
Phylogeny of the Hymenoptera: A cladistic reanalysis of Rasnitsyn's (1988) data

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The hypothesis of higher-level relationships among extinct and extant hymenopterans presented by Rasnitsyn in 1988 is widely cited but the evidence has never been presented in the form of a character matrix or analysed cladistically. We review Rasnitsyn's morphological work and derive a character matrix for fossil and recent hymenopterans from it. Parsimony analyses of this matrix under equal weights and implied weights show that there is little support for Rasnitsyn's biphyletic hypothesis, postulating a sister-group relationship between tenthredinoids and macroxyelins. Instead, the data favour the conventional view that Hymenoptera excluding the Xyelidae are monophyletic. Higher-level symphytan relationships are well resolved and, except for the basal branchings, largely agree with the tree presented by Rasnitsyn. There is little convincing support for any major divisions of the Apocrita but the Microhymenoptera and the Ichneumonidea + Aculeata appear as monophyletic groups in some analyses and require only a few extra steps in the others. The Evaniomorpha appear as a paraphyletic grade of basal apocritan lineages and enforcing monophyly of this grouping requires a considerable increase in tree length. The Ceraphronoidea are placed in the Proctotrupomorpha, close to Chalcidoidea and Platygastroidea. This signal is not entirely due to loss characters that may have evolved independently in these taxa in response to a general reduction in size. The analyses suggest that the Proctotrupomorpha may be monophyletic if the ceraphronoids are included. The Chrysidoidea are resolved in good agreement with relationships proposed by Brothers and Carpenter in 1993 but in conflict with the tree presented by Rasnitsyn. Rasnitsyn's data are largely uninformative about relationships among the Aculeata *sensu stricto*. The results are compared with those of other recent analyses of higher-level hymenopteran relationships.

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Introduction

The Hymenoptera are traditionally divided into the Symphyta (sawflies) and Apocrita, the latter being further divided into Parasitica (parasitic wasps) and Aculeata (aculeate wasps). Whereas the Apocrita and Aculeata have generally been accepted as natural groups, it has long been suspected that Symphyta are paraphyletic with respect to the Apocrita, and Parasitica with respect to the Aculeata, although the exact branching order within the Symphyta and Parasitica has been much debated. The origin of apoc-

ritan wasps from phytophagous symphytan ancestors has been a particularly contentious issue. Handlirsch (1907) suggested that apocritans evolved from primitive siricids, while others considered an origin from orussids more likely (Rohwer & Cushman 1917). On comparative morphological evidence, Ross (1936, 1937) concluded that cephids were most closely related to apocritans, while Brues (1921), Wheeler (1928) and Malyshev (1968) speculated on a possible tenthredinid-apocritan connection.

Two pivotal works that introduced Hennigian argumen-

tation to the problem were Königsmann's literature study of the phylogeny of the entire order (Königsmann 1976, 1977, 1978b, 1978a) and Brothers' cladistic analysis of aculeate relationships (Brothers 1975). Königsmann supported the notion of Apocrita and Aculeata as monophyletic groups and also presented characters indicating a sister-group relationship between the Cephidae and the Apocrita, with the remaining sawfly families forming the monophyletic sister group of this assemblage. Within the Parasitica, Königsmann only managed to resolve a few smaller groups. Subsequent work has shown many problems with Königsmann's data (e.g. Gibson 1985, 1986), and his analyses are now mainly of historical interest. The results of Brothers' aculeate study, however, have largely stood the test of time (Brothers & Carpenter 1993).

Almost a decade earlier, Rasnitsyn (1969) had described hymenopteran phylogeny explicitly in terms of nodes and synapomorphies. This was followed by a series of papers (Rasnitsyn 1968, 1969, 1975a, 1975b, 1977, 1980, 1983a, 1983b, 1983c, 1986a, 1986b, 1988, 1990; Alekseev & Rasnitsyn 1981; Dlussky 1987; Rasnitsyn & Kovalev 1988) by Russian palaeontologists on the fossil fauna of hymenopterans and the comparative morphology of extant forms. The work has led to the presentation of several, successively refined hypotheses about the higher-level phylogeny of the Hymenoptera. The most recent proposal (Rasnitsyn 1988) has been widely accepted as the best comprehensive hypothesis of higher-level hymenopteran relationships and has been used frequently for studying character evolution in the Hymenoptera, sometimes with slight modifications (e.g. Whitfield 1992; Heraty *et al.* 1994; Whitfield 1998).

Rasnitsyn's phylogenetic hypothesis is narrative and not based on an explicit cladistic analysis. Although suggested apomorphies were listed for the different groupings (Rasnitsyn 1969:800, 1980, 1988), the evidence was not presented in the form of a character matrix, making it difficult for other workers to assess the quality of the data and include the data in their own analyses.

Recently, relationships among extant higher aculeate and symphytan taxa have been subjected to comprehensive cladistic analyses (Brothers & Carpenter 1993; Vilhelmsen 1997b). To some extent, these studies have superseded the phylogenetic results presented by Rasnitsyn (1988). However, Rasnitsyn's work remains the most comprehensive study of higher-level relationships among all hymenopterans. Furthermore, it is the only detailed morphology-based hypothesis of higher-level parasitic wasp relationships, and it is unique in its incorporation of detailed and extensive fossil evidence. Hence, we believe that there is still considerable interest in making the data on which this hypothesis is based readily available to other

workers in the form of a character matrix, and to critically examine the support for various groupings proposed by Rasnitsyn through parsimony analysis of the matrix. This is what we set out to do in the present paper.

Although the data matrix presented here is based on the characters listed in Rasnitsyn (1988), it includes numerous additions and corrections. We have not considered new character systems presented in the literature since 1988, because that would have required extensive additional study of fossil specimens. The results we describe here represent the first numerical cladistic analysis of the higher-level phylogeny of the entire order Hymenoptera based on morphological evidence.

Methods

Coding principles

The character matrix was primarily derived from the tree in Rasnitsyn (1988) but complemented with numerous corrections and additions from previous and subsequent work, as well as from original observations. We have followed the character interpretations of A. P. Rasnitsyn (APR) but have attempted to list conflicting evidence, alternative interpretations, or major disagreements among current workers when present.

We only include characters that are potentially informative about relationships, i.e. we exclude unique autapomorphies of single terminal taxa. A few characters have been omitted because APR now interprets them differently or considers them to be unreliable indicators of higher-level relationships. These characters are discussed at the end of the character list (see Appendix).

The coding of polymorphic terminal taxa is a contentious issue. Many workers routinely code the terminals as being polymorphic for all the states occurring in representatives of the taxon. Such polymorphism coding is inefficient in that it will discard a considerable amount of character data informative about higher relationships (Yeates 1995). However, most polymorphisms are due to exceptional states occurring only in a few apotypic members of the taxon, and the most likely ground-plan state can be correctly inferred in many of these cases even without detailed knowledge of the phylogeny of the taxon. Therefore, we coded polymorphic terminal taxa for the likely ground-plan state whenever this could be determined with some degree of confidence. If the ground-plan state was considered by us to be uncertain, we coded the taxon as being polymorphic for all the states occurring in the taxon. Difficult cases are discussed in the character list (Appendix).

Several characteristics of fossil taxa listed by Rasnitsyn (1988) were inferred from the states of extant descendants rather than having been observed directly in the fossils themselves. The matrix presented here (Table 1; Appendix)

Table 1 Observed character states. Symbols: 0–9, A, and B = character states; p = 0/1 (uncertainty); q = 1/2; r = 0 & 1 (polymorphism); s = 0 & 1 & 2; t = 1 & 2; u = 1 & 2 & 3; v = 2 & 3 & 4; w = 7 & A; x = 0 & 2; ? = state unknown; – = state inapplicable. The following multistate characters were treated as ordered: 7, 13, 14, 17, 18, 21, 30, 36, 40, 47, 49, 53, 59, 61, 72, 76, 82, 85, 88, 94, 100, 111, 114, 120, 123, 125, 127, 128, 130, 133, 145, 152 and 155.

Taxon	1 1234567890	111111112 1234567890	222222223 1234567890	333333334 1234567890	444444445 1234567890	555555556 1234567890
Outgroup	0000-0000	000000000	000000000	000000000	0000-0000	00000000-0
Macroxyelinae	0000-0000	000000000	000000000	000000000	0000-0000	00000000-0
Xyelinae	0000-0000	000000000	001000000	000000000	0000-0000	00000000-0
Xyelotomidae	000?0-???	?000010000	00?0?000??	?0?1p00???	??????0??	????0?0-0
Blasticotomidae	0000-????	?000110000	000000010	0000000012	-----1010	01100000-0
Electrotomidae	??????????	???????????	???????????	???????????	???????????	???????????
Argidae	00000-0000	0000110000	0000000110	0000000012	-----2020	01200000-0
Pterygophoridae	00000-0000	0002--8800	0000000110	0000000010	0000-02020	01200000-0
Tenthredinidae	00000-0000	0002--8800	0000000110	0000000010	0000-021-0	01100000-0
Cimbicidae	00000-0000	0002--8800	2000000110	0000000012	-----21-0	01100000-0
Xyelydidae	00????????	?000000000	000r?000?0	?1?1p00???	??????0000	????0?0-0
Pamphilidae	0001120001	0001000000	0001000000	0100000012	-----0000	00000000-0
Praesiricidae	00????????	?000000000	00?1?000?0	?1?1p00???	??????0000	????0?0-0
Megalodontidae	0001100001	0002--0000	0001000000	0100000021	0000-01020	00000000-0
Sepulcidae	000???????	?000000000	00?0?000?0	?1?1p00???	??????0x0	????0?0-0
Cephiidae	0000100011	0002--0000	0000000000	0100000010	0000-00010	00011000-0
Gigasiricidae	000???????	?000000?0	00?0?000??	?1?1p00???	???????????	????0?0-0
Anaxyelodae	001011????	?000000000	0010?00000	01?0000010	0000-00010	00010000-0
Siricidae	0000110001	0002--0000	0000000000	0100001010	1000-00010	00010000-0
Xiphydriidae	0000110001	0002--0000	0000000100	0100012010	1000-00010	00010000-0
Paroryssidae	00????????	?002--0000	00???000?1	?1????????	???????????	????0?0-0
Orussidae	0100111111	0002--6510	0010000001	0100122020	1000-001-0	0001000121
Karatavidae	00????????	?002--0000	00?0?000?1	????p22???	???????????	????1?0?01
Ephialtidae	000??1????	?002--0000	00?0?00001	???p22???	??????21-0	0??100121
Megalyridae	001011????	?002--3300	0010?00010	?10102202?	?????021-1	0??100121
Stephanidae	0110112111	0002--0000	0010000001	0101022020	1000-021-1	0001100121
Trigonalyidae	0010112111	0002--0000	0000000111	0101222021	11101021-1	0001101121
Maimetshidae	001???????	?002--?1?0	0000?001??	?1??202???	??????21-?	0??1?1?131
Stigmaphronidae	000???????	?112--6600	0000?001??	?????22???	???????????	????1????1
Megaspilidae	0010112111	0122--6600	0000000110	01101022020	01100021-1	0001101131
Ceraphronidae	001011????	0122--6710	0000000110	11?1002021	01100021-1	0001101131
Praeaulacidae	00????????	?002--0000	00?0?000??	???p22???	?0??0?0???	????1?1121
Gasteruptionidae	0010112111	0002--4310	0010000011	0100222022	-----21-1	0001101121
Cretevaniidae	101???????	?0?2--5500	0000?1011?	?1?1222???	???????????	????1?11?1
Evaniidae	1010112111	0002--4400	0010010111	0101222021	11101021-1	0001101131
Mesoserphidae	00????????	?002--0000	00?0?000?1	???222???	???????????	0??1?????1
Peleciniidae	0010122111	0002--3300	0010000110	0101222021	01101121-0	0001101131
Proctotrupidae	0010122111	0002--4400	0000000110	0101222021	01101121-0	0001101121
Roproniidae	0010122111	0002--0000	0000000001	0101222020	1100-021-0	0001101121
Heloridae	0010122111	0002--0000	0000000010	0100222021	11101021-0	0001101131
Austroniidae	001???????	?002--3210	0000?00000	?1??222???	1100-?71-0	0??1?1131
Monomachidae	0010122111	0012--3210	0000000001	0101222020	1100-121-0	0001101121
Diapriidae	0010122111	0012--3210	0100000110	0101222021	11101021-0	0001101131
Archaeocynipidae	00????????	?002--???0	0?0?00011?	???122???	???????????	????1????1
Figitidae	0010132111	0002--3410	0110000110	0101122021	11101021-0	0001101131
Cynipidae	0010132111	0002--3410	0110000110	0101122021	11101021-0	0001101131
Ibalidae	0010132111	0002--3410	0110000110	0101122021	11101021-0	0001101131
Jurapriidae	00????????	?112--?2?0	1?0?000??	?1??222???	???????????	????1?????
Chalcidoidea	0010122111	0112--4400	1010000000	0101222120	0000-021-0	0001101121
Scelionidae	0000132111	0122--3301	2200000110	0101222021	01101121-0	0001101131
Platygastridae	0000122111	0122--7701	2200000110	0101222021	01101121-0	0001101131
Serphitidae	000013????	?122--8711	2?0?00011?	?1?1222???	???????????	0??1?????1
Mymaromatidae	0011132121	0112--4400	1000?0001?	01?120212?	1?????21-0	0??10?131

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Table 1 — *continued.*

	1	111111112	222222223	333333334	444444445	555555556
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Praeichneumonidae	00????????	?00???????	???0?0011?	???1p02???	???????????	????1????1
Ichneumonidae	0010112111	0002--0000	0010000111	0100222021	10101021-0	0001101121
Braconidae	0010112111	0002--0000	0010000111	0100222021	10101021-0	000110r131
Bethylonymidae	00????????	?002--4400	0????000?1	?1??p?2???	???????????	?????10???
Plumariidae	0000112111	?002--4400	0000001001	0111222020	1000-121-0	00011101t1
Scolecbythidae	0000112111	1002--4400	0010000001	0110222020	1000-021-0	0001100111
Dryinidae	0000112111	1102--7700	0000000001	0110222020	1000-121-0	0001101121
Sclerogibbidae	0000112111	1002--ss00	0010001001	0111222020	1000-121-0	0001101121
Embolemyidae	0010112111	1022--7700	0000000001	0111222020	10100121-0	1001121121
Bethylidae	0000112111	1002--4400	0000000001	0110222020	1000-121-0	1001121121
Chrysididae	0000112111	1102--4400	0000000001	0110222020	1000-021-0	1001120131
Sphecidae	0000112111	0002--4510	0010000002	0100022021	1001-?21-0	0001100101
Apidae	0010112111	0002--4510	0010000002	0100222021	1001-?21-0	0001130101
Pompilidae	0000112111	0002--4510	0010000002	0100222021	1001-021-0	0001100111
Rhopalosomatidae	0011112111	0002--4510	0010000002	0100222020	1000-021-0	2001100131
Sapygidae	0000112111	0002--4510	0010100001	0100222021	1001-021-0	0001130131
Tiphiidae	0000112111	0002--4510	0010100001	0100222020	1000-021-0	2001130131
Mutillidae	0000112111	0002--4510	0010101001	0100222021	1001-021-0	0001130131
Scoliidae	0000112111	0002--4510	0010100111	0101222021	1001-021-0	2001130131
Bradyobaenidae	0000112111	0002--4510	0010101001	0100222020	1000-021-0	0001130131
Sierolomorphidae	0001112111	1002--4510	0000100001	0100222020	1000-021-0	0001100131
Falsiformicidae	000???????	?002--4510	00????00?1	?1?1222???	1001-0?1-0	0????10?131
Formicidae	0000112111	0002--4510	0000100001	0100222021	1001-021-0	0001100131
Vespidae	0000112111	0002--4510	0010100111	0100222021	10101021-0	0001100131
				1	1111111111	1111111111
Taxon	666666667	777777778	888888889	999999990	000000001	111111112
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Outgroup	0-00000000	0000000000	0000000000	0000000000	0000000000	1000-00000
Macroxyelinae	0-00000000	0000000000	0000000000	0000000000	0000000000	1000-00?00
Xyelinae	0-00000000	0000000000	0000000000	0000000000	0000000000	1000-00?00
Xyelotomidae	0-????????	?000001-00	0001000000	100000?700	?000000000	1000-??700
Blasticotomidae	0-01001000	0001001-01	1001000000	1000000000	1000000000	1000-00?00
Electrotomidae	??????????	??????????	??????????	??????????	??????????	??????????
Argidae	0-01000000	0001001-00	101-000000	1000000000	1000000000	1000-00?00
Pterygophoridae	0-01000000	0001001-00	101-000000	1000000000	1000000100	1000-00?00
Tenthredinidae	0-01001000	0001001-00	1001000000	1000000000	1000000000	1000-00?00
Cimbicidae	0-01001000	0001001-01	1001000000	1000000000	0000000000	1000-00?00
Xyelydidae	0-?????0??	?000000000	1000000000	000000?000	1000000000	1000-??700
Pamphiliidae	0-00000000	0000001-00	1000000000	0000000000	0000000000	1000-00?00
Praesiricidae	0-?????0??	?000000000	1000000000	000000?700	1000000000	1000-??700
Megalodontidae	0-00000000	0000000100	1000000100	0000000000	1000000000	1000-00?00
Sepulcidae	0-?????0?0	?001100000	1000000000	000000?700	1000000000	1000-??700
Cephidae	1-00000010	0001101-00	1100000100	1000000000	1000000000	1000-00?00
Gigasiricidae	0-?????0??	?000010000	1000000000	000000?000	0000000000	1000-??700
Anaxyelidae	0-00001010	0000010000	1000200000	0000000000	01-00000000	1000-00?00
Siricidae	0-00000010	0000010100	1000000000	0000000000	1000000000	1000-00?00
Xiphydriidae	0-00001010	0001010000	1000000100	0000000000	1000000000	1000-00?00
Paroryssidae	0-????????	?001110000	1200010100	010100?710	?1-100?1??	1000-??70?
Orussidae	0-00001010	0001110000	1200010100	0101000010	1101000100	1000-00?00
Karatavitidae	1-????10??	?001110000	1100000100	000000?000	0000000000	1000-??700
Ephialtidae	1-0??210?0	?001110100	1200000100	0000001?00	1000000100	1000-?0?00
Megalyridae	2000001010	0001110100	1200000100	0002001r00	1001010110	1000-00?00
Stephanidae	2000001010	0001110100	1200210100	0102001110	10110-0111	10100-0-00
Trigonalyidae	2001001010	0001110100	1200000100	0002001000	1011000110	1000-00?01

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Table 1 — *continued.*

Taxon	666666667 1234567890	777777778 1234567890	888888889 1234567890	1 999999999 1234567890	111111111 000000001 1234567890	111111111 111111112 1234567890
Maimetshidae	200???101?	?001110100	1200010100	0102001110	10110??210	10101-0-00
Stigmaphronidae	20????10r?	?001130111	1200211-1-	-11200???	?1-11--1-1	10101-?-1?
Megaspilidae	20001-1001	0001130111	1200211-1-	-112001111	11-11--1-1	10101-0-11
Ceraphronidae	20001-1001	0101130111	120-211-1-	-112001111	11-11--1-1	10101-0-11
Praeaulacidae	21????10??	?001110100	1200000100	000200??10	?00100?100	1000-???
Gasteruptionidae	2101001010	0001110100	1200000100	0002001111	11110-01-1	1000-00?00
Cretevaniidae	21????101?	?001111-00	1200200100	0102001111	11-11--1-1	00100-?-0-
Evaniidae	2101011010	0001111-00	1200200100	0102000011	11-11--1-1	00100-0-0-
Mesoserphidae	20????10??	?001110100	1200210200	010200??10	10110-?111	1000-???
Peleciniidae	2001011011	0001110100	1200110200	0102001011	10111-01-1	2000-10?00
Proctotrupidae	2001011011	0001110100	1200110200	0102001111	10111-01-1	3000--0-00
Roproniidae	2001001011	0001110100	1200210200	0102001111	10110-01-0	10100-0-0?
Heloridae	2001001011	0001110100	1200210200	0102001111	10111-01-1	10100-0-00
Austroniidae	20????1011	0001110110	1200210201	-102001111	10111-?1-1	10100-0-0?
Monomachidae	2001001011	0001110110	1200210200	-102011111	1011010111	20100-0-01
Diapriidae	200r001011	0101110111	120021021-	-112011111	10111-11-1	10100-0-00
Archaeocynipidae	20????10??	?111110101	1200110201	011201???	?011?211-1	10101-0-0?
Figitidae	2001001011	0211110111	120-010201	-112011111	10111-11-1	00101-0-0-
Cynipidae	2001001011	0211110101	120-01021-	-112011111	10111-11-1	00101-0-0-
Ibaliidae	2001001011	0211110101	120-01021-	-112011111	10111-11-1	00101-0-0-
Jurapriidae	20????10??	?001110110	120021010?	-1120?????	10110-?1?	10???????
Chalcidoidea	20001-1011	0211110111	120-211-1-	-112011111	11111--1-1	1010r-0-00
Scelionidae	2001011011	0111110111	1200210200	-102011111	10111-01-1	1000-10?0-
Platygastridae	20011?1011	0211110111	121-211-1-	-112011111	11111-01-1	1000-10?1-
Serphitidae	20????1011	?001110111	1200210200	-10201???	10111-01-1	10100-0-00
Mymarommatidae	20?01-1011	02111-0111	120-211-1-	-1120--1--	-----	10100-0-00
Praeichneumonidae	20????10??	?001120100	1200000100	0002001000	1001010100	1000-???
Ichneumonidae	2011001011	0001130100	1200200100	0002001000	1001010100	1100-10?00
Braconidae	2011001011	0001130100	1200200100	0102001000	1011010100	1100-10-00
Bethylonmyidae	20????10??	?001110100	1200000100	000200???	?001000100	1?00-?0?0?
Plumariidae	2011001011	0001110100	1200200100	0102001100	1011010100	1000-0000?
Scolecbythidae	201???1010	0001110101	1200200100	0102011112	11-11--1-1	1000-00001
Dryinidae	201???1011	0001110100	1200210100	0102111112	11-11--1-1	1000-01001
Sclerogibbidae	201???1011	0101110101	1200200100	0102011112	11-11--1-1	1000-01001
Embolemyidae	201???1011	0001110100	1200200100	0102111112	11-11-01-1	1000-10100
Bethylidae	2011001011	0001110100	1200200100	0102011112	11-11-01-1	1000-10101
Chrysididae	2011001011	0001110100	1200210100	0102011112	11-11-01-0	1000-10-0-
Sphécidae	2011001010	1001110100	1200000100	0002000000	1001000100	1000-00?01
Apidae	2011001010	0001110100	1200000100	0002000000	1001000100	1000-00001
Pompilidae	201???1011	1001110100	1200000100	0002000000	1001000100	1000-00?01
Rhopalosomatidae	201???1011	1001130100	1200010100	0102010000	10110-0100	1000-10?01
Sapygidae	2011001010	0001110100	1200000100	0002000000	1001000100	1000-10?01
Tiphidae	2011001110	0001110100	1200000100	0002000000	1001000100	1000-10?02
Mutillidae	2011001011	0001110100	1200000100	0002000000	1001000100	1000-10?03
Scoliidae	2011001110	0001110100	1200000100	0002000000	1001000100	1000-10?02
Bradynobaenidae	201???1011	0001110100	1200000100	0?02010000	1011010100	1000-10?02
Sierolomorphidae	2011001011	0001110100	1200010100	0102011000	1001000100	1000-10?01
Falsiformicidae	20????1011	0001110100	1200000100	0002010000	1001000100	1001-10?0?
Formicidae	201r001011	0001110100	1200010100	0102000000	1001000100	1002-10?01
Vespididae	2011001010	1001110100	1200000100	0002000000	1001000100	1000-10001

