

# Review of morphological evidence on the phylogeny of basal Hymenoptera (Insecta), with a discussion of the ordering of characters

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*Received 5 August 2002; accepted for publication 17 March 2003*

In a previous study of the phylogeny of basal Hymenoptera, Vilhelmsen (2001; *Zool. J. Linn. Soc.* **131**: 393–442) compiled an extensive morphological data matrix for a phylogenetic analysis of basal Hymenoptera, comprising 38 hymenopteran genera. In this study, his characters are revised. This results in a cladogram whose relationships largely agree with those proposed by Vilhelmsen, except that the relationships at the base of the Hymenoptera are unresolved. The revised data matrix is expanded by 17 sawfly and three apocritan taxa. Moreover, 112 new morphological characters from different parts of the larval and adult morphology are also added to the data matrix, including 82 from a recent study of the terminal abdominal segments of male Hymenoptera. The addition of the new characters leads to Xyelidae, again, being the sister-group of all other Hymenoptera. The relationships among the sawfly families as proposed by Vilhelmsen are confirmed, except that the relationships among *Syntexis*, Siricidae and Xiphydriidae + Vespina are unresolved and that the monophyly of Apocrita is not convincingly supported. A separate analysis is performed which includes all extant genera of Xyelidae. The internal phylogeny of Xyelidae is determined as ((*Macroxyela Megaxyela*) *Xyelecia* (*Xyela Pleroneura*)). © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, **79**, 209–243.

ADDITIONAL KEYWORDS: morphology – ordering characters – sawflies – Symphyta – wings – Xyelidae.

## INTRODUCTION

Recently, many morphological characters for the basal lineages of Hymenoptera (sawflies) have been compiled by Vilhelmsen (2001) for phylogenetic analysis. His data matrix contains 236 characters, which were coded for six outgroup taxa, 32 sawfly genera from all 14 families, and six apocritan genera. It includes characters from his detailed studies of the mouthparts, preoral cavity and other parts of the head including antennae (Vilhelmsen, 1996, 1997a, 1999), the cervix and prothorax (Vilhelmsen, 2000a), the metathorax and anterior abdomen (Vilhelmsen, 2000b), and the ovipositor (Vilhelmsen, 2000c). Other character systems that are well represented in his data matrix are the mesothorax (Gibson, 1985; Heraty, Woolley & Dar-

ling, 1994), legs (Basibuyuk & Quicke, 1995), wings (Rasnitsyn, 1988; Basibuyuk & Quicke, 1997; Ronquist *et al.*, 1999) and larval morphology (Yuasa, 1922).

Since the publication of that data matrix, more character systems have been scrutinized. Schulmeister made detailed studies of the male external genitalia and internal reproductive organs (in press) and the tarsal plantulae (2003a). Sharkey & Roy (2002) revised Ronquist *et al.*'s (1999) wing characters. The purpose of the present paper is to combine the characters of Vilhelmsen (2001) with the characters from the recent studies of Schulmeister (2003a; in press) and Sharkey & Roy (2002) and some new morphological characters presented here.

Prior to combining these characters, I review and enlarge the data matrix of Vilhelmsen (2001). First, the coding and ordering of his characters are examined and in some cases revised, often based on examination of transformation series. Then, new taxa are

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added to his data matrix. Before making these changes I outline my approach for ordering morphological characters.

The combination of the new characters with the revised and enlarged data matrix of Vilhelmsen (2001) will lead to the most comprehensive morphological analysis of basal Hymenoptera to date, analysing 343 characters in total and covering 58 hymenopteran taxa. It will be shown that, in spite of the addition of this large amount of new data, the relationships of Vilhelmsen (2001) are largely confirmed.

## MATERIAL AND METHODS

For sawfly taxa the same species, or at least genera, were examined as those selected by Vilhelmsen (2001). In some of the outgroup taxa or apocritan taxa closely related genera were chosen due to lack of material. A number of operational taxonomic units (OTUs) were added to those used by Vilhelmsen (2001), to better test the monophyly of Tenthredinidae and Pergidae and to examine the internal phylogeny of Pamphiliidae and Siricidae. Appendix 1 lists the species used by Vilhelmsen (2001) and those included in this study; it also gives the names of the OTUs.

Most specimens were fixed in Bouin's fluid and kept in ethanol (70%) until preparation. Some were pinned museum specimens. Dissections were carried out under a Zeiss stereomicroscope Stemi SV 11 (maximum magnification 66×).

The data matrices were analysed with PAUP version 4.0b10 (Swofford, 1998) with default settings (initial tree generated with stepwise addition of taxa, hold = 1, TBR branch swapping, MulTrees = yes, Keep = no, Nbest = all, AllSwap = no, ReconLimit = infinity, ChuckScor = no) except that 1000 random sequence additions were used. Strict consensus trees were created after removing branches with a minimum length of zero (condense collapse = MinBrLen). Bremer support values were generated one by one, performing converse constraint analyses in PAUP.

## REVISION OF THE DATA MATRIX OF VILHELMSSEN (2001)

### ORDERING CHARACTERS

Before going on to revise the data of Vilhelmsen (2001), I want to give an explanation of the approach taken in the present paper for ordering and coding characters. My intention is not to provide an exhaustive discussion or a set of perfect solutions, but rather to outline my methods and to put some ideas out into the open to invite discussion of these issues.

The delimitation and ordering of character states is a complex and controversial issue. It has been discussed by Mickevich (1982), Pogue & Mickevich

(1990), Mickevich & Weller (1990), Hauser & Presch (1991), Wilkinson (1992), Hauser (1992), Lipscomb (1992), and Schuh (2000: 90–96), among others.

In principle, there are two ways to approach the problem, and both have deficiencies. First, character states can be ordered by similarity, without any reference to a tree, i.e. based on the imagination of the scientist. This approach, known as morphocline analysis, is obviously flawed because of its subjectivity. But the same approach is taken when delimiting the character states themselves – similar conditions are represented by the same character state – and therefore can hardly be excluded from morphological analysis anyway. Second, the states of a character can be mapped on a tree and the order of the states can be devised to reflect the deduced evolution of the character. This is problematic in so far as the decision is dependent on the 'starting point': if the phylogenetic hypothesis is wrong, the decision on whether and how to order the character in question could also be wrong.

The best compromise is probably to take both arguments into account by means of Hennig's reciprocal illumination ('checking, correcting, and rechecking'). If it can be imagined that a character can change directly from one state to any other, then this is an indication that the character should be treated as unordered. Those characters for which it is difficult to imagine that a change from some state X to state Z could have occurred without proceeding through state Y should be examined further. The decision as to whether to treat a character as ordered or unordered should not be based solely on the imagination of the scientist. As Mickevich (1982: 462) pointed out: 'theories of character change cannot properly be based only on prior speculation, but begins instead with the analysis of character patterns between taxa on a cladogram.' The assumption regarding the order of the character states should hence be examined in the light of background knowledge. If the assumed order of the character states is confirmed by the cladogram it should be implemented.

