Diapriidae
1 24
1 1
45 46
2 3
2 3 4 26
1 2 2 2
Platygastridae
15 36
1 2
Scelionidae
7 20 21
1 1 1
9 28 34
1 1 1
Chalcidoidea
3 15 26 27 40
0 0 0 2 0
20 36
0 2
Cynipidae
7 9 10 20 40
0 1 1 0 1
Ibaliidae
9 46
3 2
Figitidae
8 9 26 38 46
2 3 1 2 2
40
2
Liopteridae
36
3
21
2
Eucoilidae
Charipidae

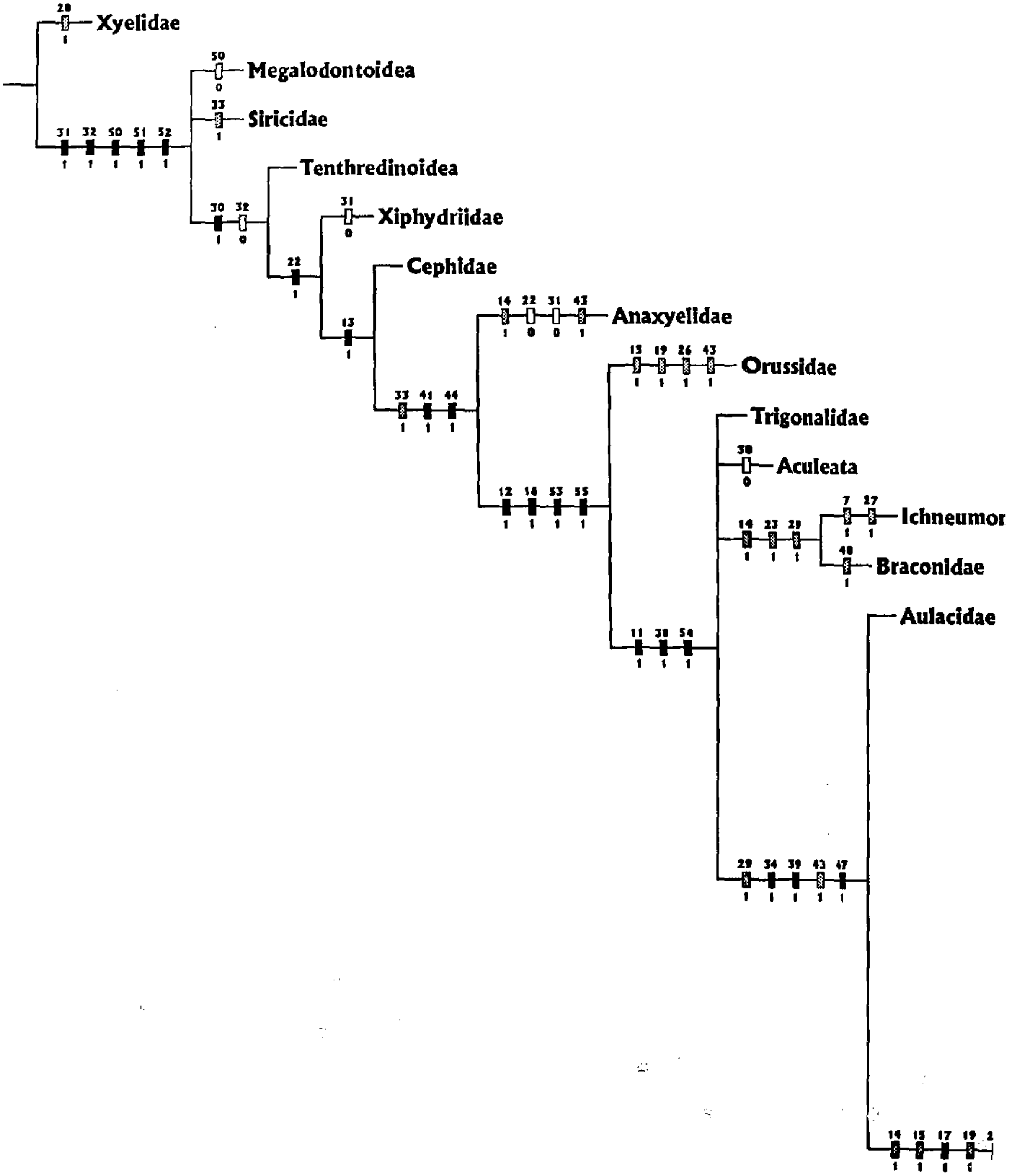
Table 3: Wing characters of Apocrita (with presence or absence of the veins only)

	0	1	2	3	4	5
	0123456789	0123456789	0123456789	0123456789	0123456789	012345
Xyelidae	0000000000	0000000000	0000000010	0000000000	0000000000	000000
Megalodontoidea	0000000000	0000000000	0000000000	0110000000	0000000000	011000
Tenthredinoidea	0000000000	0000000000	0000000000	1100000000	0000000000	111000
Xiphydriidae	0000000000	0000000000	0010000000	1000000000	0000000000	111000
Anaxyelidae	0000000000	0001100000	0000000000	1001000000	0101100000	111000
Siricidae	0000000000	0000000000	0010000000	0111000000	0000000000	111000
Cephidae	0000000000	0001000000	0010000000	1100000000	0001000000	111000
Orussidae	0000000000	0011011001	0010001000	1101000000	0101100000	111101
Ichneumonidae	0000000100	0111101000	0011000101	1101000010	0100100000	111111
Braconidae	0000000000	0111101000	001100000?	1101000010	0100100010	111111
Trigonalidae	0000000000	0111001000	001000000?	1101000010	0100100000	111111
Aculeata	0000000000	0111001000	0010000000	1101000000	0100100000	111111
Evaniidae	0000000000	0111101001	0010000000	1101010110	1111001??	1111??
Megalyridae	0000000000	0111101001	0010000000	1101011111	1111011??	1111??
Aulacidae	0000000000	0111001000	001000000?	1101100011	0101100100	111111
Stephanidae	0100000000	0111111001	001000000?	1101000011	0101100?0	111111
Gasteruptiidae	0000000000	0111111201	0010000001	1101100?11	0111100101	111111
Chalcidoidea	0100000000	0111111011	0010110010	1101010111	0111100111	1111?1
Cynipidae	0100000000	1111101011	0010110200	1101100111	0111100111	111111
Ibaliidae	0100000000	0111101011	0010?10200	1101110111	0111100111	111111
Liopteridae	0100000001	1111101011	0010110200	1101110111	0111100111	111111
Figitidae	0100000001	1111101011	0010110200	1101110111	0111100111	111111
Eucoilidae	0100000001	1111101011	0110110200	1101111111	0111110111	111111
Charipidae	0100000001	1111101011	0010110200	1101111111	0111110111	111111
Proctotrupidae	0000000000	0111111101	0010010001	1101100111	0111100101	111111
Pelecinidae	0000000000	0111111101	0010010011	1101100111	0111101?1	111111
Vanhorniidae	0000000000	0111111101	0010010001	1101100111	0111100101	111111
Heloridae	0000000000	0111111101	0010010001	1101100111	0111100101	111111
Monomachidae	0000000100	011111?01	0010010001	1101100111	0101100110	111111
Roproniidae	0000000000	0111111101	0010010001	1101100111	0111100101	111111
Peradeniidae	0000000100	011111?01	0010010001	1101100111	0111001??	111111
Austroniidae	0000000100	011111?01	0010010001	1101100111	0111100110	111111
Diapriidae	0000000100	111111?11	111001000?	1101110111	0111100111	111111
Platygastridae	0101100100	111111?11	111011100?	1101110111	0111111111	111111
Scelionidae	0100000100	1111?1?11	111011000?	1101110111	0111111111	111111
Ceraphronidae	0010111110	011111?11	11110?100?	1101000111	0111111111	111111
Megaspilidae	0010000100	011111?11	11110?100?	1101000111	011110011?	111111

Fig.3. Consensus cladogram of unweighted characters
(taking account of the presence or absence of the veins only)

numbers on top of the rectangles refer to the character,
those below the rectangle refer to the character state

■ Non-homoplastic apomorphy
▨ Homoplastic convergent apomorphy
□ Homoplastic reversal apomorphy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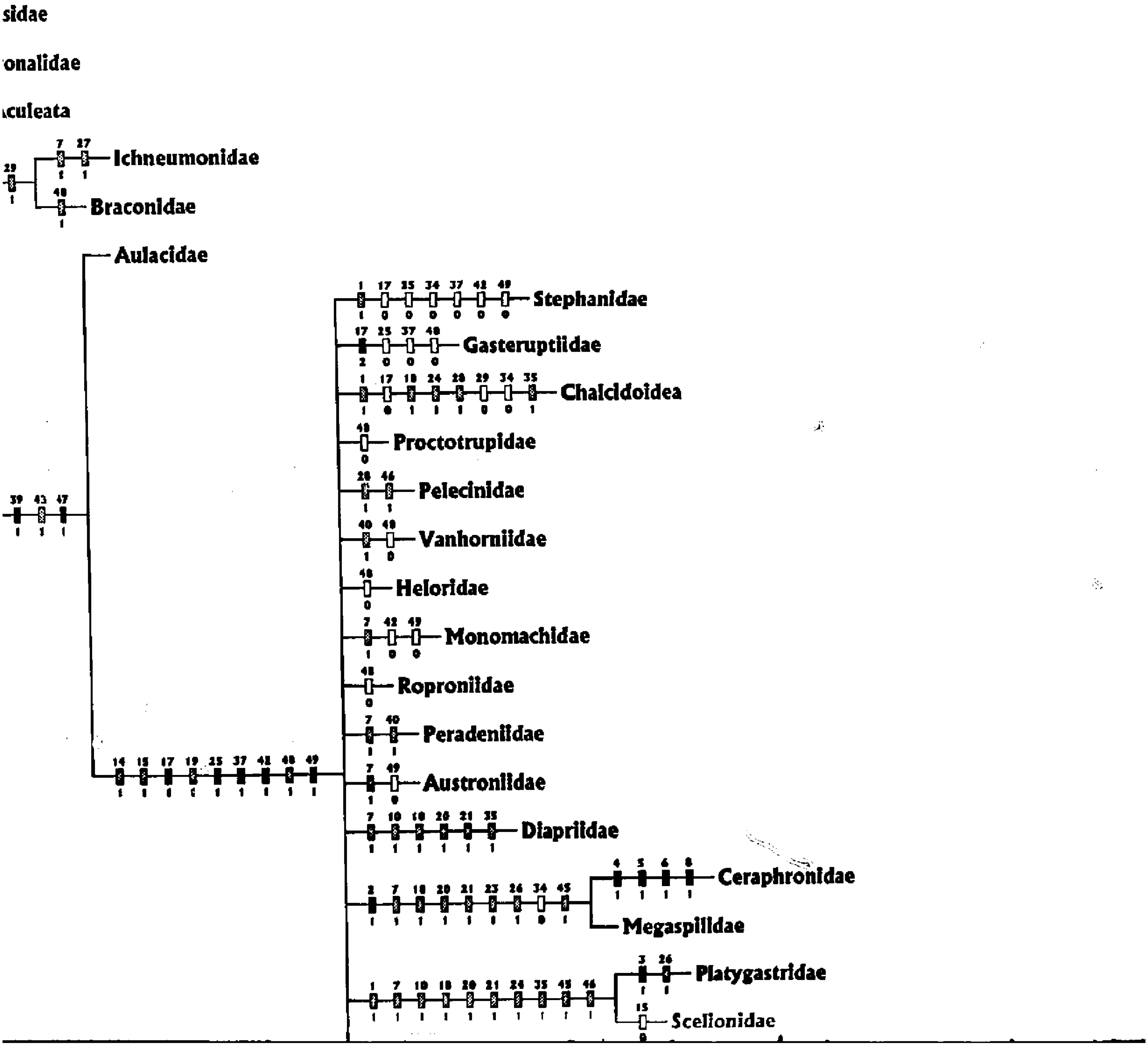
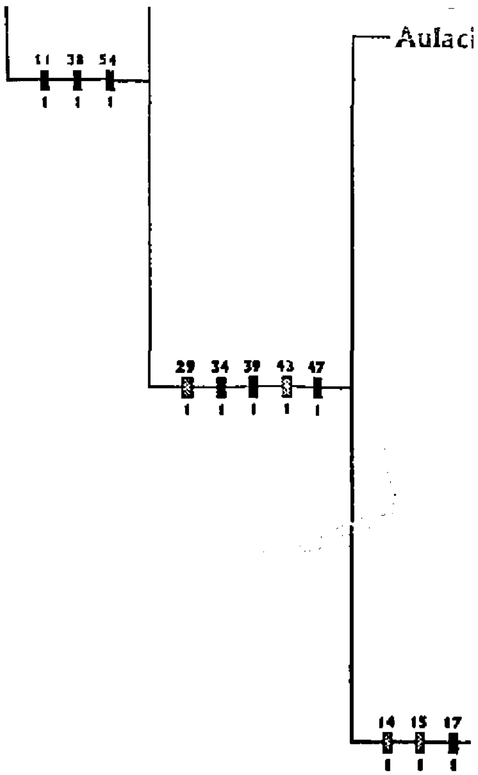
Xyelidae
50
0
Megalodontoidea
33
1
Siricidae
31 32 50 51 52
1 1 1 1 1
Tenthredinoidea
30 32
1 0
31
0
Xiphydriidae
22
1
Cephidae
13
1
14 22 31 43
1 0 0 1
Anaxyelidae
15 19 26 43
1 1 1 1
Orussidae
33 41 44
1 1 1
Trigonalidae
38
0
Aculeata
7 27
1 1
Ichneumor
14 23 29
1 1 1
48
1
Braconidae
12 18 53 55
1 1 1 1
Aulacidae
11 38 54
1 1 1
29 34 39 43 47
1 1 1 1 1
14 15 17 19 2
1 1 1 1


sidae
onalidae
culeata
Ichneumonidae
Braconidae
Aulacidae
Stephanidae
Gasteruptiidae
Chalcidoidea
Proctotrupidae
Pelecinidae
Vanhorniidae
Heloridae
Monomachidae
Roproniidae
Peradeniidae
Austroniidae
Diapriidae
Ceraphronidae
Megaspilidae
Platygastridae
Scelionidae


Aulaci
11 38 54
1 1 1
29 34 39 43 47
1 1 1 1 1
14 15 17
1 1 1

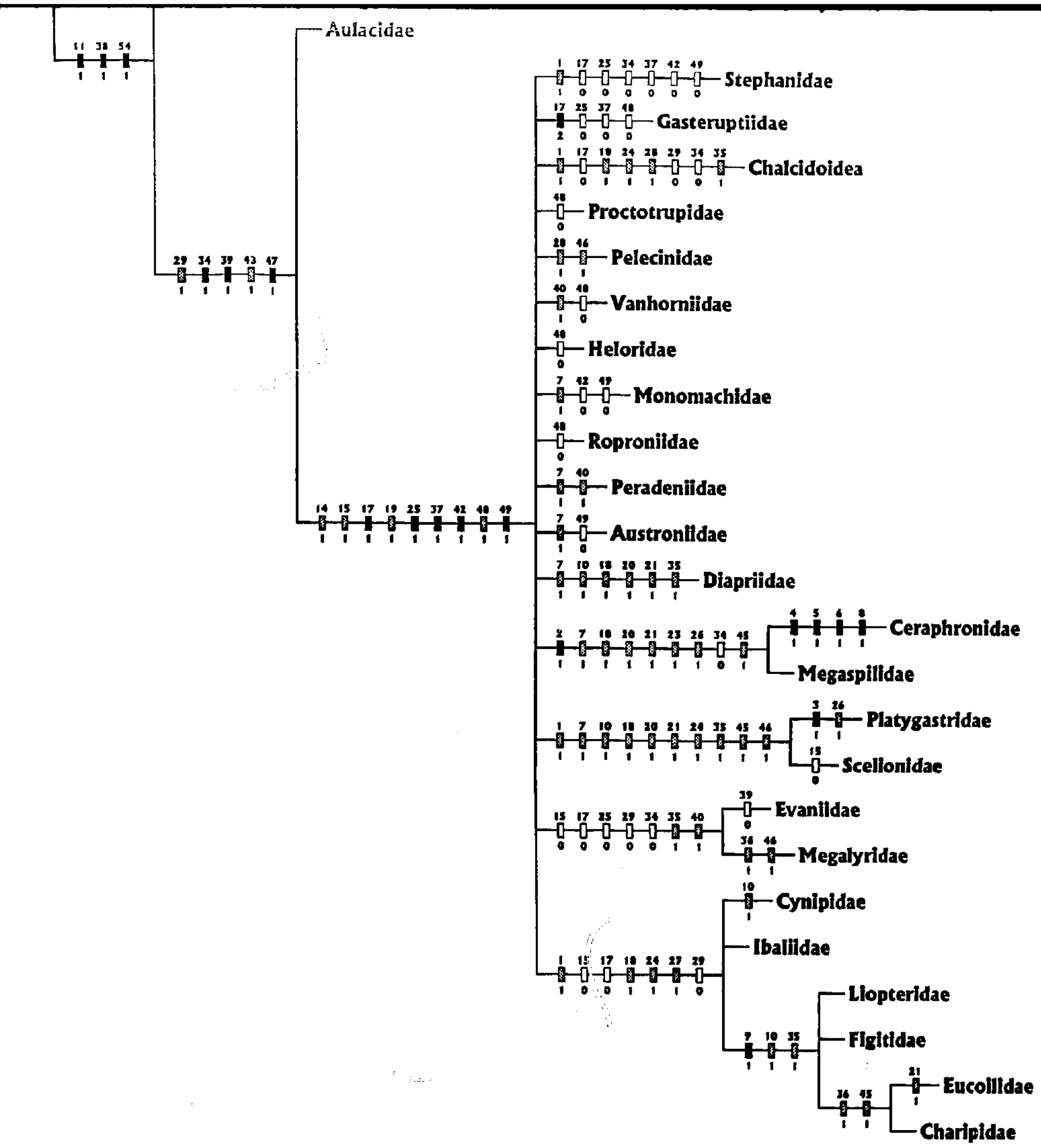
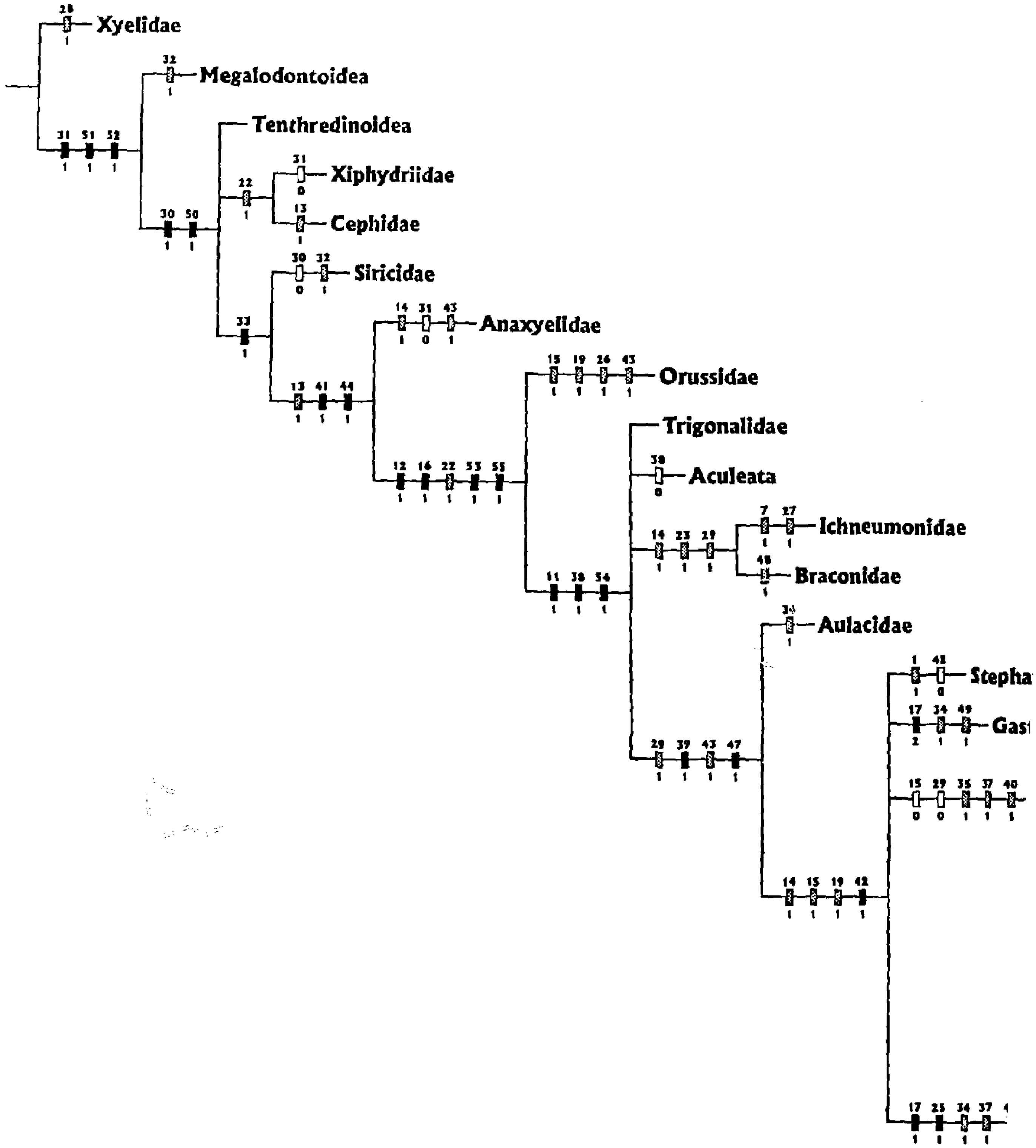
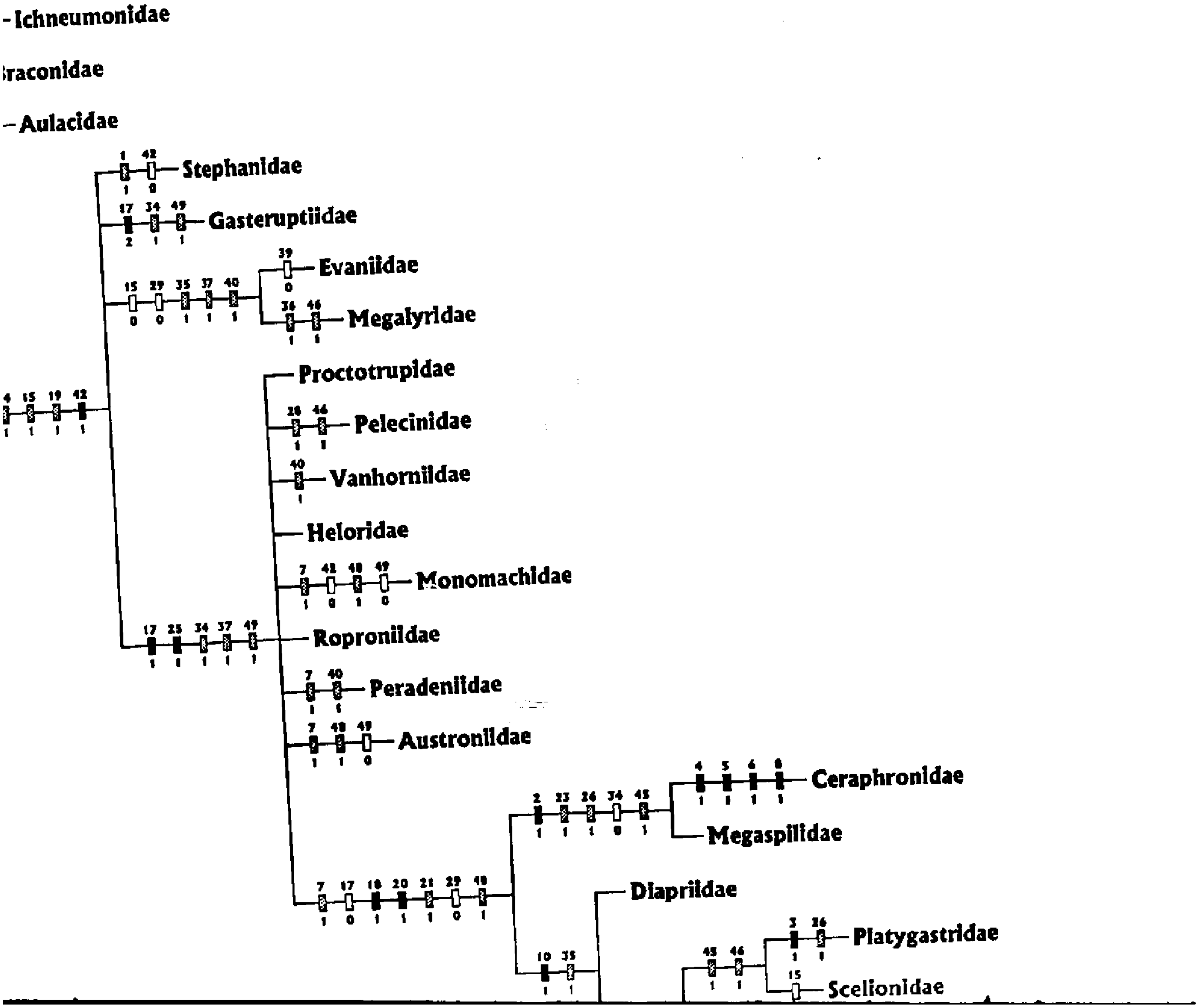

Aulacidae
Stephanidae
Gasteruptiidae
Chalcidoidea
Proctotrupidae
Pelecinidae
Vanhorniidae
Heloridae
Monomachidae
Roproniidae
Peradeniidae
Austroniidae
Diapriidae
Ceraphronidae
Megaspilidae
Platygastridae
Scelionidae
Evaniidae
Megalyridae
Cynipidae
Ibaliidae
Liopteridae
Figitidae
Eucoilidae
Charipidae

Fig.4. Consensus cladogram of weighted characters
(taking account of the presence or absence of the veins only)

numbers on top of the rectangles refer to the character,
those below the rectangle refer to the character state

■ Non-homoplastic apomorphy
▨ Homoplastic convergent apomorphy
□ Homoplastic reversal apomorphy


28 1
Xyelidae
32 1
Megalodontoidea
31 51 52 1 1 1
Tenthredinoidea
31 0
Xiphydriidae
22 1
13 1
Cephidae
30 50 1 1
30 32 0 1
Siricidae
33 1
14 31 43 1 0 1
Anaxyelidae
13 41 44 1 1 1
15 19 26 43 1 1 1 1
Orussidae
12 16 22 53 55 1 1 1 1 1
Trigonalidae
38 0
Aculeata
7 27 1 1
Ichneumonidae
14 23 29 1 1 1
48 1
Braconidae
11 38 54 1 1 1
34 1
Aulacidae
1 42 1 0
Stepha
17 34 49 2 1 1
Gas
29 39 43 47 1 1 1 1
15 29 35 37 40 0 0 1 1 1
14 15 19 42 1 1 1 1
17 25 34 37 1 1 1 1


Ichneumonidae
raconidae
Aulacidae
4 15 19 42
1 1 1 1
1 42
1 0
Stephanidae
17 34 49
2 1 1
Gasteruptiidae
15 29 35 37 40
0 0 1 1 1
39
0
Evaniidae
36 46
1 1
Megalyridae
Proctotrupidae
28 46
1 1
Pelecinidae
40
1
Vanhorniidae
Heloridae
7 42 48 49
1 0 1 0
Monomachidae
17 25 34 37 49
1 1 1 1 1
Roproniidae
7 40
1 1
Peradeniidae
7 48 49
1 1 0
Austroniidae
2 23 24 34 45
1 1 1 0 1
4 5 6 8
1 1 1 1
Ceraphronidae
Megaspilidae
7 17 18 20 21 29 48
1 0 1 1 1 0 1
10 35
1 1
Diapriidae
45 46
1 1
3 26
1 1
Platygastridae
15
Scelionidae

Combining the data from this research with those of other papers on character suites resulted in 32 most parsimonous trees with the following statistics: L= 422, CI= 0.50, RI= 0.74. Two nelson consensus trees were obtained, one with acctran optimization (Fig. 42) and the other with deltran optimization (Fig.43). The deltran option favours convergence whereas the acctran option favours losses. The deltran tree shows a similar character distribution at some nodes, but strikingly different results in other nodes when compared with the acctran tree.

The position of Xyelidae as the sister group to the remainder of the Hymenoptera is supported by nine apomorphies (31, 32, 52, 70, 77, 80, 81, 123, 145) in the acctran tree whereas the deltran tree shows a series of reversals at the basal node. Ten synapomorphies (68, 75, 85, 86, 122, 141, 142, 150, 153, 160) support the monophyly of (Xiphydriidae (Orussidae + Apocrita)) in the acctran tree but only four (122, 141, 142, 150) support the same relationship in the deltran tree (none from the wings).

In the acctran tree, the monophyly of Orussidae + Apocrita is supported by thirteen characters (12, 16, 53, 55, 118, 120, 124, 129, 130, 132, 135, 144) such as the loss of first radial and the anal crossvein in the fore wing, and the open anal cell and the orientation of the Cubitus in the hind wing. The deltran tree shows seventeen apomorphies at the same node (12, 16, 53, 55, 56, 59, 62, 99, 100, 116, 120, 124, 130, 132, 135, 143, 144). In addition, the loss of 3rs-m and m-cu, as well as the derived condition of the orientation of Rs in the hind wing are present in Anaxyelidae and Orussidae+Apocrita only (Pergidae is an exception among tenthredinoids in having lost m-cu as well). These characters are convergent in these two groups.

The results suggest that the rate of evolution of wing characters was much slower in Symphyta than in Apocrita because the time frame is larger but the differences between taxa remain relatively minor.