—*continued*

Table 1 — *continued.*

Taxon	1111111111 222222223 1234567890	1111111111 333333334 1234567890	1111111111 444444445 1234567890	1111111111 555555556 1234567890	1111111111 666666666 123456789
Outgroup	000002000	000000010	00---0000	000000000	000000000
Macroxyelinae	0?00001000	00000000t	0r---0000	000000000	000000000
Xyelinae	0?00002000	0010000020	00---0001	0001000000	000000000
Xyelotomidae	0?000010??	0?0?0?????	???????????	???????????	???????????
Blasticotomidae	0?00001000	0000001-20	00---0000	000001-000	100000000
Electrotomidae	???????????	???????????	00---?000	111201-101	--0?0????
Argidae	0?00001000	0020001-00	01---0000	1211000100	000001000
Pterygophoridae	0?00001000	0020001-00	01---0000	1211000100	010001000
Tenthredinidae	0001001000	0020001-00	0r---0000	1010001001	--0000011
Cimbicidae	0001001000	0020001-00	01---0000	1211001001	--0000011
Xyelydidae	0?000000??	0?0?0?0???	???????????	???????????	???????????
Pamphiliidae	0000000000	0000000110	0r---0001	100111--10	110010100
Praesiricidae	0?000000??	0?00?0????	???????????	???????????	???????????
Megalodontidae	0000000000	0000000110	01---0001	100211--10	110010100
Sepulcidae	0?000020??	0?0?0?????	???????????	???????????	???????????
Cephalidae	0000002000	0000001-20	01---0001	000011--10	111010100
Gigasiricidae	0?000030??	0?00?0????	???????????	???????????	???????????
Anaxyelidae	0?00003000	0000000120	00---011-	-10021--11	--1110100
Siricidae	0000003000	0000000120	0r---011-	-20021--11	--1110100
Xiphyriidae	0?00003000	0000000120	01---011-	-10121--11	--1110100
Paroryssidae	0?0?0030??	0?0?0?????	???????????	???????????	???????????
Orussidae	0000213000	0000001-20	1-0r00011-	-21131--11	--0110100
Karavitidae	0?0?0030??	0?00?0????	???????????	???????????	???????????
Ephialtidae	0?0000300?	0?00?0????	???????????	???????????	???????????
Megalyridae	0?00103000	0?000?1-20	1-?000011-	-2?131--11	--0110100
Stephanidae	0?00103000	0000001-20	1-0000011-	-21131--11	--0110100
Trigonalyidae	0?00313000	0000001-40	1-1u00011-	-21031--11	--0?10100
Maimetshidae	0?0?0030??	0?????????	???????????	???????????	???????????
Stigmaphronidae	0?0?1130??	??0?0?????	???????????	???????????	???????????
Megaspilidae	0?00313000	0000001-40	1-0?r0011-	-21031--11	--0110100
Ceraphronidae	0?10313000	0000001-40	1-1?r0011-	-21731--11	--0110100
Praeaulacidae	0?001030??	0?00?0????	???????????	???????????	???????????
Gasteruptiidae	0?00103000	0000001-40	1-0r00011-	-21031--11	--0110100
Cretevaniidae	??0?1030??	0?????????	???????????	???????????	???????????
Evanidae	0?00103000	0000001-40	1-?711011-	-21031--11	--0110100
Mesoserphidae	0?0?1030??	???????????	???????????	???????????	???????????
Pelecniidae	0?00113000	0000011-30	1-1000011-	-21731--11	--0110100
Proctotrupidae	0000103000	0000011-30	1-1000011-	-21031--11	--0110100
Roproniidae	0?00103000	0000001-20	1-1100011-	-21731--11	--0110100
Heloridae	0000113000	0000011-40	1-1500011-	-21031--11	--0110100
Austroniidae	0?001030??	0?????????	???????????	???????????	???????????
Monomachidae	0?00113000	0000011-30	1-1300011-	-21731--11	--0110100
Diapriidae	0?00113000	0000011-30	1-1300011-	-21031--11	--0110100
Archaeocynipidae	0?0?1030??	0?????????	???????????	???????????	???????????
Figitidae	0000103000	0000011-v0	1-1300011-	-21031--11	--0110100
Cynipidae	0000103000	0000011-20	01---011-	-21731--11	--0110100
Ibaliidae	0000103000	0000001-20	1-1r00011-	-21031--11	--0110100
Jurapriidae	0?0?003???	???????????	???????????	???????????	???????????
Chalcidoidea	0000103000	0001111-20	1-r?0r011-	-21031--11	--0110100
Scelionidae	0100313000	0001011-40	1-1?01011-	-21031--11	--0110100
Platygastridae	0?20313000	0001011-40	1-1300011-	-21031--11	--0110100
Serphitidae	0?00q130??	???????????	???????????	???????????	???????????
Mymaromatidae	0?00113000	0001111-??	???????????	???????????	???????????
Praeichneumonidae	0?0?0030??	0?????????	???????????	???????????	???????????
Ichneumonidae	0000003001	0000001-20	1-0000011-	-21131--11	--0010100

—*continued*

Table 1 — *continued.*

Taxon	1111111111	1111111111	1111111111	1111111111	1111111111
	2222222223	3333333334	4444444445	5555555556	6666666666
	1234567890	1234567890	1234567890	1234567890	1234567890
Braconidae	0000003001	0000001-20	1-0000011-	-21131--11	--0010100
Bethylonmidae	070700307?	077777777?	777777777?	777777777?	777777777?
Plumariidae	0710013200	1700001-??	777777777?	777777777?	777777777?
Scolecbythidae	0710013202	1100001-30	1-0000011-	-21031--11	--001010?
Dryinidae	0710013202	1200001-51	1-0810011-	-21031--11	--0010100
Sclerogibbidae	0710013200	1200001-50	1-0810011-	-21031--11	--0010100
Emboleidae	0710013202	1200001-51	1-0810011-	-21031--11	--0010100
Bethylidae	0110013212	1100001-30	1-0000011-	-21031--11	--0010100
Chrysididae	0110013212	1100001-30	1-0t00011-	-21031--11	--0010100
Sphecidae	1220013102	1100001-30	1-0w10011-	-21031--11	--0010100
Apidae	1120013102	1100001-30	01-----11-	-21031--11	--0010100
Pompilidae	1220013100	1100001-30	1-0920011-	-21131--11	--0010100
Rhopalosomatidae	1220013102	1100001-51	1-0A10011-	-21031--11	--0010100
Sapygidae	1220013100	1100001-30	1-0200011-	-21031--11	--0010100
Tiphidae	1220013102	1100001-30	1-0000011-	-21131--11	--0010100
Mutillidae	1220013102	1100001-30	1-0200011-	-21131--11	--0010100
Scolidae	1220013102	1100001-30	1-0000011-	-21031--11	--0010100
Bradynobaenidae	1220013102	1100001-30	1-0920011-	-21031--11	--0010100
Sierolomorphidae	1220013102	1100001-??	?-7777777?	777777777?	777777777?
Falsiformicidae	12270131??	??20??777?	?-??77777?	777777777?	777777777?
Formicidae	1120013102	1100001-30	1-0777111-	-21031--11	--0010100
Vespidae	1220013100	1100001-30	1-0000111-	-21031--11	--0010100

only contains entries based on original observations of actual specimens and/or published data. Some of the data have not been published previously. For instance, female character states of the Gigasiricidae are presented here for the first time, coded from an undescribed female specimen (Rasnitsyn, unpublished data).

A hypothetical ancestor coded for the likely ground-plan features of the Hymenoptera, as inferred from comparison with other insect orders (Rasnitsyn 1988), was used as the outgroup. Multistate characters were ordered if the states could reasonably be arranged in a linear sequence based on morphological evidence alone, without reference to phylogenetic relationships. The hypothesized transformation series are given in the character list (Appendix).

The character matrix is available in NEXUS format on the World Wide Web via the first author's home page (http://www.systbot.uu.se/staff/f_ronquist.html).

Terminology

Terminology of skeletal structures mainly follows Ronquist & Nordlander (1989), who provided a comprehensive and well-argued set of terms for hymenopteran skeletal morphology. Additional terms were taken from Richards (1977), Gibson (1985), Mason (1986), Gauld & Bolton (1988) and Goulet & Huber (1993). For ichneumonoid wing venation we follow the interpretation of Sharkey & Wahl (1992).

Terminal taxa

The terminal taxa in the present analysis are the same as those used by Rasnitsyn (1988) with the exception that the Baissodidae are included in the Sphecidae according to APR's current interpretation of this fossil group. In most cases, the terminals correspond to families. The classification used here and by Rasnitsyn (1988) differs slightly from that of other recent authors (e.g. Gauld & Bolton 1988; Goulet & Huber 1993; Hanson & Gauld 1995) in recognizing fewer families. Thus, Diprionidae are included in the Tenthredinidae, Aulacidae in the Gasteruptiidae, Vanhorniidae in the Proctotrupidae, Peradeniidae in the Heloridae, Liopteridae in the Ibalidae, and Heterogynaidae in the Sphecidae. These groupings are considered by other workers to be monophyletic or, in a few cases, paraphyletic grades excluding only one other lineage (Townes 1950; Townes & Townes 1981; Gibson 1985; Naumann & Masner 1985; Brothers & Carpenter 1993; Ronquist 1995a, 1995b, 1999; Dowton *et al.* 1997). The Formicidae and Vespidae were treated as superfamilies by Rasnitsyn (1988) but are lowered here to family status according to the usage in most other recent works.

Kozlov (1994) recently described a new family for *Renyxia incredibilis*, which he considered to be close to helorids based on the presence of an anellus in the flagellum. However, this is a weak character. An anellus occurs in several other groups of parasitic wasps but it is absent in

Peradenia, apparently the sister group of all other helorids (Naumann & Masner 1985). Thus, presence of the anellus cannot be taken as evidence of close relationship between helorids and *Renyxa* unless it can be shown that the anellus was secondarily lost in *Peradenia* and that the anellus does not represent a retained plesiomorphy. *Renyxa* is included here in the Roproniidae based on close similarity with fossil roproniids. Rasnitsyn's analysis did not include the Austrocynipidae, and this family was also omitted from the present analysis. The Austrocynipidae form the most basal lineage of cynipoid wasps according to the analysis of cynipoid relationships by Ronquist (1995b, 1999).

There are several well-recognized problems with paraphyletic taxa at the family level in the Hymenoptera. For instance, it is uncertain whether the two subfamilies of Xyelidae form a monophyletic unit and they were treated here as separate terminal taxa following Rasnitsyn (1988). The Sphecidae are likely to be paraphyletic relative to the Apidae, and the Scelionidae relative to the Platygastriidae, but these families are retained here as single terminal taxa. Similarly, some extinct families may also be paraphyletic but were left as single units. Such paraphyletic terminal taxa are problematic but were used here for practical reasons. First, we wanted to facilitate comparison of our results with the intuitive analysis of the data by Rasnitsyn (1988). Second, because the paraphyletic groups are likely to represent grades that exclude only one other lineage from a monophyletic taxon and because the grades were coded here for the plesiomorphic state in the characters that varied within the taxon, lumping should not affect the phylogenetic results. Third, it is difficult to divide the paraphyletic lineages into a small number of monophyletic subgroups, particularly for the fossil taxa. Finally, splitting the terminals into monophyletic subgroups would have necessitated renewed study of a substantial portion of the fossil specimens.

Phylogenetic analyses

Original analyses. Analyses of the original data matrix were performed with and without fossil taxa to examine the effect of the large proportion of missing data for many of the fossil groups. Note that the analyses restricted to extant forms did include some fossil information in determining likely ground-plan states of extant terminal taxa (cf. Appendix). All characters were treated as reversible but some characters were ordered (treated as additive) as indicated in the character list (Appendix; see also Table 1). The data were analysed using standard parsimony with all characters weighted equally and the robustness of clades was examined using bootstrapping.

Alternative assumptions. To examine the influence of certain character types on the phylogenetic results, and

explore the robustness of the results to alternative assumptions about character evolution, we identified three character sets that were differentially weighted or treated as irreversible in some analyses: 1) Characters that could reasonably be regarded as irreversible. These characters primarily involve the fusion of independent sclerites, and are labelled fusion characters in the character list (chars. 43, 44, 47, 113, 121, 124, 134, 135); 2) Loss or reduction characters, labelled loss characters in the character list (chars. 25, 39, 40, 48, 55, 64, 65, 67, 69, 72–77, 79, 80, 82, 83, 85–87, 89, 92–94, 97, 99–102, 104, 105, 108, 110, 121–125, 136–137, 148, 149, 152–156, 159, 160, 164); 3) Wing venation characters (chars. 72–95, 99–110).

Four analyses were performed: 1) wing venational characters excluded (nonvenational analysis); 2) fusion characters treated as irreversible (irreversible analysis); 3) fusion characters treated as irreversible and loss characters given one fourth the weight of the other characters (weighted analysis); and 4) loss characters excluded (no-loss analysis). The first of these analyses was designed to examine the effect of the large number of wing venational features in the data matrix; the other three were used to explore the effect of incorporating common assumptions about character evolution.

Constrained searches. To measure the degree of conflict between the data and some suggested higher groupings of hymenopterans that were not present in the shortest trees, constrained searches were performed in which the number of extra steps required to maintain the monophyly of the groupings was recorded.

Analysis under implied weights. The original data were analysed with and without fossil taxa under implied weights (Goloboff 1993) to examine the effect of weighting good characters, identified by their congruence with other characters, more heavily than poor characters. Support for clades under implied weights was examined by bootstrapping. For these searches, the *k*-value (determining the shape of the weighting function) was set to 2.

Search strategies. PAUP version 4.0d65 (Swofford 1999) was used for all analyses. The hypothetical ancestor was treated as an additional terminal taxon and was used to root the trees. Branches were collapsed when maximum length was zero. When bootstrapping, replicate matrices of the same size as the original matrix were created.

For the original data, 100 (all taxa) or 1000 (extant taxa only) random addition sequences were run, keeping one tree in each step, followed by tree-bisection-reconnection swapping. Bootstrap proportions for the all-taxon tree were calculated in 1000 replications of a simple heuristic search (10 random addition sequences, keeping 1000 trees at each step and retaining the best trees in each replication without performing branch swapping). Bootstrap propor-

tions for the pruned tree containing only extant taxa were calculated in 500 replications of a more extensive heuristic search (simple stepwise addition using the outgroup as reference taxon and keeping 100 trees in each step, followed by tree-bisection-reconnection swapping).

Shortest trees under alternative assumptions about character evolution, or compatible with alternative groupings of taxa, were calculated using 100 (extant taxa only) or 10 (all taxa) random addition sequences, keeping one tree in each step, followed by tree-bisection-reconnection swapping. The nonvenational and the irreversible analyses of all taxa resulted in more than 50 000 equally parsimonious trees. To circumvent the problems of memory overflow, branches with minimum length zero were collapsed in these searches.

When searching for trees of best fit for the original data under implied weights, uninformative characters were excluded and rounding rather than truncation of fits was used. The trees with best fit for the extant taxa was searched for in 100 random addition sequences, keeping one tree in each step, followed by tree-bisection-reconnection swapping. The same strategy failed to repeatedly find an island of best trees for the full data set, apparently because of the exaggerated precision of fit scores in PAUP, making the program halt on small local maxima in tree space. If tree space is described as a landscape with hilltops representing islands of good trees, the exaggerated precision will trick hill-climbing algorithms to stop on small pebbles on a slope rather than continuing to the hilltop. Unfortunately, the version of PAUP we used did not allow adjustment of precision. Instead, we searched for the 1000 best trees, swapping on all trees in memory, in 10 replications, each starting with a random addition sequence, keeping one tree in each step, followed by tree-bisection-reconnection swapping with a swapping neighbourhood (reconnection limit) of eight nodes (cf. Ronquist 1998).

Bootstrap proportions for the implied weight searches were calculated for extant taxa using 100 replications of one random addition sequence, keeping 20 trees in each step, followed by tree-bisection-reconnection swapping within a neighbourhood of eight nodes, retaining maximally 1000 trees in each replication. For all taxa, bootstrap proportions were obtained using simple addition with the outgroup as reference taxon, keeping one tree in each step, followed by tree-bisection-reconnection swapping within a neighbourhood of eight nodes.

Bootstrap proportions were also calculated for the data sets of Vilhelmsen (1997b) and Brothers & Carpenter (1993: Appendix 6, Table 4). This was done using 1000 replications of heuristic search (simple stepwise addition with the outgroup as reference taxon, keeping one tree in each step, followed by tree-bisection-reconnection swapping).

We preferred bootstrap proportions for comparing the support of various clades in different analyses because: (a) bootstrap proportions was the only support measure reported for some of the analyses in the literature and the raw data of these analyses were not available to us; and (b) bootstrap proportions are easier to compare between analyses than decay indices, which have to be viewed in relation to the total number of informative characters and the character weights employed.

Results and Discussion

For the entire matrix, we found two separate islands of trees with length 754, consistency index 0.36, and retention index 0.80. One island (A) contained 1404 trees and the other island (B) 28080 trees. Of 100 searches starting with random addition sequences, 95 found island B and 3 found island A. The islands differed only in that island A resolved chrysidoid and basal apocritan relationships better. In particular, all trees in island A grouped chrysidids with embolemids and had the Proctotrupomorpha, including the Ceraphronoidea, as a monophyletic clade. We limit the presentation here to the strict consensus of all trees in both islands (Figs 2, 6, 12). Only 4644 of the 29 484 most parsimonious trees remained distinct under an alternative collapsing criterion (minimum rather than maximum branch length zero).

When analyses were restricted to extant taxa, we found one island containing 196 trees of length 695, having a consistency index of 0.39, and a retention index of 0.79 (Figs 2, 7, 12). This island was hit in 676 of 1000 searches starting with random addition sequences. Collapsing branches when minimum branch length was zero resulted in a reduction to 76 distinct trees.

Searching under implied weights for all taxa, we found one island of 891 trees with fits above 112.15 (fit values ranging from 112.150 to 112.166) (Figs 3, 8, 13). In 10 replicate searches, this island was hit five times. When restricting the analysis to extant taxa, we obtained one tree of fit 112.99 (Figs 3, 9, 13). This tree was found in 27 of 100 searches starting with random addition sequences. The other searches never resulted in trees with a fit exceeding 112.97.

Bootstrap values were generally higher for the analyses excluding fossil taxa (Figs 2, 3, 6–9, 12, 13). This is due to two effects. First, many of the fossil taxa had a large proportion of missing entries in the data matrix, causing uncertainty in the phylogenetic trees and lowering bootstrap values. Second, the analyses with the fossil taxa required much longer time, necessitating more approximate searches in each bootstrap replication.