However I believe that the implications and effects of the ordering of characters should also be taken into consideration. For example, even if it is argued that the transition from state 0 to state 2 must have occurred by passing through state 1, but no close relatives of the taxa having state 2 actually exhibit state 1, then ordering this character would unnecessarily give double weight to the transformation from state 0 to state 2. This is no problem for a character in which state 1 and state 2 have been derived independently from state 0, but is somewhat problematic for a character that shows a transformation from state 0 via state 1 to state 2 in one part of the tree, and a direct transformation from state 0 to state 2 in another part of the tree.

Character 65 of Vilhelmsen (2001) is a good example of such a character; the ordering is justified but not without problems. The evolution of this character has been mapped onto the cladogram in Figure 1. The out-group taxa and most Hymenoptera have the prospinasternum entirely separate from mesosternum (state 0). Blasticotomidae have state 1 for this character (prospinasternum closely associated with mesosternum) and their sister-group, the Tenthredinoidea s.s., have state 2 (prospinasternum entirely fused with mesosternum). Apocrita also have state 2. It makes sense to order this character because state 1 is clearly intermediate between state 0 and state 2. In addition, ordering is justified because state 1 and state 2 are found in sister-groups. If the character was treated as unordered, the optimization of the character at the base of Tenthredinoidea s.l. would be ambiguous, and the character would not support the monophyly of Tenthredinoidea s.l. If, however, the character is treated as ordered, this causes the single transformation from state 0 to state 2 at the base of Apocrita to be counted as two steps. On one hand, this can be regarded as reasonable because it is a more significant transformation that might have covered two minor transformations from 0 to 1, and from 1 to 2. On the other hand, in this area of the tree it is just one evolutionary transformation, and if this is assigned a weight of two, why not assign a higher weight to other transformations as well? Moreover, if Blasticotomidae had not been included in the analysis, the intermediate state would not be observed, the character would be coded in two states and the transformation at the base of Apocrita would count only as one step. The question as to whether the transformation at the base of Apocrita is counted as one or two steps may not seem like an important issue. However, it turns out that in the final analysis of this paper, the monophyly of Apocrita depends on whether this transformation is counted as one or as two steps.

My opinion is that in an analysis like this, in which the vast majority of transformations, no matter how significant, are counted as just one step, one should have a convincing reason for giving a certain transformation twice as much weight as most others. One reviewer (of an earlier version of this paper) commented that 'when similarity is observed to be nested, it is properly scored as such' and that doing otherwise would be 'a logical mistake'. However, my argument is that in the example above, in which state 2 can be assumed to be nested within state 1 in the Tenthredinoidea s.l., state 2 is not nested within state 1 in Vespina. Another alternative, in addition to treating this character as ordered or unordered and weighting it equally to the other characters, is to give the entire character half as much weight as the other characters.

Finally, it must be noted that if different features of

a morphological structure have been combined into one character, the matter is entirely different and the reasoning above does not apply (see the discussion of character 20 below).

In recoding the data of Vilhelmsen (2001), I have also tried to avoid counting two dependent transformations twice. If two characters which are presumed to be dependent, are found to transform at the same node of the cladogram, this constitutes evidence in favour of the presumed dependencies. Or, as Pogue & Mickevich (1990: 319) put it: 'Independence is instantly recognized when differing hypothetical characters delimit different subsets of taxa.'

#### CHANGES TO THE CODING AND SCORING

Vilhelmsen's (2001) data matrix included 236 characters: 40 from Rasnitsyn (1988) as coded by Ronquist *et al.* (1999), 14 from Heraty *et al.* (1994), 12 from Basibuyuk & Quicke (1995, 1997, 1999), nine from Königsmann (1976, 1977), nine from Gibson (1985, 1986), eight from Yuasa (1922), five from Johnson (1988), four from Quicke *et al.* (1994), three from Whitfield, Johnson & Hamerski (1989), three from Kristensen (1991), two from Goulet (1993), one from Oeser (1961), one from Paulus (1979), one from Mickoleit (1966), and 124 from his own studies (Vilhelmsen, 1996, 1997a, b, 1999, 2000a, b, c).

In this section, I change the scorings of some of these characters for certain taxa and the delimitations of the states of some characters. In some cases I decided to exclude characters from phylogenetic analysis. In addition I code previously unknown states for some taxa. All the changes are mentioned and discussed below. The revised version of Vilhelmsen's data matrix is shown in Appendix 2.

Character 9 (tormae): the state of *Megalodontes cephalotes* was changed from unknown to 0 (distinct apodemes continuous with the labrum and receiving the posterior labral retractors present, not continuous medially).

Character 12 (labral compressor muscles): the state of *Urocerus* was changed from unknown to 1 (absent).