These cladograms support the monophyly of Apocrita with a number of synapomorphies (characters 11, 54, 56, 59, 62, 84, 99, 100, 117, 134, 143, 146 in the acctran tree; characters 11, 38, 84, 117, 134, 148 in the deltran tree). Character 11, loss of the second anal vein in the fore wing, and 54, the orientation of the median vein in the hind wing, are present in the ground plan of all apocritans whereas 38, the loss of second anal vein in the hind wing, may have occured several times.

The sister group relationship between Trigonalidae and the other Apocrita (excluding Aculeata and Ichneumonoidea) is supported by six uniquely derived characters (47, 57, 67, 84, 106, 175), one of which is present in the hind wing (the absence of basal hamuli). The loss of the 2rs-m crossvein in the fore wing is convergent with Ichneumonoidea, the loss of 2m-cu is also present in Orussidae in the fore wing, and the Costa in the hind wing is also lost in Orussidae.

Within Apocrita, the monophyly of all widely accepted (and well defined) superfamilies, Ichneumonoidea, Platygastroidea, Cynipoidea and Ceraphronoidea, is supported by a number of synapomorphies. The results show that Ichneumonoidea + Aculeata is a monophyletic group (characters 173, 174 are synapomorphic for these taxa) and that this assemblage is the sister group of all other Apocrita. The monophyly of Ichneumonoidea is supported by a single character, the narrow costal cell in the fore wing, which is convergently gained in Ceraphronoidea.

The absence of Rs in the hind wing of Aulacidae and Gasteruptiidae among macrohymenoptera may substantiate their sister group relationship since this vein is present in some microhymenoptera. The monophyly of this assemblage is better supported by non-wing characters such as character 135, the development of two large lobes on the third phragma (Whitfield et al. 1989).

The monophyly of the Evaniomorpha (sensu Rasnitsyn 1988) is not corroborated, although the sister group relationship between Megalyridae and Stephanidae is supported by convergences and reversals. Among these, only one can be found in the wings (the loss of the third anal vein in the hind wing, convergently with the Microhymenoptera, Aulacidae and Gasteruptiidae). Evanioidea is shown to be paraphyletic since Evaniidae is the sister group of ((Aulacidae + Gasteruptiidae) + microhymenoptera). However, the concept of Stephanoidea, reduced to Stephanidae and Megalyridae has some, albeit weak, support.

The monophyly of microhymenoptera is supported by the unique derived state of character 25: the distal abscissa of Cu in the fore wing is on the same level as the abscissa between 1-M and 2cu-a or even higher (i.e. Roproniidae). Thus, the definition of microhymenoptera in this paper is similar to the Proctotrupomorpha of Rasnitsyn (1988), with the addition of Ceraphronoidea. The apomorphic state of character 103 also supports the monophyly of this group in the acctran tree, but in the deltran cladogram, characters 73, 77 and 111 replace 103. The loss of the 3rs-m crossvein is convergent in Gasteruptiidae, Stephanidae, Ichneumonoidea and Orussidae.

The monophyly of Platygastroidea is supported by character 142 and a number of other apomorphies that are convergent in other taxa. The loss of the two cu-a crossveins (characters number20 and 21) is also present in Diapriidae+Ceraphronoidea. The loss of the distal abscissa of 1A in the fore wing is shared with Cynipoidea (except Ibaliidae) and the loss of R1 can be observed in

Eucoilidae and Charipidae.

The monophyly of Cynipoidea is supported by character 82 in the acctran tree, but also by 88 and 92 in the deltran tree. Character 27, the position of 3rs-m and shape of cell 3Rs, is also a synapomorphy for the superfamily.

The close relationship between Chalcidoidea and Platygastroidea shown by Rasnitsyn (1988) is apparent in the deltran cladogram as well (character 71 and 105 are the only synapomorphies). This assemblage is the sister group of Cynipoidea and this relationship is supported by the loss of the costal vein in the fore wing (which is convergently lost in the Stephanidae), and the loss of the stigma as well as character 64 in the deltran cladogram (numbers 64, 71 and 74 in the acctran cladogram).

Monophyly of the Proctotrupoidea is supported by character 17, the first abscissa of diagonal Rs+M, which creates a long 2-Rs+M. The absence of most of these veins in Diapriidae, Cynipoidea, Ceraphronoidea and Platygastroidea makes it difficult to evaluate this character in these taxa. The presence of Rs in the hind wing of Ceraphronoidea may indicate a close relationship with macrohymenoptera (as suggested by Rasnitsyn, 1988) or with Chalcidoidea. In either case, Ceraphronoidea is not a member of Proctotrupoidea. Within Proctotrupoidea, relationships of the different families are unresolved, except for the sister group relationship between Austroniidae and Monomachidae. This assemblage is supported by the presence of a second abscissa of M in the hind wing (a unique character state among Microhymenoptera).

The position of some groups in the cladograms based on the first data matrix of wing venation characters is somewhat erroneous because a few taxa have numerous nebulous veins, despite their large size and relative ancestry. For example, the Orussidae, where wing veins are mostly nebulous is displaced into the Apocrita. Similar phenomena occur for Stephanidae and Pelecinidae. Such a high number of nebulous veins, especially in Orussidae, is rather surprising, considering the fact that their sister species have a higher number of tubular veins. In addition, Paroryssidae, the ancestor postulated for Orussidae, was described to be much smaller (less than a third of Orussidae) and to possess a higher number of nebulous veins than its descendant (Rasnitsyn 1980, 1988). A similar relationship must be true for Pelecinidae since the other living families of Proctotrupoidea (some of which are more ancestral) are much smaller and have a more extensive tubular venation. Therefore, either the increased number of nebulous veins is the reflection of the number of specializations, or this phenomenon is an artefact due to an increased size. If size truly affects the venation in such a way, this correlation thus means that the tubular veins cannot expand as easily as the wings (with increased body size) and that the only way to accomodate the necessity of more veins is by gaining nebulous veins.

The rates of evolution of the venation of the fore and hind wing are variable and independent. This is apparent, for example, in Megalyridae, where the venation of the fore wing is rather complete, but much reduced in the hind wing (where only Rs remains). On the other hand, the fore wing venation of Ceraphronoidea is limited to C+Sc+R, R1, 1r&Rs, A (and 1-Rs, 1M, M+Cu and Cu in Megaspilidae), but the number of veins of the hind wing, although spectral is much more complete.

CONCLUSION

The difference between each phylogenetic tree based on wing characters is visible mainly in some derived taxa. The consistency and retention indexes are not particularly high in most of them, but they remain in the acceptable range in those obtained from the second data matrix (i.e. around 0.50 and 0.80 respectively). Furthermore, the combined data (wing and non-wing) result in cladograms that are relatively similar in configuration to those developed from wing characters alone (at least for the ingroups). Thus, it seems that wing characters are relatively good indicators of phylogenetic relationships: the monophyly of Cynipoidea, Ichneumonoidea and Ceraphronoidea is constant in all cladograms produced in the present paper.

The rate of transformation is different in the fore and hind wing, and the Ceraphronoidea and Megalyridae are good indicators of this effect. This variability in the rate of evolution has probably created some biases; although this is a problem of the method of analysis, it alows to maintain a proper level of objectivity that would be lost if the characters were weighted according to their estimated value as indicators of phylogenetic relationships.

Body size does affect the venation, but it is difficult to evaluate its exact effect. A decrease in the size of the insect causes a reduction in the number of veins and diminishes their strenght (often losing tracheation), but the proportion of these changes must be variable. On the other hand, an increased body size may also result in a loss of tracheation in a number of veins.

With a total of 55 characters related to wing venation, many of which were not described before, this study has achieved its main objective: to increase our knowledge of phylogenetically informative characters in Hymenoptera. Several relationships that are well recognized in the literature are also supported here by a number of characters: the sister group relationship between Monomachidae and Austroniidae, a close affiliation between Chalcidoidea, Platygastroidea and Cynipoidea, and a basal position of the Ichneumonoidea and Aculeata.

The sister group relationship between Orussidae and Apocrita (and the monophyly of the latter) is confirmed by all cladograms derived from the second data matrix (Fig.3 and 4) as well as those obtained from non-wing characters. This relationship is supported by over a dozen apomorphies in the cladograms which combine all data. The wing characters were represented by the loss of 1r and the second Anal vein in the fore wing, the opened anal cell and the orientation of the Cubitus in the hind wing. The first data matrix resulted in cladograms where Apocrita was paraphyletic because of the high number of nebulous veins in Orussidae. A similar phenomenon is also present in Stephanidae and Pelecinidae, but it does not contradict the traditional position of Orussidae, it only indicates that reduction in wing venation may occur independently in some taxa.

Symphyta is clearly not monophyletic according to any cladogram presented here and this is in agreement with previous studies (Rasnitsyn 1980, 1988; Dowton and Austin 1994); venational characters, however, offer little support for any relationship within this group. Although the interrelationships of most symphytan taxa have not been clarified in the present study (and this was not among the objectives), the Xyelidae are confirmed as the most ancestral group; they have an extra rs-m crossvein and a free basal abscissa of Cu in the hind wing.

Aculeata is the sister group of Ichneumonoidea and this assemblage is the sister group of other apocritan taxa; this is supported by Rasnitsyn (1988) and Dowton and Austin (1994). The wing venation of Aculeata is more plesiomorphic than any other member of Apocrita and the ground plan structure is the same for the two groups; this argument speaks strongly in favor of an early divergence of Aculeata.

The monophyly of Proctotrupoidea (s.s.) was not supported in any of the cladograms. The absence of Rs+M in the fore wing of Monomachidae and Austroniidae as well as the long abscissa of M between M+Cu and 1rs-m in the hind wing are peculiar characters found in no other family within this group. The venation of Pelecinidae and Diapriidae is highly reduced (especially in the latter) and that of the former is highly specialized. The monophyly of Platygastroidea is supported by cladograms derived from the second and third data matrices. The exclusion of this taxon from Proctotrupoidea is supported by the cladograms obtained from wing characters. This may be the result of a highly reduced wing venation, but the absence of the costa in the fore wing is an apomorphy that even Diapriidae has not developed.

If one admits that only monophyletic taxa should be recognized, the superfamily Siricoidea should be broken down into three families, Anaxyelidae, Siricidae and Xiphydriidae. The monophyly of Evanioidea could not be establish neither and this superfamily should also broken into three families (Evaniidae, Aulacidae and Gasteruptiidae). Proctotrupoidea are paraphyletic if Ceraphronoidea are set as a separate superfamily. However, Splitting this superfamily would render the classification of parasitic Hymenoptera very cumbersome since it includes nine families (Huber 1993) or the superfamily can be preserved for convenience, in a similar way to the Symphyta.

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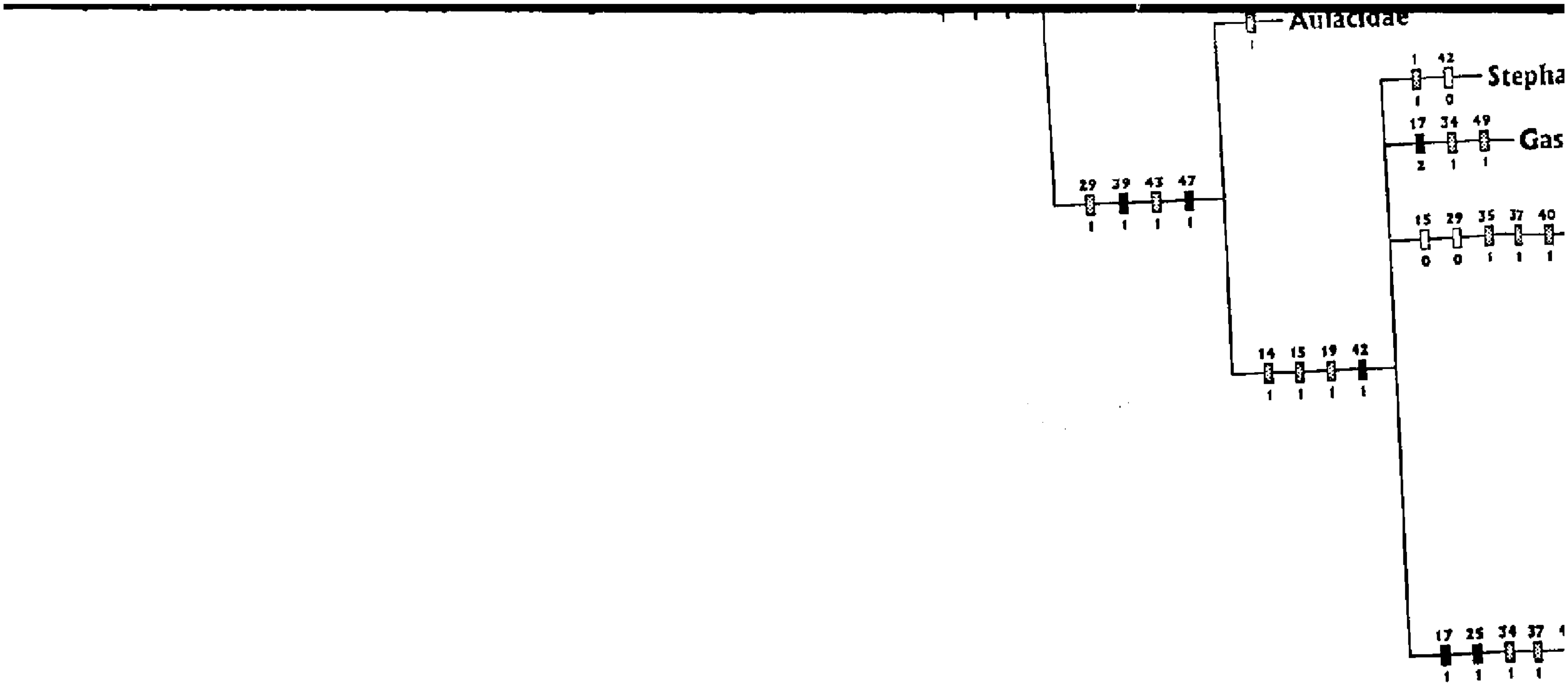
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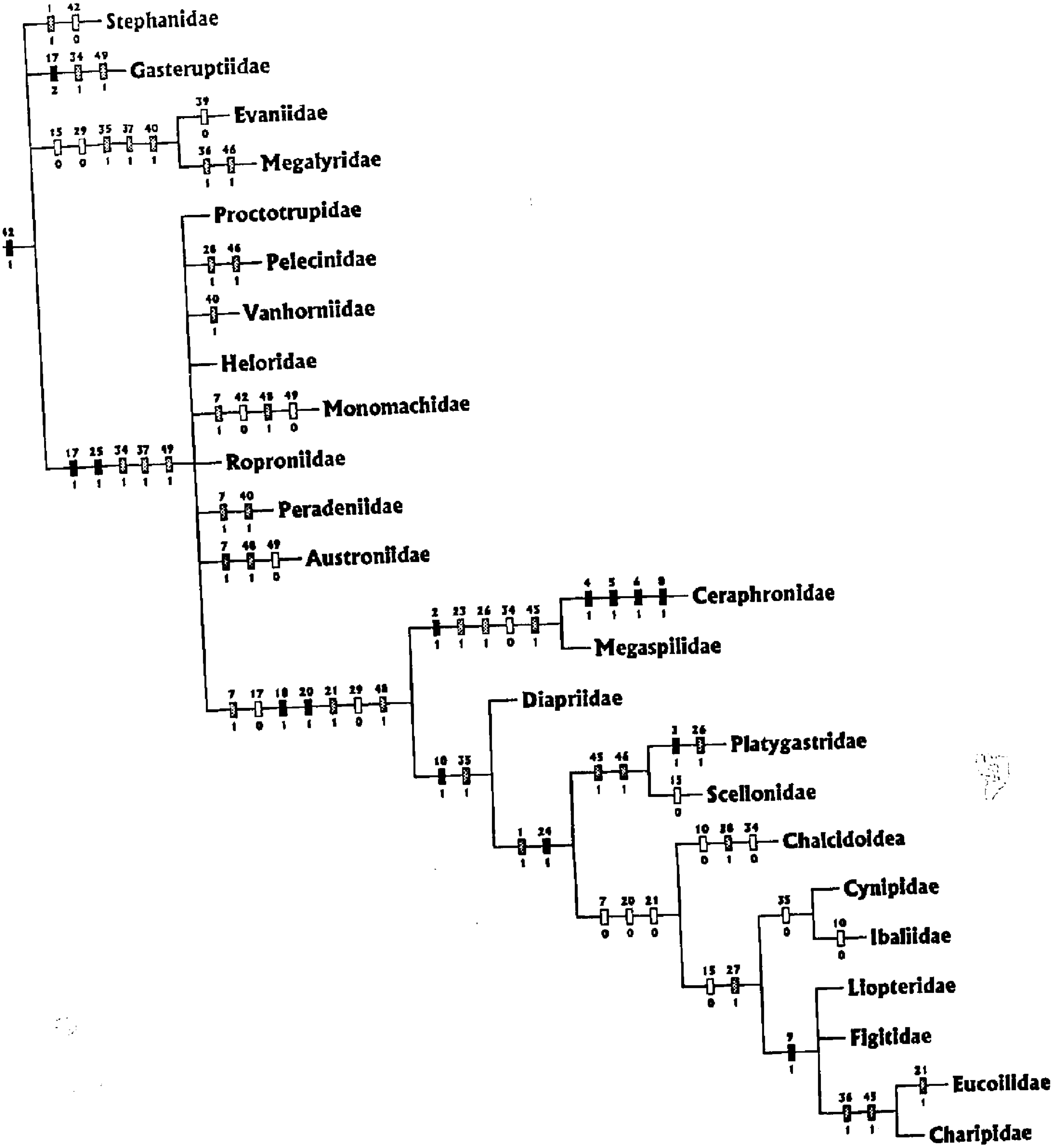
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Peradeniidae
Austroniidae
Ceraphronidae
Megaspilidae
Diapriidae
Platygastridae
Scelionidae
Chalcidoidea
Cynipidae
Ibaliidae
Liopteridae
Figitidae
Eucoilidae
Charipidae

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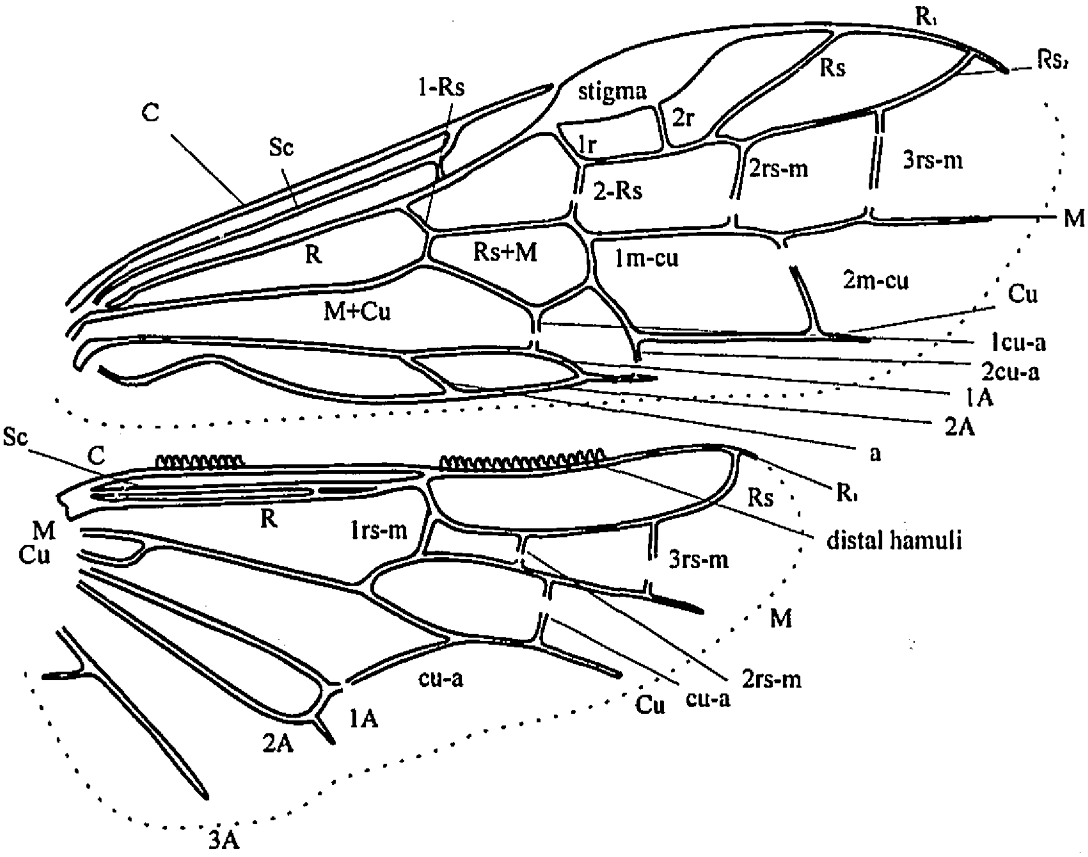
APPENDIX 1:

WING DRAWINGS

APPENDIX 1: WING DRAWINGS

Fig.5. GROUND PLAN OF THE WING VENATION OF XYELIDAE



LEGEND:

——————— Tubular vein

- - - - - - - - - - - Nebulous vein

…………………… Spectral vein

. . . . Wing border

Fig.6 GROUND PLAN OF THE WING VENATION OF MEGALODONTOIDEA

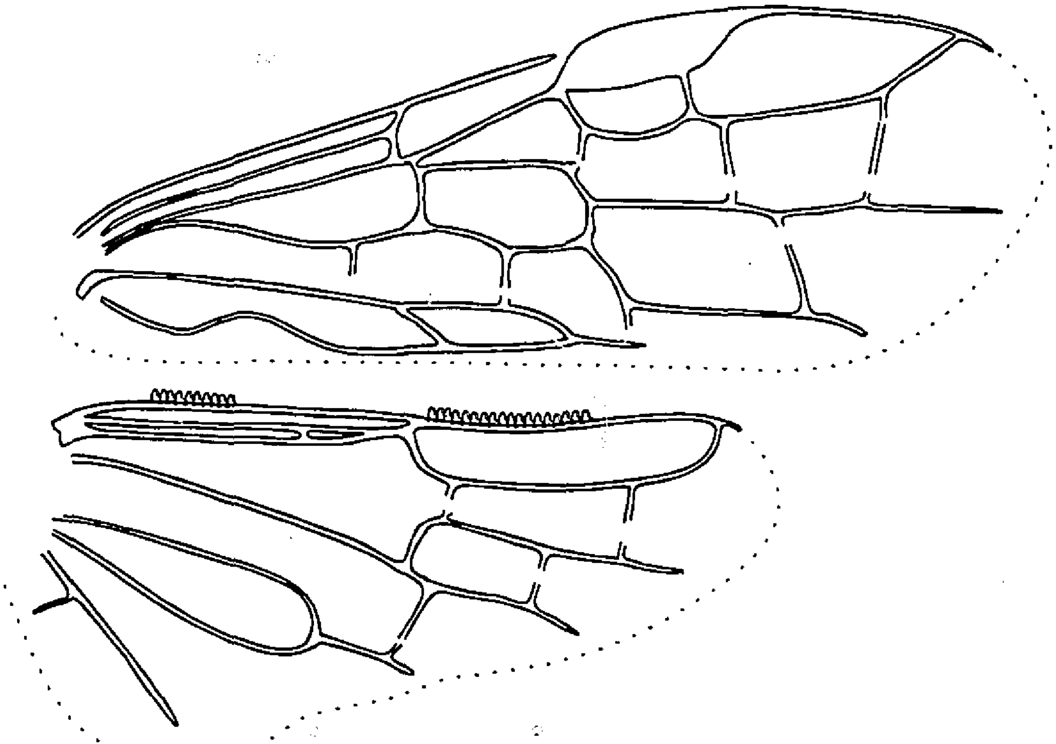


Fig.7 GROUND PLAN OF THE WING VENATION OF TENTHREDINOIDEA

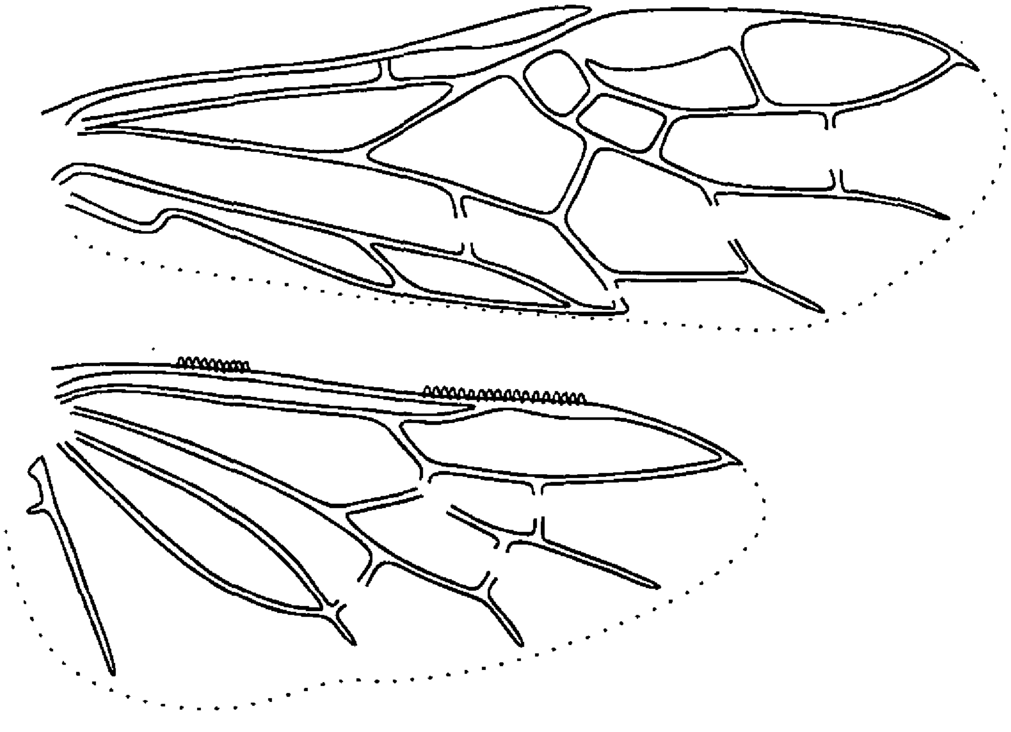


FIG.8 GROUND PLAN OF THE WING VENATION OF SIRICIDAE

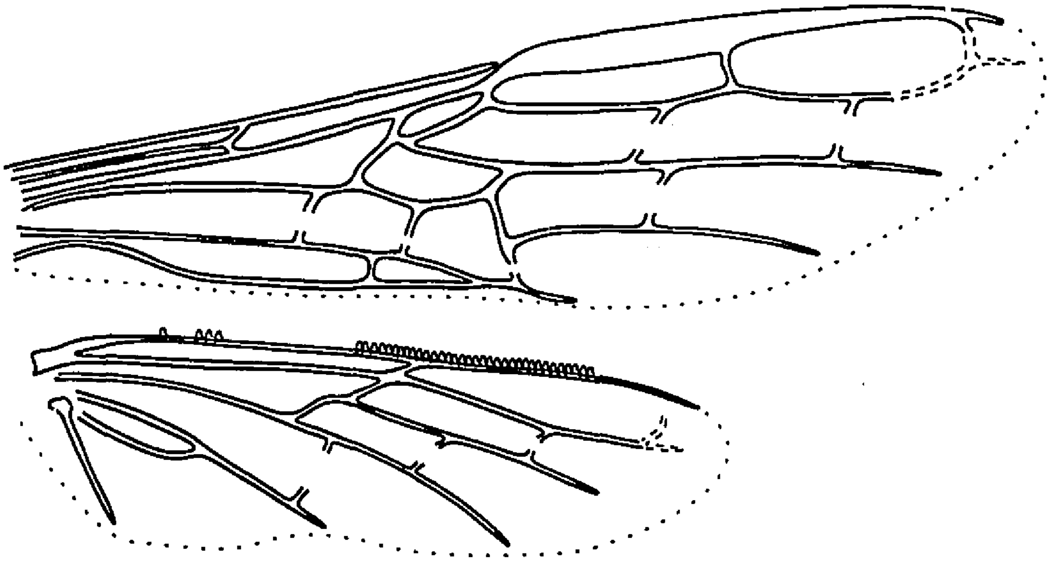


FIG.9 GROUND PLAN OF THE WING VENATION OF XIPHYDRIIDAE

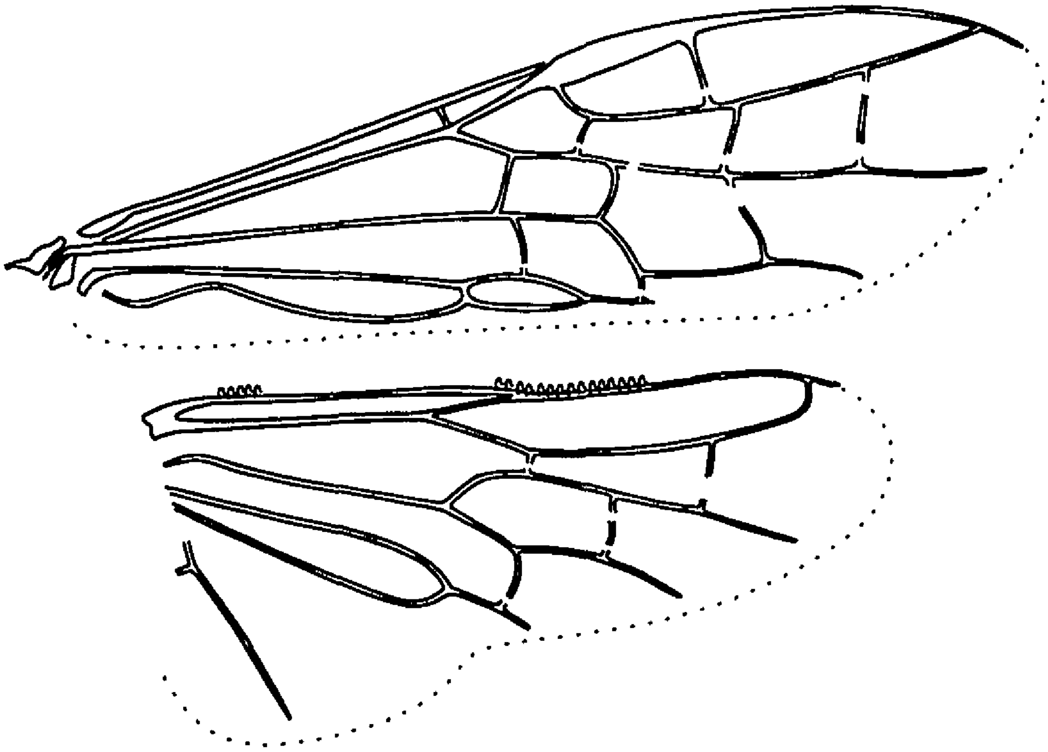


Fig.10 GROUND PLAN OF THE WING VENATION Of CEPHIDAE

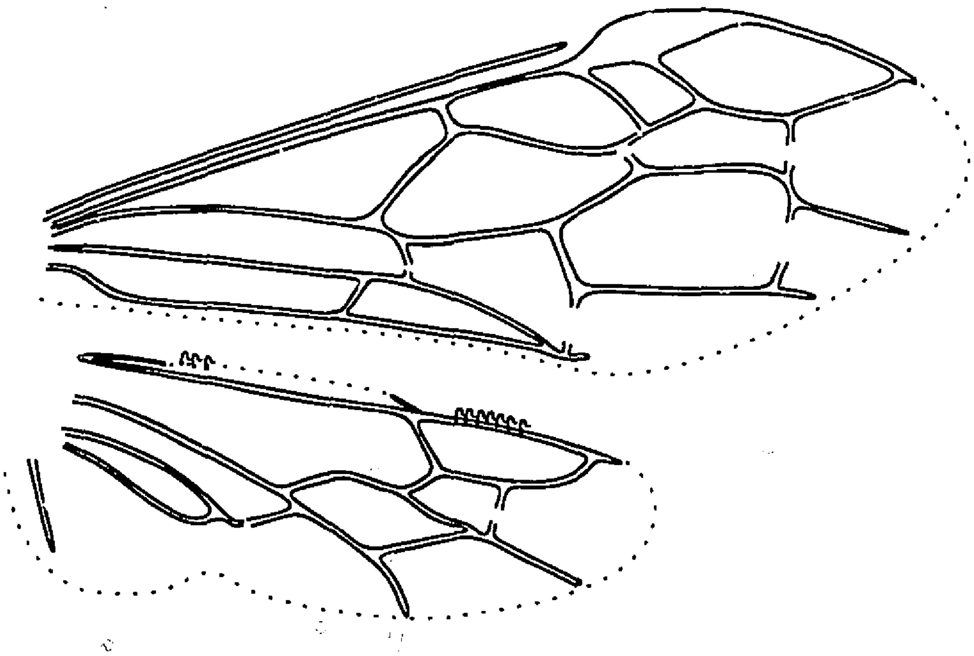


Fig.11 GROUND PLAN OF THE WING VENATION OF ORUSSIDAE

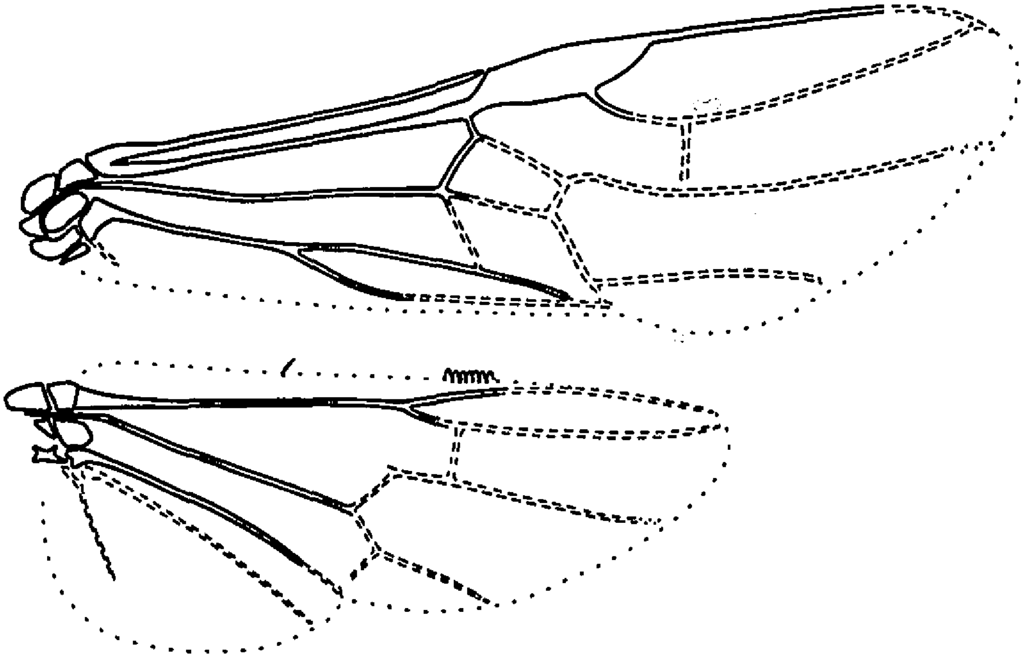


Fig.12. GROUND PLAN OF THE WING VENATION OF ACULEATA

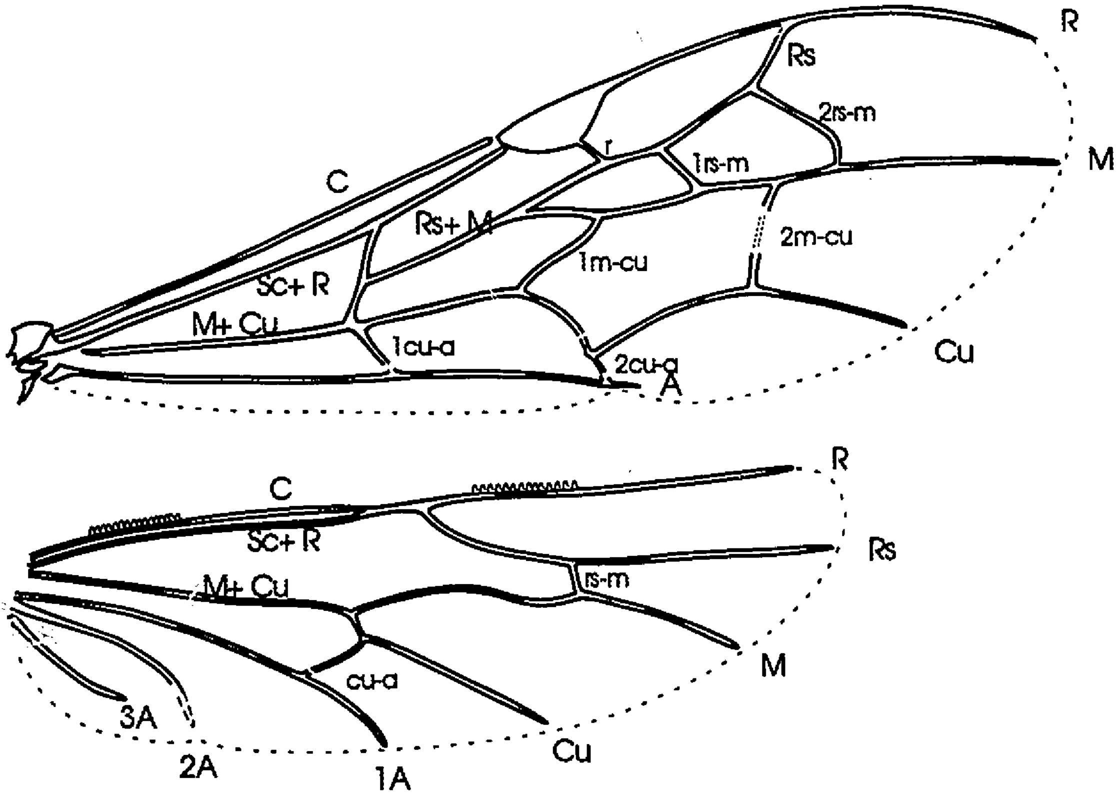


FIG.13 GROUND PLAN OF THE WING VENATION OF BRACONIDAE

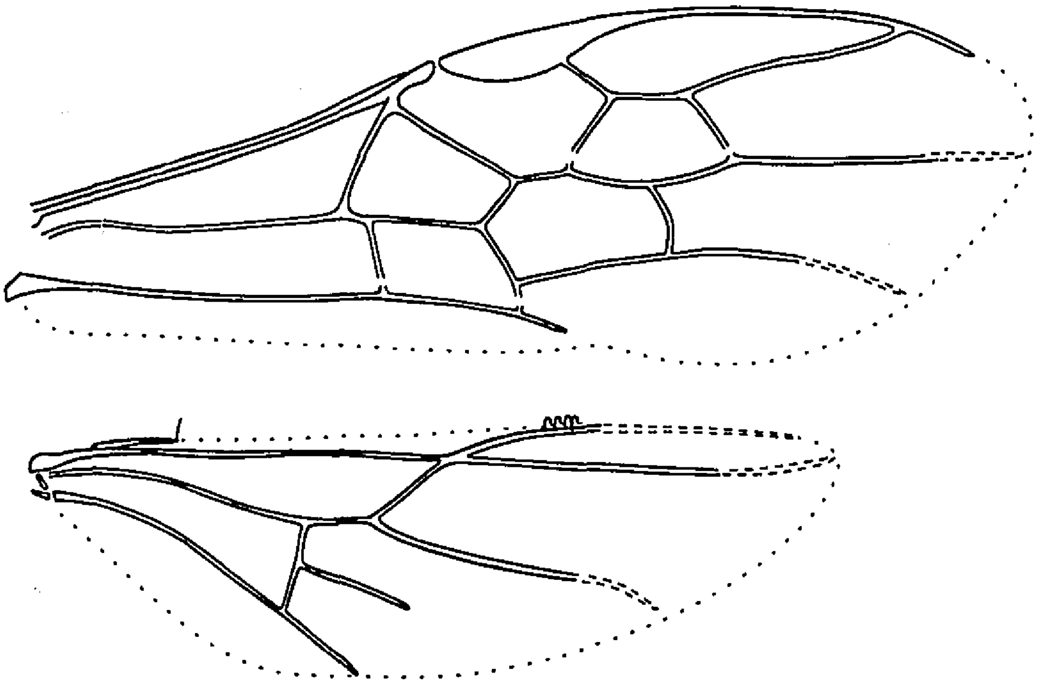


FIG.14 GROUND PLAN OF THE WING VENATION OF ICHNEUMONIDAE

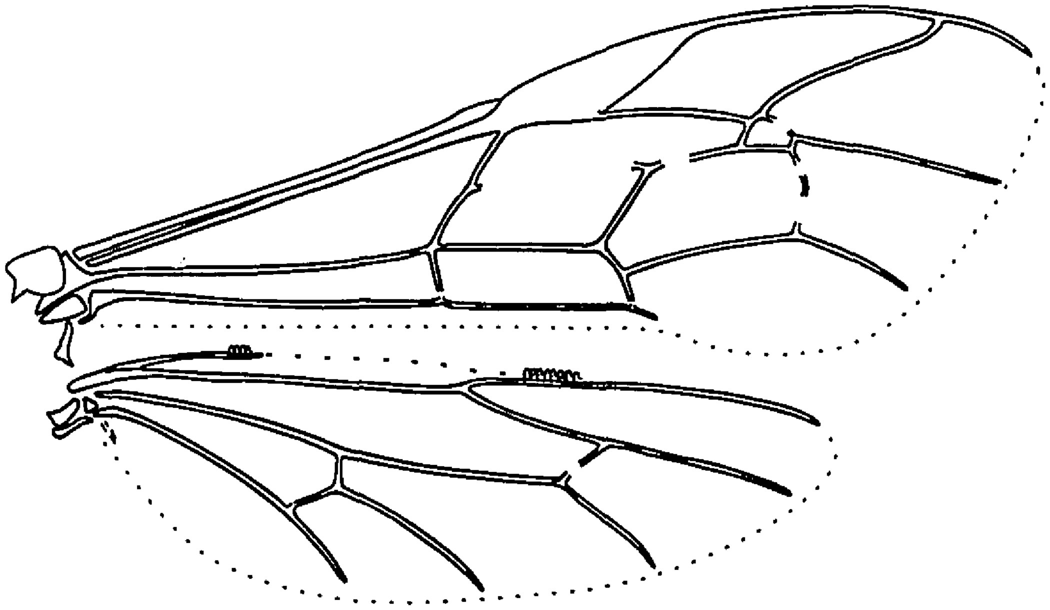


Fig.15 GROUND PLAN OF THE WING VENATION OF TRIGONALIDAE

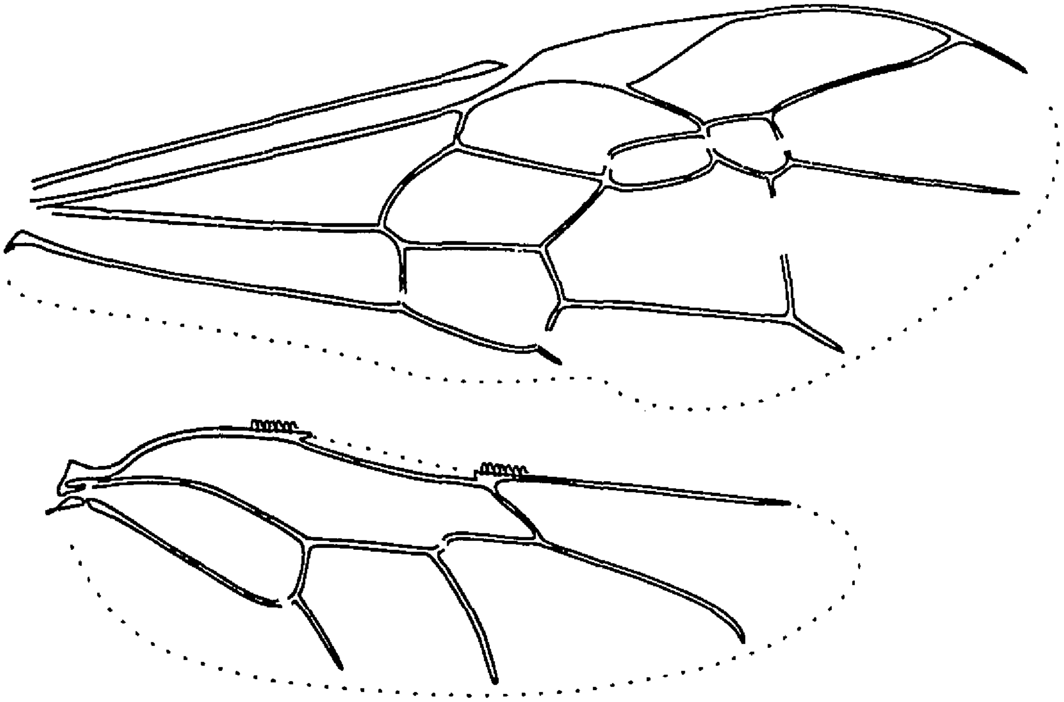


Fig.16 GROUND PLAN OF THE WING VENATION OF STEPHANIDAE

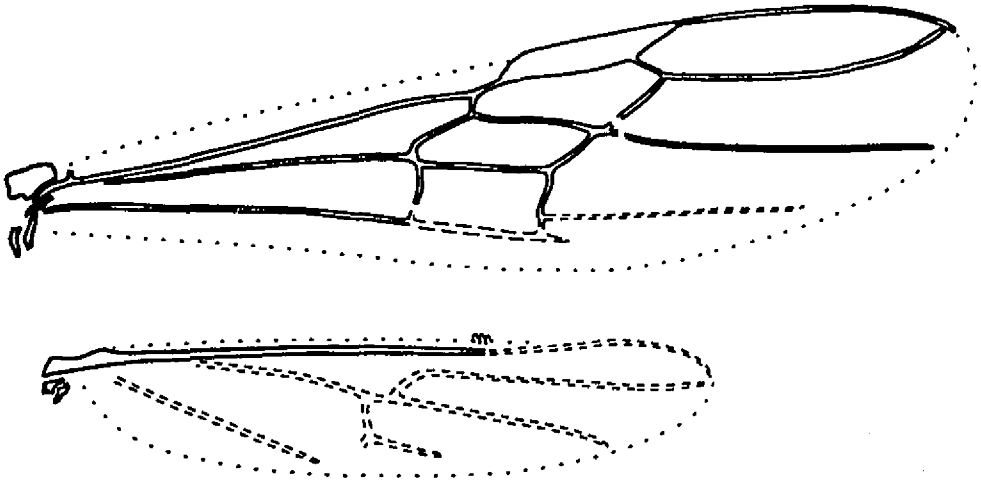


Fig.17 GROUND PLAN OF THE WING VENATION OF EVANIIDAE

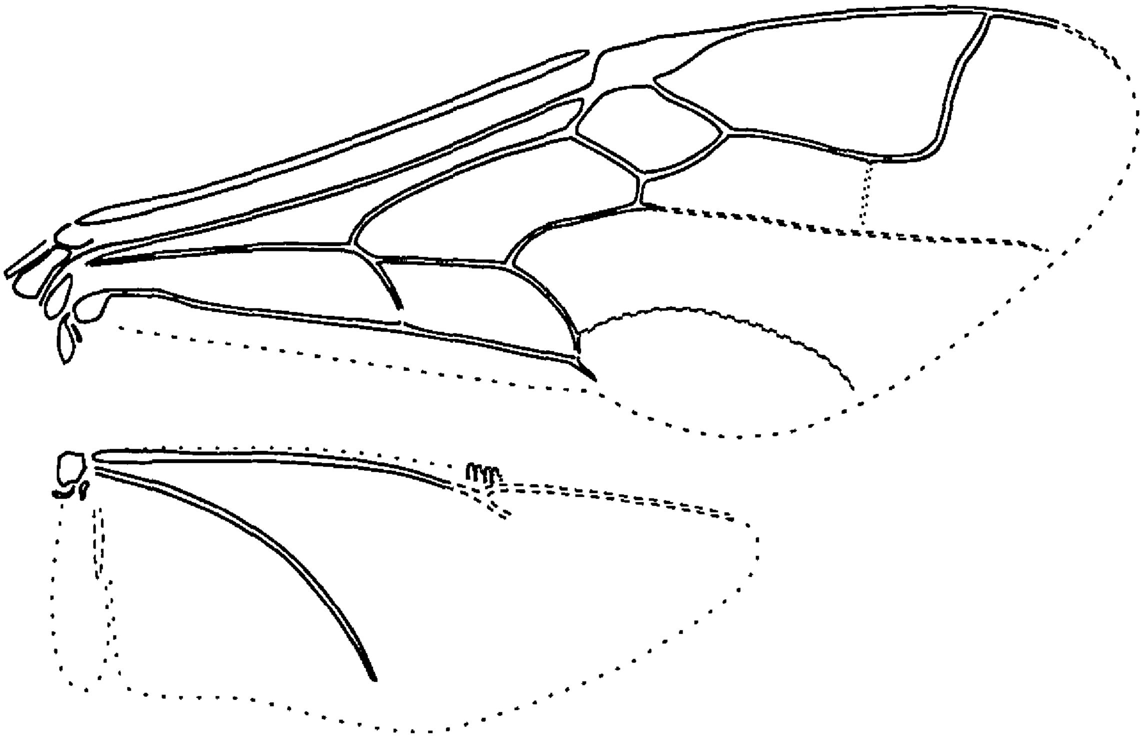


Fig.18 GROUND PLAN OF THE WING VENATION OF MEGALYRIDAE

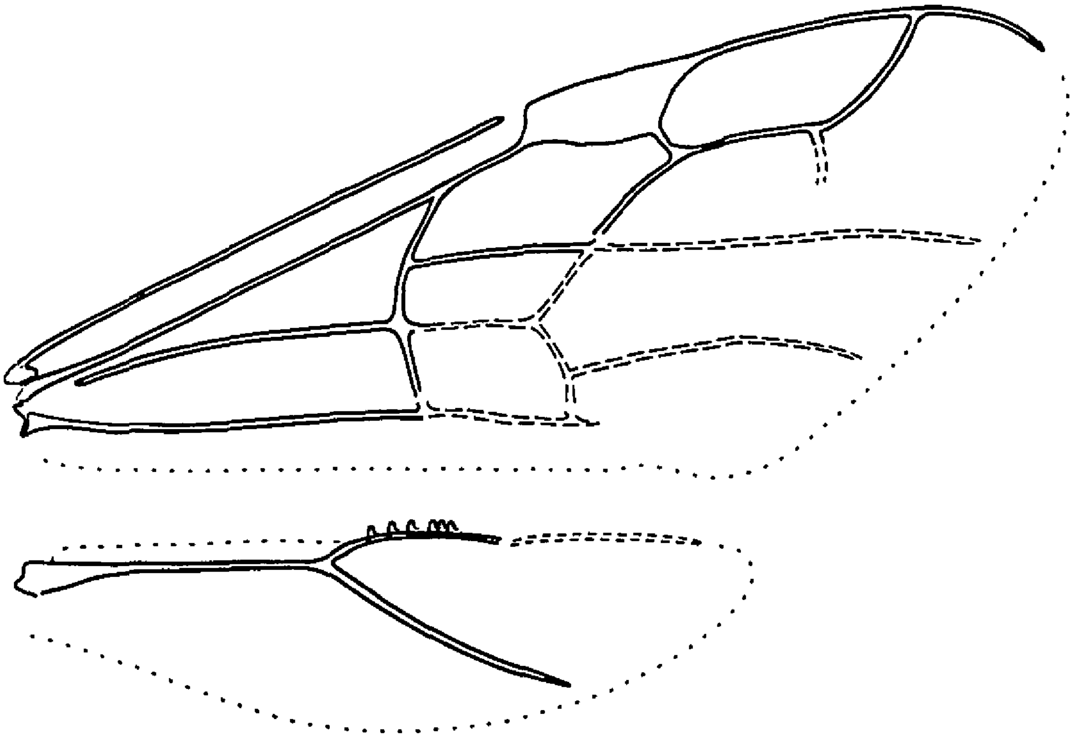


FIG.19 GROUND PLAN OF THE WING VENATION OF AULACIDAE

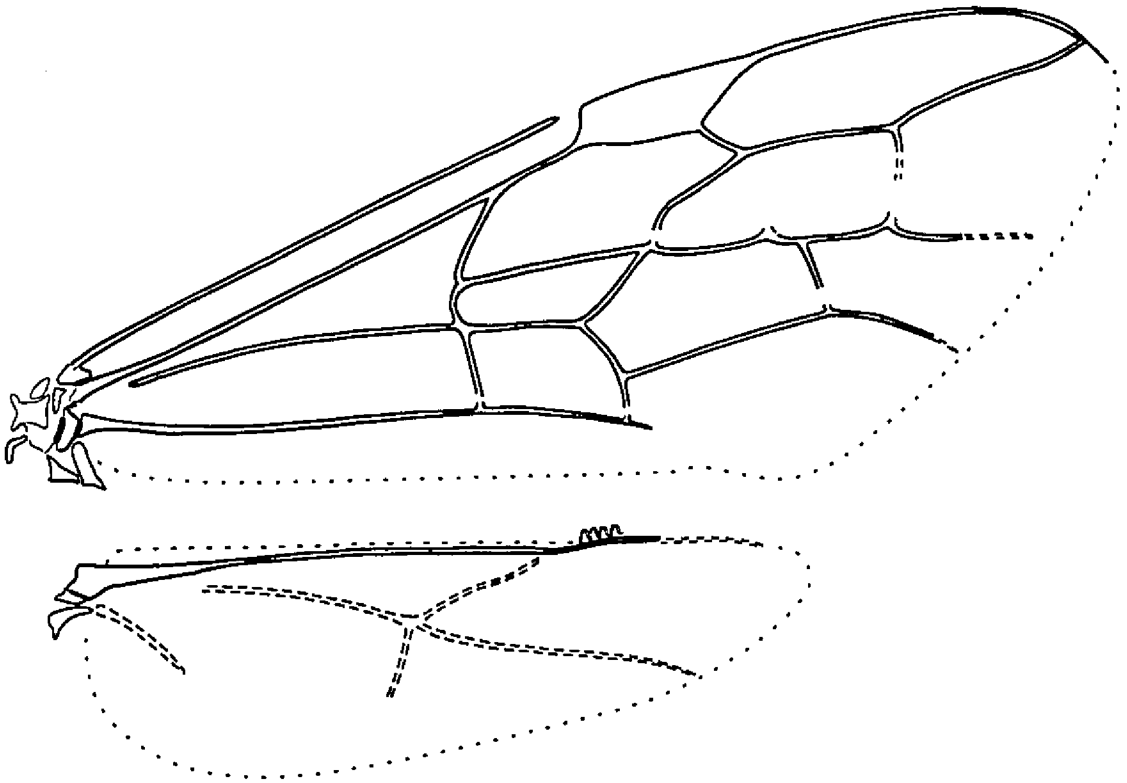


FIG.20 GROUND PLAN OF THE WING VENATION OF GASTERUPTIIDAE

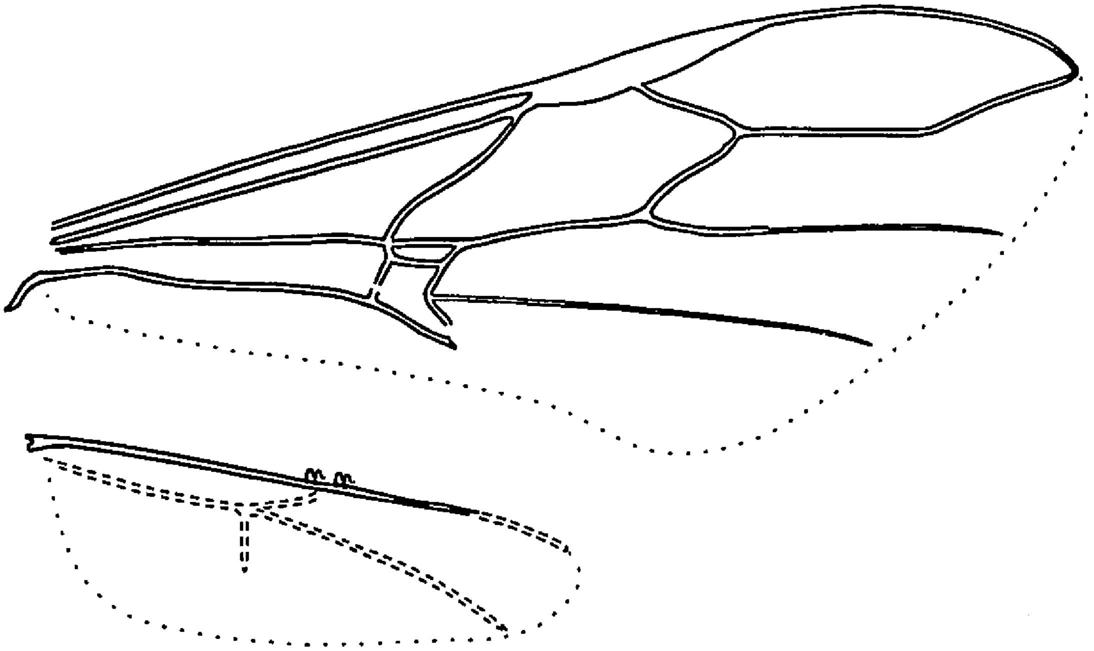


Fig.21 GROUND PLAN OF THE WING VENATION OF CYNIPIDAE

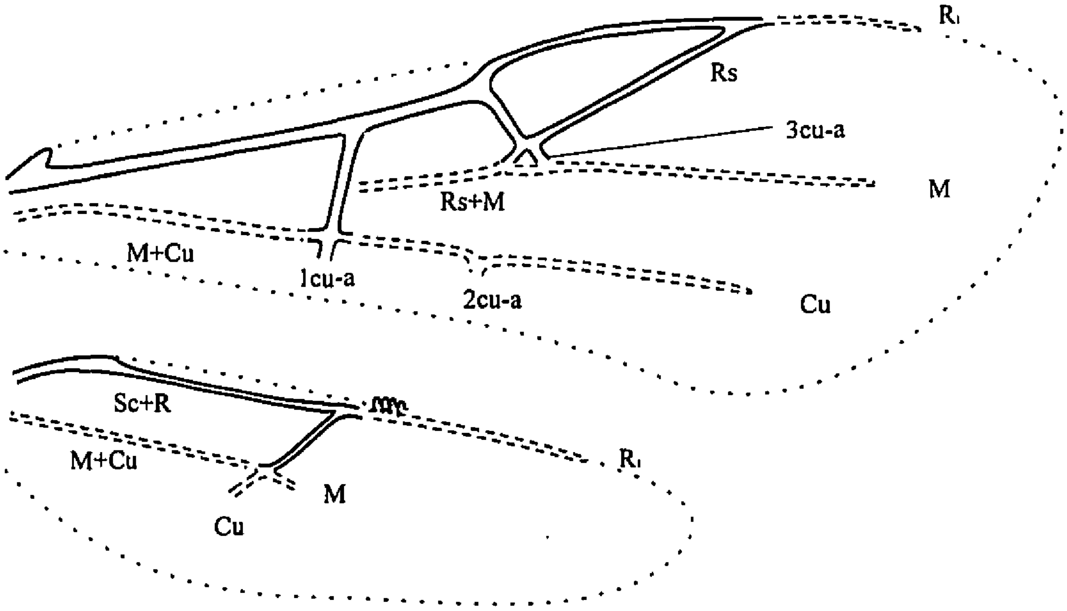


Fig.22 GROUND PLAN OF THE WING VENATION OF IBALIIDAE

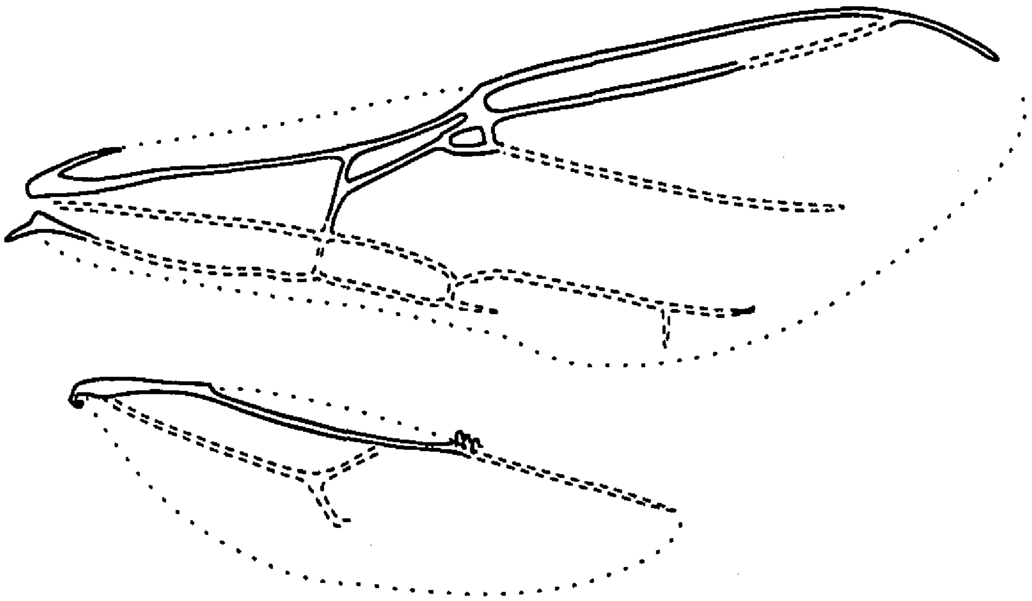


Fig.23 GROUND PLAN OF THE WING VENATION OF FIGITIDAE

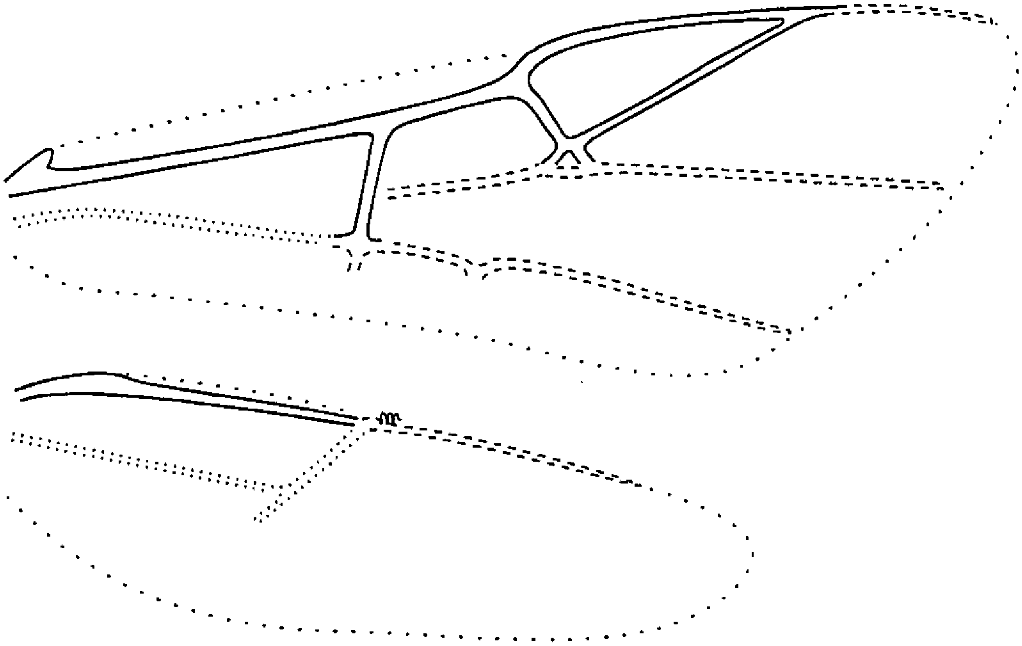


Fig.24 GROUND PLAN OF THE WING VENATION OF LIOPTERIDAE

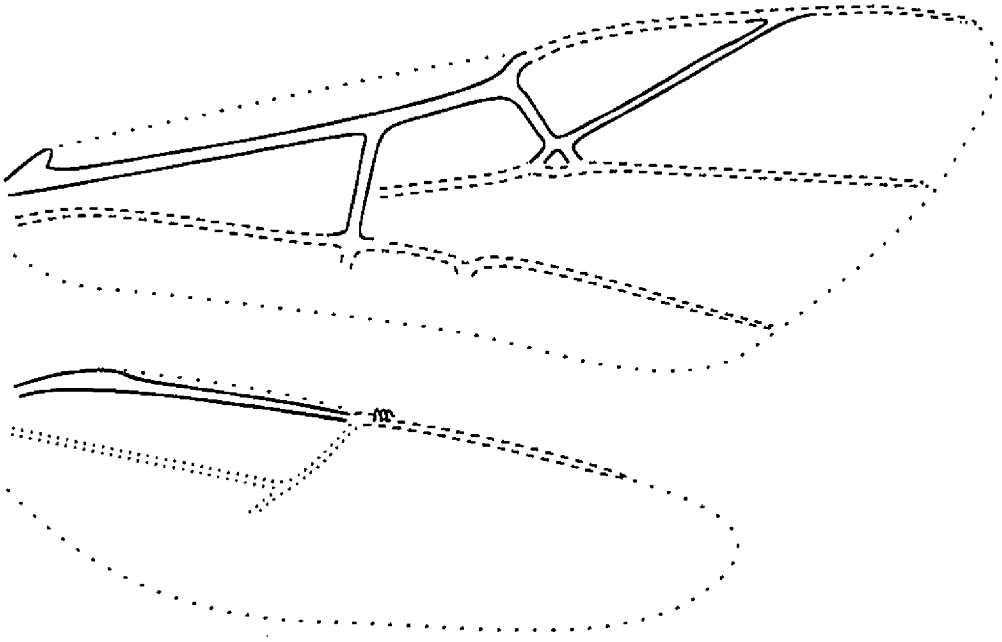


Fig.25 GROUND PLAN OF THE WING VENATION OF CHARIPIDAE

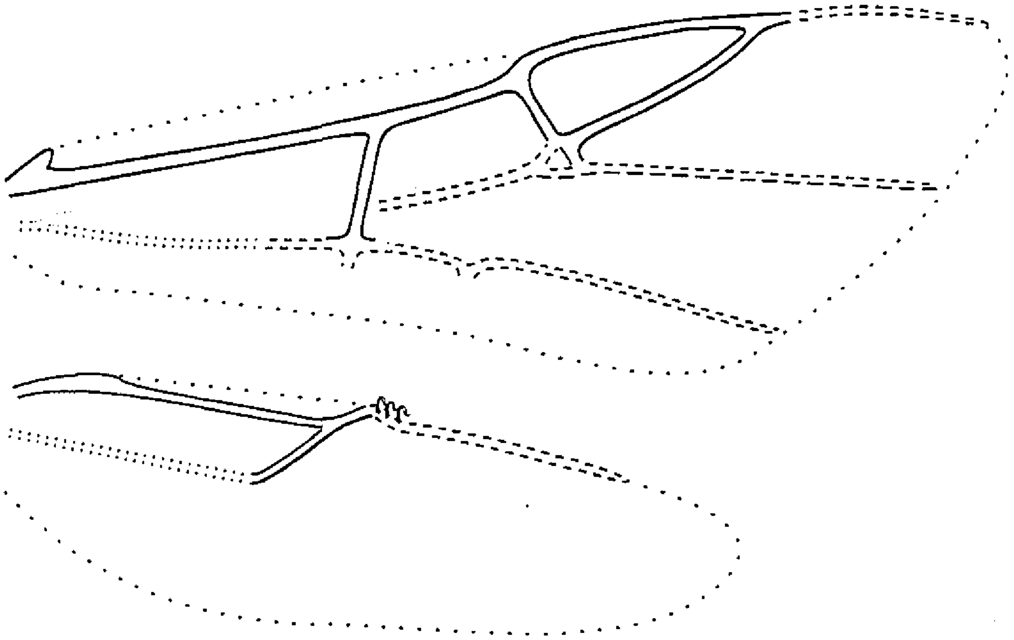


Fig.26 GROUND PLAN OF THE WING VENATION OF EUCOILIDAE

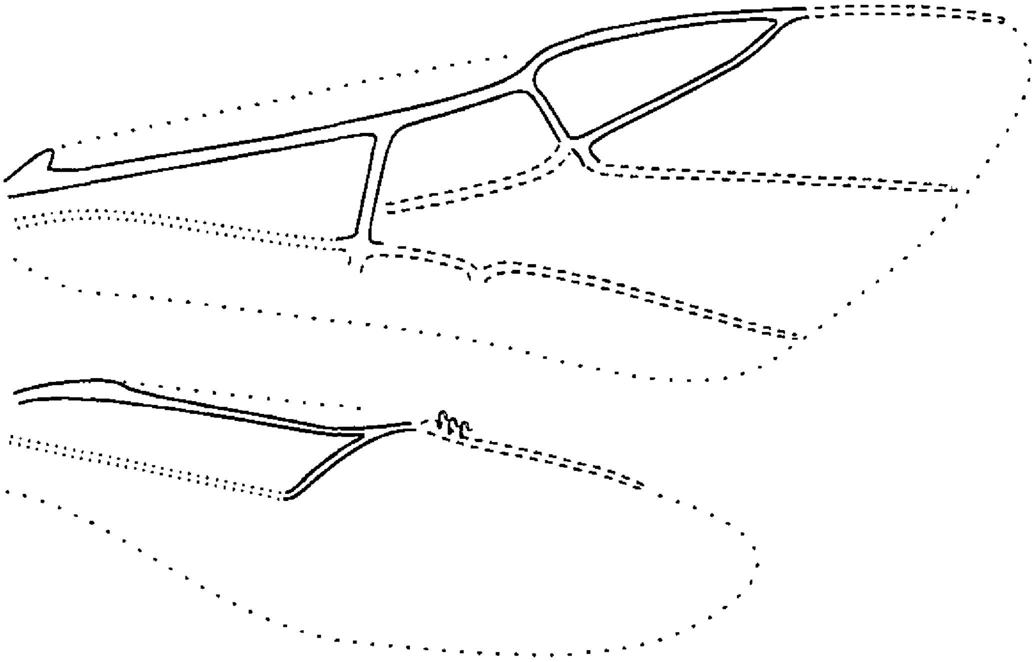


FIG.27 GROUND PLAN OF THE WING VENATION OF CERAPHRONIDAE

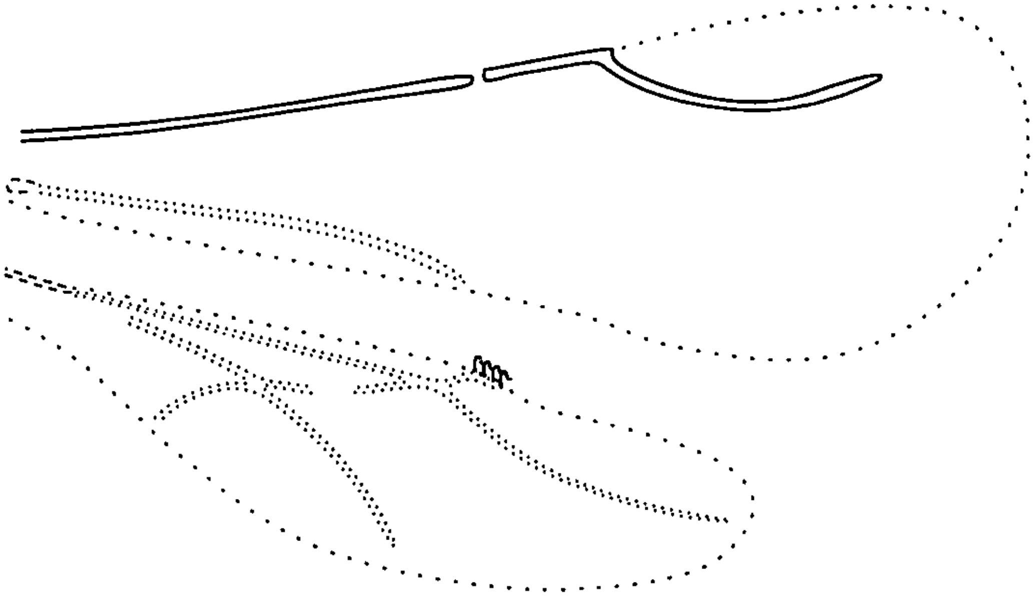


FIG.28 GROUND PLAN OF THE WING VENATION OF MEGASPILIDAE

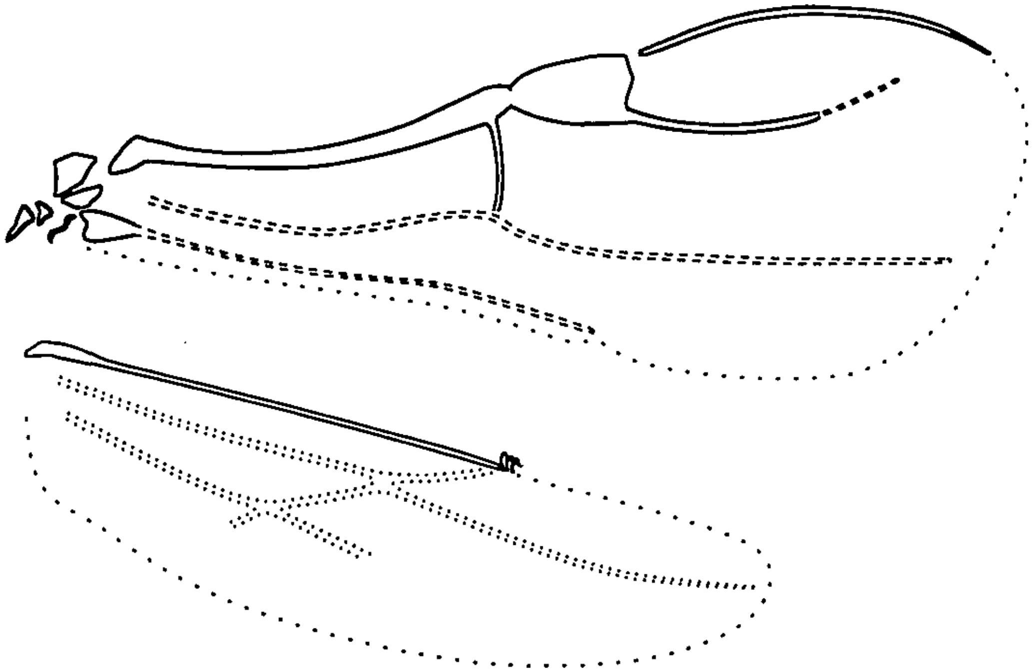


Fig.29 GROUND PLAN OF THE WING VENATION OF CHALCIDOIDEA

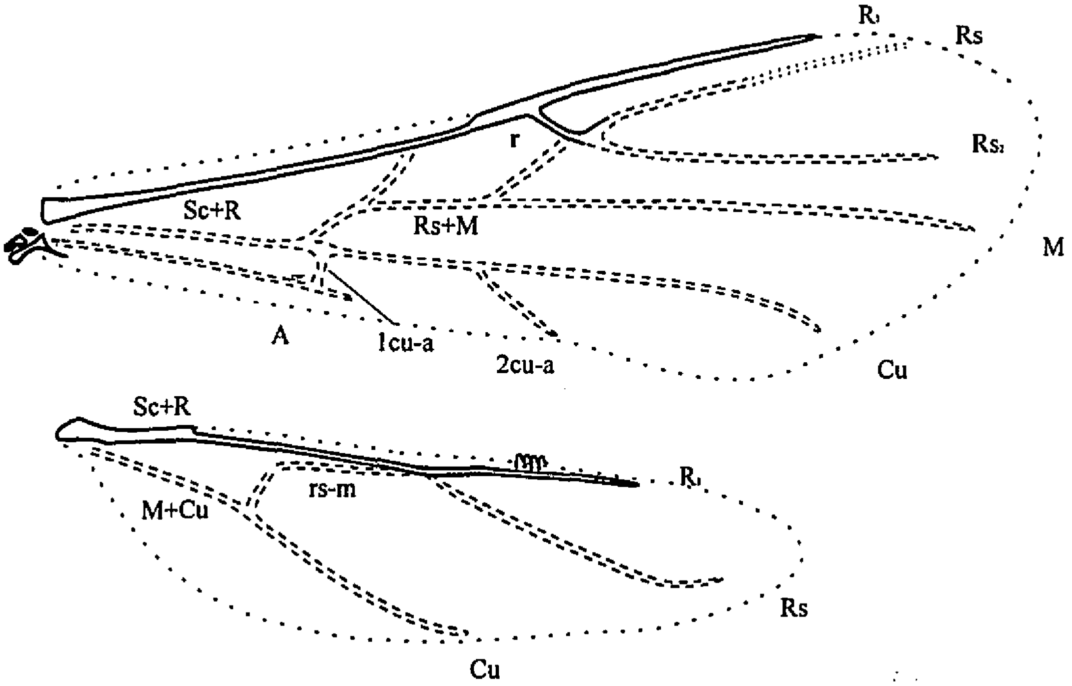


Fig.30 GROUND PLAN OF THE WING VENATION OF DIAPRIIDAE

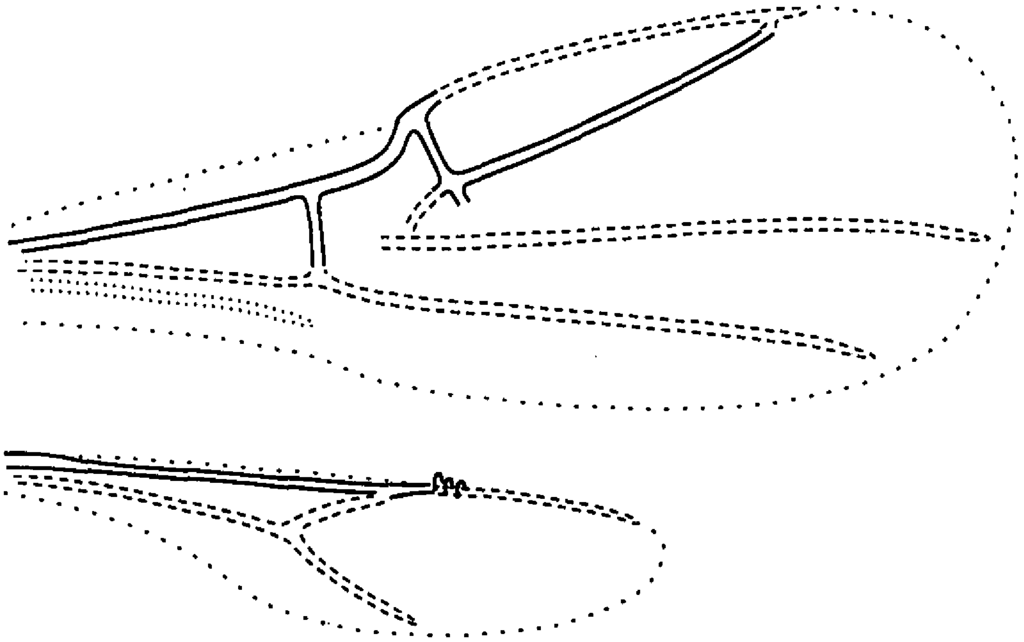


Fig.31 GROUND PLAN OF THE WING VENATION OF VANHORNIIDAE

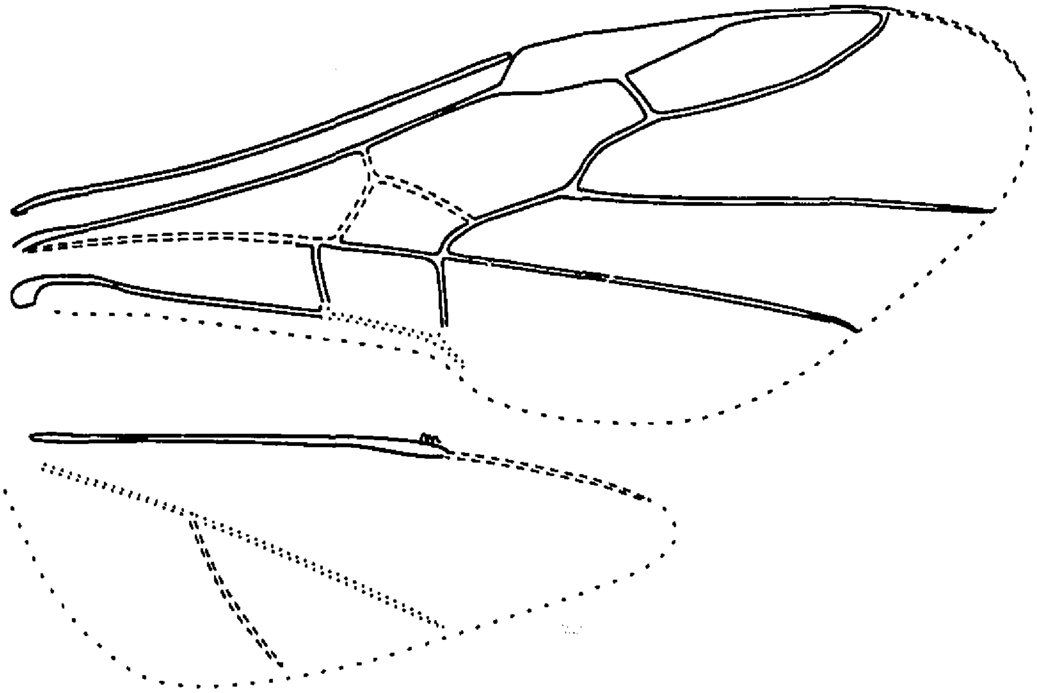


Fig.32 GROUND PLAN OF THE WING VENATION OF PERADENIIDAE

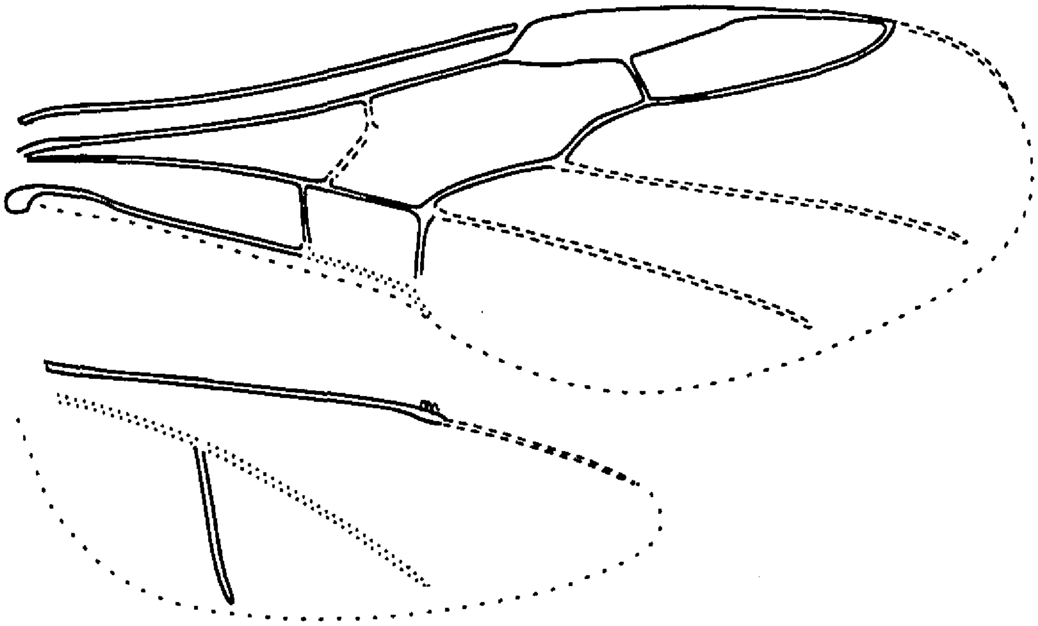


Fig.33 GROUND PLAN OF THE WING VENATION OF MONOMACHIDAE

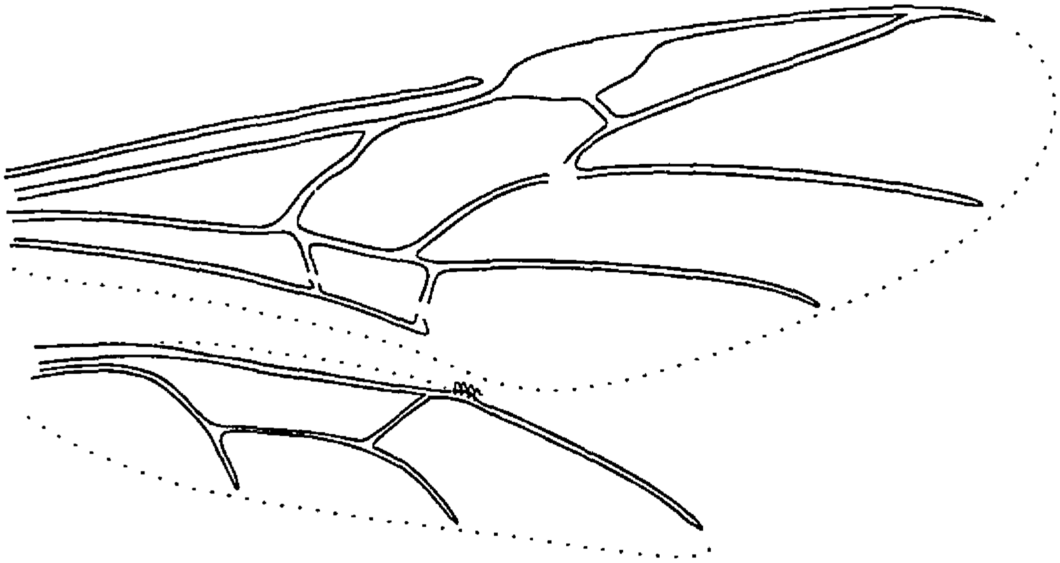


Fig.34 GROUND PLAN OF THE WING VENATION OF AUSTRONIIDAE

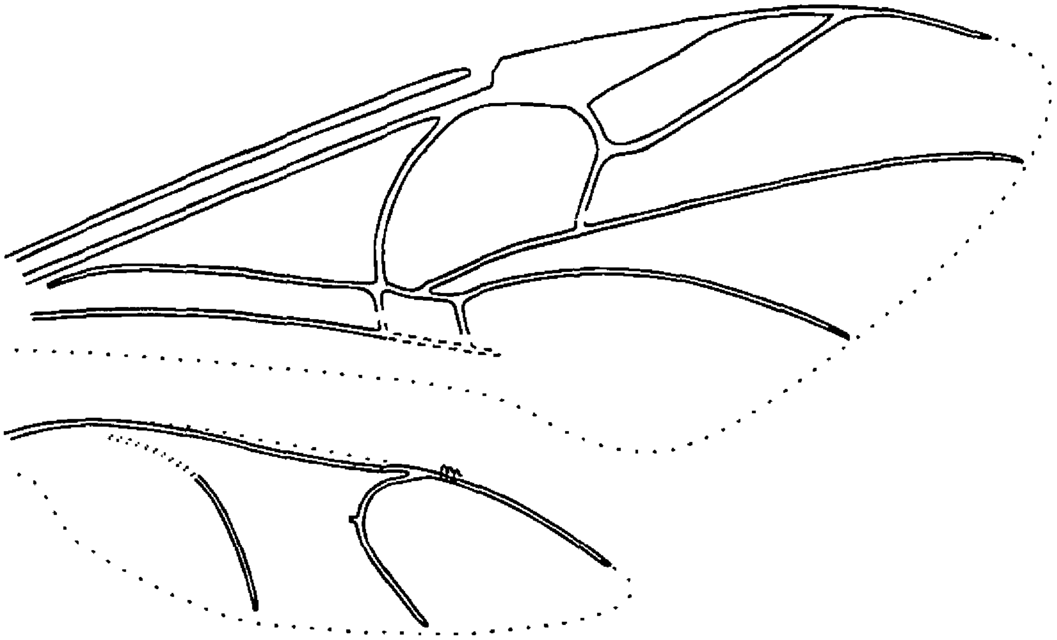


Fig.35 GROUND PLAN OF THE WING VENATION OF PROCTOTRUPIDAE

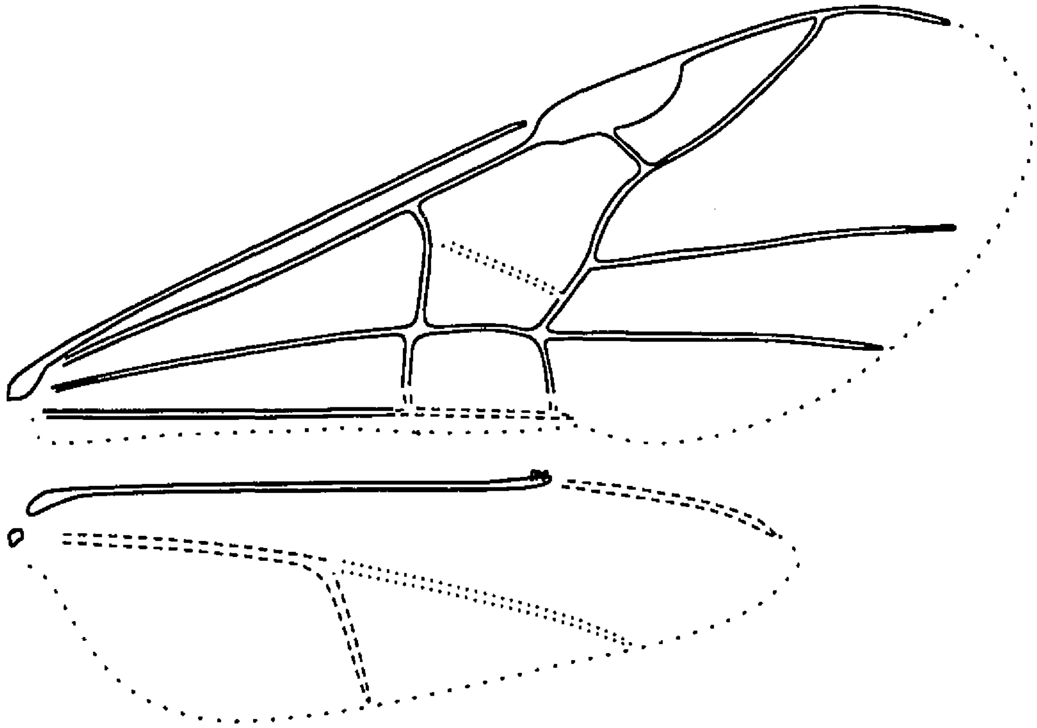


Fig.36 GROUND PLAN OF THE WING VENATION OF PELECINIDAE

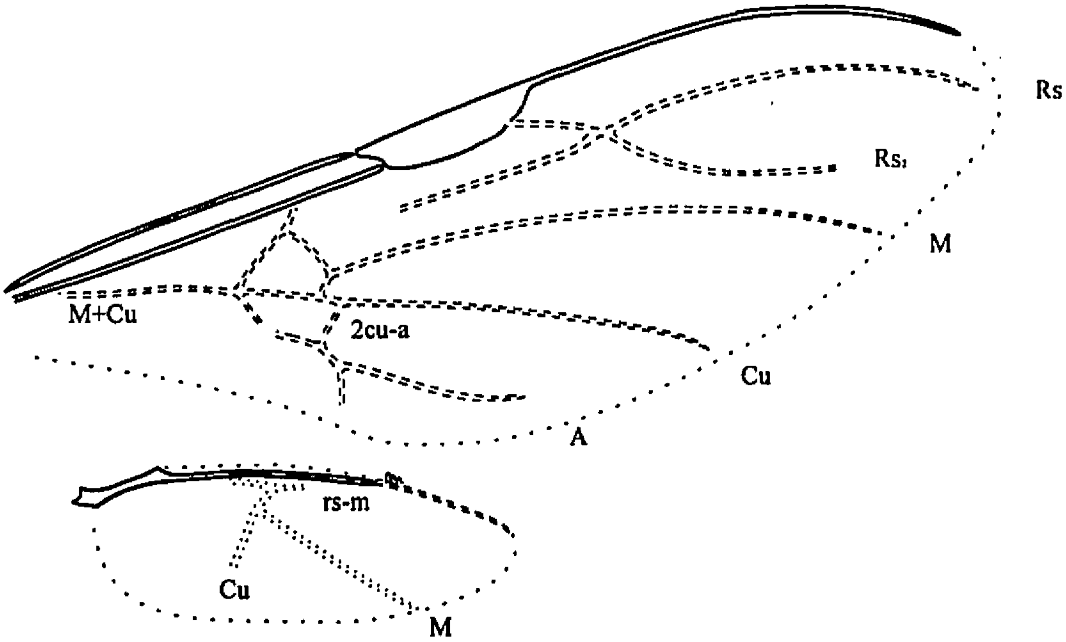


Fig.37 GROUND PLAN OF THE WING VENATION OF ROPRONIIDAE

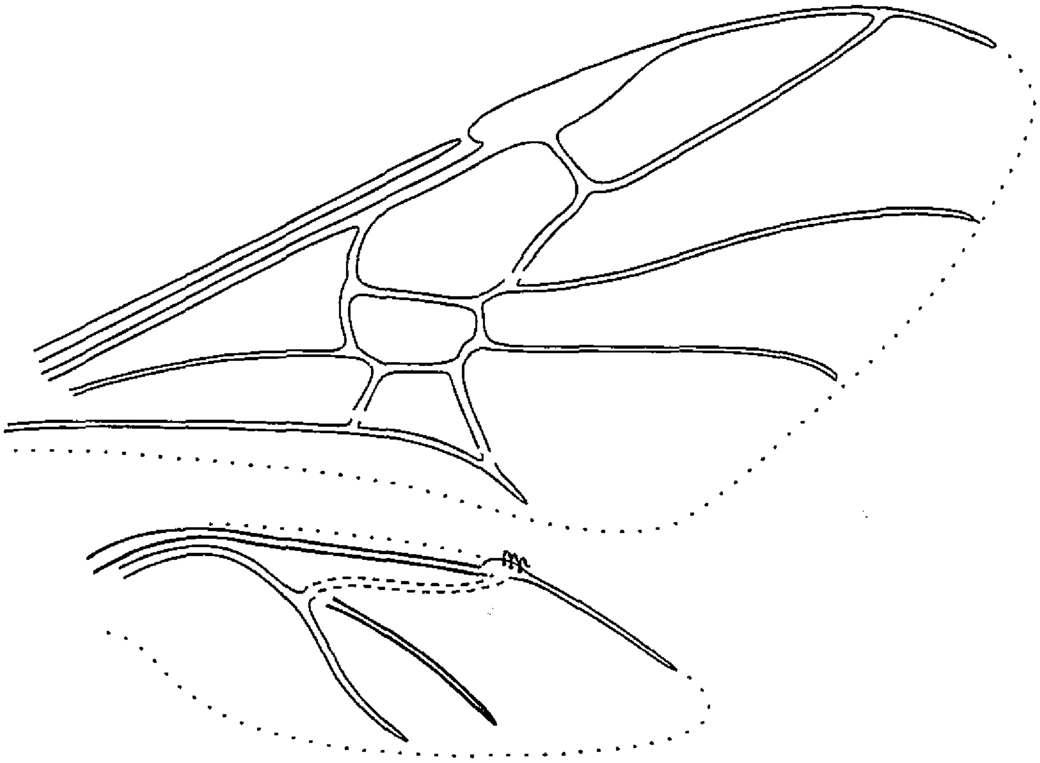


Fig.38 GROUND PLAN OF THE WING VENATION OF HELORIDAE

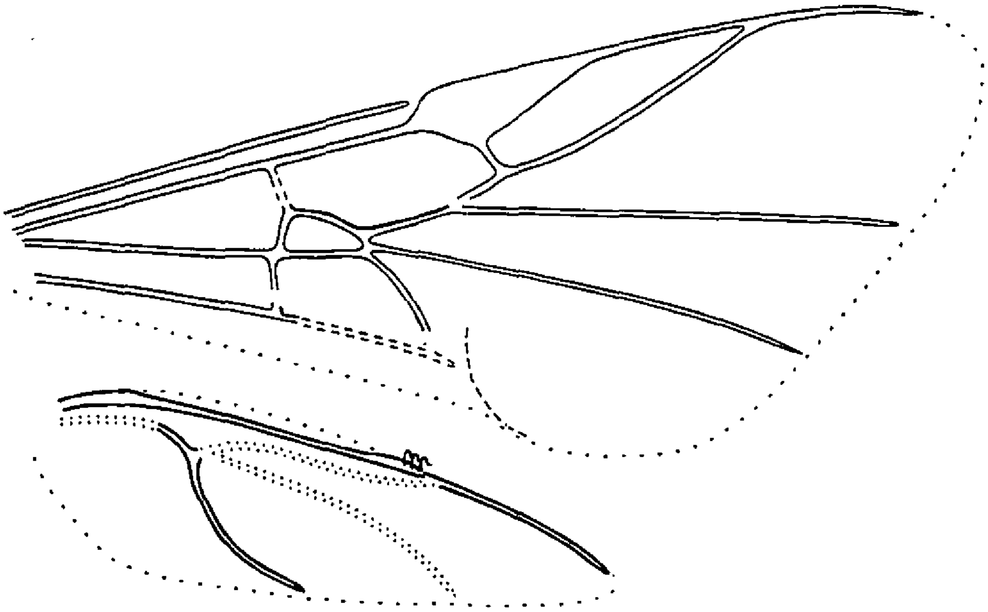


Fig.39 GROUND PLAN OF THE WING VENATION OF PLATYGASTRIDAE

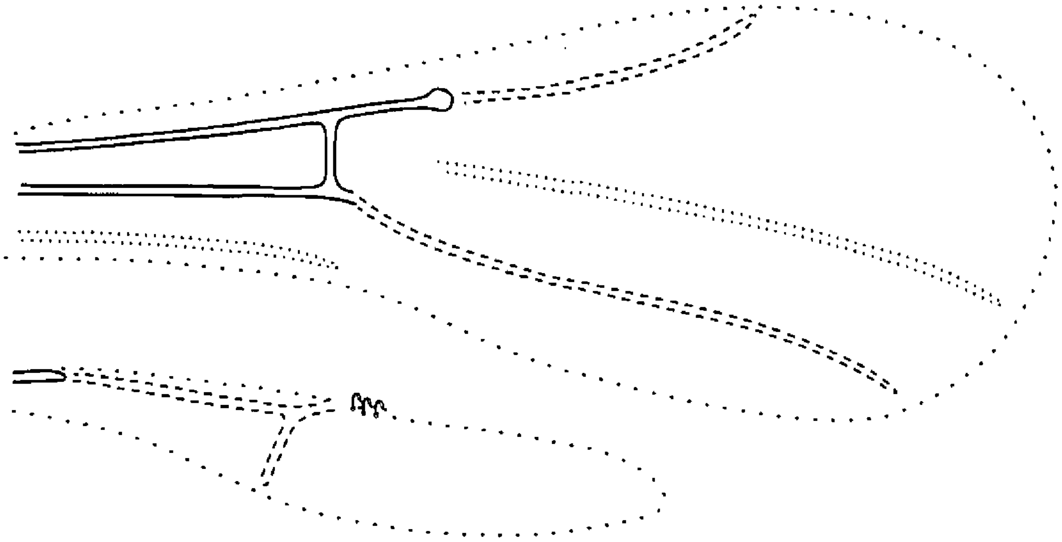
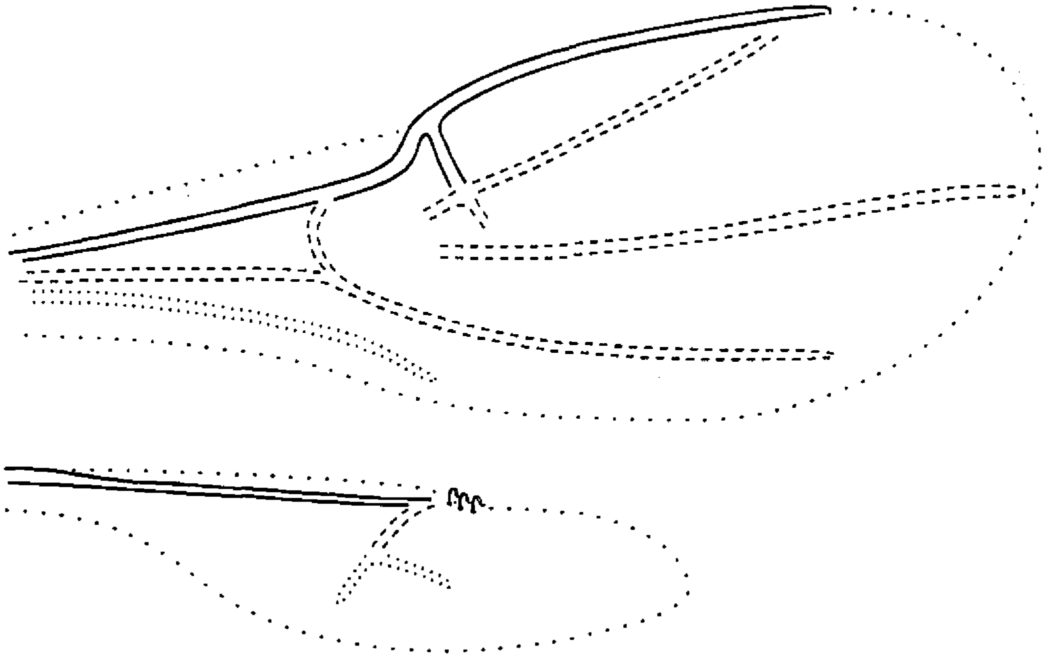


Fig.40 GROUND PLAN OF THE WING VENATION OF SCELIONIDAE



APPENDIX 2:

ANALYSIS OF NON-WING CHARACTERS

CHARACTER LIST EXTRACTED FROM THE REFERENCES

Tonapi (1958)

Homologies are rather difficult to establish for the spiracular structures of Hymenoptera because of the high specialization of this character group in some taxa. A total of 12 characters was extracted from the paper (excluding character 0 which can be one of many characters, one used to establish the monophyly of the Hymenoptera). Only character 1 was treated as non-additive because no certain polarization could be achieved from the description presented in the paper.

1. Closing mechanism of the first thoracic spiracles:

0, two movable lids (external closing system);
1, occlusor sclerite (external closing system);
2, compression of the atrium (internal closing system);
3, operculum (internal closing system).

2. Position of the first thoracic spiracle:

0, in the intersegmental membrane and exposed;
1, in the intersegmental membrane and concealed;
2, on the pronotum.

3. Position of the second thoracic spiracle:

0, exposed;
1, concealed.

4. Closing mechanism of the second thoracic spiracles:

0, two movable lids;

1, two lids, one movable;

2, one movable lid;

3, one or two flap valves.

5. Closing mechanism of the first abdominal/propodeal spiracle:

0, two levers;

1, one lever.

6. Closing muscles of the first abdominal/propodeal spiracle:

0, parallel-sided occlusor muscle;

1, cylindrical occlusor muscle.

7 Opening muscles of the first abdominal/propodeal spiracle:

0, parallel-sided dilator;

1, cylindrical dilator.

8. Closing mechanism of abdominal spiracles:

0, two levers;

1, one lever.

9. Closing muscles of the abdominal spiracles:

0, parallel-sided occlusor muscle;

1, cylindrical occlusor muscle.

10. Opening muscles of the abdominal spiracles:

0, parallel-sided dilator;

1, cylindrical dilator.

11. Number of thoracic spiracles:

0, two; 1, one

12. Number of abdominal spiracles:

0, eight;

1, two;

2, one

Daly (1963)

The polarization of muscle condition was done using Symphyta as an outgroup, but the distinction between fibrillar and closed-packed was not applied since most muscles are tubular in Apocrita and this would not improve the resolution of the cladogram. Fibrillar or closed-packed (microfibrillar) muscle fibers have nearly cylindrical contracting organelles (myofibrils) arranged in a uniform bundle and the nuclei may be scattered among the myofibrils, situated beneath the sarcolemma or both. In contrast, tubular muscles have contracting organelles present as thin lamellae which radiate from an axial core containing the nuclei. All 16 characters of this character suite were coded as being additive.

13. t2-2ph:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

14. t2-tr2:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

15. 2ph-3ph:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

16. cx3-sa3:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

17. t2-cx2:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

18. pl2-ba2b:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

19. cx2-sa2:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

20. t3-3ph:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

21. t3-pl3:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

22. cx3-ba3:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

23. t3-tr3:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

24. pl2-ba2a:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

25. t3-cx3a:

0, fibrillar or closed-packed;

1, tubular;

2, absent.

26. t3-cx3b:
0, fibrillar or closed-packed;
1, tubular;
2, absent.

27. pl3-sa3a:
0, fibrillar or closed-packed;