The results of the standard parsimony analyses and the analyses under implied weights were similar. However, the

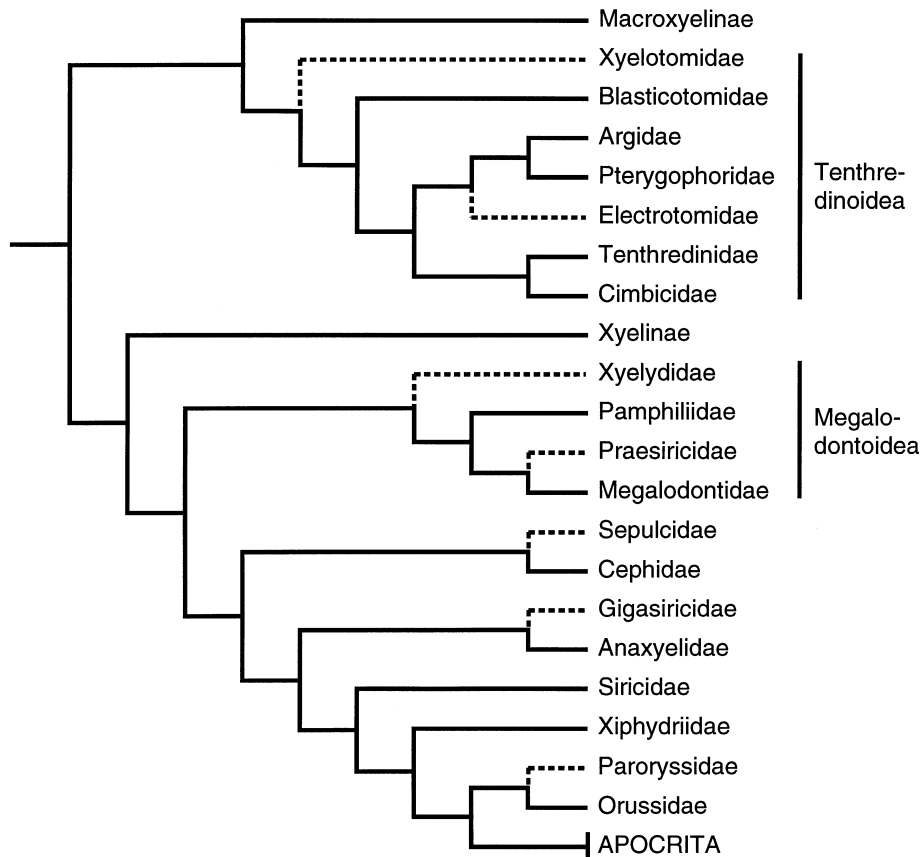


Fig. 1 Relationships among symphytan families proposed by Rasnitsyn (1988). Dashed branches lead to extinct taxa. Notice the biphyletic origin of the Hymenoptera from xyelids (the Macroxyelinae and Xyelinae).

results under implied weights consistently resembled the tree published by Rasnitsyn (1988) more than the results under equal weights. The phylogenetic implications of these and other analyses are discussed in more detail below for the Symphyta, Parasitica, and Aculeata separately.

Symphyta

For the Symphyta, our analyses resulted in well-resolved minimum-length or best-fit trees, and the topology was the same whether or not fossil taxa were included (Figs 2, 3). Most of the groupings were well supported by the data, as indicated by bootstrap values. Running the analyses with venational features excluded, fusion characters treated as irreversible, or loss characters down-weighted or excluded only changed minor details in the topology.

One of the most controversial aspects of Rasnitsyn's (1988) phylogenetic hypothesis was his suggestion that the Hymenoptera were biphyletic, with the tenthredinoids and the Macroxyelinae (one of the subfamilies of the Xyelidae) being the sister group of all other hymenopterans (Fig. 1).

In our reanalysis of Rasnitsyn's data, the biphyletic hypothesis is not confirmed; instead, the data support the view of most other workers (Gibson 1993; Heraty *et al.* 1994; Vilhelmsen 1997b), i.e. that hymenopterans excluding xyelids are monophyletic (Figs 2, 3). Nevertheless, this conclusion is somewhat sensitive to alternative assumptions of character evolution, since trees consistent with the biphyly hypothesis appeared among the shortest trees in the irreversible and no-loss analyses of all taxa.

Rasnitsyn (1988: 119) listed three apomorphic characters in support of the biphyletic hypothesis: 1) the fore wing has R joining C before the pterostigma in macroxyelines and tenthredinoids; 2) the terebra (ovipositor) is short in macroxyelines and tenthredinoids; and 3) the larval eye is situated below the level of the antenna in xyelines and other Hymenoptera. APR now agrees that the first character is not a good synapomorphy of the Macroxyelinae + Tenthredinoidea because the structural difference is subtle and not consistently distributed; hence, this character was omitted in the present analysis.

The interpretation of the ovipositor character (char. 127

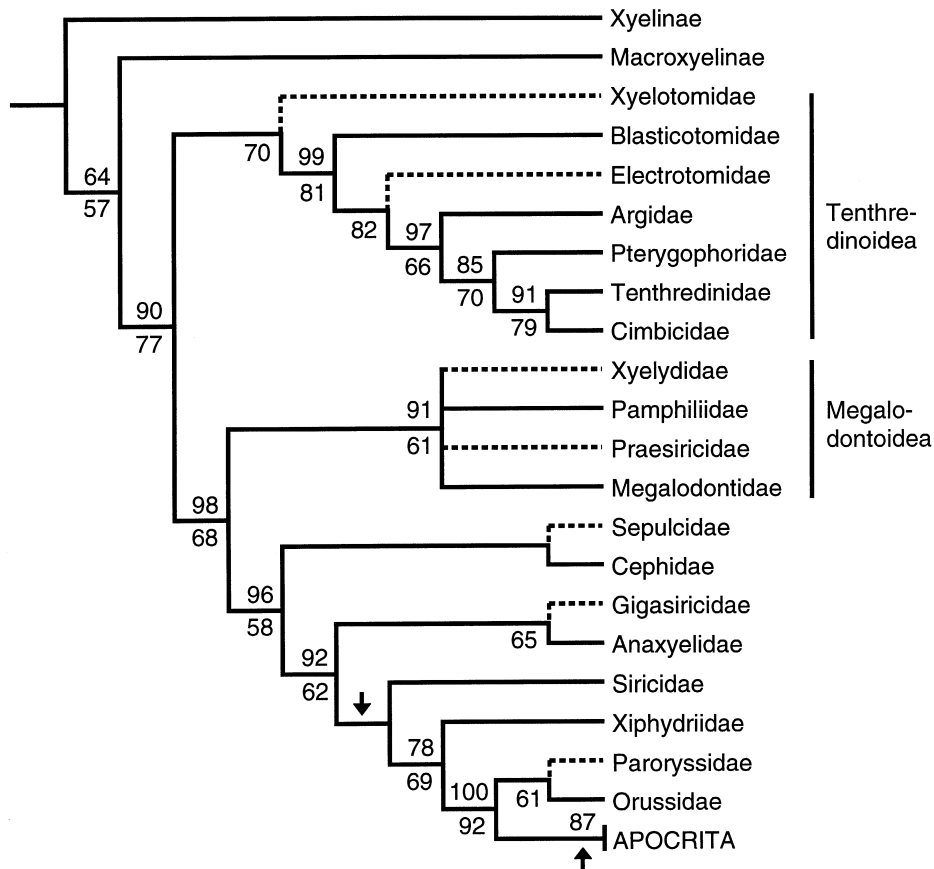


Fig. 2 Strict consensus of the most parsimonious trees of Symphytan relationships from our reanalysis of Rasnitsyn's data. Dashed branches lead to extinct taxa. Values above branches indicate bootstrap support values in the analysis excluding fossil taxa; values below branches indicate bootstrap support values in the analysis of all taxa. Bootstrap values below 50% are not reported. An arrow above a branch marks a clade that did not occur in the strict consensus of the trees excluding fossil taxa; an arrow below a branch marks a clade that did not occur in the strict consensus of the trees including all taxa.

in the present analysis) is complicated. The terebra is short and stout in macroxyelines and tenthredinoids, but longer and slender in xyelines and higher hymenopterans. Rasnitsyn (1988) indicated the latter state to be primitive for the Hymenoptera, suggesting that the short terebra is synapomorphic for macroxyelines and tenthredinoids. However, one of the most basal lineages of other hymenopterans, megalodontoids, also have a short (claw-like) terebra, which must then be assumed to have evolved independently from a long terebra. A more parsimonious explanation is that the macroxyeline and tenthredinoid state is primitive for hymenopterans excluding Xyelinae, and the long terebra of higher hymenopterans the result of secondary reversal to a more primitive state. Thus, this character cannot be maintained as a synapomorphy of macroxyelines and tenthredinoids. In addition, there is some uncertainty regarding the likely ground-plan state of this character, since most endopterygote insects have the terebra either conspicuously modified or lost. In the present analysis we

followed Rasnitsyn's (1988) suggestion that the terebra was long, like that of xyelines and the Triassic archxyelines, in the hymenopteran ground plan. However, the primitive hymenopteran terebra may well have been short and stout if xyelines and archxyelines secondarily (but early) evolved a long ovipositor.

The position of the larval antenna in relation to the eye (char. 150) does seem to support the monophyly of hymenopterans excluding macroxyelines and tenthredinoids, but provides insufficient evidence on its own. Our analysis suggests that, considering all available data, the most likely hypothesis is that the derived antennal position was independently acquired in the Xyelinae and in higher hymenopterans. In conclusion, then, the evidence presented in favour of the biphyly hypothesis is weak, and is outweighed by characters supporting the monophyly of the Hymenoptera excluding the Xyelidae (see also Gibson 1993; Vilhelmsen 1997b).

Although our results do not favour the biphyletic

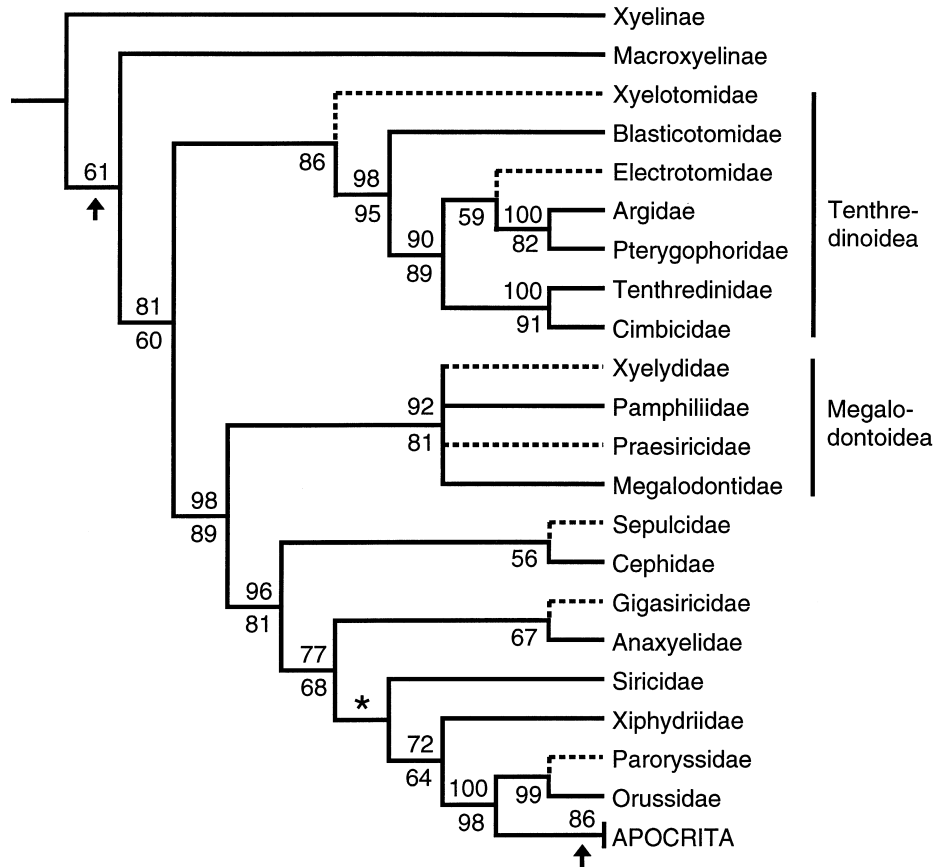


Fig. 3 Strict consensus of the most fit trees of Symphytan relationships from our reanalysis of Rasnitsyn's data. Dashed branches lead to extinct taxa. Values above branches indicate bootstrap support values in the analysis excluding fossil taxa; values below branches indicate bootstrap support values in the analysis of all taxa. Bootstrap values below 50% are not reported. The arrows mark branches that did not occur in the strict consensus of the shortest trees resulting from the analysis of all taxa. The clade marked with a star did not occur in the most fit tree resulting from the analysis of extant taxa; this tree instead had the Anaxyelidae, rather than the Siricidae, being most closely related to the Xiphydriidae, Orussidae and Apocrita.

hypothesis, they support Rasnitsyn's (1988) suggestion that the two xyelid subfamilies Macroxyelinae and Xyelinae may not form a monophyletic group. The shortest trees and some of the most fit trees in our analysis have the Xyelinae as the sister group of all other hymenopterans, in line with some previous suggestions (e.g. Heraty *et al.* 1994). However, the support for this arrangement is not convincing. The only unambiguous character change uniting hymenopterans excluding xyelines is the transformation in the ovipositor character discussed above (char. 127); its evidential value in this context is entirely dependent on correct polarization. In his recent analysis of higher-level symphytan relationships, Vilhelmsen (1997b) found two equally parsimonious arrangements of the xyelid subfamilies, one of which grouped xyelines and macroxyelines in a monophyletic lineage, and one which had macroxyelines as the sister group of all other hymenopterans. Thus, all three possible basal branching sequences have been indi-

cated in different analyses, and relationships between xyelid subfamilies and other hymenopterans remain uncertain.

The controversy surrounding xyelid monophyly may well be understood as a problem of rooting the hymenopteran tree correctly. When the root is removed, the disagreement between analyses disappears. Since hymenopterans form an isolated and highly derived group of endopterygotes, it should be expected that the hymenopteran tree is difficult to root correctly with reference to the morphology of other endopterygotes. It may well be that extensive study of many outgroups, including some exopterygotes, may be needed to resolve the question satisfactorily.

Except for the basal branchings, the results of our reanalyses are basically congruent with the relationships proposed by Rasnitsyn (1988). The only disagreement concerns the resolution of the core tenthredinoids (i.e.

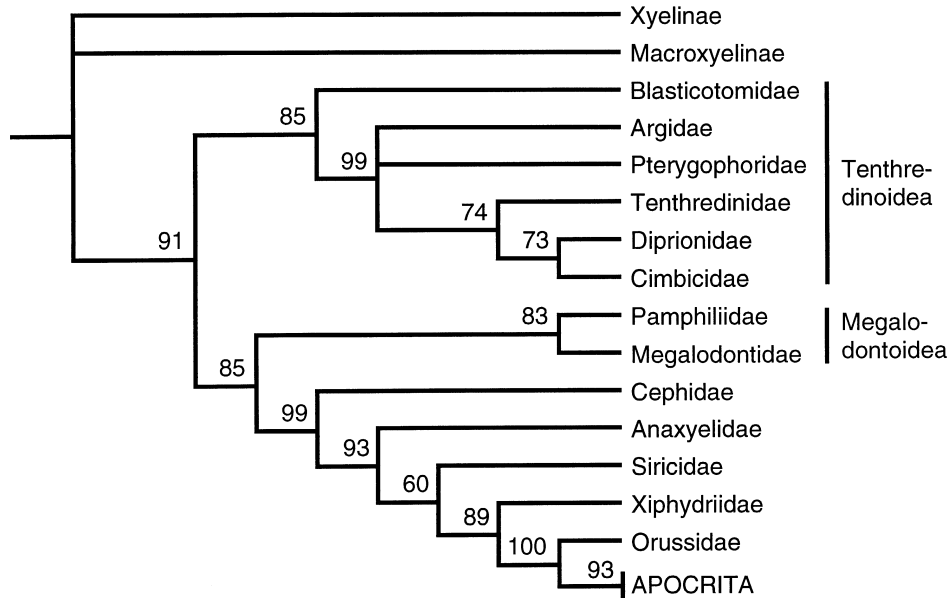


Fig. 4 Strict consensus tree from the analysis of lower hymenopteran relationships by Vilhelmsen (1997b). Bootstrap support values, as calculated by us from Vilhelmsen's data, are indicated on the branches (if larger than 50%).

tenthredinoids excluding blasticotomids). Rasnitsyn originally suggested that the Cimbicidae and Tenthredinidae, together forming a monophyletic lineage, were the sister group of the Argidae + Pterygophoridae (a senior synonym of Pergidae, see Rasnitsyn 1988) + Electrotomidae (Fig. 1). The most fit trees strongly support this set of relationships except that the placement of Electrotomidae remains somewhat uncertain (Fig. 3). The standard parsimony analyses, however, suggest that the Cimbicidae + Tenthredinidae may be more closely related to pterygophorids than to argids (Fig. 2). This arrangement is seemingly well supported, as indicated by bootstrap proportions, but the three unambiguous character changes uniting the clade all concern antennal structure and may well form states in the same complex and homoplastic transformation series. Thus, the support for this grouping in Rasnitsyn's data may be overestimated in the unweighted analysis. Other characters, not included in our analysis, indicate that a sister-group relationship between Argidae and Pterygophoridae, as originally suggested by Rasnitsyn (1988) and supported by the best-fit trees (Fig. 3), is more likely than a tenthredinid-cimbicid-ptyergophorid connection (Goulet & Huber 1993).

Vilhelmsen (1997b) recently analysed higher-level relationships among extant symphytans based on an extensive compilation of data from his own work and that of others. Only nine out of 98 characters in his analysis were taken directly from the work of Rasnitsyn, and several of these nine characters were coded differently than here. Thus, Vilhelmsen's analysis is largely independent of ours; yet,

the strict consensus tree of his analysis is perfectly congruent with the results of our analysis, and the relative support values for different groupings are also surprisingly similar (Figs 2–4). This suggests that higher-level relationships among lower hymenopterans are now fairly well understood. The remaining uncertainties concern the correct rooting of the tree, relationships among core tenthredinoids, and, to some extent, the relative position of anaxyelids and siricids.

One of the most robust clades in the symphytan tree (Figs 2–4) is Orussidae + Apocrita. In fact, this grouping is better supported than the monophyly of the apocritans themselves, both in our analysis and in Vilhelmsen's. Considering that more morphological synapomorphies of the orussid + apocritan clade are known than have yet been included in any analysis (e.g. Ronquist & Nordlander 1989; Ronquist, unpublished data), the sister-group relationship between these taxa must now be considered firmly established. It is worrying that a recent molecular analysis is in conflict with this result, suggesting that apocritans are more closely related to siricids than to orussids (Dowton & Austin 1997, 1999). Should further molecular study show that apocritans and orussids do not form a monophyletic group, there is reason to doubt all phylogenetic conclusions based on morphological evidence. However, the molecular analysis included few representatives and the support for Siricidae + Apocrita was much weaker than for Orussidae + Apocrita in the morphological analyses (72 vs. 100%). Thus, given current knowledge it seems likely that the molecular result is erroneous.

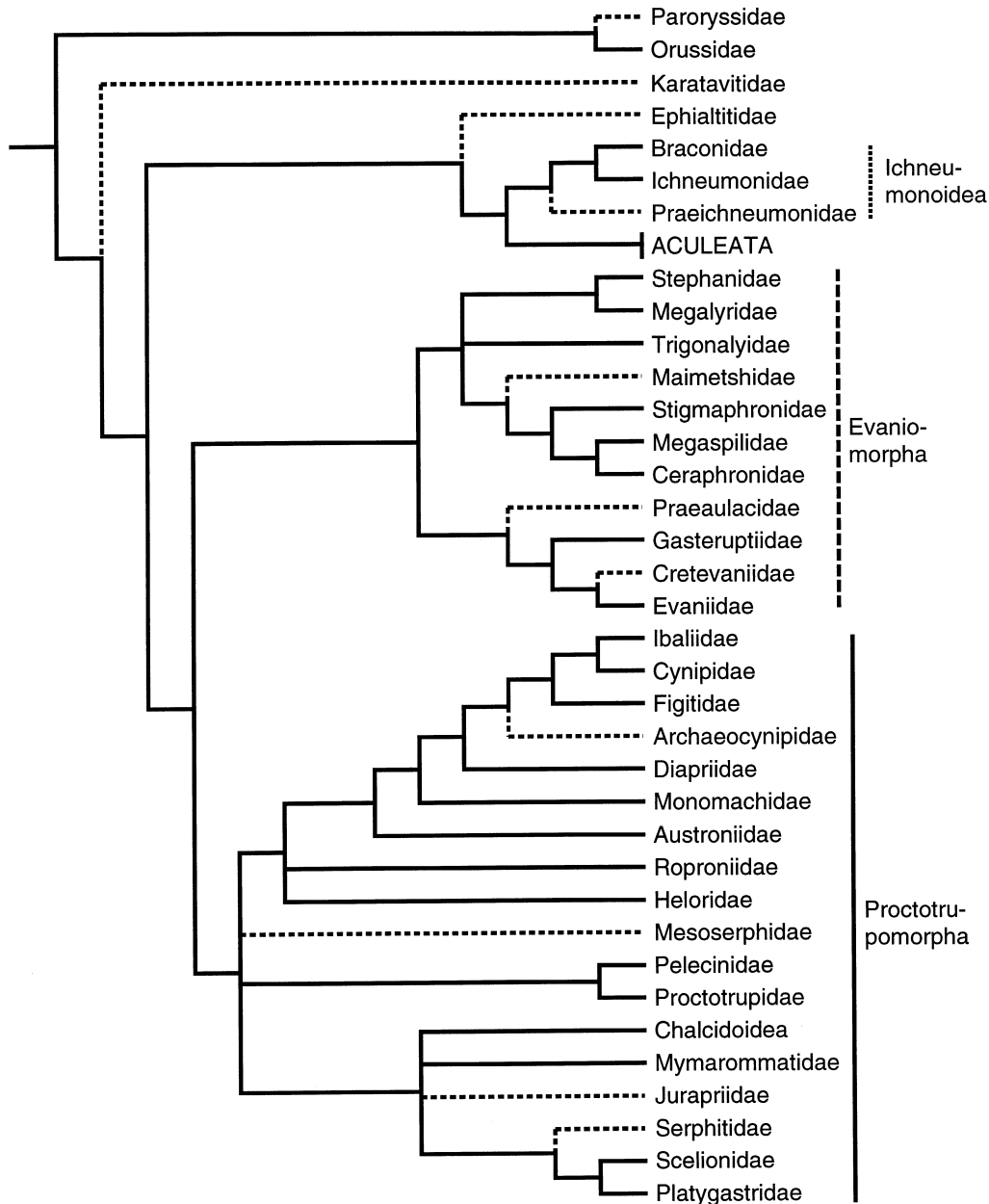


Fig. 5 Relationships among parasitic wasps proposed by Rasnitsyn (1988). Dashed branches lead to extinct taxa. The uncertainty in the position of mymarommatids is marked here as a trifurcation. Note the division of the Parasitica into three monophyletic lineages: the Ichneumonoidea, the Proctotrupomorpha, and the Evaniomorpha.