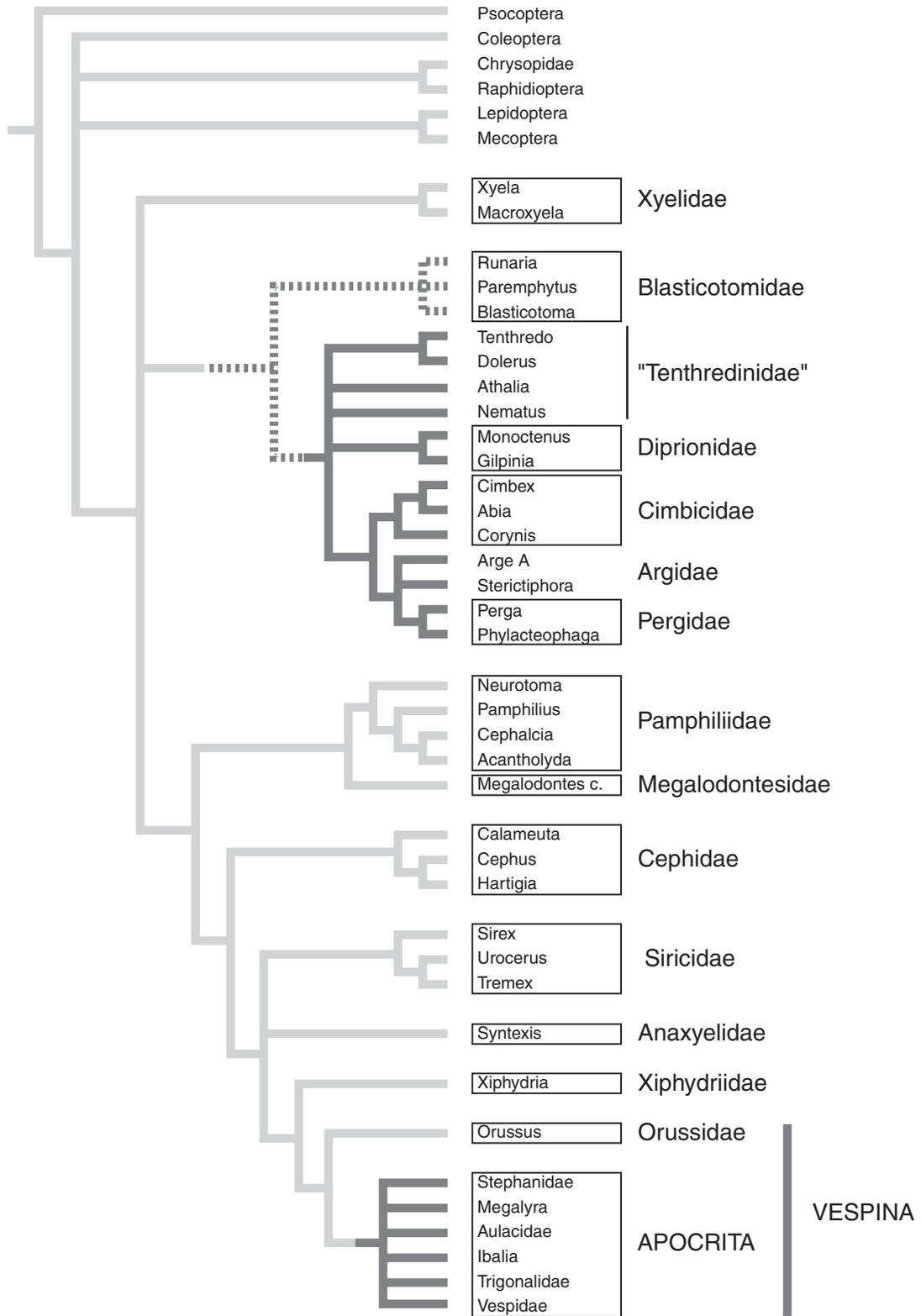
Character 13 (anterior labral retractor muscles): the state of *Urocerus* was changed from unknown to 1 (absent).

Character 14 (mandibular foramina): the state of *Runaria* was changed from unknown to 0 (confluent with the oral foramina).

Character 25 (multiporous plate sensilla): the state of *Runaria* was changed from unknown to 0 (absent).

Character 26 (mandibles): the state of *Runaria* was changed from unknown to 0 (neither highly asymmetric nor extremely long and curved).

Character 33 (shape of glossa): the state of *Runaria* was changed from unknown to 0 (flat).



**Figure 1.** Unordered analysis of the revised version of the data matrix of Vilhelmsen (2001). The cladogram is a strict consensus of 122 trees of 823 steps. The evolution of character 65 has been mapped onto the cladogram: state 0 is represented by light lines, state 1 by dashed lines, and state 2 by dark lines.

Character 34 (paraglossae): the state of *Runaria* was changed from unknown to 1 (flattened, with scale-like microtrichia in transverse rows).

Character 36 (rod-like sensilla on labial palp): the state of *Neurotoma fasciata* was changed from unknown to 1 (specialized sensilla on distal labial palp segment present, not situated in invagination). *Acantholyda* sp. also seems to have state 1. Vilhelmsen (2001) coded *Pamphilius sylvaticus* as having state 0. However, *Pamphilius middlekauffi* clearly has state 1 (as does *Pamphilius hortorum*), therefore I changed the coding of *Pamphilius* from 0 to {0,1}. *Cephalcia* sp. was checked by scanning electron microscopy and found to have state 1 as well.

Character 38 (postmentum): the postmentum of *Cephalcia* sp. (*abietis* or *arvensis*) is difficult to see, but its presence is indicated by the long setae that insert on it. The presence of the postmentum is more obvious in *Cephalcia* sp. (*fallenii*?) whose coloration is darker. The examined specimen of *Pamphilius hortorum* shows a minute pair of remnants of the postmentum. The states of *Cephalcia* and *Pamphilius* were therefore changed from 1 to 0 (present). The presence of the postmentum in *Acantholyda* was confirmed in one specimen of *Acantholyda* sp. (*erythrocephala* or *flaviceps*). The examined specimen of *Neurotoma fasciata* showed no remnant of a postmentum and the scoring of Vilhelmsen (2001) is hence confirmed.

Characters 43 (dorsal cervical sclerites) and 45 (position of cervical prominences): the dorsal cervical sclerites were coded as absent by Vilhelmsen (2001) in many taxa in which they are merely fused with the propleura, as can be seen by the insertion of setae, which are present on the cervical sclerites, but not on the propleura. Therefore, I recoded character 43 as dorsal cervical sclerites (Vilhelmsen, 2000a: character 5): 0 = absent; 1 = present, but fused to the propleura; 2 = present, separate from the propleura. Unordered: *Sterictiphora*, Pamphiliidae, and Cephidae were then assigned state 0 for character 45, because it only looks as if the cervical prominences are ventral to the anterodorsal corners of the propleura due to the presence of the fused cervical sclerites. However, because the loss or fusion of the cervical sclerites is gradual and difficult to assign with certainty, I chose to exclude character 43 from subsequent analyses. The states of character 45 are also difficult to distinguish, especially in those Apocrita where the laterocervicalia are fused to the pronotum, and this character was also excluded from the analyses.

Character 71 (posterior apical protibial spurs): Chrysopidae, Raphidioptera, and *Micropterix* were coded as inapplicable, because the homology was unclear. The entry for *Runaria* for character 71 was changed from state 0 to state 1 (reduced or absent).

Character 76 (setae on anterior part of probasitarsi): state 0 and 3 of this character were summarized. The new character state delimitation is: paddle-shaped setae on the anterior part of probasitarsi (Basibuyuk & Quicke, 1995: character K): 0 = absent, 1 = one row present, 2 = several rows present. Unordered: the state of *Tenthredo* was changed from 1 to 0, as observed in *T. mesomela*. The state of *Orthogonalys* was changed from inapplicable to 0.

Character 88 (pseudophragma of mesopostnotum): following Heraty *et al.* (1994), I changed the coding of *Orthogonalys pulchella* from 0 to state 1 (second phragma with a pair of lobes (pseudophragma) projecting anteriorly of the connection between the mesoscutellum and the mesopostnotum).

Character 89 (lateral attachment points of the mesopostnotum with the mesepimera): I assume that the absence of a connection between the mesopostnotum and the mesepimeron (state 2) is caused by the internalization of the mesopostnotum in the same clade and is hence already coded as state 2 of character 87. Therefore, I coded state 2 of character 89 as inapplicable to avoid giving undue weight to the internalization of the mesopostnotum. The character is hence reformulated as: lateral attachment points of the mesopostnotum with the mesepimera (Heraty *et al.*, 1994: character 10): 0 = broad and exposed; 1 = invaginated. Coded as inapplicable if the lateral attachment points are reduced due to internalization of the mesopostnotum.