1, tubular;
2, absent.

28. pl3-ba3:
0, fibrillar or closed-packed;
1, tubular;
2, absent.

Robertson (1968)

Very few taxa and characters were analyzed in this paper; only four characters were found in all groups presented by the author. The Chalcidoidea were included in this review even though they were not analyzed but only described by Robertson. Although the polarity of character 30 and 31 is doubtful, these were shown as being additive, following the conclusions of the author.

29. Gland filaments:
0, several filaments, grouped in a mass;
1, several filaments, branched (with several sub-branches);
2, two gland filaments, no sub-branches.

30. Muscles of the venom reservoir:

0, reservoir walls with little or no muscle;

1, reservoir walls with strong longitudinal muscles;

2, reservoir walls with strong transverse muscles.

31. Shape of the venom reservoir:

0, reservoir asymmetrical;

1, reservoir very elongated (little difference with the venom duct);

2, spindle shaped reservoir;

3, spheroid reservoir.

32. Dufour's gland:

0, absent;

1, present.

Farish (1972)

Although a table of characters was provided, the polarity of the characters had to be interpreted according the two outgroups (Tenthredinoidea and Xiphydriidae) and the cladogram that was provided. A total of 17 characters was found to have significance in the phylogeny of the taxa studied (at least one taxon had an apomorphic condition). Only the presence of a movement is considered and the data are thus considered to be additive.

33. Single antennal grooming using ipsilateral L1:

0, present; 1, absent.

34. Single antennal grooming using contralateral L1:

0, present; 1, absent.

35. Single antennal grooming using both L1:

0, absent; 1, present.

36. Double antennal grooming using both L1:

0, absent;1, present.

37. Alternative antennal grooming using ipsilateral L1:

0, present; 1, absent.

38. Alternative antennal grooming using contralateral L1:

0, present; 1, absent.

39. Alternative antennal grooming using both L1:

0, absent; 1, present.

40. Thorax grooming using L1:

0, absent; 1, present.

41. Thorax grooming using L2:

0, absent; 1, present.

42. Thorax grooming using L3:

0, absent; 1, present.

43. Thorax grooming using reflected L1:

0, absent; 1, present.

44. Wing cleaning (wing folded):

0, present; 1, absent.

45. Wing cleaning (wing held on one side):

0, absent; 1, present.

46. Wing cleaning (both L3 on one wing pair):

0, absent; 1, present.

47. L1-L1 grooming:

0, absent; 1, present.

48. L1-L1-L2 grooming:

0, absent; 1, present.

49. L1-L2-L3 grooming:

0, absent; 1, present.

50. L2-L3-L3 grooming:

0, present; 1, absent.

Richards (1972)

Two of the five characters that were extracted from this paper overlap with judge the definition or precision of the characters.

51. Position of the first thoracic spiracle:

0, in the intersegmental membrane and exposed;

1, in the intersegmental membrane and concealed;

2, on the pronotum.

52. Position of the second thoracic spiracle:

0, exposed;

1, concealed.

53. Basalar area:

0, weak or absent;

1, well developed.

54. Scutellar area:

0, well developed;

1, weak or absent.

55. Epimeral lobe:

0, well developed;

1, reduced or absent.

Iwata (1976)

Most data presented in this section are taken from a table that was provided by the author and the polarization was done with Orussidae as an outgroup for most characters. When more than one character state was present, a question mark was used, except in Chalcidoidea because one state was clearly dominant. Furthermore, the most plesiomorphic condition was chosen for ichneumonoid taxa because of their well known ancestry (they must be close to the Orussidae).

56. Feeding habit:
0, phytophagous;
1, ectoparasitoid;
2, endoparasitoid.

57. Host range:
0, monoparasitoid;
1, polyparasitoid.

58. Larva as host stage:
0, yes; 1, no

59. Coleoptera as host group:
0, yes; 1, no.

Gibson (1985)

Some characters presented in this paper overlap those shown earlier by Daly (1963), but were included in this list since the number of taxa examined by the former is much higher and because the high total number of characters of the present matrix is high enough to offset this effect. Character 64, prepectus, was the only one to be treated as non-additive.

60. t2-2ph muscle:

0, present; 1, absent.

61. fu2-tr2 muscle:

0, present; 1, absent.

62. t2-tr2 muscle:

0, present; 1, absent.

63. pl2-tr2 muscle:

0, absent; 1, present.

64. Prepectus:

0, free and exposed;
1, free and hidden;
2, fused;
3, absent.

65. Median mesoscutal sulcus:

0, absent; 1, present.

66. Notauli:

0, present; 1, absent.

67. Transscutal articulation:

0, absent; 1, present.

68. Postspiracular sclerite:

0, absent; 1, present.

Johnson (1988)

As for the previous author, there is some overlap with Daly (1963), but the same reasons apply to retain these characters on this list. All seven characters are additive.

69. Coxal groove:
0, absent;
1, present, with a broad sulcus;
2, present and deep, basicoxite reduced in size.

70. Coxal cavity:
0, large and approximated medially;
1, strongly constricted and displaced laterally.

71. Mesal lobes:
0, small;
1, elongated.

72. ba-cx muscle:
0, absent; 1, present.

73. t-cx muscle:
0, present; 1, absent.

74. fu-cxa muscle:
0, present; 1, absent.

75. fu-cxp muscle:

0, present; 1, absent.

Whitfield et al. (1989)

This paper also has some overlap with Daly (1963) and again, the same conclusions apply. The paper does not overlap with any of the other references cited nor do any of the others. All six characters are coded as additive.

76. Division of the metapostnotum (PN3):
0, absent; 1, present.

77. Division of tergite one (T1):
0, present; 1, absent.

78. Fusion of PN3 to T1:
0, none;
1, partial, with suture;
2, complete, no suture.

79. Fusion of PN3 to N3:
0, none;
1, complete with suture;
2, complete, no suture.

80. Third phragma (PH3):
0, present, normal shape;
1, absent;
2, present, with two large lobes.

81. 2ph-3ph muscle:

0, present; 1, absent.

Whitfield (1992)

Few characters were extracted and these may not be ground plan for all taxa. In addition to the reasons enumerated before for repeated characters, the author also corrected some data from Iwata. Characters 81 to 83 may not show the ground plan of each taxon, but rather a characteristic of their biology.

82. Feeding habit:

0, phytophagous;
1, ectoparasitic on xylophagous beetle larvae;
2, ectoparasitic on other insects;
3, endoparasitic.

83. Trophamnion in first instar larva:

0, absent; 1, present.

84. Teratocytes:

0, absent; 1, present.

85. Introduction of viruses during oviposition:

0, no; 1, yes.

Quicke et al. (1992a)

The table of characters provided by Quicke et al. (1992a) was used and needed to be translated into a data matrix using Symphyta to polarize the data. A total of 12 characters was kept (one was discarded since no parasitic wasp family had the apomorphic state) and they are all additive.

86. Spermatodesmata:

0, present; 1, absent.

87. Length of sperm:

0, greater than 30 micrometers;

1, less than 30 micrometers.

88. Ratio of head length to total length:

0, less than 0.4;