Parasitica

An innovative aspect of Rasnitsyn's (1988) phylogenetic hypothesis for the Hymenoptera was the suggestion that parasitic wasps form three major lineages: the Ichneumonoidea, the evaniomorphs (Evanioidae, Ceraphronoidea, Megalyridae, Stephanidae), and the proctotrupomorphs (remaining parasitic wasps) (Fig. 5). The ichneumonoids were proposed to form the sister group of the Aculeata,

and the proctotrupomorphs and evaniomorphs together constituted the Microhymenoptera.

Rasnitsyn's data do not resolve higher-level relationships in the Parasitica well. In our reanalysis, no major apocritan divisions were convincingly and consistently supported although there is suggestive evidence for some of Rasnitsyn's main lineages.

The Ichneumonoidea were grouped with the Aculeata

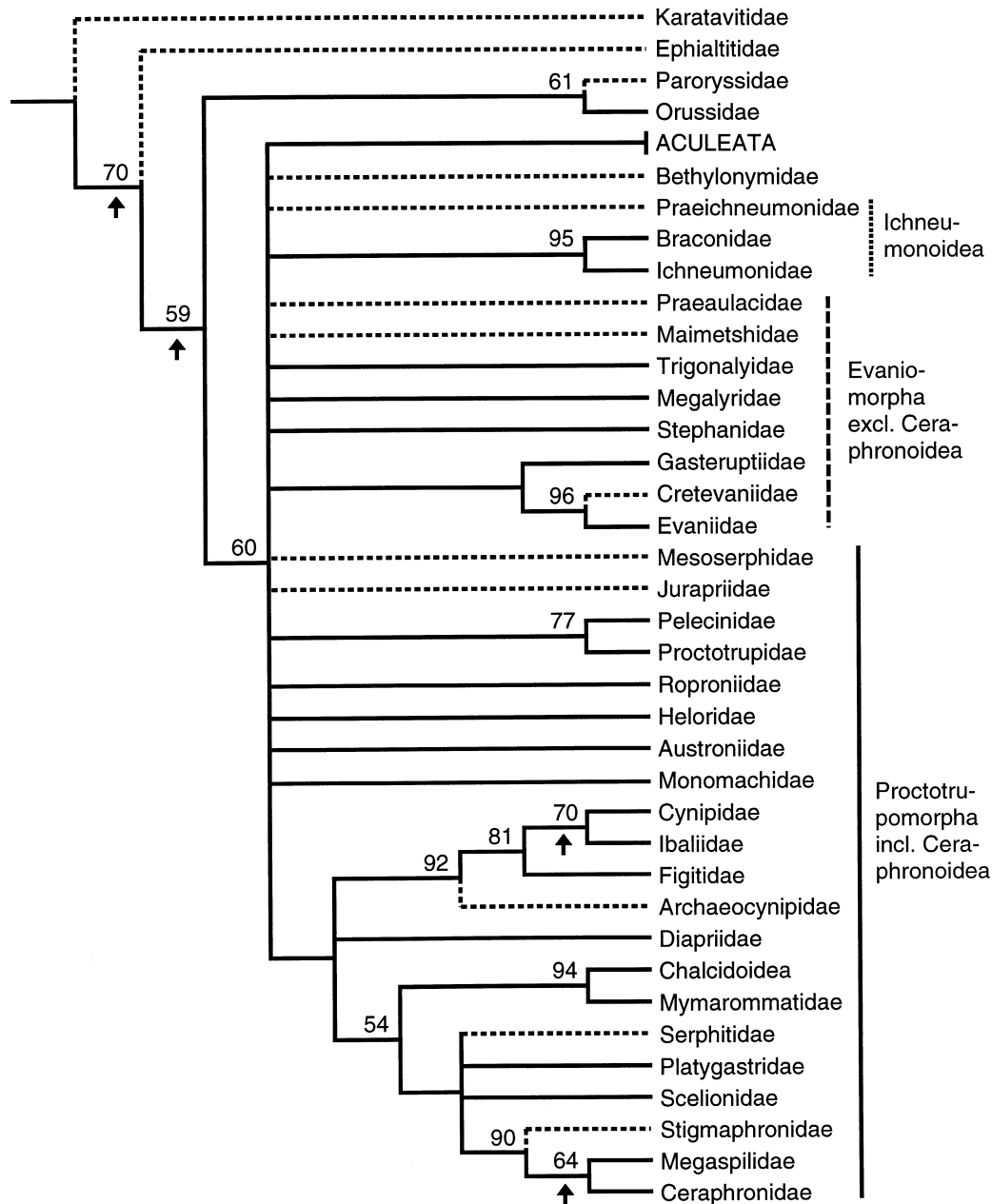


Fig. 6 Strict consensus of the most parsimonious trees of parasitic wasp relationships resulting from our reanalysis of Rasnitsyn's data. Dashed branches lead to extinct taxa. Values on branches indicate bootstrap support (if above 50%). The arrows mark branches that did not occur in all of the most parsimonious trees but received bootstrap support above 50%. Note the position of the Ceraphronoidea deeply nested within the Proctotrupomorpha. The Aculeata do not include the Bethylonymidae in this diagram.

by Rasnitsyn based on two characters: the possession of ovipositor valvilli (char. 63 in present analysis) and the presence of distinct propodeal articulating processes (char. 130). However, neither of these characters is particularly strong. The ovipositor valvilli have distinctly different structure in the Ichneumonoidea and Aculeata (Quicke *et al.* 1992), leaving some doubt as to whether they truly

represent a shared ancestral feature. Furthermore, articulating structures similar to the propodeal processes in the Aculeata and Ichneumonoidea have arisen at least once independently, in the Proctotrupeoidea (Rasnitsyn 1988). At the same time, several characters suggest that ichneumonoids are closer to other parasitic wasps than to aculeates, e.g. the structure of the mid coxae (Johnson 1988). On the

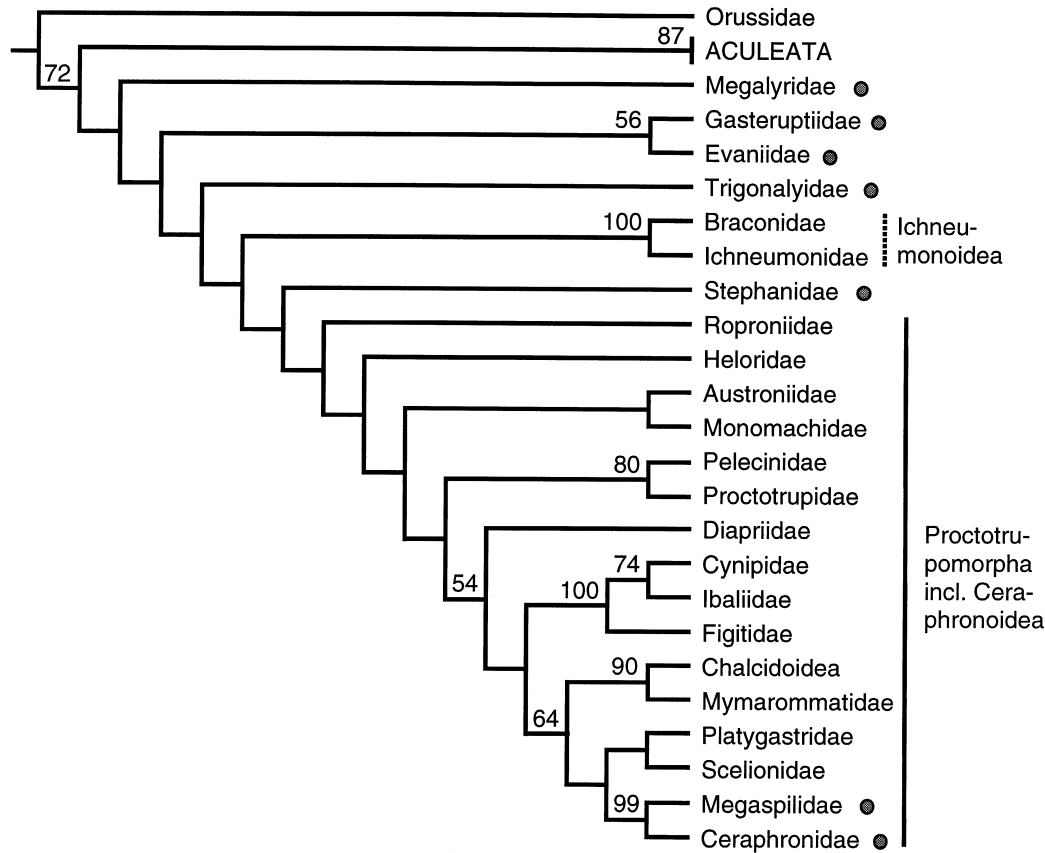


Fig. 7 Strict consensus of the most parsimonious trees of relationships among extant parasitic wasps from our reanalysis of Rasnitsyn's data. Values on branches indicate bootstrap support (if above 50%). Grey circles denote taxa included by Rasnitsyn in the Evaniomorpha. Note that the Ceraphronoidea are nested within the Proctotrupomorpha.

other hand, molecular analyses have provided some weak support for a close aculeate-ichneumonoid relationship (Dowton & Austin 1994, 1997) (Fig. 10).

In our parsimony analysis of Rasnitsyn's data, the Aculeata + Ichneumonoidea do not form a clade in any of the shortest trees (Figs 6,7). However, enforcing monophyly of this grouping requires only two to four extra steps (Table 2). Furthermore, the analyses under implied weights favour a sister-group relationship between ichneumonoids and aculeates. This lineage is robustly supported in the analysis of extant taxa (Fig. 9) and appeared in some of the most fit trees for all taxa (Fig. 8). Taken together, Rasnitsyn's data do not provide conclusive evidence but do suggest the existence of an ichneumonoid-aculeate clade, at least under implied weights.

Rasnitsyn's Evaniomorpha are characterized by having the mesal articulation of the mid coxa displaced from the basal rim (char. 50 in the present analysis). Early work by Rasnitsyn (1975a, 1980) suggested that the Stephanidae did not have this modification but they were later included

in the Evaniomorpha (Rasnitsyn 1988: 136) on the assumption that the stephanid state represents a slight modification of the typical evaniomorph state. Johnson (1988) studied the midcoxal articulation of hymenopterans in detail and confirmed that the Evaniomorpha share a derived position of the mesal articulation but did not consider stephanids to have this condition. However, his scanning electron micrograph of a stephanid mesocoxa (Johnson 1988: Fig. 13) indicates that the mesal articulation of stephanids may actually be slightly displaced from the basal rim. In our analysis, we followed Rasnitsyn (1988) in coding stephanids as having the derived evaniomorph condition but the evidence for inclusion of stephanids in the Evaniomorpha is obviously weak.

Several unique features are shared by orussids and stephanids, but absent in all other hymenopterans. These characters include an ocellar corona, an extremely large basalare, and presence of labral apodemes (Gibson 1985; Vilhelmsen 1996). Assuming that the Apocrita are monophyletic and that secondary loss is more likely than inde-

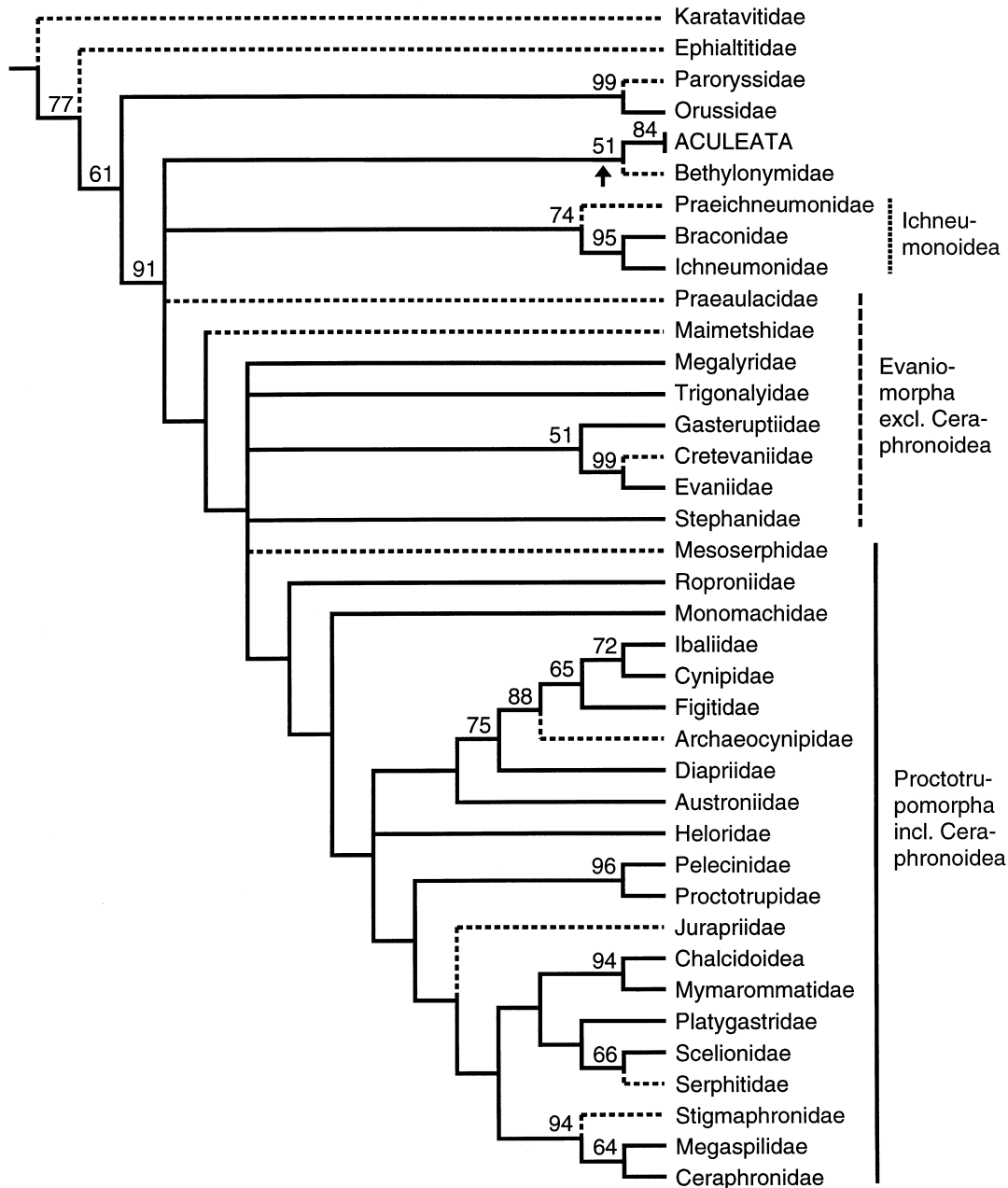


Fig. 8 Strict consensus of the most fit trees of parasitic wasp relationships resulting from our reanalysis of Rasnitsyn's data. Dashed branches lead to extinct taxa. Values on branches indicate bootstrap support (if above 50%). The arrow marks a branch that did not occur in all of the most parsimonious trees but received bootstrap support above 50%. The Aculeata do not include the Bethylonymidae in this diagram.

pendent gain, these characters suggest that the Stephanidae may be the sister group of the remaining Apocrita (cf. also Whitfield 1992). Early analyses of 16S rRNA sequences provided some evidence that the Apocrita excluding stephanids are monophyletic (Dowton & Austin 1994). However, peculiarities of the stephanid mitochondrial

sequence examined (Dowton & Austin 1995, 1997) make this conclusion uncertain, and the most recent analysis of apocritan 16S data did not include the stephanid sequence at all (Fig. 10).

Some morphological data, in addition to the midcoxal structure, are at least consistent with a monophyletic

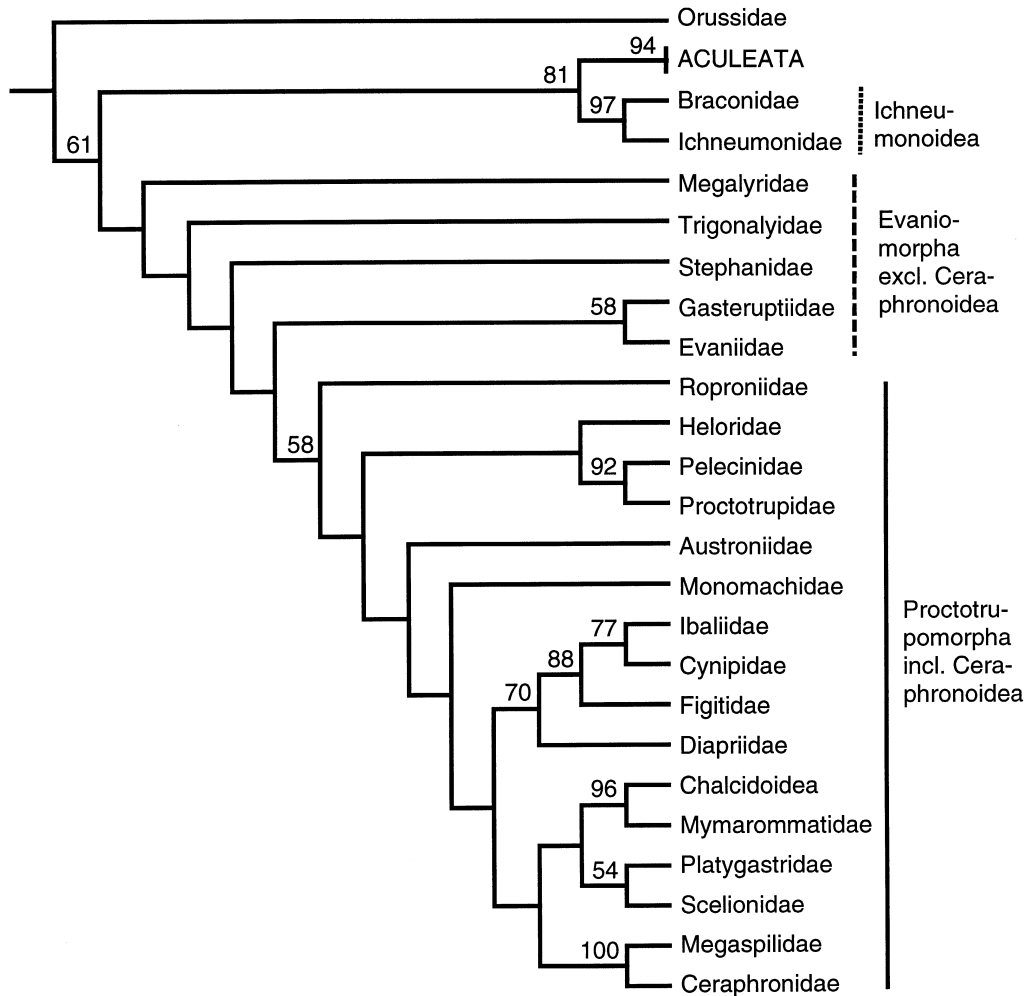


Fig. 9 The most fit tree of relationships among extant parasitic wasps from our reanalysis of Rasnitsyn's data. Values on branches indicate bootstrap support (if above 50%). Note the support for the Ichneumonoidea + Aculeata and that the Microhymenoptera (Proctotrupomorpha and Evaniomorpha) appear as a monophyletic clade.

Table 2 Some alternative apocritan groupings and the number of extra steps, compared with the most parsimonious trees, they require with Rasnitsyn's data in unweighted analyses.

Grouping	Extra steps in searches with	
	extant taxa	all taxa
Proctotrupomorpha (excl. Ceraphronoidea)	11	7
Evaniomorpha	18	15
Evaniomorpha excl. Stephanidae	12	11
Evaniomorpha excl. Ceraphronoidea	8	9 ¹
Evaniomorpha excl. Stephanidae & Ceraphronoidea	4	3
Diapriidae + Cynipoidea	1	3
Microhymenoptera	5	0
Ichneumonoidea + Aculeata	4	2 ¹

¹ Most parsimonious tree island was hit rarely or tree overflow occurred during searches, indicating that shorter trees compatible with the constraints may exist.