Character 95 (occlusor muscles of the posterior thoracic spiracles): the coding for *Tenthredo* was changed from unknown to 1 (arise from the posterior margin of the mesepimera ventrally of the spiracles), as observed in *T. mesomela*.

Character 97 (configuration of mesopseudosternal sulci): all species that were coded as having state 1 for character 96 (mesopseudosternal sulci at most shallow grooves without internal ridges) were coded as inapplicable for character 97 by Vilhelmsen (2001). However, the mesopseudosternum is often delimited in some way, even in those species that do not have internal ridges, so statements about its form can be made. Hence, I coded *Runaria*, *Cephalcia*, *Acantholyda*, and *Pamphilius* as having state 0 (not reaching the anterior margins of the mesepisterna, terminating in the discrien of the mesothorax), as was coded for character 49 by Ronquist *et al.* (1999). The latter authors coded this character as inapplicable only for those species that have no sulcus. However, because the mesopseudosternal sulcus separates the insertion sites of two muscles, the insertion of these muscles can reveal where the sulcus would be if present. Taking this into account, *Gilpinia* sp., and *Nematus* sp. have state 1 (terminating in the anterior margin of the mesepisterna), corresponding to state 1 with the cod-

ing of Ronquist *et al.* (1999), whereas *Monoctenus juniperi*, *Tenthredo mesomela*, *Athalia rosae*, and *Corynis crassicornis* also have state 1 but state 2 with the coding of Ronquist *et al.* (1999). Because the difference between states 1 and 2 in the coding of character 49 of Ronquist *et al.* (1999) is only slight and seems to vary within Diprionidae, I use the coding of Vilhelmsen (2001). *Orussus* is lacking the muscle inserting medially on the mesosternum and the character was therefore coded as inapplicable for *Orussus*. In summary, the coding of character 97 was changed to: mesopseudosternum (or insertion site of the muscle inserting medially on the mesosternum) (Ronquist *et al.*, 1999: 49): 0 = not reaching the anterior margin of the mesonotum; 1 = reaching the anterior margin of the mesonotum.

Character 117 (shape of cenchri): Vilhelmsen (2001) coded the shape of the cenchri in two states: 'less than twice as broad as long' and 'at least twice as broad as long'. The latter state was coded by Vilhelmsen (2001) for all Diprionidae, Cimbicidae, Argidae, Pergidae, and Megalodontesidae. I noticed that, within Tenthredinidae, the cenchri of the nematine species were approximately twice as broad as long and hence intermediate between the remaining Tenthredinidae and the taxa mentioned above. In order to include this information in the analysis, I decided to code this character in three states instead of just two: shape of cenchri (Vilhelmsen, 2000b: character 5 in part): 0 = about as broad as long (more or less round); 1 = about twice as broad as long (oval); 2 = about three times as broad as long or more (very narrow). Ordered.

Character 128 (metapostnotum): Whitfield *et al.* (1989) stated that no apocritans have a divided metapostnotum and mention this specifically for *Orthogonalys* and *Megalyra*. I therefore changed the coding of these two taxa from 1 to 0 (continuous medially).

Character 130 (petiolar foramen): 0 = not developed; 1 = posterior margin of T1 constricted, petiolar foramen confluent with coxal foramina; 2 = petiolar foramen separated from coxal foramina by sclerotized bridges (ordered). As stated by Vilhelmsen (2001), this character is based on character 57 of Ronquist *et al.* (1999). However, character 57 had only two states: petiolar foramen confluent with/separated from coxal foramina. Vilhelmsen (2001) split the first state up into two states (see above) and treated the character as ordered. The ordering leads to the circumstance that state 1, which is in essence the presence of a constriction between T1 and T2, comes out as a synapomorphy of Apocrita. This is problematic because Vilhelmsen (2001) also coded the presence of this constriction in Apocrita as state 2 of character 185, where this synapomorphy receives a weight of two (see below). Hence, the presence of a waspwaist receives a total weight of three steps in Vilhelmsen's (2001) ordered analysis,

which seems unjustified especially if one considers that such constriction appeared twice in the evolution of the Hymenoptera. In order to remove this undue weight, I changed the coding of character 185 (see below) and used the coding of Ronquist *et al.* (1999) for the present character: relation between metacoxal foramina and petiolar foramen (Ronquist *et al.*, 1999: character 57): 0 = continuous; 1 = separate.

Character 136 (anapleural clefts in the metathorax): this character was excluded from the analysis because the difference between the absence and presence of the clefts is so subtle that I was not certain when to assign state 0 and when state 1.

Character 138 (metepimera): I coded *Sterictiphora*, *Perga*, and *Phylacteophaga* as state 0 (posterior parts of metepimera reduced) instead of as inapplicable.

Character 139 (association between T1 and metepimera): I added a fourth state to this character. For taxa in which state 4 occurs, character 140 was coded as inapplicable. The new wording is: association between the first abdominal tergite and the metepimera (Vilhelmsen, 2000b: character 25 in part, character 26): 0 = entirely separate; 1 = articulating posteriorly; 2 = closely abutting along their entire length; 3 = totally fused; 4 = fused anteriorly. Unordered. (One reviewer suggested that this character should be ordered. However, looking at the cladograms, it can be seen that states 1, 2, 3, and 4 all arise independently from state 0).

Character 140 (articular inflections on the metepimera): if the metepimeron and T1 are anteriorly or completely fused, it is to be expected that the articular inflection on the metepimeron is absent. This character was therefore coded as inapplicable if the previous character was coded as state 3 or 4.

Character 158 (metatibial preapical spurs): *Micropterix* was changed from 1 to inapplicable because it has a number of thickened setae and it is unclear whether these are homologous to the preapical spurs of Hymenoptera.