1, greater than 0.4.

89. Detachable, extracellular, acrosomal sheath:

0, absent; 1, present.

90. Number of axonemal central singlets:

0, two; 1, one.

91. Mitochondrial derivatives (overlap of nucleus):

0, not or hardly overlapping nucleus;

1, overlapping nucleus considerably.

92. Mitochondrial derivatives (size):

0, normal size;

1, reduced.

93. Mitochondrial derivatives (symmetry):

0, markedly asymmetric;

1, nearly symmetric.

94. Mitochondrial derivatives (shape):

0, circular or radially elongate;

1, depressed.

95. Axoneme and derivatives:

0, untwisted;

1, spiraled.

96. Number of deltoid accessory bodies:

0, two; 1, one.

97. Development of deltoid accessory bodies:

0, well developed, triangular;

1, reduced, ill-defined shape.

Quicke et al. (1994)

As for the previous paper, the characters had to be polarized since they were listed in a table and the zeros did not necessarily indicate a plesiomorphic state. The character from Quicke et al. (1992b), the ovipositor valvilli, was added to this list. All ten characters are treated as additive.

98. Division of upper valve:

0, divided at apex;

1, not divided at apex.

99. Number of lumina of upper valve:

0, one lumen;

1, two lumina.

100. Olistheters:

0, diverging ventrally;

1, approximately vertical;

2, converging ventrally.

101. Olistheter mechanism:

0, densely covered with large scales;

1, with only sparse, weak scaling.

102. Ventral wall of upper valve:

0, evenly thickened;

1, more strongly thickened medially, making the upper valve lumen reniform in section.

103. Ventral part of lower valves:

0, abutting;

1, overlapping.

104. Dorsal part of upper valves:

0, without asymmetric cleft;

1, with asymmetric cleft.

105. Ovipositor:

0, strongly compressed laterally;
1, more or less oval or round;
2, strongly dorso-ventrally compressed.

106. Medio ventral part of the lower valves:
0, without seal;
1, with seal.

107. Ovipositor valvilli:
0, absent; 1, present

Heraty et al. (1994)

Since a data matrix was provided, it was used with few changes and these were made when more than one character state was established for a single taxon. In such cases, the most plesiomorphic condition was considered to be the ground plan. A total of 12 characters was detailed by the authors.

108. Mesofurcal bridge:
0, no arms;
1, furcal arms long, robust, and separated along their entire length;
2, furcal arms reduced but well separated;
3, furcal arms narrow and elongate, joined at the extreme apices;
4, furcal arms elongate and fused along most of their length;
5, furcal arms completely fused and forming a transverse mesofurcal bridge;
6, furcal arms completely fused and bowed, with a strong median anterior process;
7, mesofurcal bridge absent.

109. Laterophragma of mesopostnotum:

0, laterophragma forming a lobe;

1, laterophragma excised between the elongate apodeme and the posterior lobe (pn2);

2, laterophragma reduced to a narrow triangular process;

3, axillary lever deflected ventrally;

4, axillary lever reduced, forming a short, broad process;

5, axillary lever robust and strongly appressed to the inner surface of the second phragma.

110. Furcal-laterophragmal muscle:

0, only fu2-pn2 muscle present;

1, division of fu2-pn2 into fu2-pn2a and fu2-pn2b;

2, loss of fu2-pn2b;

3, loss of fu2-pn2a.

111. t2-pn2 muscle:

0, t2-pn2 attaching between the mesonotum and the anterior face of the laterophragmal lobe;

1, t2-pn2 and the associated posterior lobe of the laterophragma is lost.

112. Mesopostnotum and scutellar-metanotal muscle:

0, mesopostnotum weakly sclerotized medially and appears to be split, t2-t3 internal;

1, mesopostnotum broadly exposed dorsally, t2-t3 internal;

2, mesopostnotum exposed dorsally, t2-t3 external;

3, mesopostnotum weakly sclerotized medially and appears to be split, t2-t3 internal;

4, mesopostnotum and t2-t3 completely internal.

113. Formation of the pseudophragma:

0, anterior margin of mesopostnotum broadly attached to the anterior margin of the mesonotum;

1, anterior margin of mesopostnotum developed into a broad bilobed internal plate (pseudophragma).

114. Furcal-spina muscle (fu2-sps1):

0, present; 1, absent.

115. Furcal-spina muscle (fu2-sps2):

0, present; 1, present.

116. Furcal-basalare muscle (fu2-ba3):

0, absent; 1, present.

117. Lateral articulation of mesopostnotum:

0, mesopostnotum broadly and evenly joined to the upper mesepimeron;

1, juncture invaginated and connected by weak cuticle, strong connection at the anteriormost point of attachment;

2, mesopostnotum completely internal and connection reduced to the anteriormost point of attachment.

118. Fusion of lateral arms of mesofurca and metafurca:

0, lateral arms of mesofurca and metafurca broadly separated, interfurcal muscle present;

1, lateral arms of both furcae fused at the junction with the mesofurcal bridge, interfurcal muscle lost.

119. Furcal process for trochanteral muscle (fu2-tr2):

0, fu2-tr2 attaching to the lateral arms of the mesofurca;

1, fu2-tr2 attaching to the anterior extensions of the lateral furcal arms.

Sharkey (1994)

This paper is short but provides an interesting character to include in this study; the polarization was done according to the author.

120. Labial silk production in larvae:

0, present; 1, absent.

Table 4: Data matrix of non-wing character suites of Apocrita

	Tonapi	Daly	Robertson
	0 1	2	3
	0123456789012	3456789012345678	9012
Xyelidae	0000000000000	0001000000010010	????
Megalodontoidea	0????????????	????????????????	????
Tenthredinoidea	0000010010000	0211201001212211	0000
Xiphydriidae	0000111011000	????????????????	????
Anaxyelidae	0????????????	????????????????	????
Siricidae	00001010010??	0020000002011110	0001
Cephidae	0000000000000	0010000000222210	????
Orussidae	0????????????	????????????????	0???
Ichneumonidae	0101211101100	2211201222212211	1010
Braconidae	0101311101100	2211201222212211	1120
Trigonalidae	0????????????	????????????????	????
Aculeata	0300300?10000	2211201002212211	1230
Evaniidae	0210310?10001	????????????????	????
Megalyridae	0????????????	????????????????	????
Aulacidae	0????????????	2211201202212211	????
Stephanidae	0????????????	????????????????	????
Gasteruptiidae	0220310?10?01	????????????????	????
Chalcidoidea	031??00?00?11	2012211212122211	2??0
Cynipidae	021??00?0??11	0211211112122221	????
Ibaliidae	0????????????	0211211112122221	????
Liopteridae	0????????????	????????????????	????
Figitidae	0????????????	????????????????	????
Eucoilidae	0????????????	????????????????	????
Charipidae	0????????????	????????????????	????
Proctotrupidae	02212111??02	????????????????	????
Pelecinidae	0????????????	????????????????	????
Vanhorniidae	0????????????	????????????????	????
Heloridae	0????????????	????????????????	????
Monomachidae	0????????????	????????????????	????
Roproniidae	0????????????	????????????????	????
Peradeniidae	0????????????	????????????????	????
Austroniidae	0????????????	????????????????	????
Diapriidae	0????????????	????????????????	????
Platygastridae	0????????????	????????????????	????
Scelionidae	0????????????	????????????????	????
Ceraphronidae	02212111??02	????????????????	????
Megaspilidae	0????????????	????????????????	????