Evaniomorpha excluding the Stephanidae. For instance, evaniids and trigonalysids (but not gasteruptiids) share two apomorphies in the structure of the antenna cleaner (Basi-buyuk & Quicke 1995). Ceraphronoids and megalysids possibly both have the prepectus secondarily exposed and fused to the pronotum and completely surrounding the mesothoracic (apparently prothoracic) spiracle (Gibson 1985, 1986). This has been taken as evidence for the monophyly of this heterogeneous group of giants (megalysids) and dwarfs (ceraphronoids). Unfortunately, the occlusor muscle apodeme is absent in megalysids, at least in the single representative dissected so far (Gibson 1985). The occlusor muscle apodeme is primitively situated on a free prepectus and it is used as the main indicator of the fate of the prepectus when the latter is fused to other sclerites. Its absence makes the hypothesis of prepectal fusion

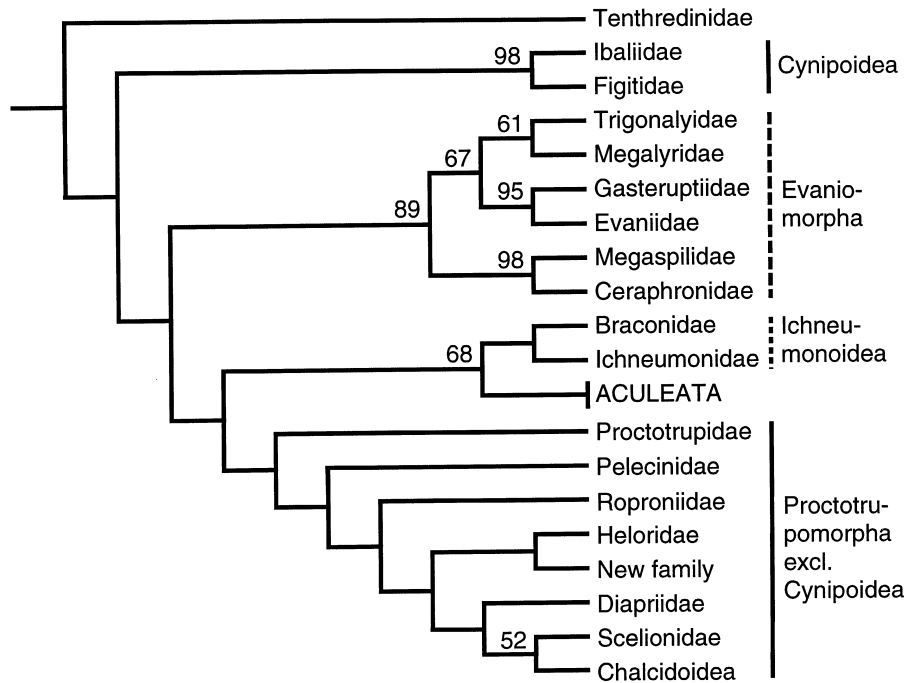


Fig. 10 Relationships among parasitic wasps as indicated by analyses of mitochondrial 16S rDNA sequences (Dowton *et al.* 1997). Bootstrap values are those reported by the original authors. Note the exclusion of the Cynipoidea from the Proctotrupomorpha and the support for the Evaniomorpha.

to the pronotum in megalyrids uncertain, weakening the evidence for a megalyrid-ceraphronoid connection.

Other evidence favours splitting of the evaniomorphs. For instance, megalyrids have some rare or unique archaic apocritan features, including the structure of the first metasomal segment and the presence of subantennal grooves (Vilhelmsen 1997a), suggesting a very basal position within the Apocrita. Furthermore, a secondarily exposed prepectus occurs in chalcidoids in addition to ceraphronoids (and possibly megalyrids) (Gibson 1985). Thus, this character could be interpreted as a synapomorphy grouping ceraphronoids (and possibly megalyrids) with chalcidoids rather than with other evaniomorphs, although the position of the mesothoracic spiracle is quite different in chalcidoids and in ceraphronoids/megalyrids.

Our analyses of Rasnitsyn's data (Figs 6–9) suggest that the Evaniomorpha is an unnatural group and that megalyrids, stephanids, trigonalyids, and evanioids form a paraphyletic assemblage of basal apocritan lineages. Constraining the Evaniomorpha *sensu* Rasnitsyn 1988 to be monophyletic requires 15–18 extra steps under standard parsimony (about 2–3% length difference) (Table 2). It is particularly the Ceraphronoidea, and to a lesser extent the Stephanidae, that fit poorly in the Evaniomorpha; the data are less strongly in conflict with monophyly for the remaining

Evaniomorpha (Table 2). Also the analyses using implied weights split the Evaniomorpha (Figs 8, 9).

The ceraphronoids consistently group with chalcidoids and platygastroids, deep inside the Proctotrupomorpha, in the shortest and the most fit trees (Figs 6–9). These three groups are among the smallest parasitic hymenopterans, suggesting that parallel reductions due to small size, particularly in the large number of wing venational characters, may be responsible for pulling them together in the shortest trees. However, similar phylogenetic results were obtained in the nonvenational and the weighted analyses, as well as in the analysis where loss characters were excluded, suggesting that this phylogenetic signal was not due entirely to shared homoplastic losses. Some nonreductional characters that favour a position of the ceraphronoids close to chalcidoids and platygastroids are the geniculate antennae, the tubular petiole, and the exposed prepectus.

Contrary to our results, but in support of the original tree published by Rasnitsyn (1988), evaniomorphs including ceraphronoids were supported as a monophyletic group in a recent analysis of mitochondrial 16S sequence data (Dowton *et al.* 1997) (Fig. 10; stephanids were not studied). On the other hand, new morphological evidence seems to support a ceraphronoid-proctotrupomorph connection. For instance, Basibuyuk & Quicke (1997)

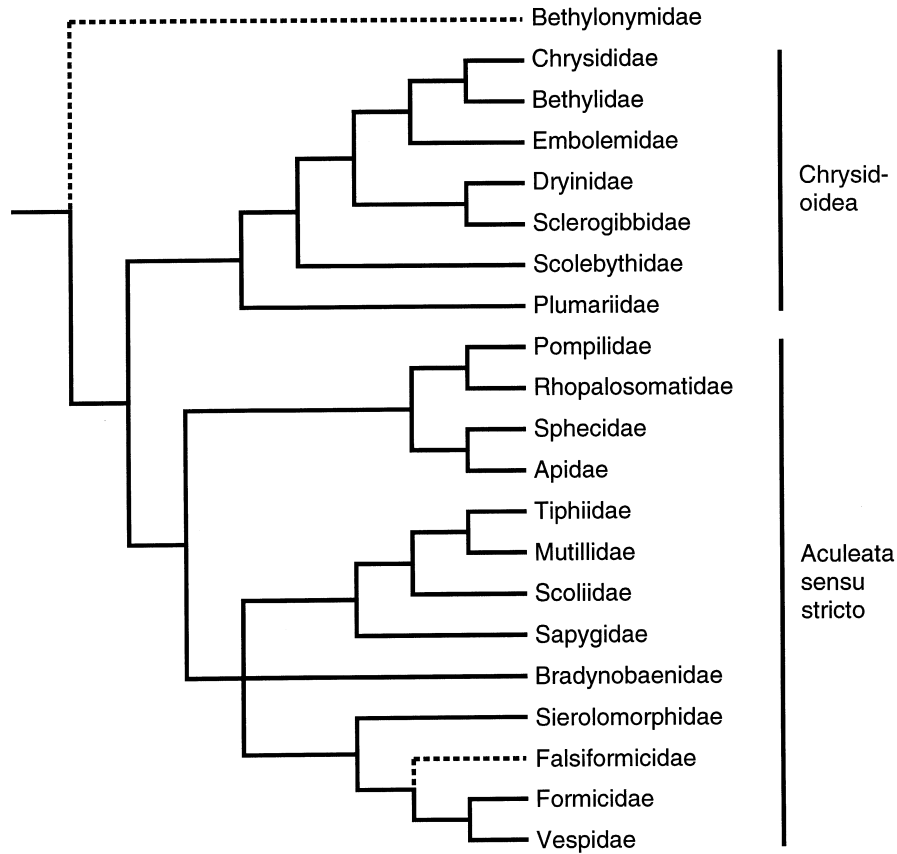


Fig. 11 Aculeate relationships proposed by Rasnitsyn (1988). Dashed lines lead to extinct taxa. The uncertainty concerning the position of the Bradynobaenidae was resolved by placing this family basally in the clade in which it belongs according to Rasnitsyn (1988).

found that diapriids, chalcidoids, and ceraphronoids share the presence of small, stiff setae opposing the distal hamuli, a unique feature in the Apocrita. Ceraphronoids are also similar to proctotrupomorphs but unlike some evaniomorphs in lacking secondary hamuli (Basibuyuk & Quicke 1997).

Rasnitsyn (1988) based his Proctotrupomorpha on several characters, most of which show some reversals within the group or parallel gains outside the group. Our analyses basically support or are consistent with the Proctotrupomorpha being monophyletic, given that the Ceraphronoidea are included (Figs 6–9). However, the clade never received convincing support in bootstrap resampling analyses. The branching order within the Proctotrupomorpha in the optimal trees is similar but not identical to the order in Rasnitsyn's original tree (Fig. 5). The proctotrupomorphs, excluding ceraphronoids, have appeared as a monophyletic group in molecular analyses (Dowton & Austin 1994), although the support is not convincing and the latest analysis places the Cynipoidea outside the Proctotrupomorpha (Dowton *et al.* 1997) (Fig. 10).

In support of the monophyly of the Microhymenoptera (i.e. Evaniomorpha + Proctotrupomorpha), Rasnitsyn (1988) listed two characters: 1) reduction in the anal veins of the fore wing and 2) reduction of the second to seventh abdominal spiracles. Neither character is strong, and the latter character is weakened by the fact that orussids have the same abdominal spiracles reduced as the microhymenopterans (Ronquist, unpublished data). This suggests that either: 1) the polarity of the character is the reverse, i.e. that the well-developed spiracles on the second to seventh abdominal segments in the Aculeata and Ichneumonoidea are a derived neotenic feature instead of a retained plesiomorphy; or 2) the same spiracles have been reduced at least twice independently, in which case further homoplastic changes in the Apocrita may have occurred. The fact that most apocritan larvae have the spiracles well developed lends some credibility to the neoteny hypothesis. On the other hand, orussids have apparently evolved from ancestors of minute size, perhaps explaining independent reduction of spiracles. In any case, it is not surprising that the Microhymenoptera do not receive convincing support in our analyses. Neverthe-

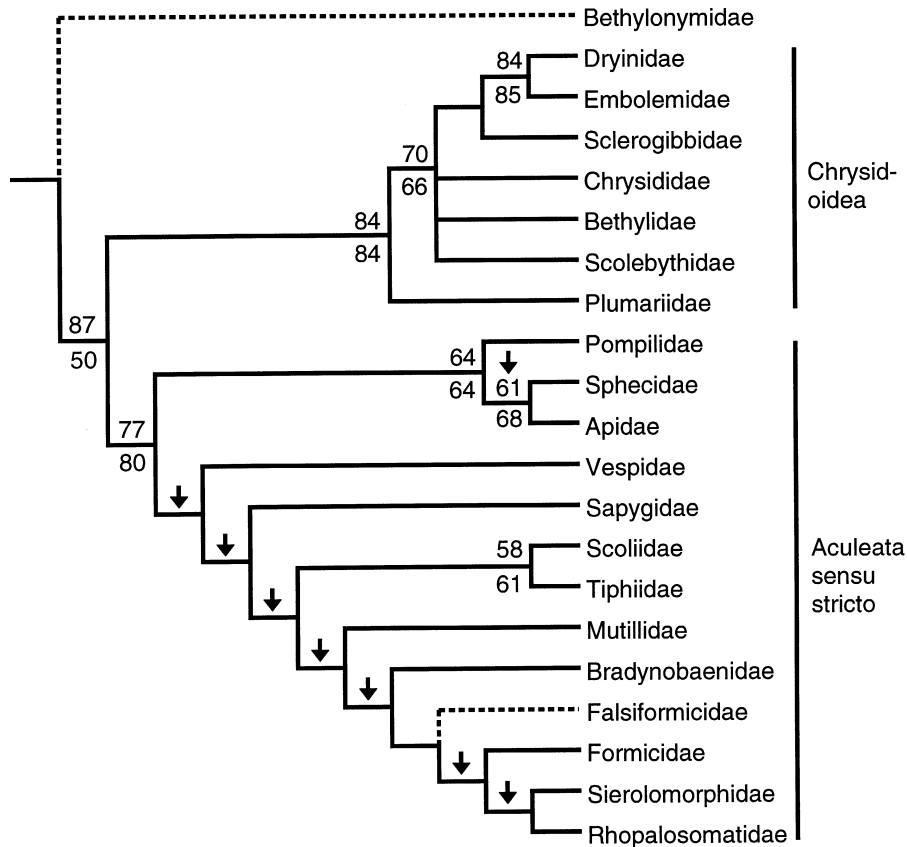


Fig. 12 Strict consensus tree of the most parsimonious trees of aculeate relationships resulting from our reanalysis of Rasnitsyn's data. Dashed lines lead to extinct taxa. Values above branches represent bootstrap support for the analysis of extant taxa; values below branches are bootstrap support for the analysis of all taxa. Branches with arrows did not appear in the strict consensus of the most parsimonious trees of extant taxa.

less, there is some suggestive evidence for the clade, particularly in the analyses under implied weights, in which the clade occurred in the most fit tree (extant taxa) or in some of the most fit trees (all taxa). Even under standard parsimony, the Microhymenoptera appeared as a monophyletic group in some of the shortest tree in the analysis of all taxa and relatively few extra steps were needed to obtain a monophyletic Microhymenoptera in the analysis of extant taxa (Table 2).

Rasnitsyn (1988) expressed some doubt as to the position of mymarommatids, but our analysis of his data (corrected and updated for mymarommatids) strongly group mymarommatids with chalcidoids, a conclusion previously reached by Gibson (1986).

Our reanalysis indicates that the higher-level cynipoid relationships proposed by Rasnitsyn (Fig. 5) are in good agreement with his data (Figs 6–9) but the conclusions are still questionable. The signal is mainly due to one character informative about higher-level cynipoid relationships (char. 90), and the interpretation of this character is

contentious (Ronquist 1995b). Furthermore, Rasnitsyn's analysis does not include the Austrocynipidae, a taxon that differs considerably from other cynipoids. Ronquist (1995b) recently analysed family level cynipoid relationships, including austrocynipids, based on 59 informative characters and reached the conclusion that cynipids and figitids are sister groups, not cynipids and ibaliids as suggested by Rasnitsyn.

The Platygastroidea (Scelionidae + Platygastridae) did not always appear as a monophyletic group in the shortest or most fit trees because no unique autapomorphies of the superfamily were listed by Rasnitsyn (1988). Subsequent work has convincingly shown that the group is monophyletic (Austin & Field 1997).

Concerning the fossil groups of parasitic wasps, our analysis (Figs 6, 8) suggests that the phylogenetic positions proposed by Rasnitsyn (Fig. 5) are in good agreement with the available data for most taxa. Notable exceptions include the families Praeaulacidae, Maimetshidae, Ephialtidae and Karatavitidae, which all occur in more basal posi-

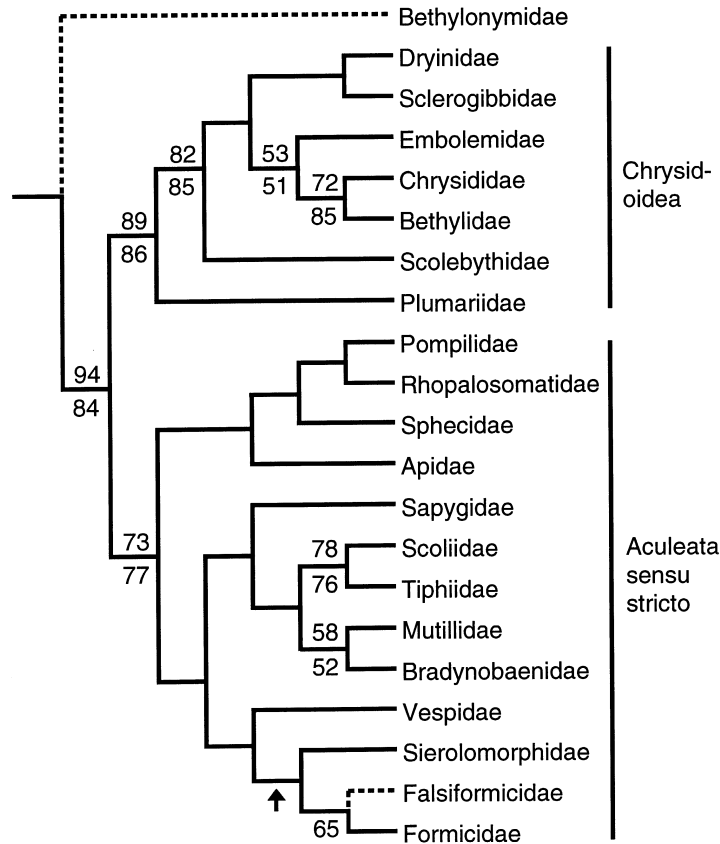


Fig. 13 Strict consensus tree of the most fit trees of aculeate relationships resulting from our reanalysis of Rasnitsyn's data. Dashed lines lead to extinct taxa. Values above branches represent bootstrap support for the analysis of extant taxa; values below branches are bootstrap support for the analysis of all taxa. The branch with an arrow did not appear in all of the most fit trees from the analysis of all taxa.

tions than in Rasnitsyn's tree. It is possible that the basal placement of these taxa is due to the inclusion in them of some specimens that have primitive states of key features, whereas most members are relatively more advanced and have closer affinities with modern forms.

Aculeata

It is now accepted by most workers (e.g. Brothers 1975; Carpenter 1986; Brothers & Carpenter 1993) that the Aculeata fall into two major monophyletic lineages, the Chrysidoida and the Aculeata *sensu stricto* (Vespoidea + Apoidea), an hypothesis that goes back to the detailed comparative work on the hymenopteran ovipositor by Oeser (1961). This dichotomy was also recognized by Rasnitsyn (1988) (Fig. 11) and is supported in our reanalysis of his data (Figs 12, 13).

In the Chrysidoida, Rasnitsyn (1988) suggested that embolemids were most closely related with bethylids + chrysidids (Fig. 11), a phylogenetic scheme that was at odds with work by Carpenter (1986) indicating that embolemids were the sister group of dryinids. The conclusions

of Carpenter were later supported in a comprehensive analysis of higher-level relationships among extant aculeates by Brothers & Carpenter (1993) (Fig. 14).

Brothers & Carpenter (1993) reassessed Rasnitsyn's characters on aculeate relationships and concluded that parsimony analysis of the data resulted in a chrysidoid phylogeny more similar to theirs than to the tree published by Rasnitsyn. Our more detailed reanalyses of Rasnitsyn's data essentially confirm their findings. In a standard parsimony context, Rasnitsyn's data strongly suggest that embolemids and dryinids are sister groups, whether or not fossil taxa are excluded from consideration (Fig. 12). There is some lack of resolution among other chrysidoids but there is no disagreement with the results of the analysis of Brothers and Carpenter (Fig. 14). The implied weights analyses of Rasnitsyn's data give slightly different results (Fig. 13) but the trees are also here congruent with those of Brothers and Carpenter except for the grouping of the Embolemidae with Chrysididae and Bethylidae, a clade which is poorly supported in bootstrap resampling analyses (Fig. 13).

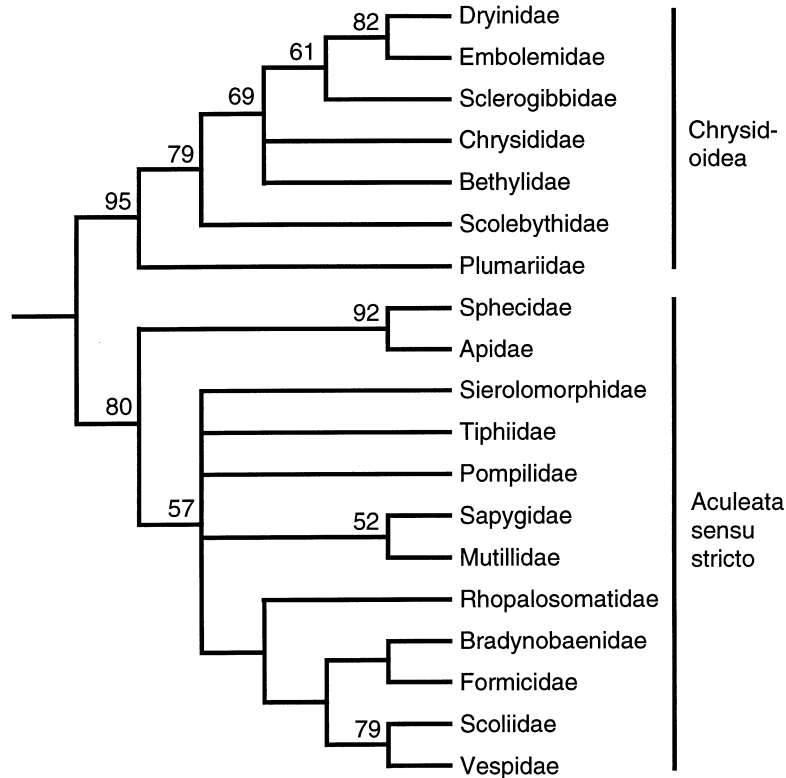


Fig. 14 Aculeate relationships indicated by the analysis of Brothers & Carpenter (1993: fig. 9A). The tree is the strict consensus of the most parsimonious trees resulting from their analysis based on extensive branch swapping on all the data without weighting. Values on branches are bootstrap support values for interfamily relationships, as calculated by us from Brothers and Carpenter's data. The cladogram has been simplified by including the Heterogynaidae in the Sphecidae and retaining Sapygidae as a monophyletic group, although these results were not supported in all of the most parsimonious trees. Similarly for simplicity, subfamilies were grouped into families, and *Olixon* was included in the Rhopalosomatidae.