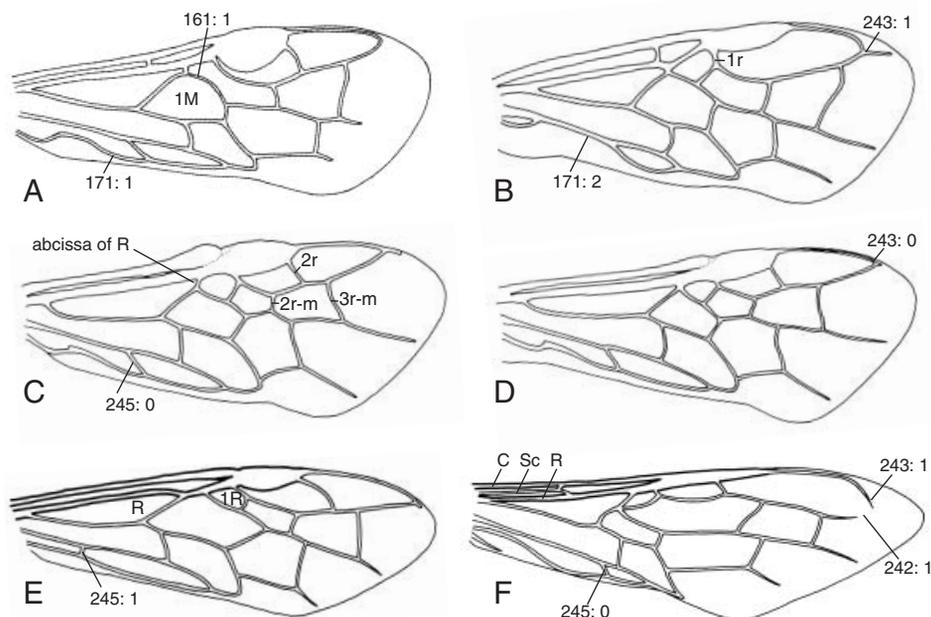
Character 159 (subcosta of forewing): Vilhelmsen (2001) coded state 1 (fused with R) for *Xyela*. However, the subcosta is not completely absent in this genus; it runs adjacent to the radius and is not entirely fused with it (see Benson, 1945b; the drawing in Goulet & Huber, 1993: 127). Because neither state 1 nor state 0 (distinct, separate longitudinal vein) apply to *Xyela*, I decided to introduce a third state for this character: subcosta of forewing (Ronquist *et al.*, 1999: character 74): 0 = distinct, separate longitudinal vein; 1 = running adjacent to R, but not entirely fused with it; 2 = fused with R, at most short transverse anterior branches present. Unordered. (Even though state 1 is an obvious potential intermediate between state 0 and state 2, there are no taxa showing state 2 closely related to the taxon exhibiting state 1 (*Pleroneura*,

which is probably the sister-group of *Xyela*, clearly has state 0), meaning that ordering this character would unnecessarily give double weight to the transition from 0 to 2 and from 2 to 0).

Character 161 (first abscissa of forewing Rs): Vilhelmsen (2001) divided this character into the two states 'present' and 'absent', the latter state being found in all Tenthredinoidea *s.s.* except for *Athalia*. I do not agree with this delimitation. The genus *Athalia* shows a variety of conditions, even within one species: some species/specimens (Fig. 2C) have a short abscissa like Blasticotomidae (Fig. 2A), some have no abscissa (Fig. 2D) like other Tenthredinoidea *s.s.*, for example *Arge* (Fig. 2B). Thus, there is no gap (discontinuity) between the conditions found in Blasticotomidae, the genus *Athalia*, and the rest of Tenthredinoidea. Ronquist *et al.* (1999: character 77) divided this character into the two character states 'long' and 'short or absent'. However, the abscissa of *Xylecia* is hardly longer than those of Blasticotomidae and those of some Pamphiliidae are even shorter than those of Blasticotomidae. Within the genus *Acantholyda*, *A. fasciata* shows no abscissa, whereas a specimen of *Acantholyda* sp. (*erythrocephala* or *flaviceps*) does have an abscissa, which is of similar length as those of Blasticotomidae. In sum, all intermediate conditions between a long abscissa and no abscissa can be found, and there is some variation within a genus or even within a species, so that I support neither the coding of Vilhelmsen (2001) nor that of Ronquist *et al.* (1999).

Instead, I considered coding the condition 'M is displaced basally and joins vein R+Rs instead of Rs alone, so that cells R and 1R do not meet', found in some Tenthredinoidea (see Fig. 2E) as a separate state, which is used in some determination keys. However, all intermediate conditions are found, between cells R and 1R barely touching and being widely separate, so this coding cannot be used either. Hence, this character should not be used at all. In order to retain the numbering of the following characters, it is here replaced with another character. In Blasticotomidae, the cell 1M is round anteriorly and hence has the shape of a half-circle (Fig. 2A). In other taxa the cell 1M is angular anteriorly (Fig. 2B–F). I therefore replace Vilhelmsen's (2001) character 161 with the following: cell 1M of forewing (present study): 0 = angular anteriorly (Fig. 2B–F); 1 = round anteriorly (Fig. 2A).

Character 165 (length of crossvein 1r of forewing): Vilhelmsen (2001) coded this character as inapplicable when vein 2r is absent, because he measured the length of 1r in relation to that of 2r. However, the character is the length of vein 1r and this is still present if 2r is absent. In this case, the length of 1r can be compared to the length that 2r would have if it was present, i.e. the distance between the stigma and vein Rs. Hence, for those taxa in which this character was coded as inapplicable by Vilhelmsen (2001), I assigned a state in the present revision. Vilhelmsen (2001) coded Xyelidae as having state 0, 'at most as long as



**Figure 2.** Forewings of basal Hymenoptera. A. *Paremphtytus flavipes* (Blasticotomidae). B. *Arge gracilicornis* (Argidae). C. *Athalia* sp. (Tenthredinidae). D. *Athalia rosae* (Tenthredinidae). E. *Tenthredo campestris* (Tenthredinidae). F. *Urocerus gigas* (Siricidae).

2r'. However, in Xyelidae, 1r is slightly longer than 2r. I therefore change the wording of this character to: Cross vein 1r of forewing (Ronquist *et al.*, 1999: character 82): 0 = shorter or at most slightly longer than 2r; 1 = significantly longer than 2r.

Character 167 (position of crossvein 2r of forewing relative to 2r-m): in accord with Ronquist *et al.* (1999), I changed the coding of *Ibalia* to 'inapplicable'.

Character 168 (crossvein 2r-m of forewing): *Nematus* is polymorphic for this character, even within one species, so I changed the coding from state 0 to {0,1}.

Character 171 (anal cell of forewing): In order to provide better resolution for the enlarged sample of Tenthredinoidea s.s., I divided the character state 'anal cell complete or constricted in the middle, not reaching wing margin' into two separate states, so that there are now five instead of four character states: anal cell of forewing (Königsmann, 1976; Ronquist *et al.*, 1999: character 94): 0 = complete, reaching posterior wing margin; 1 = complete, not reaching posterior wing margin (Figs 2A,C–F); 2 = constricted in the middle (i.e. posterior anal vein fused to anterior anal vein in the middle), not reaching wing margin (Fig. 2B); 3 = petiolate (i.e. posterior anal vein absent proximally of 1a), not reaching wing margin; 4 = absent (i.e. posterior anal vein and 1a entirely absent). Ordered.

Character 174 (distal hamuli placement): The state of *Corynis* was changed from 1 to 0 (in zigzag lines), those of *Cephalcia* and *Neurotoma* from 0 to 1 (in straight lines).