	Farish	Richards	Iwata	Gibson
	4 5			6
	345678901234567890	12345	6789	012345678
Xyelidae	??????????????????	?????	0???	000000000
Megalodontoidea	??????????????????	0000?	0???	000020001
Tenthredinoidea	000000000000000000	00011	0???	003000001
Xiphydriidae	011101100000001001	?????	0???	000010011
Anaxyelidae	??????????????????	?????	0???	000000001
Siricidae	??????????????????	0000?	0???	000010100
Cephidae	??????????????????	?????	0???	000000001
Orussidae	??????????????????	???1?	1000	120011?10
Ichneumonidae	001100110000111000	00011	1000	112021?11
Braconidae	0010001100001110?0	00011	1000	11202?011
Trigonalidae	??????????????????	000??	1100	122011??1
Aculeata	011101011011101000	2?111	10??	11200??11
Evaniidae	001100100101100001	2001?	1011	112111?11
Megalyridae	??????????????????	1?01?	??00	111020?11
Aulacidae	??????????????????	0001?	1100	112021?11
Stephanidae	??????????????????	2?11?	??00	101010011
Gasteruptiidae	??????????????????	2011?	1000	112000?11
Chalcidoidea	011101110001011110	2????	1?00	121000?11
Cynipidae	??????????????????	1??1?	????	012011011
Ibaliidae	??????????????????	?????	1?01	012011011
Liopteridae	??????????????????	?????	????	?????????
Figitidae	101110100001011000	?????	2001	012011011
Eucoilidae	??????????????????	?????	????	012011011
Charipidae	??????????????????	?????	????	?????????
Proctotrupidae	??????????????????	1?011	2?0?	112111??1
Pelecinidae	??????????????????	1?011	2000	112111?11
Vanhorniidae	??????????????????	?????	????	012111?11
Heloridae	001100100001101100	1?011	????	112011?11
Monomachidae	??????????????????	?????	????	012011?11
Ropronidae	??????????????????	1?011	????	112011?11
Peradeniidae	??????????????????	?????	????	?????????
Austroniidae	??????????????????	?????	????	1120?1?11
Diapriidae	001100100001101100	?????	2?01	001011?11
Platygastridae	??????????????????	?????	2?0?	1?2?11?11
Scelionidae	??????????????????	?????	201?	122111?11
Ceraphronidae	??????????????????	?????	1001	021030011
Megaspilidae	??????????????????	?????	????	021030011

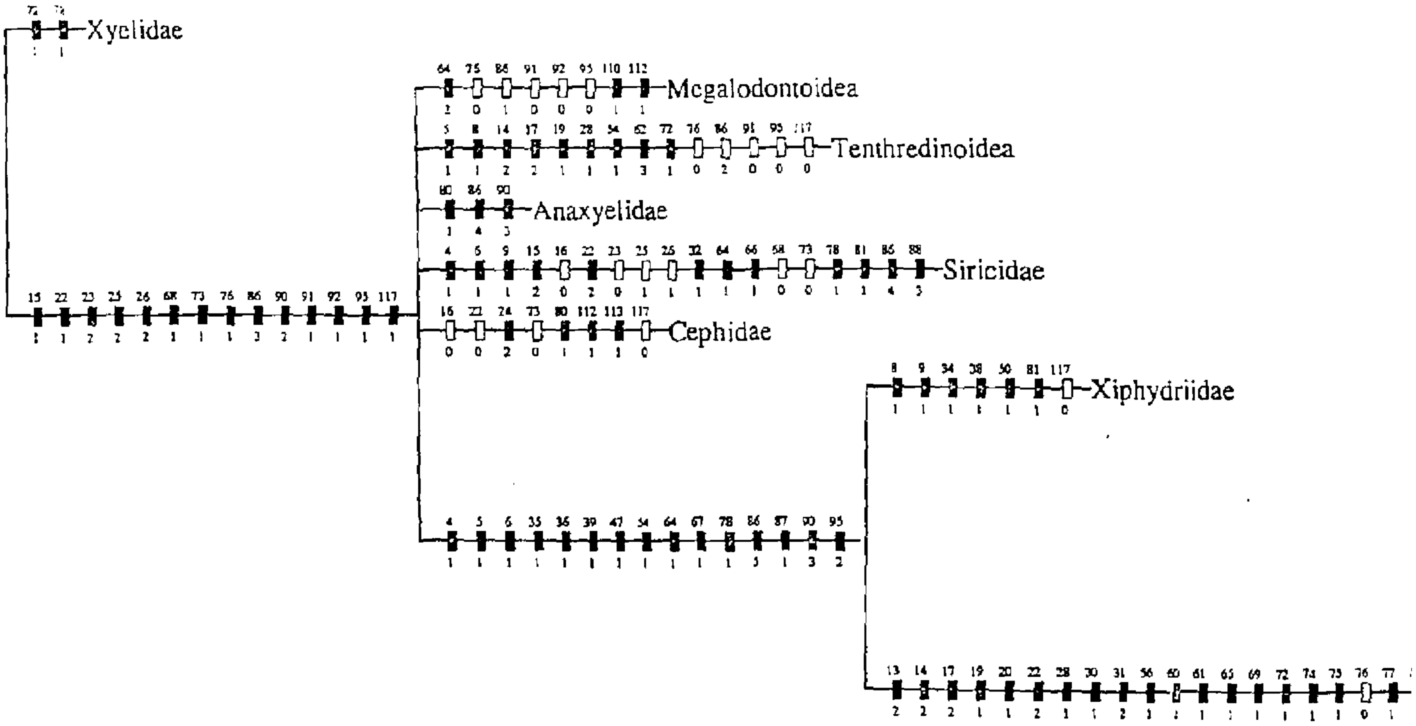
	Johnson	Whitfield+al	Whitfield
	7	8	
	9012345	678901	2345
Xyelidae	0001000	001000	0000
Megalodontoidea	0000100	000000	0000
Tenthredinoidea	0001100	000000	0000
Xiphydriidae	0000100	101001	0000
Anaxyelidae	???????	100010	0000
Siricidae	0000000	101001	0000
Cephidae	0000000	100010	0000
Orussidae	1001111	011000	1000
Ichneumonidae	2101111	011100	1101
Braconidae	2101111	011100	1111
Trigonalidae	1011111	011100	?000
Aculeata	?001111	??????	?000
Evaniidae	1011111	011100	2000
Megalyridae	?011111	011100	1000
Aulacidae	1011111	011120	3000
Stephanidae	1001111	011100	1000
Gasteruptiidae	1011111	011120	3000
Chalcidoidea	1101111	011100	3000
Cynipidae	???????	011100	3?0?
Ibaliidae	1101111	011100	3?0?
Liopteridae	???????	??????	3?0?
Figitidae	???????	011100	3?0?
Eucoilidae	???????	??????	3?0?
Charipidae	???????	??????	3?0?
Proctotrupidae	???????	011100	3000
Pelecinidae	2101111	011100	3000
Vanhorniidae	???????	??????	3000
Heloridae	???????	011100	3000
Monomachidae	???????	??????	3000
Roproniidae	???????	??????	3000
Peradeniidae	???????	??????	3000
Austroniidae	???????	??????	3000
Diapriidae	?101111	011100	3000
Platygastridae	2101111	011100	311?
Scelionidae	2101111	011100	300?
Ceraphronidae	?011111	01221?	3000
Megaspilidae	1011111	01221?	3000

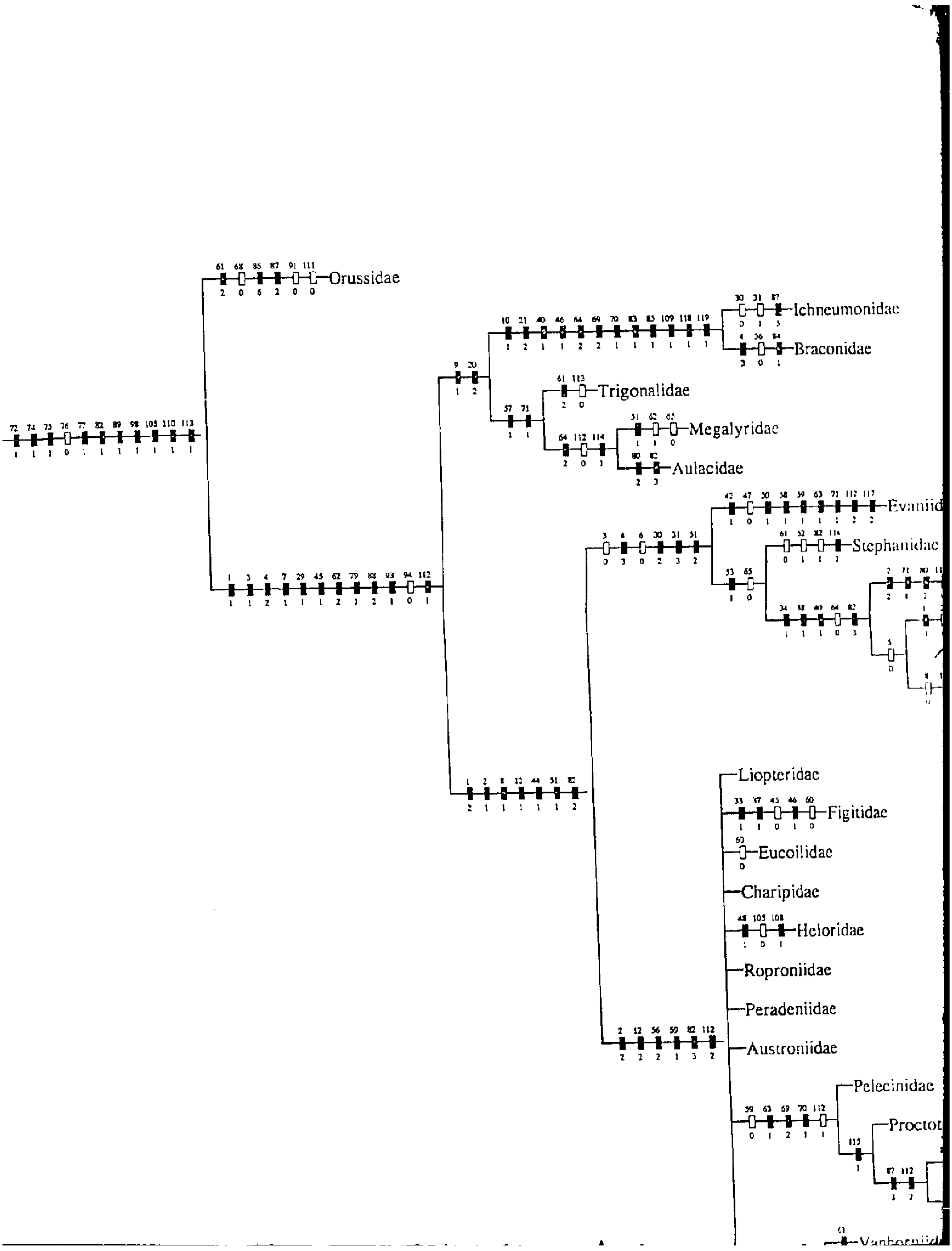
	Heraty + al	Quicke 1992	Quicke 1994	Sharkey
		1	1	1
	9	0	1	2
	678901234567	890123456789	0123456789	0
Xyelidae	101010001000	000000000000	010?000000	0
egalodontoidea	101020001000	????????????	1110000100	0
Tenthredinoidea	201020101000	0000000000?0	0100000000	0
Xiphydriidae	511031101200	????????????	0100000000	0
Anaxyelidae	401031101100	????????????	0100000100	0
Siricidae	403021101100	????????????	0100000100	0
Cephidae	301021101100	0000000?00?0	0111000000	0
Orussidae	62?130101200	????????????	1001000100	0
Ichneumonidae	552131110200	100?00010001	1?11000111	0
Braconidae	512131110200	1???00?1000?	1?11000111	0
Trigonalidae	512131110200	????????????	11100????0	0
Aculeata	512131110200	100000010000	1121000111	0
Evaniidae	512131110200	????????????	1121000200	1
Megalyridae	??2?31110200	????????????	1101100100	1
Aulacidae	512131110200	????????????	1101100100	0
Stephanidae	512131110200	????????????	1111100100	1
Gasteruptiidae	512131110200	100?????????	1101?00100	0
Chalcidoidea	512131110200	10000101110?	1121011100	1
Cynipidae	512131110200	????????????	1111000100	1
Ibaliidae	512131110200	????????????	1111100100	1
Liopteridae	512131110200	????????????	??????????	1
Figitidae	512131110200	100000010000	1121000100	1
Eucoilidae	512131110200	????????????	1121000100	1
Charipidae	512131110200	????????????	1121000100	1
Proctotrupidae	512131110200	100?????????	1111010100	1
Pelecinidae	??2?31110200	????????????	1111000100	1
Vanhorniidae	512031110200	????????????	1121010100	1
Heloridae	512131110200	1??000?00010	1121000100	1
Monomachidae	512031110200	????????????	1121010100	1
Roproniidae	512131110200	????????????	1121000100	1
Peradeniidae	??2?31110200	????????????	??????????	1
Austroniidae	512?31110200	????????????	??????????	1
Diapriidae	512031110200	10?0010?1100	11?1010100	1
Platygastridae	732131110200	????????????	1121010100	1
Scelionidae	532131110200	????????????	1121010100	1
Ceraphronidae	712031110200	????????????	??????????	1
Megaspilidae	712031110200	????????????	1121010100	1

Fig. 41. Cladogram of non-wing characters

numbers on top of the rectangles refer to the character, those below the rectangle refer to the character state

■ Non-homoplastic apomorphy
▨ Homoplastic convergent apomorphy
□ Homoplastic reversal apomorphy


Xyelidae
Megalodontoidea
Tenthredinoidea
Anaxyelidae
Siricidae
Cephidae
Xiphydriidae


Orussidae
Ichneumonidae
Braconidae
Trigonalidae
Megalyridae
Aulacidae
Evaniid
Stephanidae
Liopteridae
Figitidae
Eucoilidae
Charipidae
Heloridae
Roproniidae
Peradeniidae
Austroniidae
Pelecinidae
Proctot
Vanhorniid

APPENDIX 3:

ANALYSIS OF THE COMBINED DATA

Table 5 Data matrix of combined data on character suites

Wing characters (present study)

	0	1	2	3	4	5
	0123456789	0123456789	0123456789	0123456789	0123456789	0123
Xyelidae	0000000000	0000000000	0000000010	0000000000	0000000000	0000
Megalodontoidea	0000000000	0000000000	0000000000	0110000000	0000000000	0010
Tenthredinoidea	0000000000	0000000000	0000000000	1100000000	0000000000	1110
Xiphydriidae	0000000000	0000000000	0010000000	1000000000	0000000000	1110
Anaxyelidae	0000000000	0001100000	0000000000	1001000000	0101100000	1110
Siricidae	0000000000	0000000000	0010000000	0110000000	0000000000	1110
Cephidae	0000000000	0001000000	0010000000	1100000000	0001000000	1110
Orussidae	0000000000	0011011001	0010001000	1101000000	0101100000	1111
Ichneumonidae	0000000100	0111101000	0011000101	1101000010	0100100000	1111
Braconidae	0000000000	0111101000	001100000?	1101000010	0100100010	1111
Trigonalidae	0000000000	0111001000	001000000?	1101000010	0100100000	1111
Aculeata	0000000000	0111001000	0010000000	1101000000	0100100000	1111
Evaniidae	0000000000	0111101001	0010000000	1101010110	11111001??	1111
Megalyridae	0000000000	0111101001	0010000000	1101011111	11111011??	1111
Aulacidae	0000000000	0111001000	001000000?	1101100011	0101100100	1111
Stephanidae	0100000000	0111111001	001000000?	1101000011	01011001?0	1111
Gasteruptiidae	0000000000	0111111201	0010000001	1101100?11	0111100101	1111
Chalcidoidea	0100000000	0111111011	001011001?	1101010111	0111100111	1111
Cynipidae	0100000000	1111101011	0010110100	1101100111	0111100111	1111
Ibaliidae	0100000000	0111101011	0010?10100	1101110111	0111100111	1111
Liopteridae	0100000001	1111101011	0010110100	1101110111	0111100111	1111
Figitidae	0100000001	1111101011	0010110100	1101110111	0111100111	1111
Eucoilidae	0100000001	1111101011	0110110100	1101111111	0111110111	1111
Charipidae	0100000001	1111101011	0010110100	1101111111	0111110111	1111
Proctotrupidae	0000000000	0111111101	0010010001	1101100111	0111100101	1111
Pelecinidae	0000000000	0111111101	0010010011	1101100111	01111011?1	1111
Vanhorniidae	0000000000	0111111101	0010010001	1101100111	0111100101	1111
Heloridae	0000000000	0111111101	0010010001	1101100111	0111100101	1111
Monomachidae	0000000100	0111111?01	0010010001	1101100111	0101100110	1111
Roproniidae	0000000000	0111111101	0010010001	1101100111	0111100101	1111
Peradeniidae	0000000100	0111111?01	0010010001	1101100111	01111001?1	1111
Austroniidae	0000000100	0111111?01	0010010001	1101100111	0111100110	1111
Diapriidae	0000000100	1111111?11	111001000?	1101110111	0111100111	1111
Platygastridae	0100100100	1111111?11	111011100?	1101110111	0111111111	1111
Scelionidae	0101000100	11111?1?11	111011000?	1101110111	0111111111	1111
Ceraphronidae	0010011110	0111111?11	11110?100?	1101000111	0111111111	1111
Megaspilidae	0010000100	0111111?11	11110?100?	1101000111	0111100110	1111

	Tonapi	Daly	Robertson
	6	7 8	
	6789012345678	9012345678901234	5678
Xyelidae	0000000000000	0001000000010010	????
Megalodontoidea	0????????????	????????????????	????
Tenthredinoidea	0000010010000	0211201001212211	0000
Xiphydriidae	0000111011000	????????????????	????
Anaxyelidae	0????????????	????????????????	????
Siricidae	00001010010??	0020000002011110	0001
Cephidae	0000000000000	0010000000222210	????
Orussidae	0????????????	????????????????	0???
Ichneumonidae	0101211101100	2211201222212211	1010
Braconidae	0101311101100	2211201222212211	1120
Trigonalidae	0????????????	????????????????	????
Aculeata	0300300?10000	2211201002212211	1230
Evaniidae	0210310?10001	????????????????	????
Megalyridae	0????????????	????????????????	????
Aulacidae	0????????????	2211201202212211	????
Stephanidae	0????????????	????????????????	????
Gasteruptiidae	0220310?10?01	????????????????	????
Chalcidoidea	031??00?00?11	2012211212122211	2??0
Cynipidae	021??00?0??11	0211211112122221	????
Ibaliidae	0????????????	0211211112122221	????
Liopteridae	0????????????	????????????????	????
Figitidae	0????????????	????????????????	????
Eucoilidae	0????????????	????????????????	????
Charipidae	0????????????	????????????????	????
Proctotrupidae	02212111???02	????????????????	????
Pelecinidae	0????????????	????????????????	????
Vanhorniidae	0????????????	????????????????	????
Heloridae	0????????????	????????????????	????
Monomachidae	0????????????	????????????????	????
Roproniidae	0????????????	????????????????	????
Peradeniidae	0????????????	????????????????	????
Austroniidae	0????????????	????????????????	????
Diapriidae	0????????????	????????????????	????
Platygastridae	0????????????	????????????????	????
Scelionidae	0????????????	????????????????	????
Ceraphronidae	02212111???02	????????????????	????
Megaspilidae	0????????????	????????????????	????

	Farish	Richards	Iwata	Gibson
	1	1		1
	9 0	1		2
	901234567890123456	78901	2345	678901234
Xyelidae	??????????????????	?????	0???	000000000
Megalodontoidea	??????????????????	0000?	0???	000020001
Tenthredinoidea	000000000000000000	00011	0???	003000001
Xiphydriidae	011101100000001001	?????	0???	000010011
Anaxyelidae	??????????????????	?????	0???	000000001
Siricidae	??????????????????	0000?	0???	000010100
Cephidae	??????????????????	?????	0???	000000001
Orussidae	??????????????????	???1?	1000	120011?10
Ichneumonidae	001100110000111000	00011	1000	112021?11
Braconidae	0010001100001110?0	00011	1000	11202?011
Trigonalidae	??????????????????	000??	1100	122011??1
Aculeata	011101011011101000	2?111	10??	11200??11
Evaniidae	001100100101100001	2001?	1011	112111?11
Megalyridae	??????????????????	1?01?	??00	111020?11
Aulacidae	??????????????????	0001?	1100	112021?11
Stephanidae	??????????????????	2?11?	??00	101010011
Gasteruptiidae	??????????????????	2011?	1000	112000?11
Chalcidoidea	011101110001011110	2????	1?00	121000?11
Cynipidae	??????????????????	1??1?	????	012011011
Ibaliidae	??????????????????	?????	1?01	012011011
Liopteridae	??????????????????	?????	????	?????????
Figitidae	101110100001011000	?????	2001	012011011
Eucoilidae	??????????????????	?????	????	012011011
Charipidae	??????????????????	?????	????	?????????
Proctotrupidae	??????????????????	1?011	2?0?	112111??1
Pelecinidae	??????????????????	1?011	2000	112111?11
Vanhorniidae	??????????????????	?????	????	012111?11
Heloridae	001100100001101100	1?011	????	112011?11
Monomachidae	??????????????????	?????	????	012011?11
Ropronidae	??????????????????	1?011	????	112011?11
Peradeniidae	??????????????????	?????	????	?????????
Austroniidae	??????????????????	?????	????	1120?1?11
Diapriidae	001100100001101100	?????	2?01	001011?11
Platygastridae	??????????????????	?????	2?0?	1?2?11?11
Scelionidae	??????????????????	?????	201?	122111?11
Ceraphronidae	??????????????????	?????	1001	021030011
Megaspilidae	??????????????????	?????	????	021030011

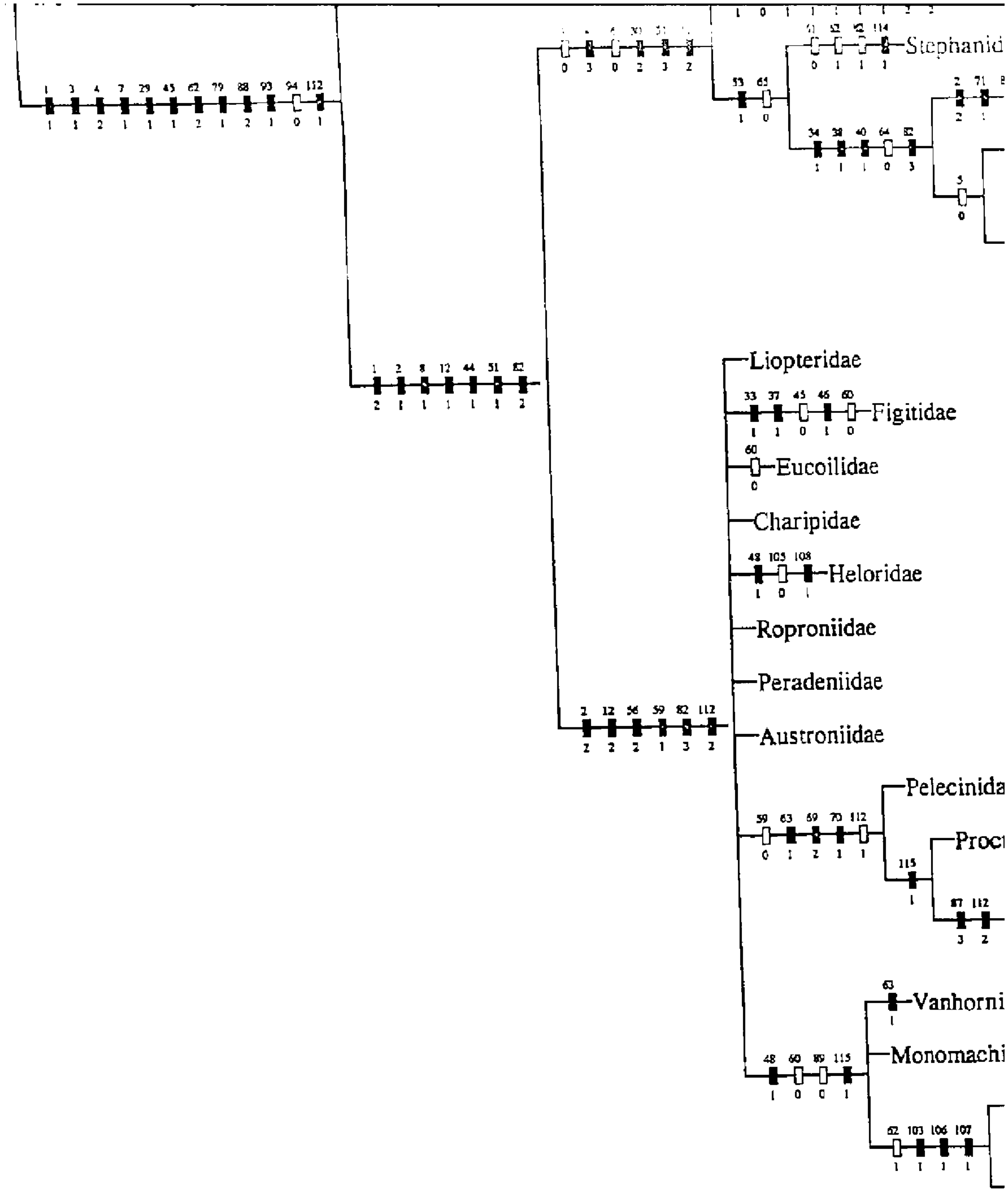
	Johnson	Whitfield+al	Whitfield
	1	1	
	3	4	
	9012345	678901	2345
Xyelidae	0001000	001000	0000
Megalodontoidea	0000100	000000	0000
Tenthredinoidea	0001100	000000	0000
Xiphydriidae	0000100	101001	0000
Anaxyelidae	???????	100010	0000
Siricidae	0000000	101001	0000
Cephidae	0000000	100010	0000
Orussidae	1001111	011000	1000
Ichneumonidae	2101111	011100	1101
Braconidae	2101111	011100	1111
Trigonalidae	1011111	011100	?000
Aculeata	?001111	??????	?000
Evaniidae	1011111	011100	2000
Megalyridae	?011111	011100	1000
Aulacidae	1011111	011120	3000
Stephanidae	1001111	011100	1000
Gasteruptiidae	1011111	011120	3000
Chalcidoidea	1101111	011100	3000
Cynipidae	???????	011100	3?0?
Ibaliidae	1101111	011100	3?0?
Liopteridae	???????	??????	3?0?
Figitidae	???????	011100	3?0?
Eucoilidae	???????	??????	3?0?
Charipidae	???????	??????	3?0?
Proctotrupidae	???????	011100	3000
Pelecinidae	2101111	011100	3000
Vanhorniidae	???????	??????	3000
Heloridae	???????	011100	3000
Monomachidae	???????	??????	3000
Roproniidae	???????	??????	3000
Peradeniidae	???????	??????	3000
Austroniidae	???????	??????	3000
Diapriidae	?101111	011100	3000
Platygastridae	2101111	011100	311?
Scelionidae	2101111	011100	300?
Ceraphronidae	?011111	01221?	3000
Megaspilidae	1011111	01221?	3000