Rasnitsyn's hypothesis for the Aculeata *sensu stricto* also differed considerably from the relationships advocated by Brothers & Carpenter (1993) (Figs 11, 14). Our analyses indicate that there is no convincing and consistent support for any groupings within the Aculeata *sensu stricto* based on Rasnitsyn's data. The relationships suggested by the optimal trees (Figs 12, 13) are largely unresolved and sometimes specify relationships that are both in conflict with Rasnitsyn's original tree and the results presented by Brothers and Carpenter. In their reanalysis of Rasnitsyn's data, the latter authors arrived at a result for the Aculeata *sensu stricto* that was different in detail from ours, but similar in being largely unresolved. Thus, the two reanalyses of Rasnitsyn's data agree well not only for the Chrysid-oidea, but also for the Aculeata *sensu stricto*.

Although Rasnitsyn's data do not provide much resolution in the Aculeata *sensu stricto*, it should be noted that Brothers and Carpenter also had considerable difficulties in resolving relationships among higher aculeates. Their preferred tree is based on character weighting; strict

consensus trees of their unweighted analyses were at least partly unresolved for relationships among higher aculeates (Brothers & Carpenter 1993).

The number of characters (225) in the analysis of Brothers & Carpenter (1993) is impressive compared to the characters informative about aculeate relationships in Rasnitsyn's data, but the difference partly results from the coding procedure Brothers and Carpenter used for character complexes. Most of these were described in terms of branching character state trees and then broken into a number of simple, often additive representation variables. These representation variables are interdependent, and the coding procedure is appropriate only if the character state tree is a reasonable representation of the character system. For instance, consider their characters 121–122, both treated as ordered (additive):

- '121. Metatibial spines (first variable): Many scattered spiniform setae (or neither spines nor spiniform setae) = 0. Scattered weak (or very strong) spines = 1. Scattered moderately strong spines = 2. Spines moderate and present only apically = 3. Spines very strong and present only apically = 4.

122: Metatibial spines (second variable): Spines weak or absent (or strong but present only apically) = 0. Scattered very strong spines = 1.'

Their coding of taxa implies that the character system evolves according to a character state tree where state 1 of the second character branches off from state 1 in the first character. Other workers might have wanted to consider other transformation series hypotheses or coded the character complex as a single, unordered character. We do not want to detract from the value of the analysis of Brothers and Carpenter. However, a large portion of the phylogenetic information in their data stems from the hypothesized character state trees and this must be borne in mind when comparing the number of characters and the evolutionary assumptions in their analysis with other studies of aculeate relationships.

Conclusions

Our reanalysis of Rasnitsyn's (1988) data has pointed out parts in which his much cited hymenopteran phylogeny is well-supported, and parts in which the evidence is weak or conflicting. Higher-level symphytan relationships are largely well supported by Rasnitsyn's data. The topology largely agrees with Rasnitsyn's original tree except for the biphyletic hypothesis, and even better with the results of other workers. In the Chrysidoidea, our analyses indicate that Rasnitsyn's data are in good agreement with the phylogeny presented by Brothers and Carpenter (Brothers & Carpenter 1993), although his original tree was not. For the remaining Apocrita, Rasnitsyn's data are weak. None of his major apocritan lineages consistently appear among the shortest trees in parsimony analyses of his data, but many of the groupings occur in trees that are only slightly longer. Interestingly, implied weights analyses provide some evidence for the monophyly of the Aculeata + Ichneumonoidea and for the Microhymenoptera.

The results of numerical parsimony-based cladistic analysis are indicative, not decisive, and in cases of insufficient knowledge (as for the Parasitica), manual evaluation based on intuitive (but preferably explicit) character weighting may be superior to unweighted analysis of raw data (Rasnitsyn 1996). An additional difficulty with numerical cladistic analysis is to express all the available morphological variation in terms of discrete characters, and some important information that is available for an experienced worker formulating an intuitive phylogenetic hypothesis may evade character definition attempts. The Evaniomorpha provide a possible case in point, where Rasnitsyn's (1988) original tree agrees better with some molecular results (Dowton & Austin 1997) than our cladistic reanalysis of the data.

Even though the difference was small, it is notable that the implied weights analysis consistently produced results more similar to the manually constructed tree (Rasnitsyn 1988) than standard parsimony analysis did. Future studies will have to show whether this occurred simply because implied weights analysis is more similar to manual reconstruction of phylogeny, or if implied weights analysis (and manual reconstruction) is (are) also more efficient in retrieving phylogenetic information from noisy data sets.

The character matrix we have presented here by no means includes all the available morphological evidence, nor necessarily does it represent the optimal coding of the included data. We have restricted ourselves entirely to the characters presented by Rasnitsyn (1988) and have omitted subsequent work describing novel character systems. Furthermore, the inclusion of fossil evidence has sometimes necessitated a more crude definition of character states than would otherwise have been possible. We are convinced that future comparative morphological studies will provide a wealth of additional characters informative about higher-level hymenopteran relationships and hope that this paper will stimulate such work.

Acknowledgements

Katarina Eriksson and Magnus Lindgren initially coded characters for nonaculeate Hymenoptera and Alain Roy for Aculeata. Alex Rasnitsyn and Fredrik Ronquist (FR) checked and corrected the codings, and FR finished the analyses and a first draft of the manuscript. Lars Vilhelmsen and Jim Carpenter kindly provided digital copies of their symphytan and aculeate character matrices, respectively. For critical comments on the manuscript, we would like to thank Lars Vilhelmsen, Donald Quicke, Mike Fitton, Gary Gibson, Lubomir Masner, and two anonymous referees. This research was supported in part by the Swedish Natural Science Research Council (grant to FR).

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Appendix. Characters used for phylogenetic analysis

In the character list below, numbers in square brackets following a character state description refer to the nodes in Rasnitsyn's (1988) tree where the corresponding apomorphy was listed. The first state is the assumed plesiomorphic state for the Hymenoptera, except for a few ordered, multistate characters where one of the intermediate states is suggested to be plesiomorphic for the Hymenoptera. In

the latter case, the plesiomorphic state is marked with node number 0. References to a node interval (e.g. 14–15) means that the state is unknown for one or more fossil taxa branching off in this interval. Each character description is followed by corrections of the coding implied by Rasnitsyn's tree, and a discussion of ground-plan assumptions and alternative character interpretations. The character list is followed by a list of excluded characters. R88 refers to Rasnitsyn (1988). Observed states are given in Table 1 above.

1. Structure of head and anterior part of mesosoma: (0) mesosoma gradually narrowed anteriorly, propleura sloping, head not flattened posteriorly, highly movable; (1) mesosoma truncated abruptly anteriorly forming flat vertical surface, propleura vertical, head flattened posteriorly and tightly appressed to mesosoma, only weakly movable [46].

2. Ring of cuticular teeth around anterior ocellus (ocellar corona): (0) absent; (1) present [30, 36].

3. Position of antennal foramina: (0) contiguous or subcontiguous with clypeus [67]; (1) distinctly separated from clypeus, usually distant from clypeus [33, 74–75, 89]. State 0 was inadvertently omitted from node 40; state 1 from node 21, 96, and 99 in R88. Stephanids have the antennal foramina close to the clypeus, but still distinctly separated from it, i.e. state 1. There is considerable intra-taxon variation in sphecids, pompilids, vespids, and formicids; antennal foramina contiguous with clypeus is here assumed to be the ground-plan state.

4. Oral and mandibular foramina: (0) contiguous; (1) isolated [14–15]. Sphecids have both states, but the foramina are likely to be contiguous in the ground plan (Bohart & Menke 1976: 9). The same is true for Tiphidae, Scoliidae, Mutillidae, and Bradynobaenidae (Osten 1988).

5. Occipital foramen: (0) open ventrally, continuous with oral foramen; (1) closed ventrally [13].

6. (Subdivision of 5:1) Nature of sclerotization closing occipital foramen ventrally: (0) hypostomal bridge [13]; (1) postgenal bridge [20–21, 24, 25, 28]; (2) external sclerotization of tentorial origin (lower tentorial bridge *sensu* Rasnitsyn 1988) [16, 49, 74–75]. (3) composite bridge consisting of tentorial and postgenal or hypostomal elements. Unordered. State 3 should have been listed under nodes 59–60, 69, and 71 in R88. Ichneumonids and braconids have a postgenal bridge in their ground plans (state 1; state 2 was erroneously given in R88; cf. Rasnitsyn 1980: 79), although there is a strong tendency towards the development of a lower tentorial bridge in both families. Diapriidae except *Ismarus* have the lower tentorial bridge replaced by a composite bridge (Rasnitsyn 1980: 88) but the state in *Ismarus* (pure lower tentorial bridge) is consid-

ered to be the likely ground plan of the family. APR's division of the sclerotization closing the occipital foramen ventrally into different states rests on subtle differences in structure that other workers fail to appreciate. Vilhelmsen (1997b) divided the symphytan head closure into three states: a wide, rectangular area in pamphiliids and megalodontids, a narrow rectangular area in cephids, and an at least partly linear structure (i.e. postgenae meet medially at least for some distance) in anaxyelids, siricids, xiphidriids, orussids and apocritans; these three states forming a linear transformation series. FR agrees with this interpretation.

7. Size of tentorial bridge (syn. with anterior or upper tentorial bridge *sensu* Rasnitsyn 1988): (0) broad; (1) narrow, stripe-like [28]; (2) thin, rod-like [31–32]. Ordered 012.

8. Shape of tentorial bridge: (0) straight (1) distinctly arched [28].

9. Corpotendon (anterior process from upper tentorial bridge forming the tendon of the posterior contractor of the pharynx): (0) absent; (1) present [20–21, 28].

10. Basal position of anterior tentorial arms: (0) issuing from anterior part of tentorial bridge; (1) issuing below level of tentorial bridge [13].

11. Structure of anterior tentorial arms: (0) broad; (1) thin, rodlike [80]. State 1 was inadvertently omitted from node 109 in R88.

12. Structure of antenna: (0) simple; (1) geniculate [58, 65, 86, 92, 112]. State 1 was erroneously not mentioned for node 39 in R88. Formicids [node 112] were coded here as having simple antennae in their ground plan based on the structure in fossil ants. Most diapiiids [node 58] have the antennae weakly bent but not as distinctly geniculate as in the other taxa coded as having state 1. Because of this and the apparently simple antennae of ismarine diapiiids, diapiiids were coded as having simple antennae in their ground plan.

13. Length of scape: (0) short; (1) moderately long [56, 65]; (2) very long [67, 89]. Ordered 012. This character was inadvertently omitted from some nodes in R88: node 58 should have state 1, node 39 state 1 and node 41 state 2. There is considerable variation in length of scape among chalcidoids and diapiiids; a scape of moderate length is here considered to be the ground-plan state in these groups. Many aculeates also show considerable variation, but are likely to have the scape short in the ground plan as demonstrated by archaic representatives (even in ants, where particularly male Armaniinae have a short scape). For proctotrupoids, see also Naumann & Masner (1985).

14. Structure of the first flagellomere: (0) composed of several flagellomeres, thick and long; (1) composed of several flagellomeres, not thicker than other flagellomeres but usually slightly longer with some subdivisions indicated; (2) apparently simple, flagellomeres subequal in

length [10, 11, 15, 24]. Ordered 012. There is fossil evidence to support a composite flagellomere in the ground plan of anaxyelids but not in that of cephids (Rasnitsyn 1996). Additional data from Rasnitsyn (1996) were used in the present coding.

15. (Subdivision of 14:0 and 1) Number of flagellomeres beyond the composite first: (0) more than one; (1) one or none [4, 9]. Loss character.

16. (Subdivision of 14:0 and 1) Structure of flagellomeres beyond the composite one: (0) normal width; (1) thick [2].

17. Number of articles in male antenna: (0) more than 16 [0, 87]; (1) 16 [87]; (2) 15 [87]; (3) 14 [44, 54, 67]; (4) 13 [45, 46, 51, 66, 78, 93]; (5) 12 [47]; (6) 11 [39]; (7) 10 [70, 86, 89]; (8) 9 or less [71]. Ordered 012345678. This character was incompletely accounted for in R88, and the coding has been updated. Extant helorids have 16 articles and extant roproniids 14 (Naumann & Masner 1985). R88 erroneously specified the number of articles in the helorid and roproniid ground plan as either 14 or 15. Fossil roproniids had 14–24 articles (Rasnitsyn 1990) and the Jurassic helorid *Protobelorus mesozoicus* had 20 articles (Kozlov 1968). Both families are likely to have more than 16 articles in the ground plan (Rasnitsyn 1996). Taxa with a thick, composite flagellomere were coded as having more than 16 articles, although a much smaller number might actually be discernible. Tenthredinids are considered to have 9 articles or less in the ground plan although some extant representatives have more.

18. Number of articles in female antenna: (0) more than 16 [0, 52, 53, 87]; (1) 16 [38, 52, 53, 87]; (2) 15 [52, 54, 65, 87]; (3) 14 [44, 52, 67]; (4) 13 [46, 51, 66, 78]; (5) 12 [47, 93]; (6) 11 [39]; (7) 10 [42, 70, 71, 86, 89]; (8) 9 or less. Ordered 012345678. See comments under the previous character concerning complementary coding and for the helorid and roproniid states. Mymarommatids are considered here to have 13 articles in the female-antenna ground plan (R88). Extant female mymarommatids have maximally 11 articles, but the last article is evidently a composite structure (Gibson 1986). Fossil mymarommatid females had either 12 or 13 articles (Kozlov & Rasnitsyn 1979; Gibson 1986). Taxa with a thick, composite flagellomere were coded as having more than 16 articles, although a smaller number might actually be discernible. Tenthredinids are considered to have 9 articles or less in the ground plan although some extant representatives have more. Extant orussids have 10 flagellomeres in the female antenna, but APR considers the ground-plan number to be 12 in this sex based on fossil evidence (Rasnitsyn 1980: fig. 87).

19. Sexual dimorphism in the number of flagellomeres: (0) absent [39, 44, 46, 51, 52, 66, 67, 70]; (1) present [42,

45, 54, 71, 93]. Coding used here reflects characters 17–18 and not the states implied by R88, if conflicting.

20. Shape of flagellum in females: (0) straight; (1) distinctly bent [67].

21. Shape of apical part of flagellum of females: (0) simple, more or less cylindrical; (1) subclavate [65]; (2) strongly clavate [12, 67]. Ordered 012.

22. Structure of basal flagellomeres (F1-F3) in male antenna: (0) no basal flagellomere modified; (1) one of the flagellomeres excavated and equipped with a glandular ridge [57]; (2) one of the flagellomeres swollen and with a glandular area or peg [68]. Unordered. For more information, see Ronquist & Nordlander (1989), Ronquist (1995b), Bin & Vinson (1986), and Isidoro *et al.* (1996). Modifications of the male flagellomeres, often in the form of ridge-like structures and presumably associated with glands, are more widespread among the Apocrita than implied by the coding used here (e.g. Naumann & Masner 1985; Isidoro *et al.* 1996). It is possible that the states in diapriids, cynipoids and platygastroids form parts of a more complex transformation series involving states in other apocritan taxa, rather than being isolated apomorphies.

23. Multiporous plate sensilla on flagellum: (0) absent; (1) present [59–60, 66]. This character was coded after Basibuyuk & Quicke (1999), who recorded multiporous plate sensilla from many more taxa than those listed as having them in R88.

24. Structure of mandible: (0) not extremely long and curved; (1) very long, about half width of head, crossing for about full length at rest, curved, with two strong teeth in moving plane [14–15]. Xyelydidae fossils have both states and were coded as polymorphic.

25. Pubescence of hypopharynx: (0) well developed; (1) reduced [100]. Loss character.

26. Structure of thorax or mesosoma: (0) oblong; (1) short and high, strongly sclerotized [46].

27. Wings of females: (0) present; (1) absent [81, 87, 105, 107]. Loss character.

28. Length of pronotum medially in dorsal view: (0) long; (1) moderately short to short [3, 27, 44, 50, 57, 67, 74, 106, 113]. State 1 not mentioned for node 37 and 38 in R88 by mistake. Megalyrids are considered to have the pronotum long medially in the ground plan based on Mesozoic fossils (Rasnitsyn 1975b: fig. 54), although extant megalyrids have the pronotum short.

29. Pronotal-mesepisternal attachment: (0) loose attachment, often with one or a few interposed, small sclerites; (1) pronotum rigidly attached to anterior mesopleural margin [44, 50, 57, 67, 74, 106, 113]. State 1 was inadvertently omitted from nodes 3, 27, and 38–41 in R88. For helorids and megalyrids there is uncertainty concerning

the state in fossils; they were coded here as having state 1 based on extant representatives.

30. Pronotal lobe covering mesothoracic spiracle: (0) absent; (1) present, not enlarged but covering the spiracle in lateral view [28]; (2) enlarged, inflated [94]. Ordered 012. In nonaculeate apocritans, a distinct spiracular lobe is only present in the Stephanidae, Trigonalysidae, Gasteruptiidae, Evaniidae, and Ichneumonoidea (Gibson 1985). An indistinct lobe also covers the spiracle laterally in roproniids and monomachids. The codings in the present matrix were corrected accordingly. Brothers & Carpenter (1993: chars. 34–36) interpret this character complex differently in the Aculeata.

31. Position of spiracular occlusor muscle apodeme: (0) at about mid-height of posterolateral margin of pronotum; (1) close to ventral margin of pronotum [38–41].

32. Structure of propleura: (0) not contiguous ventromedially; (1) contiguous ventromedially [13].

33. Shape of profurca: (0) vertical; (1) proclined [80].

34. Prosternum: (0) exposed; (1) concealed [81, 87, 89]. This character was used only for chrysidoids in R88; the coding has been complemented for other hymenopterans. Extant megalyrids have the prosternum concealed but fossil specimens have different mesosomal structure and it is possible that they have the prosternum exposed. Until this is definitely shown, however, the family must be coded for the state occurring in extant forms.

35. Structure of median mesoscutal line: (0) sulcus with corresponding apodeme; (1) impression without apodeme [59]; (2) absent [37, 44, 49, 74, 80, 100]. Unordered. State 2 should also have been mentioned for node 96 and 97 in R88. A median mesoscutal sulcus is present in fossil sphecids (Baissodidae) (Rasnitsyn 1975b: 122, figs 135, 136, 137; Rasnitsyn 1988: 138), and this is considered here as the ground-plan state of sphecids although extant species lack a median mesoscutal line. Some argids, pterygophorids, tenthredinids, and cimbicids lack the median mesoscutal line (Benson 1938), as well as some stephanids (Gibson 1985), but the line is likely present in their ground plans. For additional information, see Gibson (1985).

36. Parapsidal signum: (0) absent; (1) incipient [26]; (2) well developed [28]. Ordered 012. State 0 was inadvertently omitted from nodes 38, 42, and 72 in R88. The signum is present in the Archaeocynipidae (Rasnitsyn, unpublished data).

37. Transscutal line or fissure: (0) absent; (1) represented by oblique mesoscutal grooves [24]; (2) represented by a straight, transverse transscutal fissure (line of articulation). Unordered. State 2 should have been mentioned for node 26 in R88. The mesonotal structure of siricids is distinctly different from that of xiphydriids, orussids and

apocritans (Gibson 1985). The hypothesis that these two states are homologous, as suggested in R88, is based mainly on phylogenetic relationships indicated by other characters and is difficult to defend solely on morphological evidence. In the present analysis, a separate state was therefore recognized for siricids and the feature treated as an unordered multistate character. Proctotrupids, most Ichneumonoidea, and some Cynipoidea and Chalcidoidea have the fissure only partly developed, but these cases evidently represent secondary reversals (Gibson 1985).

38. Sheath-like apodeme (axillar phragma) from anterior margin of axilla for the insertion of the tergal part of the mesotrochanteral depressor: (0) absent; (1) present [66 + mymarommatids].

39. Postspiracular sclerite: (0) present but incompletely detached from the mesopleuron (anepisternum); (1) present as a free sclerite; (2) absent [28]. Unordered. Loss character. State 2 should have been mentioned for node 18 in R88 (see Gibson 1985). The difference in structure between xyelids (state 0) and other symphytans with a postspiracular sclerite (state 1) (Shcherbakov 1980; Shcherbakov 1981; Gibson 1985, 1993) was inadvertently omitted from R88.

40. Prepectus: (0) large; (1) reduced in size [44–48, 50, 57, 67, 74–75, 113]; (2) absent [45]. Ordered 012. Loss character. State 1 should have appeared under nodes 37, 53, 95, 98, 102, 105, 106, and 110; and state 2 under nodes 4, 9, 12, and 16 in R88 (Gibson 1985; Vilhelmsen 1997b). Extant Megalyridae have been hypothesized to have a large exposed prepectus fused to the pronotum to enclose the spiracle (Gibson 1985). However, the absence of the occlusor muscle apodeme in the single megalyrid dissected so far makes this hypothesis uncertain. The occlusor muscle apodeme is primitively situated on the free prepectus and is one of the few indicators of the fate of the prepectus when the latter has been lost as an independent sclerite. Megalyrids were therefore coded as having state unknown for this character and others referring to the prepectus. Fossil megalyrids (at least the holotype of *Cleistogaster buriatica*, present observation) lack an externally exposed spiracle, indicating that the family may have had a small concealed prepectus in their ground plan. However, some extant megalyrids have an extremely small spiracle, and it may be that the spiracle is exposed in the fossils but has not been detected because of its small size (G. Gibson, personal communication).