Character 177 (costa of hindwing): Vilhelmsen (2001) distinguished only between the absence and presence of a costa, but Sharkey & Roy (2002) distinguished between presence, partial reduction (Cephidae, *Syntexis*) and absence. As the partial reduction in Cephidae is probably correlated with the 'fusion' of Sc+R with C (Fig. 5E) in Cephidae, which is treated in a different character below (character 246), using the coding of Sharkey & Roy would give double weight to these (probably) dependent transformations at the base of Cephidae, and the partial reduction in *Syntexis* is autapomorphic anyway. I therefore follow Vilhelmsen.

Character 185 (constriction between T1 and T2: 0 = absent; 1 = dorsoventrally; 2 = dorsoventrally and laterally): if mapped on the consensus tree resulting from the unordered analysis, states 1 and 2 must be assumed to have been derived independently. Treating this character as ordered was probably used by Ronquist *et al.* (1999) and Vilhelmsen (2001) to test the hypothesis that a slight waspwaist is a synapomorphy of Cephidae and Apocrita. Unfortunately, this treatment results in a double weight on the transition from state 0 to state 2 (formation of the waspwaist) at the base of Apocrita, which I find unjustified. (One reviewer commented that it is justified because state 1

was intermediate between state 0 and state 2. However, the current knowledge on the phylogeny of Hymenoptera tells us that this is probably wrong – states 1 and 2 were apparently independently derived from state 0.) A better way of testing the homology of the constriction in Cephidae and Apocrita, without giving undue weight to the synapomorphy in Apocrita is to code the character with only two states, with state 1 being assigned to both Cephidae and Apocrita. (This way, any perceived differences in the configuration of the constriction in Cephidae and Apocrita are neglected.) Another way of coding this character without giving double weight to the transformation at the base of Apocrita would be to recognize different states for Cephidae and Apocrita and to treat the character as unordered. This would mean that any possibility of the constriction of Cephidae and Apocrita being homologous would be excluded a priori and that this possibility would not be tested in the analysis. Even though this can be justified based on current background knowledge, I am not yet ready to discard the possibility of testing the homology of the conditions in Cephidae and Apocrita; even though the waspwaist in Cephidae and Apocrita look different, one could still be derived from the other. I therefore code this character as: constriction between first and second abdominal tergite (Königsmann, 1977: character 7): 0 = absent; 1 = present.

Character 190 (abdominal spiracles, females): the state of *Sterictiphora* was changed from unknown to 0 (spiracles on abdominal segments 1–8 well developed).

Character 191 (abdominal spiracles, males): the state of *Syntexis* was changed from unknown to 0 (spiracles on abdominal segments 1–8 well developed) and of *Megalyra* from unknown to 1 (spiracles on abdominal segments 2–7 reduced).

Characters 190 and 191: the coding shows that the spiracles were reduced (state 1 of 190 and states 1 and 2 of 191) in the females and males of the same species of the taxa included in the analysis. This indicates that the two characters (respectively this one character in the two sexes) are not independent. I therefore decided to exclude one character from all analyses in order to avoid giving unjustified weight to the reduction of the spiracles. Because character 190 is divided into two states, whereas 191 is divided into three states and hence provides more information, character 190 was excluded.

Character 212 (sawteeth on dorsal margin of second valvulae): I excluded this character from subsequent analyses because even taxa that had been coded by Vilhelmsen (2001) as not having teeth showed tiny serration, while in those taxa coded as having teeth, these teeth were hardly any larger.

Character 217 (basal ring in the male copulatory apparatus): the basal ring is secondarily absent in all

Pergidae (see Schulmeister, in press). The coding was therefore corrected from state 1 (present) to state 0 (absent) in all pergid species. *Megalyra* has state 1.

Character 218 (paramere = latimere): *Orthogonalys* does have the paramere (latimere/gonoforceps) subdivided into gonostipes and harpe, but there is no musculature between the two. It was hence assigned a new state; state 2 = subdivided, musculature absent. The state of *Megalyra* was changed from unknown to 1 (undivided, musculature absent). The new wording is: male latimere (Königsmann, 1977: character 8): 0 = subdivided into gonostipes and harpe, with intrinsic musculature; 1 = undivided, musculature absent; 2 = subdivided, musculature absent. Unordered. (At first glance, it looks as if state 2 was intermediate between states 0 and 1 and that the character should be ordered as 0–2–1. However, based on phylogenetic background knowledge, state 2 must be assumed to be derived from state 1, the subdivision of the gonoforceps in *Orthogonalys* being secondary (another indication being the lack of musculature)).

Character 219 (gonomacula): Vilhelmsen (2001) coded the gonomacula as absent even in those taxa that lack a harpe. However, I argue that, in the taxa lacking a harpe this character should be coded as inapplicable. The cause for the absence of the harpe in Cephidae and Apocrita is either that it fused with the gonostipes or that it was simply reduced. We do not know which is the case. If the latter applies, then the gonomacula is absent because the harpe is absent. In this case, coding the gonomacula as absent in Cephidae and Apocrita would mean counting the reduction of the harpe twice. But even if the harpe had fused to the gonostipes in the stem lineages of Cephidae and Apocrita rather than being reduced, this would likely have caused the reduction of the gonomacula, because the inflexibility of the gonoforceps would have rendered the gonomacula useless. Therefore, the lack of a gonomacula in all taxa that do not have a harpe is probably correlated with the absence of the harpe, regardless of whether the absence of the harpe is due to fusion or reduction. The absence of a gonomacula in all taxa without a harpe provides some confirmation for the hypothesis that the loss of these two features is correlated. I therefore coded this character as inapplicable for species that do not have a harpe in order to avoid counting these correlated reductions twice. The state of *Tremex* was changed from unknown to state 1 (present). The formulation of this character is: Gonomaculæ (Königsmann, 1977: character 6): 0 = absent; 1 = membranous discs (with associated muscle v) situated distally on male harpe. Coded as inapplicable for taxa in which a separate harpe is missing.

Character 220 (volsellae): the state of *Megalyra* was changed from unknown to 1 (present).

Character 230 (larval abdominal legs): according to

Lorenz & Kraus (1957), the reduction of the larval abdominal legs in Xyelinae is not total as in Pamphilioidea, Cephioidea, Siricoidea and Orussoidea (and Apocrita). According to them, the legs in Xyelinae are 'querwulstartig'. Therefore, I recode this character in three states: larval abdominal legs (Yuasa, 1922; Lorenz & Kraus, 1957): 0 = present, well developed; 1 = present as bulges; 2 = completely absent. Unordered. Judging by the figures in Smith (1967), Macroxyelinae have state 1. State 1 is therefore assigned to *Xyela* and *Macroxyela*.