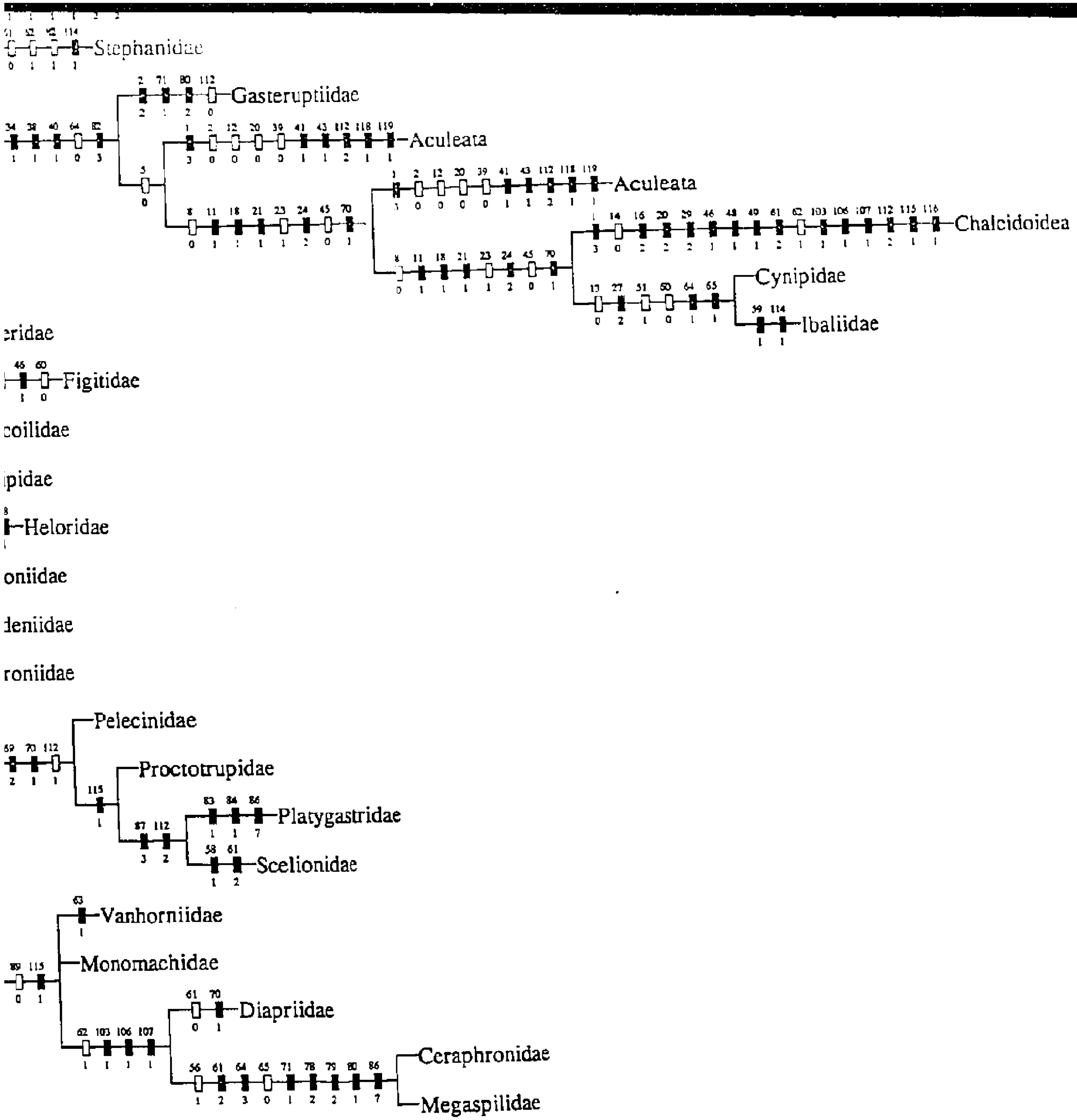
	Heraty + al	Quicke 1992	Quicke 1994	Sharkey
	1	1	1	1
	5	6	7	8
	678901234567	890123456789	0123456789	0
Xyelidae	101010001000	000000000000	010?000000	0
Megalodontoidea	101020001000	????????????	1110000100	0
Tenthredinoidea	201020101000	0000000000?0	0100000000	0
Xiphydriidae	511031101200	????????????	0100000000	0
Anaxyelidae	401031101100	????????????	0100000100	0
Siricidae	403021101100	????????????	0100000100	0
Cephidae	301021101100	0000000?00?0	0111000000	0
Orussidae	62?130101200	????????????	1001000100	0
Ichneumonidae	552131110200	100?00010001	1?11000111	0
Braconidae	512131110200	1???00?1000?	1?11000111	0
Trigonalidae	512131110200	????????????	11100????0	0
Aculeata	512131110200	100000010000	1121000111	0
Evaniidae	512131110200	????????????	1121000200	1
Megalyridae	??2?31110200	????????????	1101100100	1
Aulacidae	512131110200	????????????	1101100100	0
Stephanidae	512131110200	????????????	1111100100	1
Gasteruptiidae	512131110200	100?????????	1101?00100	0
Chalcidoidea	512131110200	10000101110?	1121011100	1
Cynipidae	512131110200	????????????	1111000100	1
Ibaliidae	512131110200	????????????	1111100100	1
Liopteridae	512131110200	????????????	??????????	1
Figitidae	512131110200	100000010000	1121000100	1
Eucoilidae	512131110200	????????????	1121000100	1
Charipidae	512131110200	????????????	1121000100	1
Proctotrupidae	512131110200	100?????????	1111010100	1
Pelecinidae	??2?31110200	????????????	1111000100	1
Vanhorniidae	512031110200	????????????	1121010100	1
Heloridae	512131110200	1??000?00010	1121000100	1
Monomachidae	512031110200	????????????	1121010100	1
Roproniidae	512131110200	????????????	1121000100	1
Peradeniidae	??2?31110200	????????????	??????????	1
Austroniidae	512?31110200	????????????	??????????	1
Diapriidae	512031110200	10?0010?1100	11?1010100	1
Platygastridae	732131110200	????????????	1121010100	1
Scelionidae	532131110200	????????????	1121010100	1
Ceraphronidae	712031110200	????????????	??????????	1
Megaspilidae	712031110200	????????????	1121010100	1

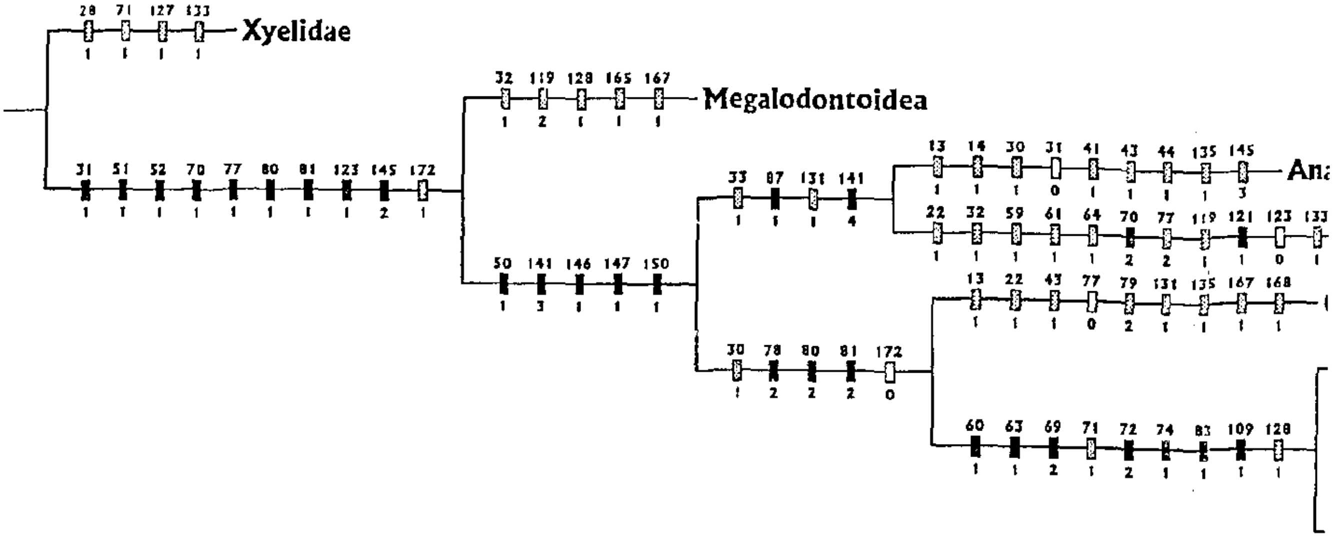
Fig. 42. Acctran cladogram of the total evidence

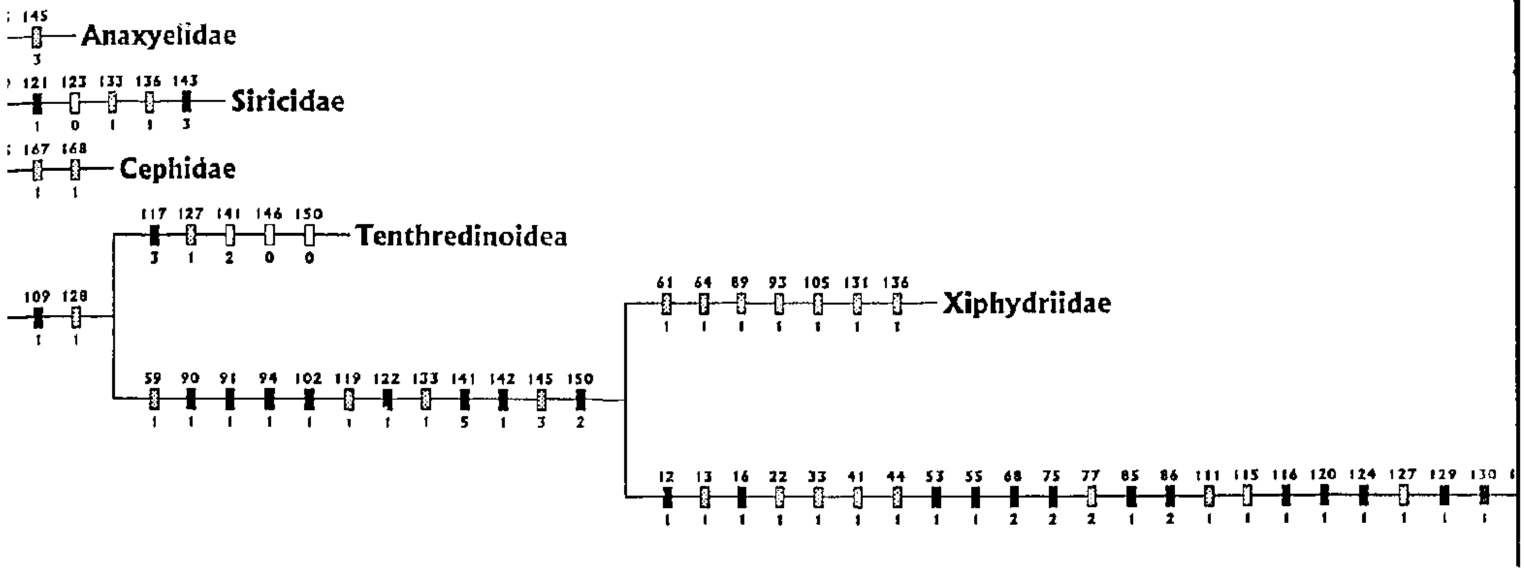
numbers on top of the rectangles refer to the character, those below the rectangle refer to the character state

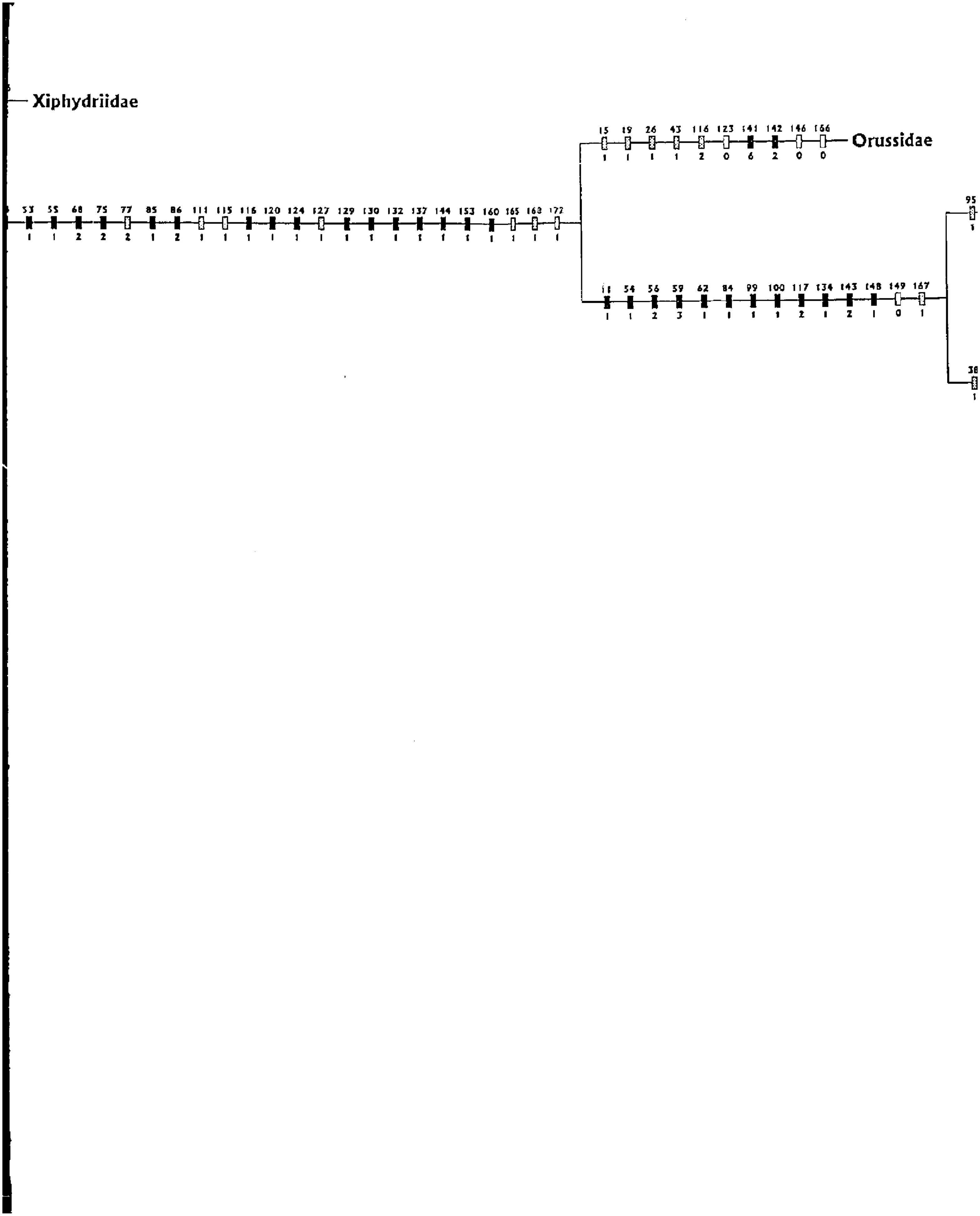
■ Non-homoplastic apomorphy
▨ Homoplastic convergent apomorphy
☐ Homoplastic reversal apomorphy

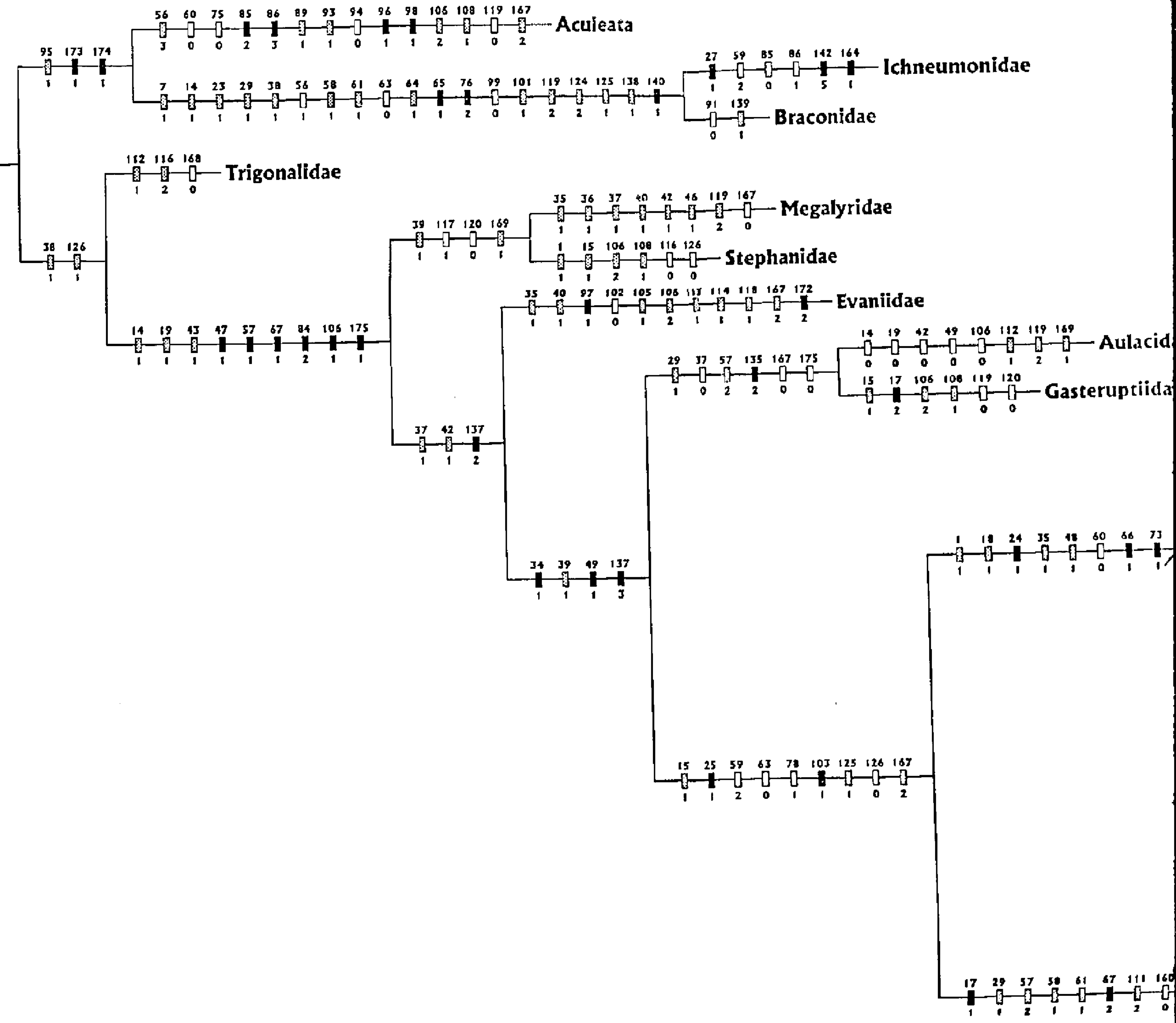

Stephanid
Liopteridae
Figitidae
Eucoilidae
Charipidae
Heloridae
Roproniidae
Peradeniidae
Austroniidae
Pelecinida
Proc
Vanhorni
Monomachi


Stephanidae
Gasteruptiidae
Aculeata
Aculeata
Chalcidoidea
Cynipidae
Ibaliidae
eridae
Figitidae
coilidae
ipidae
Heloridae
oniidae
deniidae
roniidae
Pelecinidae
Proctotrupidae
Platygastridae
Scelionidae
Vanhorniidae
Monomachidae
Diapriidae
Ceraphronidae
Megaspilidae

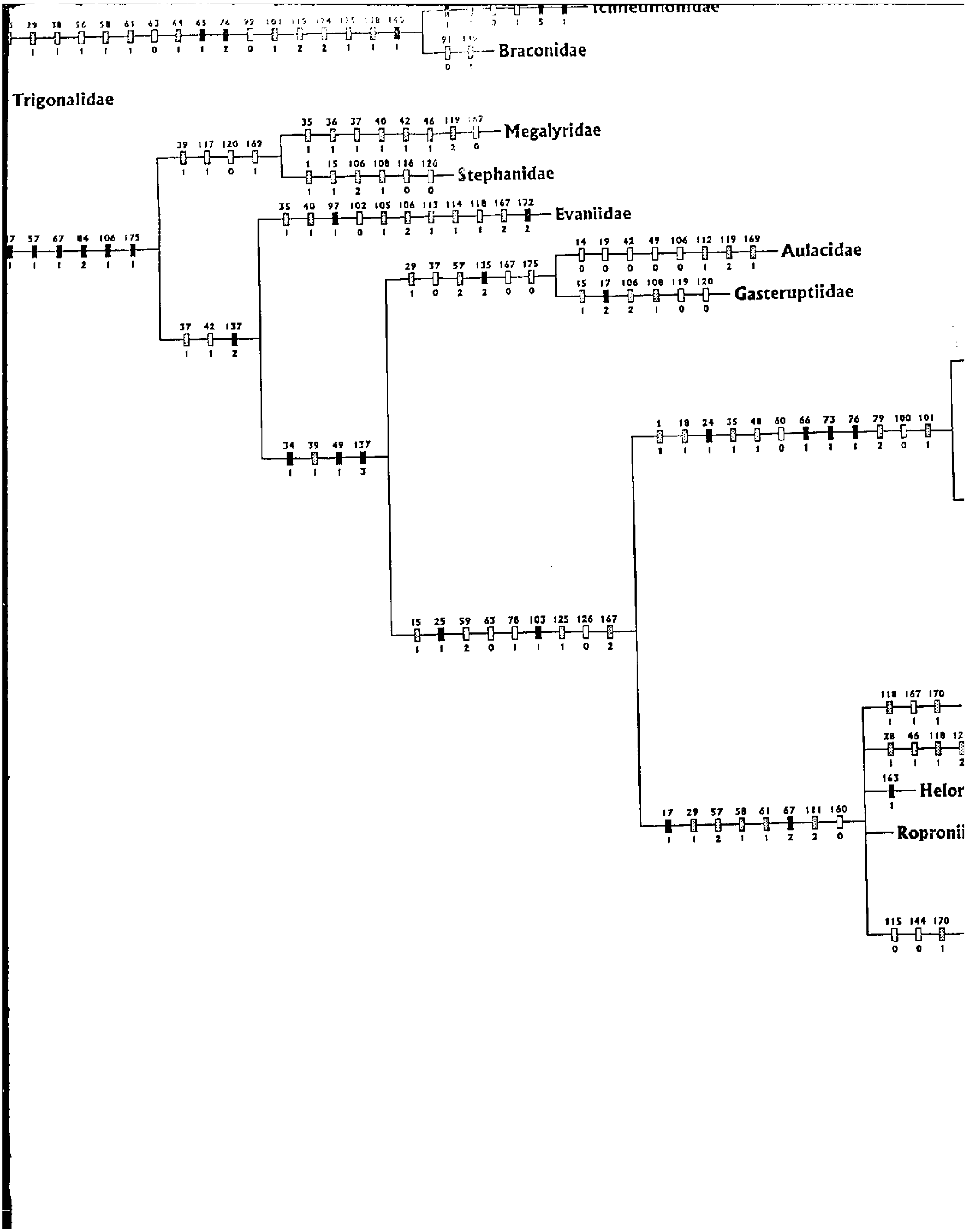

Xyelidae
Megalodontoidea
An


145
3
Anaxyelidae
121 123 133 136 143
1 0 1 1 3
Siricidae
167 168
1 1
Cephidae
117 127 141 146 150
3 1 2 0 0
Tenthredinoidea
109 128
1 1
59 90 91 94 102 119 122 133 141 142 145 150
1 1 1 1 1 1 1 1 5 1 3 2
61 64 89 93 105 131 136
1 1 1 1 1 1 1
Xiphydriidae
12 13 16 22 33 41 44 53 55 68 75 77 85 86 111 115 116 120 124 127 129 130
1 1 1 1 1 1 1 1 1 2 2 2 1 2 1 1 1 1 1 1 1 1


Xiphydriidae
Orussidae
15 19 26 43 116 123 141 142 146 166
1 1 1 1 2 0 6 2 0 0
53 55 68 75 77 85 86 111 115 116 120 124 127 129 130 132 137 144 153 160 165 168 172
1 1 2 2 2 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
11 54 56 59 62 84 99 100 117 134 143 148 149 167
1 1 2 3 1 1 1 1 2 1 2 1 0 1
95
1
38
1



Acuieata
Ichneumonidae
Braconidae
Trigonalidae
Megalyridae
Stephanidae
Evaniidae
Aulacid
Gasteruptiida
95 173 174
1 1 1
56 60 75 85 86 89 93 94 96 98 106 108 119 167
3 0 0 2 3 1 1 0 1 1 2 1 0 2
7 14 23 29 38 56 58 61 63 64 65 76 99 101 119 124 125 138 140
1 1 1 1 1 1 1 1 0 1 1 2 0 1 2 2 1 1 1
27 59 85 86 142 164
1 2 0 1 5 1
91 139
0 1
38 126
1 1
112 116 168
1 2 0
14 19 43 47 57 67 84 106 175
1 1 1 1 1 1 2 1 1
39 117 120 169
1 1 0 1
35 36 37 40 42 46 119 167
1 1 1 1 1 1 2 0
1 15 106 108 116 126
1 1 2 1 0 0
37 42 137
1 1 2
35 40 97 102 105 106 113 114 118 167 172
1 1 1 0 1 2 1 1 1 2 2
34 39 49 137
1 1 1 3
29 37 57 135 167 175
1 0 2 2 0 0
14 19 42 49 106 112 119 169
0 0 0 0 0 1 2 1
15 17 106 108 119 120
1 2 2 1 0 0
15 25 59 63 78 103 125 126 167
1 1 2 0 1 1 1 0 2
1 18 24 35 48 60 66 73
1 1 1 1 1 0 1 1
17 29 57 58 61 67 111 160
1 1 2 1 1 2 2 0



Ichneumonidae
5 29 38 56 58 61 63 64 65 74 92 101 115 124 125 138 145
1 1 1 1 1 1 0 1 1 2 0 1 2 2 1 1 1
91 112
0 1
Braconidae
Trigonalidae
17 57 67 84 106 175
1 1 1 2 1 1
39 117 120 169
1 1 0 1
35 36 37 40 42 46 119 167
1 1 1 1 1 1 2 0
Megalyridae
1 15 106 108 116 126
1 1 2 1 0 0
Stephanidae
37 42 137
1 1 2
35 40 97 102 105 106 113 114 118 167 172
1 1 1 0 1 2 1 1 1 2 2
Evaniidae
34 39 49 137
1 1 1 3
29 37 57 135 167 175
1 0 2 2 0 0
14 19 42 49 106 112 119 169
0 0 0 0 0 1 2 1
Aulacidae
15 17 106 108 119 120
1 2 2 1 0 0
Gasteruptiidae
15 25 59 63 78 103 125 126 167
1 1 2 0 1 1 1 0 2
1 18 24 35 48 60 66 73 76 79 100 101
1 1 1 1 1 0 1 1 1 2 0 1
17 29 57 58 61 67 111 160
1 1 2 1 1 2 2 0
118 167 170
1 1 1
28 46 118 12
1 1 1 2
163
1
Helor
Roproni
115 144 170
0 0 1

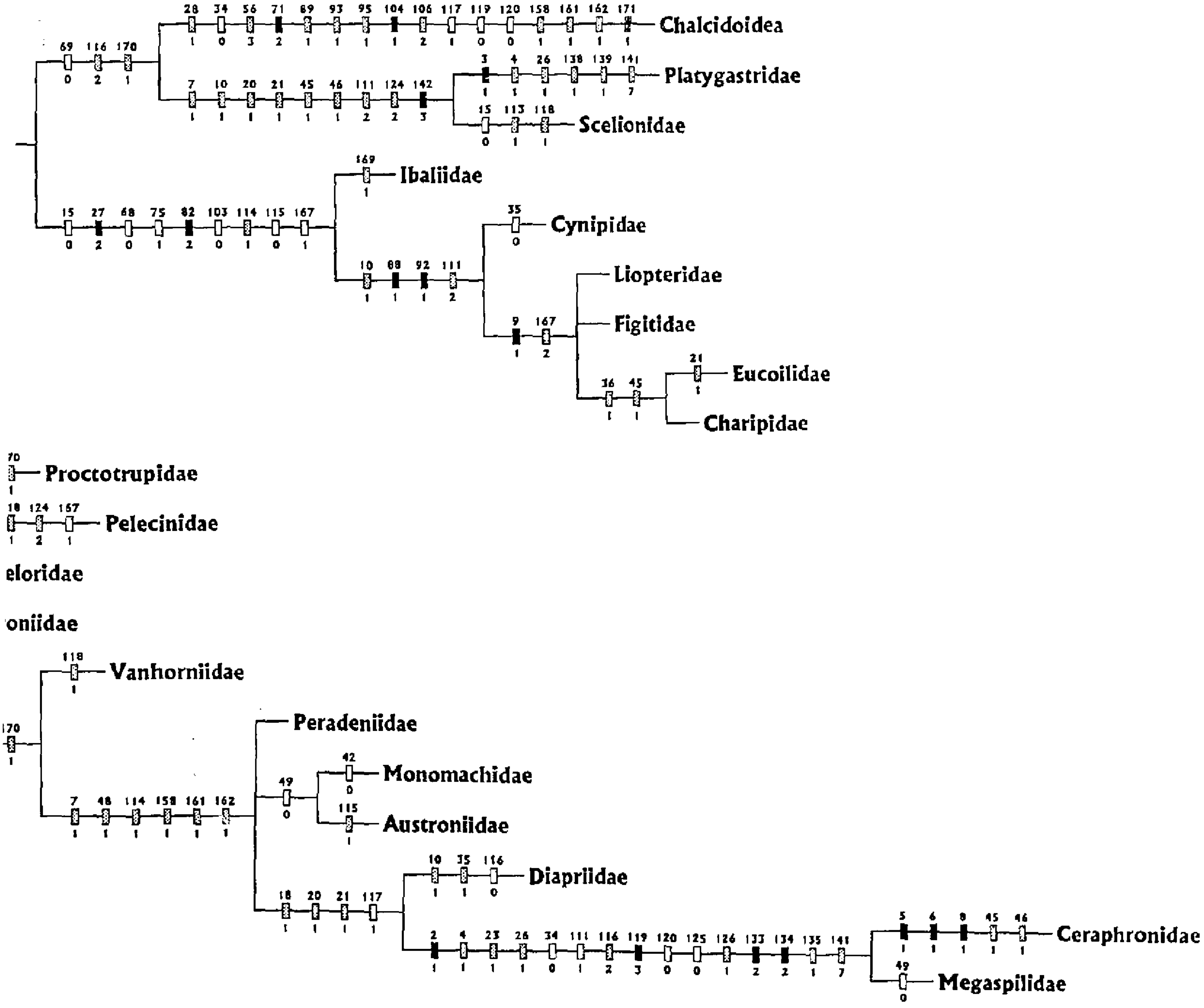
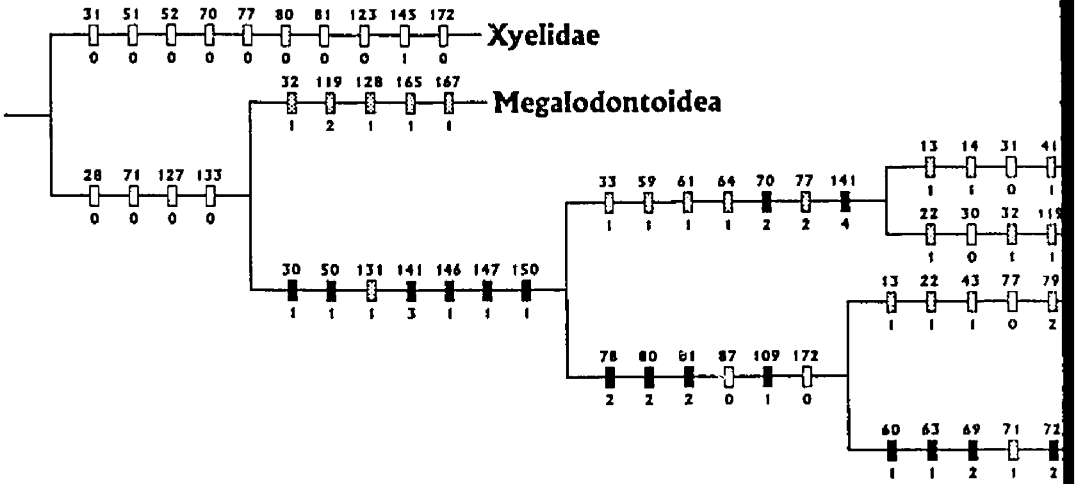
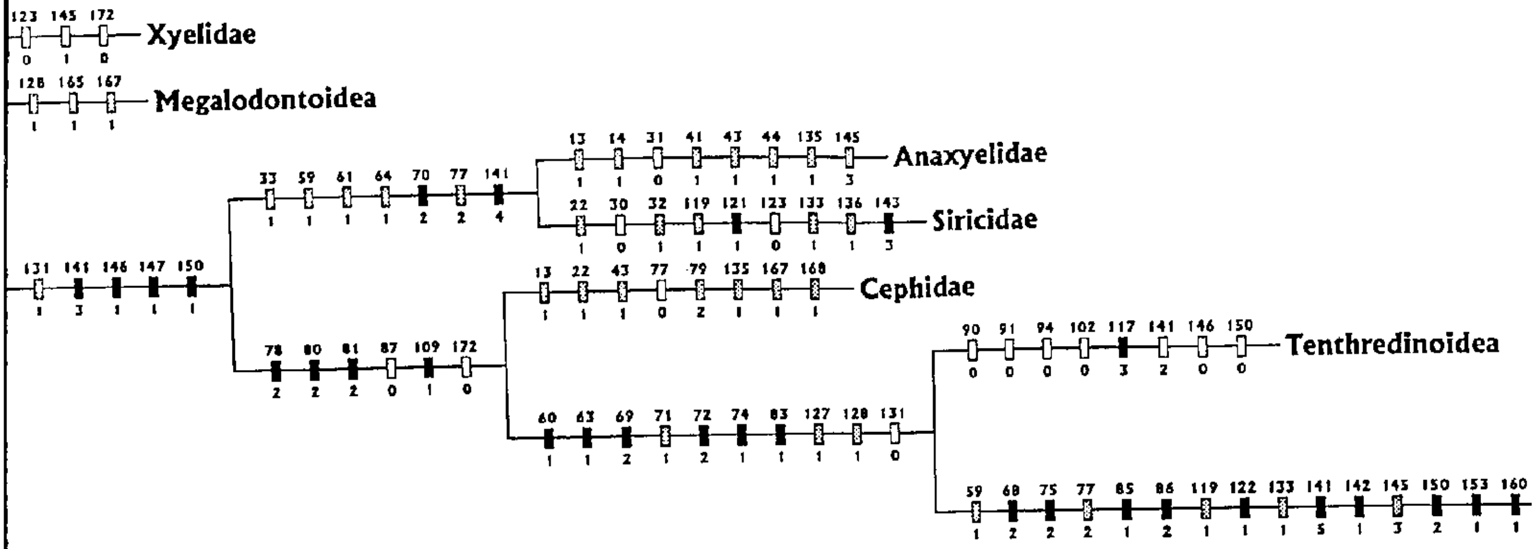