41. Structure of prepectus (first variable): (0) exposed, visible externally [0, 66]; (1) concealed [24]. State 0 was inadvertently omitted from nodes 39–41, 50, and 67 in R88. Considered inapplicable when the prepectus is absent. Position of the spiracle on the pronotum or the presence of a netrion is taken here as evidence that the

prepectus is at least partly exposed (Rasnitsyn 1980) (for a different view, see Masner 1979; Gibson 1985). Megalyrids were coded as having state unknown (see char. 41).

42. Structure of prepectus (second variable): (0) not extending behind and above mesothoracic spiracle; (1) extending behind and above mesothoracic spiracle [44–48, 49]. State 0 should have been mentioned for node 66 in R88. Coded as inapplicable when the prepectus is absent, and unknown for the Megalyridae (see char. 41).

43. Structure of prepectus (third variable): (0) independent sclerite or not fused to pronotum; (1) fused to pronotum [38–41, 44–48, 50, 57, 67, 74–75, 89, 113]. Fusion character. State 1 should have been mentioned for nodes 37 and 53 in R88. Considered inapplicable when the prepectus is absent, and unknown for the Megalyridae (see char. 41).

44. Structure of prepectus (fourth variable). (0) independent sclerite or not fused to mesopectus; (1) fused to mesopectus [106, 111]. Fusion character. State 1 was inadvertently omitted from nodes 95, 98, 102, and 105 in R88. Considered inapplicable when the prepectus is absent, and unknown for the Megalyridae (see char. 40). The position of the occlusor muscle apodeme in apids, sphecids, mutillids, pompilids, scoliids and formicids supports the interpretation that these taxa have the prepectus fused to the mesopectus (Gibson 1985). See also Brothers & Carpenter (1993: chars. 48–53).

45. Structure of prepectus fused to pronotum: (0) not forming a ridge-like internal structure; (1) forming a ridge-like posterior pronotal inflection [44–48, 50, 57, 67, 74–75, 113]. State 1 should also have appeared under nodes 37 and 53 in R88. Coded as inapplicable when the prepectus is not fused to the pronotum or absent. State unknown for the Megalyridae (see char. 40).

46. Interrelation of prepecti: (0) not in broad contact ventrally; (1) in broad contact or fused ventrally, forming an annular pronotum if prepecti fused laterally to pronotum [50, 68, 84]. State 0 should have been mentioned for node 92 and state 1 for nodes 56 and 81 in R88. Many chalcidoids have the prepecti in broad contact or fused ventrally (Gibson 1985), but this is considered here to be secondarily derived within the group. Brothers & Carpenter (1993: chars. 48–53) interpret the character differently in aculeates. First, they consider scolebythids, plumariids, apids, and sphecids to have the prepecti in broad contact or fused medially. Second, they interpret prepecti in broad contact to be the plesiomorphic state for Aculeata. Apids and sphecids were coded here as having state unknown since the prepectus is fused to the mesopectus, and the exact delimitation of the area of prepectal origin is uncertain. We disagree with Brothers and Carpenter concerning the state for plumariids, scolebythids and the ancestral

aculeate. See also Brothers (1975) for additional information. Coded as inapplicable when the prepectus is absent.

47. Spinisternum: (0) independent sclerite; (1) attached to anterior margin of mesopectus [2–3]; (2) incorporated in mesothoracic venter anteromesally [5, 31–32]. Ordered 012. Fusion character. State 1 should have been mentioned for node 18 in R88 (Rasnitsyn 1969: 103).

48. Mesopseudosternal sulci *sensu* Shcherbakov (1980): (0) present, delimiting a pseudosternal area of the mesopectus; (1) absent or indistinct [11, 28]. Loss character.

49. Shape of mesopseudosternum *sensu* Shcherbakov (1980): (0) short, not reaching anterior mesopectal margin [0, 17]; (1) narrowly reaching anterior mesopectal margin [2–3]; (2) widely reaching anterior mesopectal margin [6–8]. Ordered 012. State 1 should have been included at nodes 21 and 22 and state 2 at node 18 in R88. Coded as inapplicable when mesopseudosternal sulci absent. Sepulcidae have both states 0 and 2.

50. Mesal articulation of mesocoxa: (0) close to the basal margin of the coxa; (1) far removed from the basal margin of the coxa [34]. Johnson (1988) regarded stephanids as having state 0, but the articulation in stephanids is slightly more distant from the basal margin of the mesocoxa than in most other taxa with state 0, as is evident from the illustrations in Johnson's paper. Thus, we follow R88 here in coding stephanids as having state 1. Some workers consider the 0 state in most microhymenopterans to be different from the state in symphytans (Gibson 1999), but here we follow the interpretation of APR.

51. Structure of mesosubpleuron: (0) subpleuron smoothly truncate posteriorly [105]; (1) subpleuron produced between mesocoxae [88]; (2) subpleuron with a lamella overlying mesocoxae [103]. Unordered. Mesoserphidae coded after a specimen of *Mesoserphus dubius* in which the mesosubpleuron could be observed (Rasnitsyn 1986a). Brothers & Carpenter (1993: chars. 56–57) interpret this character complex differently in the Aculeata. Rasnitsyn regarded chrysidids as having the subpleuron produced between the mesocoxae in the groundplan, and that this process was secondarily lost in most species except the Amiseginae, but Brothers and Carpenter coded chrysidids as having the subpleuron smoothly truncate posteriorly in the groundplan. According to Brothers and Carpenter, all aculeates except plumariids, chrysidids, dryinids, and scolytids have the subpleuron produced in some way, with bradynobaenids, formicids, scoliids and vespids having articular processes.

52. Structure of lateral arms of meso- and metafurca: (0) thin, not hollow; (1) thick, hollow [23].

53. Length of anterior arms of meso- and metafurca: (0) long; (1) short [23]; (2) very short [68]. Ordered 012.

54. Shape of anterior mesofurcal arms: (0) free; (1) fused for some distance [19].

55. Cenchri with associated area aspera and loop of anal vein in fore wing: (0) present; (1) absent [21, 31]. Loss character.

56. Structure of metasubpleuron: (0) more or less flat; (1) projecting anteromesally in females but not in males [81]; (2) projecting between mesocoxae as bicarinate plate in both sexes [88]; (3) elevated between meso- and meta-coxae [101]. Unordered. The coding for sphecids used here is based on the state in Sphecinae (state 0); most other sphecids have state 2. Brothers & Carpenter (1993: chars. 73–76, 78) interpreted this character complex completely differently in the Aculeata.

57. Relation between metacoxal and petiolar foramina: (0) foramina continuous; (1) foramina isolated [39]. State 1 should have been mentioned also for nodes 37, 38–41, 43, 49, 76, 86, and 91 in R88. Most ichneumonids have metacoxal and petiolar foramina isolated, and this was assumed here to be the ground-plan state of the family. The open condition is apparently found only in some apical clades, e.g. *Syrphoctonus* (Diplazontinae); *Stethantyx* (Tersilochinae), *Idiogramma*, and *Netelia* (Tryphoninae). Many braconids of various subfamilies have the foramina contiguous, whereas others have them isolated. The Braconidae were therefore coded as being polymorphic for this character. The foramina are likely to be isolated in the ground plan of chalcidoids (G. Gibson, personal communication).

58. Relation between first abdominal tergum and metapostnotum: (0) tergum movably connected with subvertical postnotum, deep and narrow transverse gap in front of tergum; (1) tergum and subhorizontal metapostnotum immovably abutting or fused, no gap but sometimes a broad furrow [28].

59. Structure of abutting metapostnotum (subdivision of 58:1): (0) strongly enlarged posteromesally to form propodeal triangle [95]; (1) slightly enlarged posteromesally, small and triangular in shape; [83]; (2) transverse, medium size, distinct [0]; (3) very short or absent, at least medially [92, 99, 100]. Ordered 0123. State 1 should have been mentioned for node 98 and state 3 for nodes 38, 41, 48, 50 (but not 51), 53, 54 (but not 56), 67, and 77 in R88. Plumariids have both states 1 and 2. Brothers & Carpenter (1993: chars. 63–65) coded this character complex completely differently in aculeates.

60. Structure of first abdominal tergum: (0) medially split; (1) not medially split [28].

61. Size of foramen between first and second abdominal segments: (0) no distinct constriction, foramen about as large as following intersegmental foramina; (1) propodeum sloping posteroventrally, posterior foramen dorsoventrally narrow but laterally wide, thus enhancing rocking movements between the segments [31]; (2) propodeum sloping

posteroventrally, posterior foramen dorsoventrally and laterally narrow [32–33, 73]. Ordered 012. State 1 was inadvertently omitted from node 21 in R88.

62. (Subdivision of 61:2) Position of small propodeal foramen on propodeum: (0) low; (1) high [43].

63. Articulation between first and second abdominal segments: (0) not involving specialized, elongate condyli; (1) involving a pair of distinct, tooth-like condyli [73]. Proctotrupids and some scelionids have unspecialized articular processes on the propodeum (Rasnitsyn 1968, 1988). They were coded here as having state 0.

64. Mesonotal part of the mesotrochanteral depressor: (0) present [66]; (1) absent [2–3, 43–44, 49, 74–75]. Loss character. The coding implied by R88 is incomplete and was complemented using Gibson (1985). Ceraphronoids were considered by R88 to lack the muscle, but this is not the case (Gibson 1985). The muscle is present in megalodontids (APR, unpublished data).

65. Mesopectal part of the mesotrochanteral depressor (mesofurcal-mesotrochanteral muscle, or its hypothesized homologue): (0) present; (1) absent [41, 66 (not *mym.*), 70]. Loss character. The coding implied by R88 is incomplete and was complemented using Gibson (1985). The muscle is absent in platygastriids (as observed in *Isocibus* sp.; R88) but present in megalodontids (APR, unpublished data).

66. (Subdivision of 65:0) Origin of the mesopectal part of the mesotrochanteral depressor: (0) lateral arms of furca; (1) partly or entirely from pleuron [48, 50, 69]. The coding implied by R88 is incomplete and was complemented using Gibson (1985). Megalodontids have this muscle originating from the lateral arms of the furca (APR, unpublished data).

67. Preapical tibial spurs: (0) present; (1) absent [11, 22]. Loss character. State 1 should have been mentioned for node 4 in R88. Siricidae are coded after Mesozoic Auliscinae (Rasnitsyn 1969); extant siricids lack preapical spurs.

68. Spines on outer surface of meso- and metatibiae: (0) spines absent or inconspicuous [0, 102, 105]; (1) strong fossorial spines [101]. According to Brothers and Carpenter (Brothers & Carpenter 1993: chars. 118–123), moderate to strong meso- and metatibial spines occur in a number of additional aculeate taxa, including formicids and pompilids.

69. Posterior (outer) protibial spur: (0) present [0, 41]; (1) rudimentary to absent [19]. Loss character. Stigmaphronidae have the spur either present or absent (Rasnitsyn 1975b). For further information, see Basibuyuk & Quicke (1995).

70. Mesocoxal base: (0) wide, basal foramen approximately as wide as coxa; (1) narrow, mesocoxa abruptly narrowed basally, diameter of basal foramen distinctly

smaller than maximum diameter of coxa [97, 109, 111]. State 1 should also have been mentioned for nodes 38–41, 49, 74–75, 81, 85, 89, 91, 105, and 107 in R88. See Johnson (1988) for additional information.

71. Inner (posterior) metatibial spur: (0) simple; (1) modified into a calcar [95, 110]. State 0 should have been mentioned for node 96 and state 1 for node 97 in R88. R88 listed this character as a synapomorphy of formicids and vespids, and possibly of apids and sphecids assuming that the simple spur in *Astata* (Sphecidae) and Apidae is a secondary reversal. However, APR now considers the modification in formicids to be too slight to be considered as a real synapomorphy of the taxa subtended by node 110. Therefore, formicids were coded as having an unmodified spur. According to Brothers & Carpenter (1993: chars. 132–133), pompilids and rhopalosomatids have one type of calcar, and heterogynoids (here treated as sphecids) and vespids a second type, a distinction which is not recognized here.

72. Pterostigma: (0) large, distinct; (1) small [59]; (2) absent [60, 66, 70]. Ordered 012. Loss character. State 1 was inadvertently omitted from nodes 42, 58, 69, and 87 in R88. Ronquist (1995b) argued that the reduction in cynipoids (excluding austrocynipids) must have been independent from that in other parasitic wasps because of differences in the structure of the stigmal remnant. The pterostigma is small but distinct in fossil and some extant diapiroids, and this is taken here to be the ground plan of the Diapiroidae.

73. Costal vein (C) of fore wing: (0) present; (1) absent [59, 66, 70]. State 1 should have been mentioned for node 69 in R88. Loss character.

74. Subcosta (Sc) of fore wing basal to anterior branch: (0) distinct, separate vein; (1) appressed to or fused with R, or lost [3, 26]. Loss character. State 1 was not mentioned for node 20 in R88 by mistake.

75. Anterior branch of subcosta (Sc) of fore wing: (0) present, at least as a crossvein in costal space; (1) absent [20, 28]. Loss character.

76. Costal cell of fore wing: (0) wide; (1) moderately narrow [22]; (2) very narrow [74]; (3) missing [39, 75]. Ordered 0123. Loss character. Rhopalosomatids have the costal cell missing (state 3) (Goulet & Huber 1993: 205); this was inadvertently omitted in R88.

77. First abscissa of Rs of fore wing (before joining M): (0) long; (1) short or absent [2, 21]. Loss character. State 1 should also have appeared at nodes 16 and 46 in R88.

78. (Subdivision of 77:0) Direction of first abscissa of Rs: (0) inclivous; (1) subvertical to reclivous [25, 32]. State 1 should also have been mentioned for node 18 in R88.

79. Vein $R_s + M$ of fore wing: (0) present [59]; (1) absent, at least basal to 1m-cu [39, 54, 61, 65, 76]. Loss character. Extant ichneumonids lack $R_s + M$, but the

vein is present in the fossil *Tanychora* (Townes 1973), and this is taken here as the ground-plan state of the Ichneumonidae.

80. Abscissa of radial sector (Rs) of fore wing between cell 1R (or 1R + 2R) and cell Rs (i.e. after distal branching of $R_s + M$): (0) present at least partly as tubular vein; (1) absent as tubular vein [4, 12, 39, 57, 66, 70, 83, 87]. Loss character. State 1 should also have been mentioned for node 65 in R88.

81. Structure of Rs of fore wing apically: (0) furcate; (1) not furcate [13]. State 1 was not mentioned for node 2–3 in R88 by mistake. Xyelotomids had the vein bifurcate in the ground plan as shown by the archaic representative *Pseudoxyela* (Rasnitsyn 1969: fig. 82, 1996).

82. Crossvein 1r of fore wing: (0) short, equal to or shorter than 2r; (1) long, longer than 2r [28]; (2) incomplete or absent [29, 32]. Ordered 012. Loss character. State 1 should also have appeared at node 21 in R88.

83. Crossvein 2r of fore wing: (0) present; (1) absent [6–8, 70]. Loss character.

84. (Subdivision of 83:0) Position of crossvein 2r of fore wing: (0) from middle of pterostigma to position basal to or close to 2r-m; (1) from apex of pterostigma to position distinctly distal to 2r-m [2]. Inapplicable to ceraphronids and taxa with the stigma absent.

85. Crossvein 2r-m of fore wing: (0) tubular; (1) nebulous [39, 50, 59]; (2) absent [23, 36, 47, 48, 49, 66, 70, 75, 80, 106]. Ordered 012. Loss character. Node 39 in Rasnitsyn (1988) should have had state 2 and nodes 60 and 106 state 0. Following R88, we assume here that r-m in Embollemidae is 3r-m secondarily displaced basally compared with 2m-cu.

86. Crossvein 3r-m of fore wing: (0) tubular; (1) nebulous to absent [29, 36, 38, 49, 66, 70, 86, 92, 109, 112]. Loss character. State 1 should also have appeared at node 99 in R88.

87. Media and cubitus of fore wing: (0) present, at least partly as tubular veins; (1) completely absent as tubular veins [39, 66, 70]. Loss character.

88. Shape of M + Cu and Cu: (0) curved or angular; (1) straight basal to 1m-cu, distinctly bent backwards at 1m-cu [18, 21, 26]; (2) straight throughout [49]. Ordered 012. Coded as inapplicable when M and Cu absent.

89. Crossvein 1m-cu of fore wing: (0) present; (1) absent [39, 57, 62, 66, 70]. Loss character. State 1 should have appeared at node 58 and not node 57 in R88. FR interprets this character differently in cynipoids (Ronquist 1995b).

90. Position of 1m-cu of fore wing: (0) meeting Cu_1 far from the fork of M and Cu; (1) meeting Cu_1 close to the fork of M and Cu [54]. Monomachids should have had state 0 in R88 (cf. Naumann & Masner 1985). Coded as inapplicable when 1m-cu absent.

91. Wing cell basal to 1m-cu of fore wing (cell 1m): (0) small to intermediate [38, 82]; (1) large [2, 21]. APR now considers that a reduction in the size of the cell was incorrectly used in R88 to distinguish Maimetshidae from other evaniomorphs (node 38) and plumariids from other chrysidoids (node 82). These taxa were coded here as having the plesiomorphic state.

92. Crossvein 2m-cu of fore wing: (0) tubular; (1) nebulous to absent [29, 36, 38, 48, 49, 66, 70, 80, 89, 109, 112]. Loss character. Node 46 instead of 48, node 77, and node 99 should have been mentioned as having state 1 in R88.

93. Crossvein cu-a of fore wing: (0) tubular; (1) nebulous to absent [39, 57, 66, 70]. Loss character.

94. Posterior anal vein (A_{2+3}) and cross-vein 1a of fore wing: (0) present; (1) A_{2+3} absent basal to 1a [29]; (2) A_{2+3} and 1a entirely absent [33]. Ordered 012. Loss character. State 2 should also have been mentioned under node 73 in R88.

95. Adventitious vein closing cell 2Cu (cell outside crossvein 1cu-a) posteriorly: (0) absent; (1) present [86, 89].

96. Shape of hind wing: (0) maximum width at base; (1) maximum width beyond anal region [55, 67]. State 1 should also have appeared at nodes 66, 82, 99, 107, 109, and 111 (but not 112) in R88.

97. Jugal lobe of hind wing: (0) separated from vannus [0, 48, 93]; (1) dedifferentiated, incorporated into vannus or lost [32, 109]. Loss character.

98. Number of distal hamuli: (0) numerous (1) reduced in number, almost always 3 [49, 82]. State 1 was inadvertently omitted at nodes 36, 38, 45, 47, and 81, and state 0 at node 50 (but not 51) in R88. Extant megalyrids have 2–6 hamuli (Basibuyuk & Quicke 1997), and were coded here as polymorphic. Extant orussids have 4–6 hamuli, which is less than most other taxa with state 0 (Basibuyuk & Quicke 1997), but they were coded here as having the plesiomorphic state since they never have as few as 3 hamuli.

99. Costa (C) of hind wing: (0) present; (1) absent (except possibly basally) [83, 85, 89, 90]. Loss character. State 1 should also have been mentioned at nodes 29, 36, 38, 43, and 49 in R88. Presence of a percurrent C in the hind wing of *Parnopes* (Chrysididae) is considered a reversal due to secondary increase in size (R88).

100. Radius (R) of hind wing: (0) R and Rs at least partly tubular; (1) Rs completely nebulous to absent [39, 44, 49, 65]; (2) Rs and distal part of R absent as tubular vein [83, 85, 90]. Ordered 012. Loss character. State 2 was inadvertently omitted from node 89 in R88. Mesoserphids have a small but tubular Rs (state 0), and not state 1 as implied by Rasnitsyn's (1988) tree (Rasnitsyn 1980). The percurrent R in Chrysis is interpreted to be a reversal due to secondary increase in size (R88).

101. Subcosta (Sc) of hind wing: (0) present; (1) absent [17, 83, 85]. Loss character. The loss of this vein was erroneously only mentioned for a few nodes in R88. The hind wing subcosta is only present in xyelids, pamphiliids, gigasiricids, karatavitids, some cimbicids, and some anaxyelids (Rasnitsyn 1980: 125 and fig. 91).

102. Crossvein 1r-m of hind wing: (0) tubular; (1) nebulous to absent [23, 29, 39, 44, 66, 82, 83, 85]. Loss character. State 1 was inadvertently omitted from node 70 in R88. The single r-m crossvein in anaxyelids is considered here to be 3r-m.

103. Direction of 1r-m of hind wing: (0) subvertical [65]; (1) reclivous [49, 77]. State 1 was inadvertently omitted from nodes 36, 37, 38, 45, 99, and 107 in R88. Extant formicids have r-m reclivous; the coding here is based on the Sphecomyrminae, which have r-m subvertical. Coded as inapplicable when 1r-m is absent.

104. Crossvein 3r-m of hind wing: (0) tubular; (1) nebulous to absent [29, 39, 44, 57, 66, 82, 83, 85]. Loss character. State 1 was inadvertently omitted from node 32–33 and 32–73 in R88. Among ephialtitids, 3r-m only exists in *Leptephialtites gigas* (Rasnitsyn 1975: fig. 19); this was assumed here to be the ground-plan state of the family.

105. Media + cubitus (M + Cu) and free media (M) of hind wing: (0) tubular; (1) nebulous to absent [39, 47, 66, 83, 85]. Loss character. State 1 should have been mentioned at nodes 50, 52, 66, 67, and 88 and state 0 at node 56 in R88. Roproniids were coded as having state 0 based on *Renyxa*; other roproniids have state 1.