#### REVISION OF THE ORDERING OF THE CHARACTERS

The revised data matrix of Vilhelmsen (2001) was subjected to a parsimony analysis in which all characters were treated as unordered and the characters 43, 45, 136, 190 and 212 were excluded. This was carried out in order to provide a basis for examining the ordering of the characters. This analysis resulted in 122 most parsimonious trees of 823 steps. The strict consensus is shown in Figure 1.

The multistate characters 89, 130 and 185 were recoded above to binary characters. Characters 43, 117, 159, 218 and 230 were recoded from binary characters to multistate characters. All multistate characters were examined with respect to their ordering by mapping their character state distribution on the tree in Figure 1. Those characters for which I decided to change the ordering as well as some interesting additional cases are now discussed:

Character 20 (shape of tentorial bridge): judging from their distribution on the consensus tree resulting from the unordered analysis, the states 1 and 2 of this character are likely to be independently derived. This would speak for treating this character as unordered. However, this reasoning does not apply to this character, as it combines two features of the tentorial bridge: 'broad' (state 0) vs. 'narrow' (states 1 & 2) and 'not arched' (states 0 & 1) vs. 'arched' (state 2). (These two features were actually coded as two separate characters by Ronquist *et al.* (1999).) In order to imply the homology of the condition 'narrow', the character must be treated as ordered. Treating the character as ordered gives double weight to the direct transition from 'broad, not arched' (state 0) to 'narrow, arched' (state 2) (for example at the base of the Vespina). In this case this is justified as there really are two transitions: from 'broad' to 'narrow' and from 'not arched' to 'arched'. In this type of character, in which two features are combined (none of which refers to absence vs. presence), state 1 is not necessarily understood as an intermediate between state 0 and state 2. I hence continue to treat this character as 'ordered'.

Character 44: judging from their distribution on the consensus tree resulting from the unordered analysis

(Fig. 1), state 1 (found in *Syntexis*) and state 2 (some Apocrita) of this character are independently derived. Ordering would hence give unproportional weight to the synapomorphy 'state 2'. Therefore, I treat this character as unordered.

Character 65: this is an example for a character in which the ordering is justified but not without problems, as discussed above. The evolution of this character is mapped in Figure 1. I first did all the analyses in this study with character 65 treated as ordered and the results are presented. In addition, all analyses were repeated with character 65 treated as unordered and it was found that the strict consensi of the first two ordered analyses remained the same. However, in the final analysis, the unordering of this character caused the Apocrita to collapse.

Character 75: state 1 (found in Cephidae and *Syntexis*) and state 2 (Vespina) of this character must be assumed to be independently derived. I hence decided to treat this character as unordered.

Character 94 (posterior thoracic spiracles): when this character was mapped on the consensus tree resulting from the unordered analysis, it could not be decided whether state 1 (spiracles accommodated in distinct concavities of the mesepimera) or state 2 (spiracles covered laterally by mesepimera) is more plesiomorphic with respect to the other. Moreover there is no reason to assume that either state 1 or state 2 is a necessary intermediate between the other two states. I therefore treated this character as unordered.

Character 188: Kristensen (1991) suggested that it is an autapomorphy of Hymenoptera to have the abdominal spiracles lying within the lateral parts of the tergites. In the outgroup taxa examined by Vilhelmsen (2001) the spiracles are situated within the lateral membranous parts of the abdomen. In *Xyela*, *Blasticotomidae*, *Cimbicidae*, *Pamphiliidae* and *Xiphydria*, the lateral parts of the tergites are separated from the dorsal parts by membranous lines; in all other Hymenoptera included in the present analyses, this is not the case. Vilhelmsen (2001) argued that 'it seems reasonable to assume that' the state in which the lateral parts are separated from the dorsal parts (state 1) 'represents an intermediate step in a transformation series leading from having the spiracles lying in membranous cuticle (state 0) to having them surrounded by sclerotized cuticle which is continuous with the abdominal terga (state 2)' and used this argument to order this character as 0–1–2. However, it can just as well be assumed that the sclerotization of the parts of the integument surrounding the spiracles is merely a ventral extension of the dorsal sclerotization, and originally not separated from the latter. The greater sclerotization would have provided better protection for the abdomen, but would have made it somewhat inflexible. This could have led to the introduction