69 116 170
0 2 1
28 34 56 71 89 93 95 104 106 117 119 120 158 161 162 171
1 0 3 2 1 1 1 1 2 1 0 0 1 1 1 1
Chalcidoidea
7 10 20 21 45 46 111 124 142
1 1 1 1 1 1 2 2 3
3 4 26 138 139 141
1 1 1 1 1 7
Platygastridae
15 113 118
0 1 1
Scelionidae
169
1
Ibaliidae
15 27 68 75 82 103 114 115 167
0 2 0 1 2 0 1 0 1
35
0
Cynipidae
10 68 92 111
1 1 1 2
Liopteridae
Figitidae
9 167
1 2
21
1
Eucoilidae
36 45
1 1
Charipidae
70
1
Proctotrupidae
18 124 167
1 2 1
Pelecinidae
eloridae
oniidae
118
1
Vanhorniidae
170
1
Peradeniidae
42
0
Monomachidae
49
0
115
1
Austroniidae
7 48 114 158 161 162
1 1 1 1 1 1
10 35 116
1 1 0
Diapriidae
18 20 21 117
1 1 1 1
5 6 8 45 46
1 1 1 1 1
Ceraphronidae
2 4 23 26 34 111 116 119 120 125 126 133 134 135 141
1 1 1 1 0 1 2 3 0 0 1 2 2 1 7
49
0
Megaspilidae

Fig. 43. Deltran cladogram of the total evidence

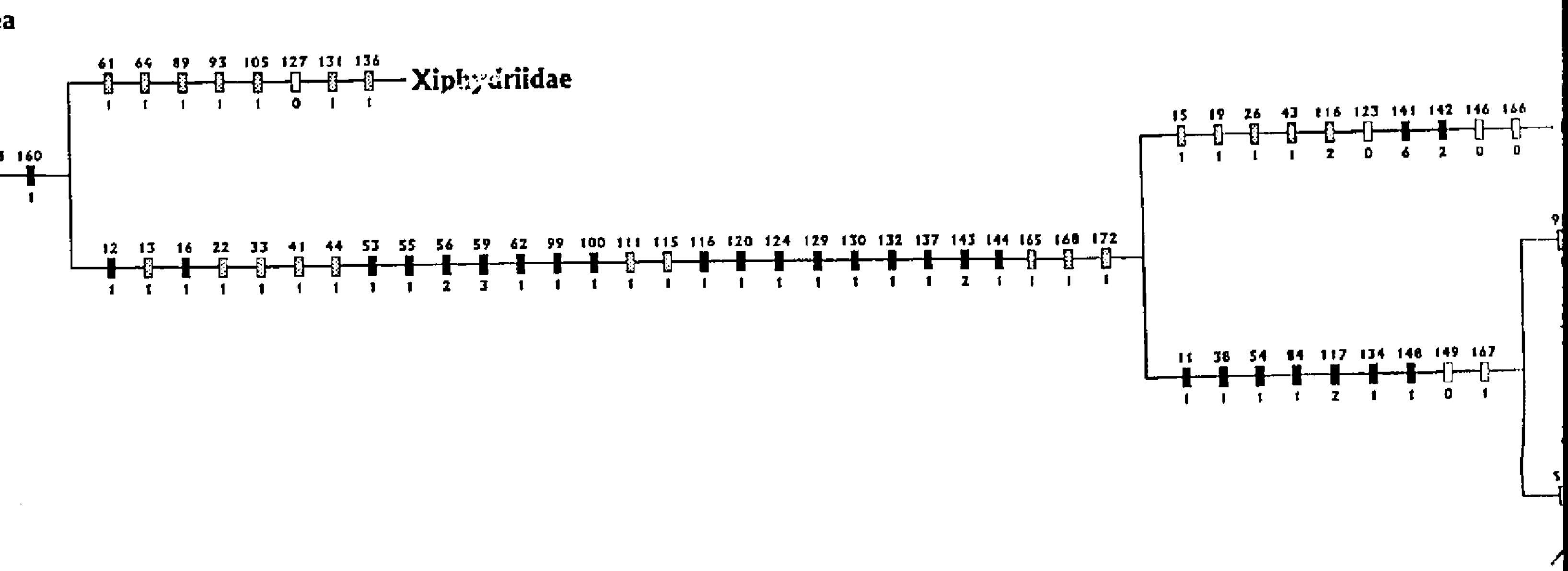
numbers on top of the rectangles refer to the character,
those below the rectangle refer to the character state

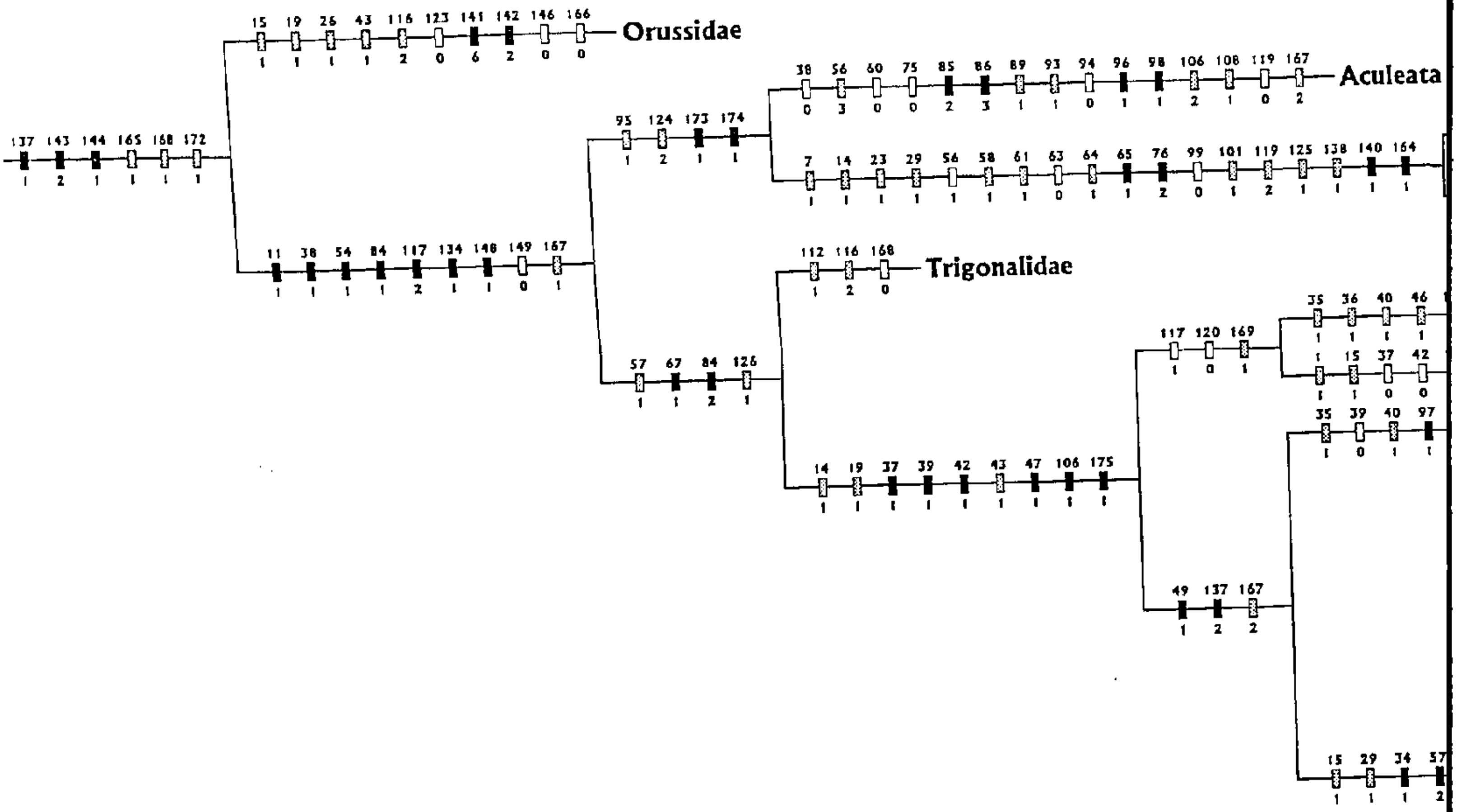
█ Non-homoplastic apomorphy
▒ Homoplastic convergent apomorphy
□ Homoplastic reversal apomorphy

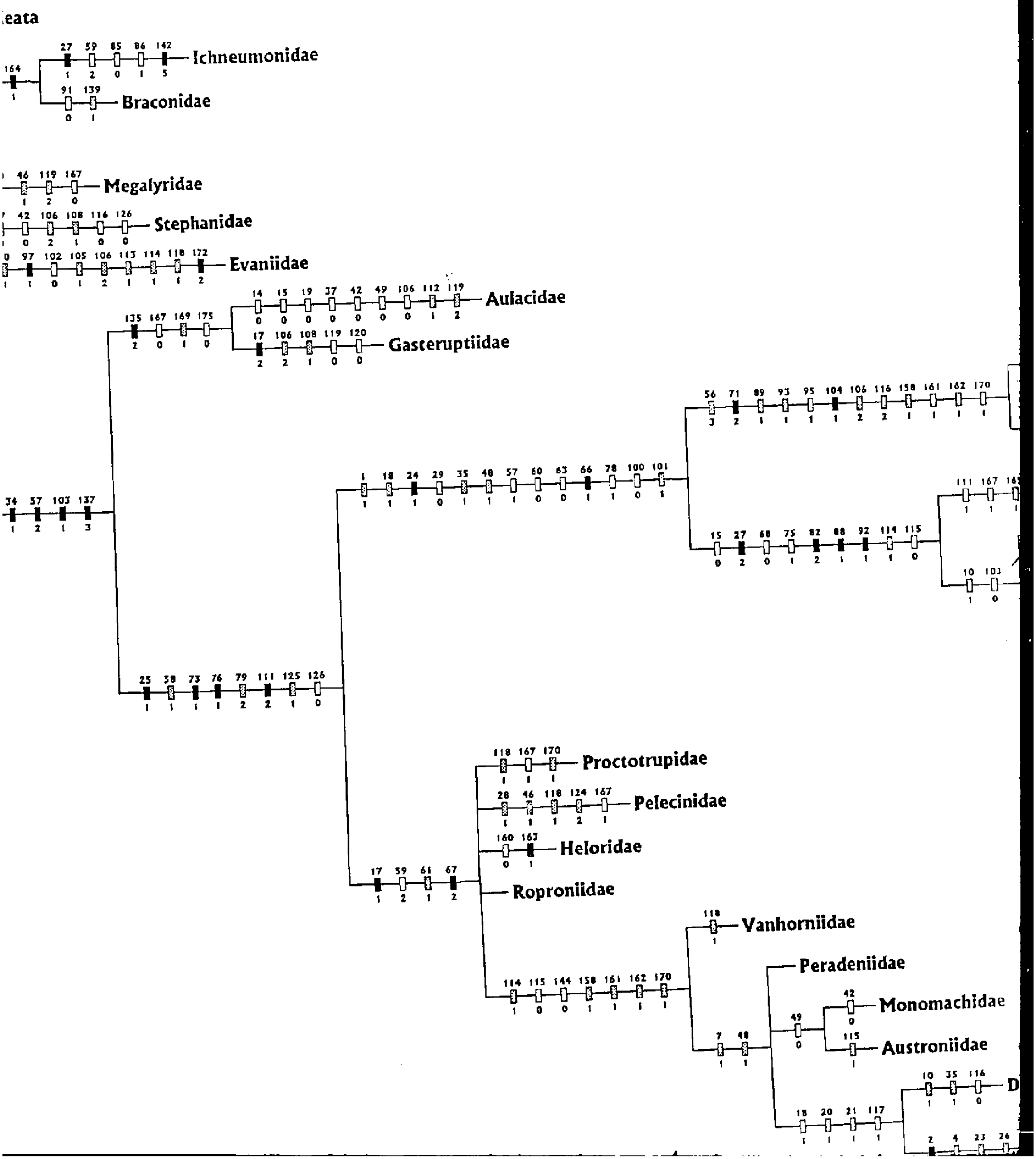

31 51 52 70 77 80 81 123 145 172
0 0 0 0 0 0 0 0 1 0
Xyelidae
32 119 128 165 167
1 2 1 1 1
Megalodontoidea
28 71 127 133
0 0 0 0
30 50 131 141 146 147 150
1 1 1 3 1 1 1
33 59 61 64 70 77 141
1 1 1 1 2 2 4
78 80 81 87 109 172
2 2 2 0 1 0
13 14 31 41
1 1 0 1
22 30 32 11
1 0 1 1
13 22 43 77 79
1 1 1 0 2
60 63 69 71 72
1 1 2 1 2



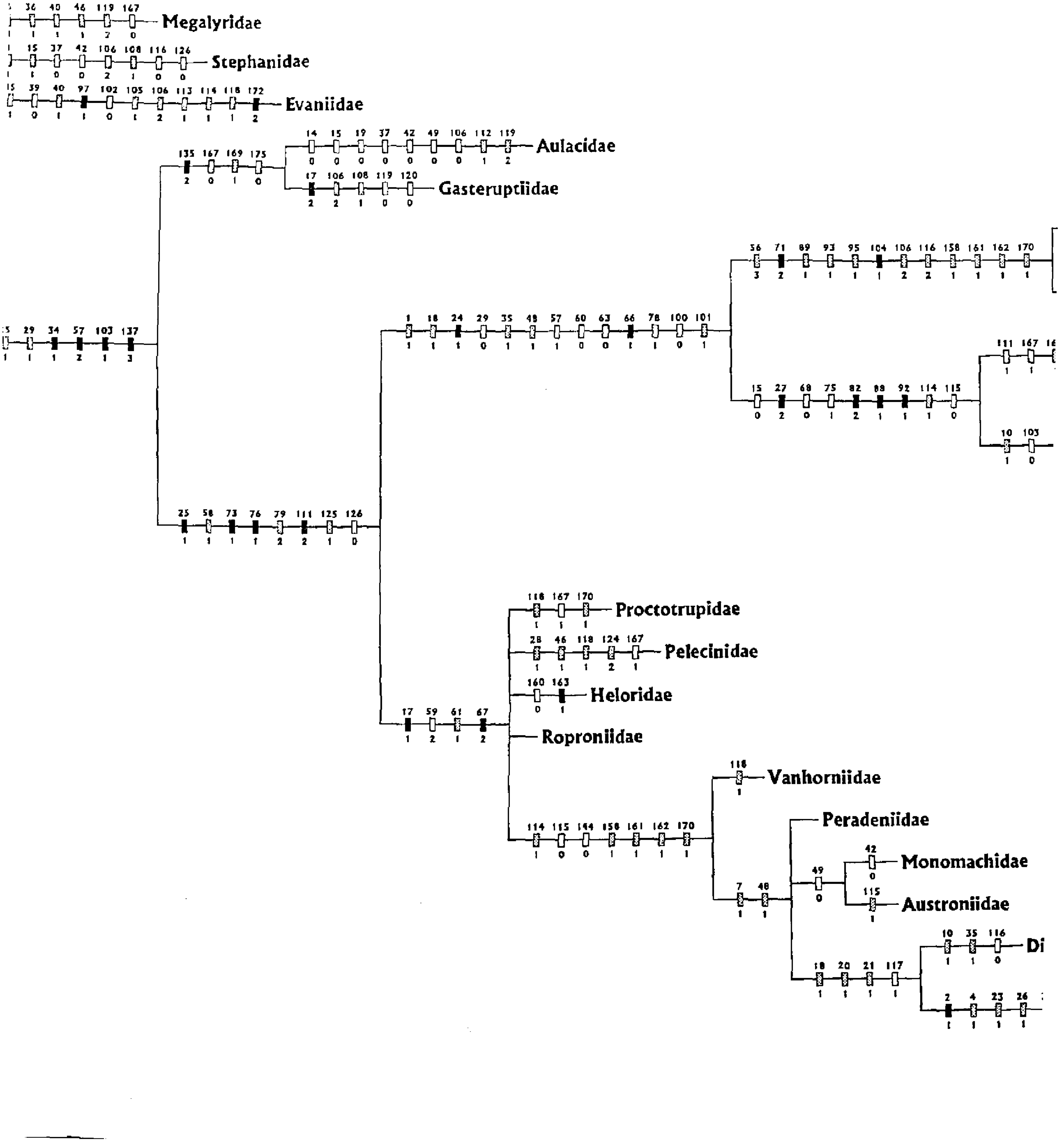
123 145 172
0 1 0
Xyelidae
128 165 167
1 1 1
Megalodontoidea
13 14 31 41 43 44 135 145
1 1 0 1 1 1 1 3
Anaxyelidae
22 30 32 119 121 123 133 136 143
1 0 1 1 1 0 1 1 3
Siricidae
33 59 61 64 70 77 141
1 1 1 1 2 2 4
131 141 146 147 150
1 3 1 1 1
13 22 43 77 79 135 167 168
1 1 1 0 2 1 1 1
Cephidae
78 80 81 87 109 172
2 2 2 0 1 0
90 91 94 102 117 141 146 150
0 0 0 0 3 2 0 0
Tenthredinoidea
60 63 69 71 72 74 83 127 128 131
1 1 2 1 2 1 1 1 1 0
59 68 75 77 85 86 119 122 133 141 142 145 150 153 160
1 2 2 2 1 2 1 1 1 5 1 3 2 1 1


ea
160
1
61 64 89 93 105 127 131 136
1 1 1 1 1 0 1 1
Xiphydriidae
12 13 16 22 33 41 44 53 55 56 59 62 99 100 111 115 116 120 124 129 130 132 137 143 144 165 168 172
1 1 1 1 1 1 1 1 1 2 3 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1
15 19 26 43 116 123 141 142 146 166
1 1 1 1 2 0 6 2 0 0
11 38 54 84 117 134 148 149 167
1 1 1 1 2 1 1 0 1


137 143 144 165 168 172
1 2 1 1 1 1
15 19 26 43 116 123 141 142 146 166
1 1 1 1 2 0 6 2 0 0
Orussidae
11 38 54 84 117 134 148 149 167
1 1 1 1 2 1 1 0 1
95 124 173 174
1 2 1 1
38 56 60 75 85 86 89 93 94 96 98 106 108 119 167
0 3 0 0 2 3 1 1 0 1 1 2 1 0 2
Aculeata
7 14 23 29 56 58 61 63 64 65 76 99 101 119 125 138 140 164
1 1 1 1 1 1 1 0 1 1 2 0 1 2 1 1 1 1
57 67 84 126
1 1 2 1
112 116 168
1 2 0
Trigonalidae
14 19 37 39 42 43 47 106 175
1 1 1 1 1 1 1 1 1
117 120 169
1 0 1
35 36 40 46
1 1 1 1
1 15 37 42
1 1 0 0
35 39 40 97
1 0 1 1
49 137 167
1 2 2
15 29 34 57
1 1 1 2



eata
164 / 1
27 59 85 86 142 / 1 2 0 1 5
Ichneumonidae
91 139 / 0 1
Braconidae
46 119 167 / 1 2 0
Megalyridae
42 106 108 116 126 / 0 2 1 0 0
Stephanidae
97 102 105 106 113 114 118 172 / 1 0 1 2 1 1 1 2
Evaniidae
14 15 19 37 42 49 106 112 119 / 0 0 0 0 0 0 0 1 2
Aulacidae
135 167 169 175 / 2 0 1 0
17 106 109 119 120 / 2 2 1 0 0
Gasteruptiidae
34 57 103 137 / 1 2 1 3
56 71 89 93 95 104 106 116 158 161 162 170 / 3 2 1 1 1 1 2 2 1 1 1 1
1 18 24 29 35 48 57 60 63 66 78 100 101 / 1 1 1 0 1 1 1 0 0 1 1 0 1
111 167 / 1 1
15 27 68 75 82 88 92 114 115 / 0 2 0 1 2 1 1 1 0
10 103 / 1 0
25 58 73 76 79 111 125 126 / 1 1 1 1 2 2 1 0
118 167 170 / 1 1 1
Proctotrupidae
28 46 118 124 167 / 1 1 1 2 1
Pelecinidae
160 163 / 0 1
Heloridae
17 59 61 67 / 1 2 1 2
Roproniidae
118 / 1
Vanhorniidae
114 115 144 158 161 162 170 / 1 0 0 1 1 1 1
Peradeniidae
42 / 0
Monomachidae
49 / 0
115 / 1
Austroniidae
7 48 / 1 1
10 35 116 / 1 1 0
D
18 20 21 117 / 1 1 1 1
2 4 23 26



36 40 46 119 167
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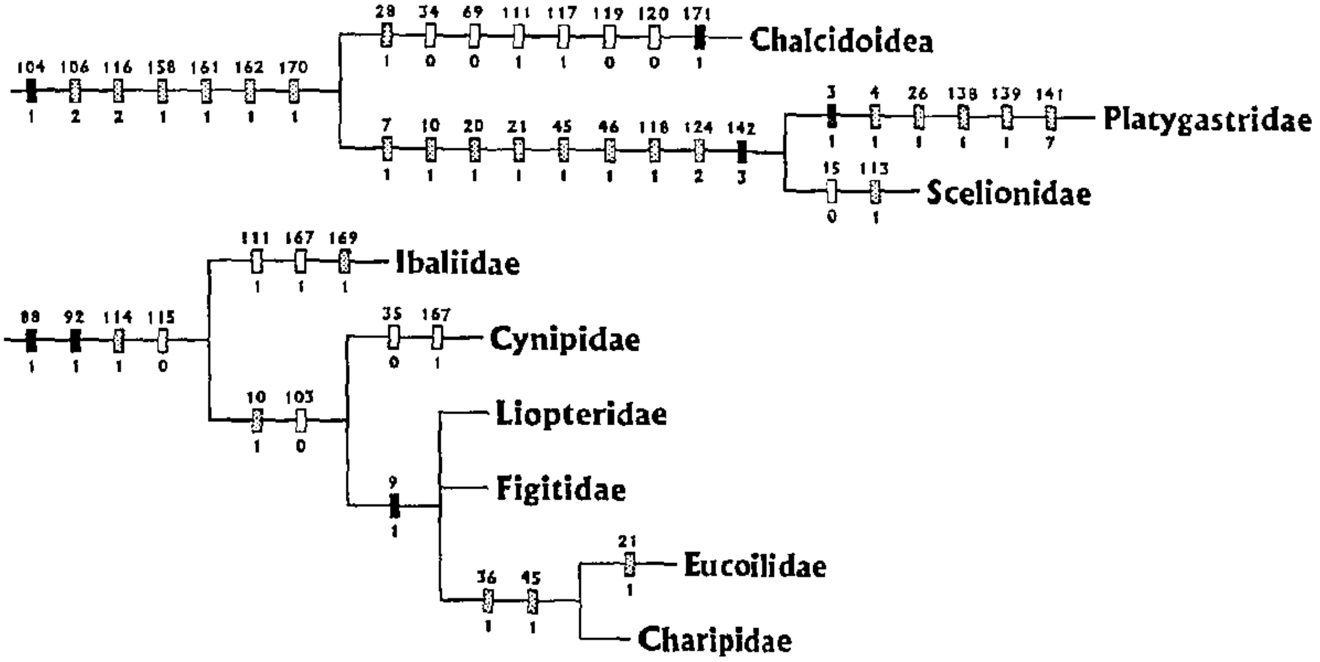
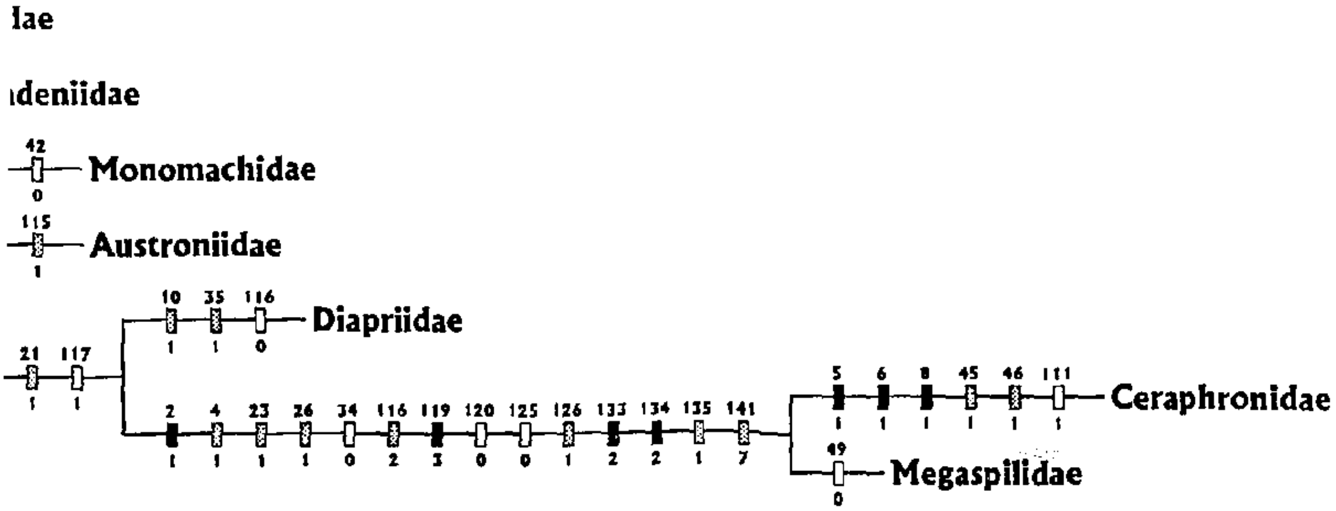
Megalyridae
15 37 42 106 108 116 126
1 0 0 2 1 0 0
Stephanidae
15 39 40 97 102 105 106 113 114 118 172
1 0 1 1 0 1 2 1 1 1 2
Evaniidae
14 15 19 37 42 49 106 112 119
0 0 0 0 0 0 0 1 2
Aulacidae
135 167 169 175
2 0 1 0
17 106 108 119 120
2 2 1 0 0
Gasteruptiidae
56 71 89 93 95 104 106 116 158 161 162 170
3 2 1 1 1 1 2 2 1 1 1 1
15 29 34 57 103 137
1 1 1 2 1 3
1 18 24 29 35 48 57 60 63 66 78 100 101
1 1 1 0 1 1 1 0 0 1 1 0 1
111 167
1 1
15 27 68 75 82 88 92 114 115
0 2 0 1 2 1 1 1 0
10 103
1 0
25 58 73 76 79 111 125 126
1 1 1 1 2 2 1 0
118 167 170
1 1 1
Proctotrupidae
28 46 118 124 167
1 1 1 2 1
Pelecinidae
160 163
0 1
Heloridae
17 59 61 67
1 2 1 2
Roproniidae
118
1
Vanhorniidae
Peradeniidae
42
0
Monomachidae
114 115 144 158 161 162 170
1 0 0 1 1 1 1
49
0
7 48
1 1
115
1
Austroniidae
10 35 116
1 1 0
Di
18 20 21 117
1 1 1 1
2 4 23 26
1 1 1 1


Chalcidoidea
Platygastridae
Scelionidae
Ibaliidae
Cynipidae
Liopteridae
Figitidae
Eucoilidae
Charipidae


lae
ideniidae
Monomachidae
Austroniidae
Diapriidae
Ceraphronidae
Megaspilidae