106. Shape of media (M) of hind wing between M + Cu and r-m: (0) distinctly bent; (1) almost straight [74]. State 1 should have been mentioned at nodes 35, 56, 81, and 107 in R88. Considered inapplicable when this abscissa of M is short or absent. The character varies in extant trigonalids, but fossils have M distinctly bent (APR, unpublished data), and this is considered here to be the ground-plan state of the family.

107. Structure of M + Cu of hind wing: (0) convex from above; (1) concave from above [57].

108. Crossvein m-cu of hind wing: (0) tubular; (1) nebulous to absent [10, 29, 36]. Loss character. State 1 was inadvertently omitted from node 32 in R88.

109. Cell Cu in hind wing: (0) closed apically by cu-a crossvein; (1) closed apically by Cu, which is bent sharply posteriorly first and then apically just before the anal fold, there replacing free apical abscissa of A which is lost together with cu-a [35, 49]. Considered inapplicable when cell Cu is open laterally and vein Cu absent apically. State 1 should also have been mentioned at nodes 37 and 38 in R88.

110. First anal vein (A1) of hind wing: (0) tubular or nebulous; (1) spectral to absent [39, 44, 57, 65, 83, 85].

Loss character. State 1 was inadvertently omitted from nodes 36, 49, 89, and 91 in R88. Roproniids were coded as having state 0 based on *Renyxa*; other roproniids have state 1.

111. Length and shape of female metasoma: (0) short, laterally compressed [46]; (1) moderately elongate, slightly depressed [0]; (2) distinctly elongate and slender [50, 56]; (3) moderately elongate in normal repose but strongly extendable in length during oviposition [51]. Ordered 0123. State 0 should have been mentioned for node 60 in R88. The metasoma is laterally compressed in gasteruptiines, but this is regarded here as secondarily derived compared to the rounded metasoma of aulacines. The metasoma of roproniids is considered moderately elongate and slightly depressed in the ground plan based on the state in fossil roproniids and in *Renyxa* (Lelej 1994).

112. Structure of anterior metasomal sterna: (0) sclerotized throughout; (1) divided by longitudinal, membranous lines or stripes. State 1 should have been mentioned for node 74–75 in R88.

113. Structure of second abdominal segment (first variable): (0) tergum and sternum free sclerites; (1) tergum and sternum fused, with or without a visible suture, forming a distinct tubular or ringlike petiole in both sexes (the petiole may be very short and partly hidden) [36, 38, 46, 52, 56, 66, 71]. Fusion character.

114. Structure of second abdominal segment (second variable): (0) not forming a nodelike petiole set off from third abdominal segment; (1) forming a nodelike petiole in females but not in males [111]; (2) forming a nodelike petiole in both sexes [112]. Ordered 012.

115. (Subdivision of 113 : 1) Length of tubular petiole in females: (0) about the same length or longer than each of the following metasomal segments; (1) much shorter than each of the following metasomal segments, ringlike [38]. State 1 should also have been mentioned for node 59 in R88. The superficially ringlike structure in proctotrupids is only the specialized anterior part of the petiole, and is not considered homologous to the annular petiole of cynipoids and ceraphronoids. Chalcidoids often have a ringlike petiole, but it is uncertain whether this is a ground-plan feature; chalcidoids were therefore coded here as being polymorphic for this character.

116. Structure of posterior margin of second abdominal sternum: (0) distinctly overlapping anterior margin of third abdominal sternum; (1) weakly or not overlapping third abdominal sternum [88, 100]. State 1 should have been listed under node 99 in R88. Considered inapplicable when the petiole is tubular or when the second sternum is fused to the third. The variation in the structure of the posterior part of the second abdominal sternum in the Aculeata was coded differently by Brothers & Carpenter

(1993: char. 154). Considered inapplicable to forms with abdominal segment 2 tubular or ringlike, or with abdominal sterna 2 and 3 fused.

117. Structure of anterior margin of third abdominal sternum. (0) straight or smoothly curved [88]; (1) angularly notched [85].

118. Structure of anterolateral apophyses of abdominal sternum 3: (0) apophyses small, muscles mainly attached to elongated anterolateral corners of the sclerite; (1) apophyses large, finger-like, sclerite behind apophyses desclerotized [88]. Considered inapplicable to taxa with tubular or ringlike petiole (cf. char. 110) and those that lack the apophyses (Chrysididae, Braconidae). Rasnitsyn (1980) only examined chrysidoids; data for other groups were added from the literature (Duncan 1939; Michener 1944; Alam 1956).

119. Size of abdominal segment 3: (0) about the same length as other metasomal segments; (1) conspicuously enlarged [39, 70].

120. Shape of abdominal sternum 7 of females: (0) plate-like (not modified as below); (1) more or less conical, with short or no notches delimiting lateral lobes, apical slit narrow [102]; (2) depressed, flattened below, with long notches making apical slit wide [101]; (3) depressed, flattened below, with no notches, making apical opening small [105]. Ordered 0123. State 1 should have been mentioned for nodes 37, 41, 56, 83, 85, 91, and 93 in R88. Coded as inapplicable when sternum 7 is internalized or folded along midline in forms with laterally compressed metasoma, and as unknown for the Roproniidae because of uncertainty concerning the state of *Renyxa*. The transformation series hypothesis requires justification. The ventral flattening of the conical sternum can be explained as an adaptation, making the apex of the terebra more freely movable, if it is associated with opening of lateral notches. There is no such adaptive explanation for flattening of the sternum without associated changes in the apical slit. Therefore it is considered more likely that state 2 rather than state 3 evolved from state 1.

121. Structure of abdominal tergum 8 in females: (0) usually external and fully sclerotized, if internal then not desclerotized medially; (1) fully internal, desclerotized medially except for antecosta, spiracles hypertrophied [93]. Fusion and loss character.

122. Basal apophyses (posterior to apodeme) of abdominal tergum 9 in females: (0) present; (1) absent [79]. Loss character. Coded based on data from Oeser (1961), Copland & King (1971), Ronquist & Nordlander (1989), and Ronquist (unpublished data).

123. Cercus of female: (0) present; (1) reduced [79]; (2) absent [70, 93]. Ordered 012. Loss character. Accord-

ing to Brothers & Carpenter (1993: char. 198), the cercus is absent also in females of Chrysididae.

124. Structure of abdominal sternum 8 in males: (0) well sclerotized, not excised apically; (1) membranous, strongly excised apically [11]. Fusion and loss character.

125. Spiracles on abdominal segments 2–8: (0) well developed; (1) in both sexes strongly reduced or absent on 2–7, well developed on 8 [33]; (2) in females strongly reduced on 2–7, in males strongly reduced on 2–8; (3) strongly reduced or absent on 2–8 [37, 38–41, 67]. Ordered 0123. Loss character. Orussids (node 30) have state 2 (FR, unpublished data), and the coding implied by R88 was corrected accordingly. Serphitid females have the spiracles reduced on abdominal segments 2–7 but well developed on segment 8, as indicated by one well preserved specimen (Gibson 1986). However, the state is unknown in males. Serphitids were therefore coded as having either state 1 or state 2.

126. Apex of female metasoma and external visibility of ovipositor: (0) metasomal apex open at rest, ovipositor at least partially visible externally [51, 78]; (1) metasomal apex closed at rest, apical tergum and sternum fit each other concealing the ovipositor [30, 37, 39, 50, 53, 56, 58, 67, 68, 79]. The apical sternum of evaniids does not close the metasoma in rest, the ovipositor being concealed only by the terga. Evaniids were therefore coded as having state 0.

127. General structure of terebra: (0) small, clawlike [14]; (1) compact, sawlike [1a]; (2) long and thin, laterally compressed [0]; (3) needlelike, subcircular in section [22]. Ordered 0123.

128. Structure of second valvifer (first variable): (0) not divided; (1) subdivided by a deep postarticular incision into anterior and posterior, interconnected parts [79]; (2) fully bipartite, intra-articulated [80]. Ordered 012.

129. Structure of second valvula: (0) articulating basally with proximal part of second valvifer; (1) displaced apically, not articulating with second valvifer [90].

130. Valvilli on first valvula of ovipositor: (0) absent [98, 113]; (1) two lamellae attached separately by capitate base to fossae on the inner surface of the valvula; (2) a pair of lamellae borne on a single valvular outgrowth [79, 93]. Ordered 012. Rasnitsyn's (1980, 1988) interpretation of the Chrysididae is not correct; the present coding is based on Quicke, Fitton & Ingram (1992).

131. Structure of third valvula: (0) unisegmented; (1) divided into two segments [79]. See Rasnitsyn (1980: 100).

132. Furcula: (0) absent; (1) free sclerotization of membrane; (2) fused with base of second valvulae as evident from their elongated base [85, 89]. Unordered. State 1 should have been entered under node 79 in R88. A simple tendon-like sclerotization, as can be found in some

Braconidae (Oeser 1961: fig. 41), is not considered here to constitute a true furcula. Ichneumonids lack such a sclerotization.

133. Orientation of male genitalia: (0) not rotated (orthandrous) at rest; (1) orthandrous in pupa, rotated 180 degrees (strophandrous) in adult; (2) strophandrous in both pupa and adult [5]. Ordered 012. State 1 occurs in extant Xyelinae (Snodgrass 1941; Rasnitsyn 1980: 138), but the state is unknown for the extinct, archaic xyeline tribe Liadoxyelini. Blasticotomids have orthandrous and not strophandrous genitalia (Togashi 1970; Vilhelmsen 1997b).

134. Structure of male phallus: (0) parameres and aedeagus independent; (1) parameres and volsellae fused to form genital tube around aedeagus [65]. Fusion character.

135. Basal ring of male phallus: (0) free; (1) fused to rest of phallus [66]. State unknown for austroiniids (cf. Gibson 1985). Fusion character. A megalyrid (*Megalyra fasciipennis*) was dissected by APR (unpublished data) and was found to have a large, free basal ring.

136. Cuspis of male phallus: (0) present; (1) absent [50, 53, 54–55, 65]. Loss character. State unknown for austroiniids (Gibson 1986). A megalyrid (*Megalyra fasciipennis*) was dissected by APR (unpublished data). This species had a volsellar lobe without delimited digitus or cuspis. Because it is uncertain whether the volsellar lobe includes the cuspis, Megalyridae were coded here as having state unknown. Contrary to the claims of Gibson (1986), the cuspis is present in Ibaliidae (Ronquist & Nordlander 1989). However, it may be absent in other cynipoids (cf. Gibson 1986), and so it is coded absent here for figitids and cynipids.

137. Gonomaculum (apical membranous disc) of male phallus: (0) present; (1) absent [2–3, 20, 28]. Loss character.

138. (Subdivision of 137:0) Position of gonomaculum: (0) apical; (1) subapical [13].

139. Habitat of larva: (0) externally on plant [8, 11]; (1) externally or subinternally on plant under silk tent [0, 1a, 1415]; (2) internally in plant [4, 28, 63]; (3) in rotten plant material or in soil [50, 78]; (4) inside shelter made by host — cocoon, ootheca, etc. — but otherwise exposed; (5) externally on free-living, active host [85, 89, 99]. Unordered. The coding in R88 is incomplete and was complemented using information from Gauld & Bolton (1988), Goulet & Huber (1993), and Ronquist (1995b) except that R88 was followed in treating state 2 as primitive for the Chalcidoidea and Ichneumonoidea and state 3 as primitive for most Aculeata. The R88 tree implies that Macroxyelinae and Xyelinae larvae feed in male conifer cones (state 1). However, Xyelinae larvae feed both in cones (state 1) and inside shoots (state 2), and Macroxyeli-

nae larvae feed inside shoots (state 2) and externally on leaves (state 0) (Smith 1979; Gauld & Bolton 1988).

140. Larval protective behaviour: (0) larva not protected by case; (1) larva protected by a case constructed from the egg shell and previous larval skins [86, 99]. State 1 should also have been listed under node 89 in R88; larvae of embolemids construct cases like dryinids and rhopalosomatids (Brothers & Carpenter 1993; Goulet & Huber 1993).

141. Larval feeding mode: (0) phytophagous [63, 96]; (1) carnivorous [28]. The coding of the Electrotomidae is based on its morphology (Rasnitsyn 1977).

142. Food of phytophagous larva: (0) nonangiosperm plants; (1) angiosperms [18, 21, 27]. The coding implied by R88 is incomplete and was complemented with data from Gauld & Bolton (1988) and Goulet & Huber (1993). The Electrotomidae were coded as feeding on conifers because the fossil larval specimens are embedded in conifer resin (Rasnitsyn 1977). Coded as inapplicable to carnivorous larvae.

143. Feeding behaviour of carnivorous larva: (0) feeding externally on host (ectoparasitic); (1) feeding internally in host, at least in early instars (endoparasitic) [49]. State 1 should have been listed under nodes 37 and 42 in R88. Rasnitsyn (1988: 126) supposed that fully ectoparasitic development evolved secondarily in chalcidoids. However, most chalcidoids are ectoparasitic and the groundplan structure cannot be determined with confidence based on current evidence. The Chalcidoidea were therefore coded as polymorphic for this character. Evaniids are endoparasitic according to some authors (Brown 1973) and ectoparasitic according to others (Edmunds 1954), and were coded here as having state unknown.

144. Host of carnivorous larva (first variable): (0) Coleoptera [50, 62]; (1) Hymenoptera: Symphyta [28, 62]; (2) Hymenoptera: Apocrita [92, 102, 105]; (3) Diptera [54–55]; (4) Lepidoptera; (5) Neuroptera; (6) Thysanoptera; (7) Blattodea [46–48]; (8) Homoptera [89]; (9) Arachnida [98]; (10) Orthoptera [99]; (11) Embioptera [87]. Unordered. Considered inapplicable to phytophagous larvae. The coding implied by R88 is incomplete; data have been added from Gauld & Bolton (1988) and Goulet & Huber (1993) except that the ground-plan assumptions of R88 were accepted when reasonable. Following R88, the ground-plan host of chrysidids and mutillids is assumed to be apocritans, and the ground-plan host of sphecids is considered unknown. The vespidae coding is based on the state in the Euparaginae.

145. Host of carnivorous larva (second variable): (0) endopterygote; (1) exopterygote [85, 94]; (2) noninsect. Ordered 012. Coding implied by R88 complemented with data from Gauld & Bolton (1988) and Goulet & Huber (1993). Considered inapplicable to phytophagous larvae.

146. Stage of host primarily eaten by carnivorous larva: (0) larva, nymph or adult [28, 50, 55, 79, 105]; (1) egg [46–48, 67]. State 0 should have been mentioned for node 70 in R88 (Gauld & Bolton 1988; Goulet & Huber 1993). Chalcidoids were coded as polymorphic for this character because of uncertainty concerning the ground-plan state. Aulacines oviposit into the host egg but feed on later instars whereas gasteruptioneans eat the host egg; the former condition (state 0) is considered here to be primitive for the Gasteruptioneidae.

147. Oviposition behaviour of females: (0) female finds larval food (plant, host or prey) first, then oviposits; (1) female oviposits first (in empty nest), then finds prey [108–110].

148. Intrasegmental annulation: (0) present; (1) absent [22]. Loss character.

149. Larval eye: (0) present; (1) absent [22]. Loss character.

150. Relative position of larval eye and antenna: (0) eye above level of antenna; (1) eye below level of antenna [1b]. Coded as inapplicable to those lacking the larval eye.

151. Distance between larval eye and antenna: (0) short; (1) long [5, 14–15]. Coded as inapplicable to those lacking the larval eye.

152. Segmentation of larval antenna: (0) more than three segments/articles; (1) three segments [6]; (2) one segment [8, 12, 28]. Ordered 012. Loss character. In addition to the taxa mentioned by R88, xiphydriids and anaxyelids have three-segmented antennae and siricids have one-segmented antennae (Gauld & Bolton 1988).

153. Incisive molar flange of larval mandible: (0) present; (1) absent [5]. Loss character.

154. Larval metathoracic spiracle: (0) present, well developed; (1) rudimentary, nonfunctional [104]. Loss character. State 1 should have been listed under nodes 6, 12, 16, 27, and 74–75 in R88. Pompilidae (node 98) also have the metathoracic spiracle reduced (Brothers & Carpenter 1993). In many Symphyta, the metathoracic spiracle is small but functional (Rasnitsyn, unpublished data); thus, our coding differs somewhat from the information in Yuasa (1922). Stephanids, megalyrids, and trigonalids were coded after Vilhelmsen (1997b: char. 92).

155. Larval thoracic legs: (0) well developed and distinctly segmented with segments of different size; (1) shortened, with segmentation simplified (segments of equal size) [14–15, 19]; (2) vestigial, unsegmented [22]; (3) completely absent [28]. Ordered 0123. Loss character. Most cephid larvae have the thoracic legs unsegmented. However, in *Syrista* the legs are very short but still distinctly segmented (Rasnitsyn 1969: fig. 257). Cephidae were therefore coded as having state 1 in the ground plan.

156. Larval prolegs: (0) present; (1) absent [13]. Loss character. State 1 should also have been mentioned for nodes 4 and 7 in R88; the prolegs are absent both in blasticotomids (Lorenz & Kraus 1957) and in electrotomids (Rasnitsyn 1977). In addition, they are extremely reduced, but still present, in Xyelinae and some Macroxyelinae (Smith 1967).

157. Structure of larval prolegs: (0) unsegmented; (1) two-segmented [11]. Coded as inapplicable when prolegs are absent.

158. Subspiracular and suprapedal lobes of larva: (0) separate; (1) fused [6]. Coded as inapplicable when these lobes are absent.

159. Longitudinal and oblique sulci of larval abdominal sterna: (0) present; (1) absent [13]. Loss character.

160. Subanal appendage of larva: (0) present; (1) absent [11, 19]. Loss character. Contrary to the implications of R88, the subanal appendage is absent in the Electrotomidae (Rasnitsyn 1977) and present in the Cephidae (Rasnitsyn 1969). The subanal appendages are absent in the Arginae (Lorenz & Kraus 1957), but are likely to be present in the ground plan of the Argidae.

161. Segmentation of subanal appendage of larva; (0) unsegmented [0, 8]; (1) segmented [2–3, 13]. The appendage is segmented in some cephids, as seen in *Syrista* (Rasnitsyn 1969: fig. 257), and this state is assumed here to be primitive for the family. Coded as inapplicable when the subanal appendage is lacking.

162. Position of subanal appendage: (0) removed from base of anal slit; (1) situated at base of anal slit [13]. Coded as inapplicable when the subanal appendage is lacking. State 1 should also have been mentioned for node 4 in R88.

163. Supraanal horn of larva: (0) absent [0, 28]; (1) present [19].

164. Salivary gland: (0) capable of producing silk; (1) not capable of producing silk [19]. Loss character. State 0 was inadvertently omitted from node 73, and should have been mentioned at node 22 instead of 19. Gasteruptioneans, scelio-nids, and many chalcidoids spin cocoons, but the silk is not produced by salivary glands but by anal secretion from a pair of hypertrophied Malpighian tubules (Malyshev 1964, 1968; Rasnitsyn 1980:83). Thus, these taxa are coded here as having state 1. The character was coded as unknown for trigonalids; they spin cocoons (Clausen 1929; Yamane 1973), but it is not known whether they use the salivary glands or anal secretions for this.

165. Common envelope of larval salivary gland: (0) absent; (1) present [13].

166. Larval salivary glands: (0) without secondary ducts; (1) with secondary ducts [8].

167. Shape of salivary duct in cross-section: (0) rounded; (1) quadrangular [13]. Quadrangular salivary duct was only

explicitly recorded from the Siricidae by Maxwell (1955), but pamphiliids, cephids and xiphytriids were mentioned as having the same state as siricids in the summary of the paper (Maxwell 1955: 106).

168. Size of salivary duct: (0) narrow; (1) wide [11]. The end of the last sentence under node 11 in R88 reads ‘...and with ductus of salivary gland ...’. It should read: ‘...and with wide ductus of salivary gland ...’.

169. Arrangement of glandular cells of salivary gland duct of larva: (0) not arranged into distinct rows; (1) arranged into two distinct rows [11]. A state similar to state 1 also occurs in xyelids (Maxwell 1955), but we follow R88 in coding xyelids as having state 0.

Deleted characters

Characters used in R88 but omitted here are listed below:

1. Mandible of cutting type [93]. APR no longer considers the simple distinction between chewing and cutting type of mandible in aculeates as a good indicator of higher-level relationships.
2. Basal ring of femur absent on at least one pair of legs but not on all [50]; absent on all legs [69, 82]. APR now regards this as an unreliable higher-level character because of considerable intrataxon variability.
3. Tarsal arolium and orbicula small [100]. APR now considers this character to involve too subtle differences to be a reliable indicator of higher-level relationships.
4. Radius (R) of fore wing joining C before pterostigma [1a]. APR now considers this character to be incorrect, since G. Gibson (pers. comm.) has convincingly shown that there is a weak connection between C and R before the pterostigma also in xyelines.
5. Wing cell above Rs of hind wing minute [49]. This state is only observable in Mesoserphidae (Rasnitsyn 1980); all other proctotrupomorphs have lost Rs, making it impossible to determine the size of the cell above Rs.
6. Hind wing crossvein 1r-m meeting R distinctly basad distal group of hamuli [0, 54, 65]; meeting R near distal group of hamuli [49]. This character is now considered unreliable for higher-level relationships by APR.
7. Hard metasomal sterna (convex when dried), at least in female [37, 78–79]. APR now regards this as a poor character.