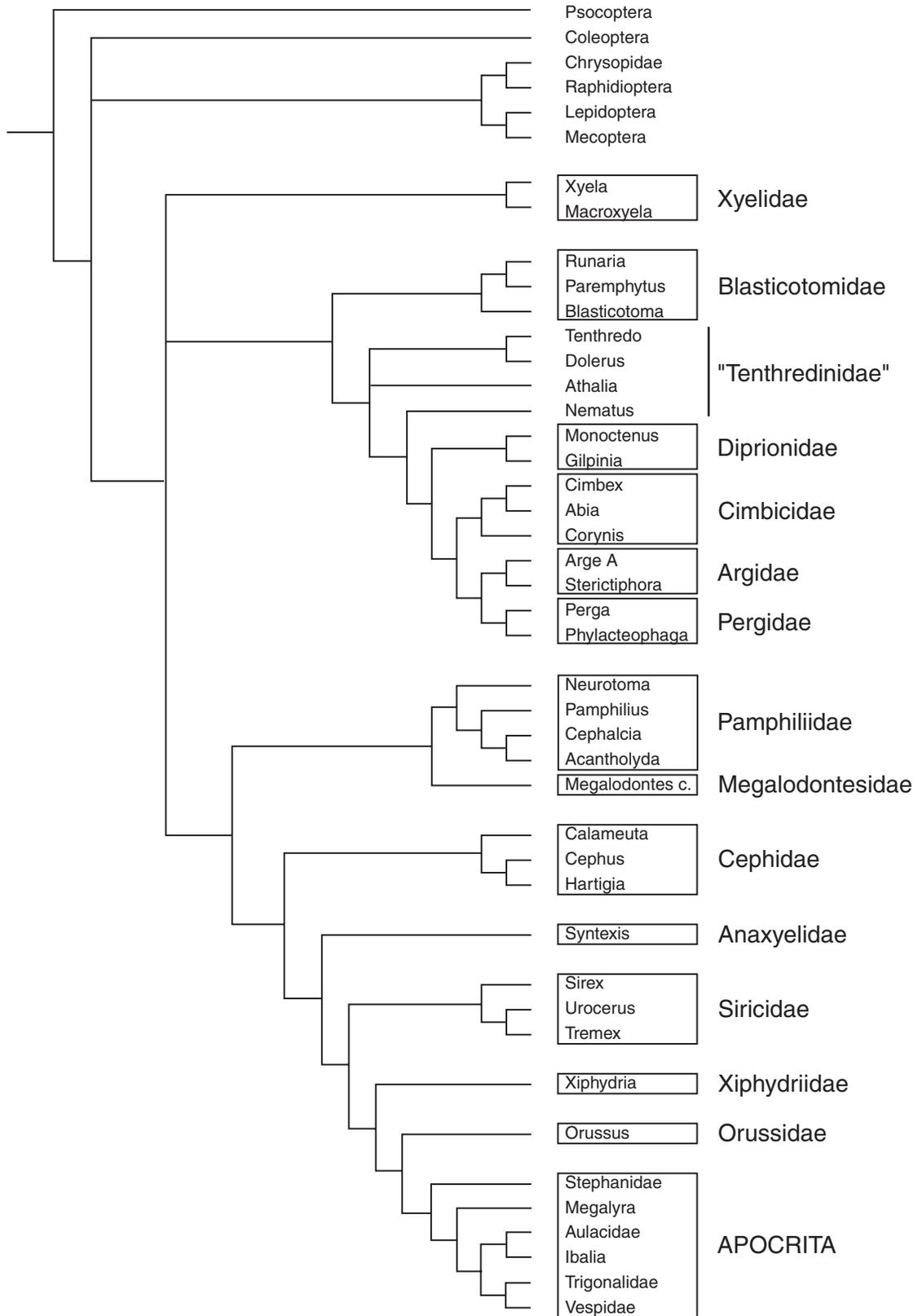
of membranous lines in some taxa, to provide more flexibility and enable the abdomen to be flattened, as in *Pamphiliidae* and *Cimbicidae*. This scenario would mean that state 2 (complete sclerotization) is intermediate between state 0 and state 1. If these two scenarios are mapped on the consensus tree derived from the unordered analysis (Fig. 1) the ordering of Vilhelmsen (2001) requires seven steps on the tree. Even then, it must be assumed that state 2 in *Cimbicidae* and *Xiphydria* were derived from state 1, not state 0. The latter scenario, on the other hand, which assumes that state 1 is always derived from state 2, requires only six steps on the tree. (The same applies for the consensus trees of the unordered and ordered trees of Vilhelmsen (2001).) This result shows that it is more parsimonious to assume that the tergites and 'pleurites' were completely fused in the groundplan of Hymenoptera and that the membranous lines between them (in some hymenopteran taxa) are derived. The latter scenario and the ordering 0–2–1 are hence more parsimonious and should therefore be preferred. In order to change the ordering of the states from 0–1–2 to 0–2–1, state 1 was simply renamed as 2, and state 2 as 1 in this study (and the corresponding changes introduced to the data matrix). The new formulation is thus: pleural region of abdominal segments (Vilhelmsen, 2001: character 188): 0 = pleural regions of second to fifth abdominal segments membranous; 1 = pleural regions sclerotized and continuous with the tergites, membranous lines absent; 2 = pleural regions around the spiracles sclerotized, but at least partly separated from the tergum of the corresponding segment by weakly sclerotized or membranous lines. Ordered.

Character 196: state 1 (found in *Pamphilioidea*) was clearly derived from state 0 (all other Hymenoptera) and not from state 2 (*Psocoptera* and *Raphidioptera*). In order to avoid giving double weight to the transitions from state 0 to state 2 within the outgroup, I treat this character as unordered.

#### ORDERED ANALYSIS OF THE REVISED VERSION

The revised version of the matrix of Vilhelmsen (2001) (shown in Appendix 2) was subjected to an analysis in which the characters 20, 23, 27, 30, 35, 36, 41, 42, 46, 48, 59, 65, 78, 79, 99, 112, 117, 134, 146, 157, 171, 188, 191, 192, 193, 224, 228 and 229 were treated as ordered (additive), and the characters 43, 45, 136, 190 and 212 were excluded. This analysis resulted in three most parsimonious trees of 845 steps. The strict consensus of these trees is depicted in Figure 3.

Within Hymenoptera, the strict consensus shown in Figure 3 agrees with the strict consensus of the resulting trees from the unordered analysis (shown in Fig. 1), except that *Runaria* + *Paremphtus* are now unambiguously monophyletic, the relationships



**Figure 3.** Ordered analysis of the revised version of the data matrix of Vilhelmsen (2001). The cladogram is a strict consensus of three trees of 845 steps.

within Tenthredinoidea s.s. are somewhat more resolved, Argidae are resolved as monophyletic, the relationships among *Syntexis*, Siricidae and Xiphydriidae + Vespina are resolved, and that the relationships within Apocrita are also resolved. The relationships among Xyelidae, Tenthredinoidea s.l., and the remaining Hymenoptera are still not resolved.

Compared to the final hypothesis of Vilhelmsen (2001: fig. 11) the most significant difference is the lack of resolution at the base of the hymenopteran tree. The only other difference is that the relationship of *Athalia* is unresolved.

### ADDITIONAL TAXA

In order to better test the monophyly of Tenthredinidae and Pergidae, closer examine the internal phylogeny of Pamphiliidae and Siricidae, and to improve the optimization of the characters on the cladogram (especially for the molecular characters added in Schulmeister (2003b)), 19 taxa were added to those used by Vilhelmsen (2001): *Aglaostigma*, *Selandria*, *Strongylogaster*, *Monophadnoides*, *Metallus*, *Taxonus*, *Hoplocampa*, *Nematinus*, *Cladius* (all Tenthredinidae), *Diprion* (Diprionidae), *Lophyrotoma*, *Acordulecera*, *Decameria* (Pergidae), *Onycholyda* (Pamphiliidae), *Megalodontes skorniakowii* (Megalodontesidae), *Xeris* (Siricidae), Ichneumonidae sp. A, Ichneumonidae sp. B, and *Sceliphron* (Apoidea). The genus *Arge* was split up into two taxonomic units, *Arge* A and *Arge* B. (While the characters of Vilhelmsen (2001) (Appendix 2) are coded only for *Arge* A, and the characters presented here (Appendix 3) are coded only for *Arge* B, the characters of the male terminalia (Appendix 4) are coded for both *Arge* A and *Arge* B.)

If not mentioned otherwise, the codings for these additional taxa are based on personal observations. The labial palp of *Onycholyda amplexa* was examined by scanning electron microscopy and found to have state 1 for character 36. Specimens of this species do not show a sclerotized postmentum (character 38), but a few setae remain in its place.

— *Lophyrotoma*, *Diprion pini*, *Xeris spectrum*, and *Sceliphron* were coded after Basibuyuk & Quicke (1997) for characters 172–176.

— *Strongylogaster*, *Taxonus*, *Hoplocampa*, and *Acordulecera* were coded after Gibson (1985) for character 80.

— *Strongylogaster*, *Diprion*, and *Acordulecera* were coded after Heraty *et al.* (1994) for characters 68, 81–86, 88, 89, 98 and 99.

— *Aglaostigma*, *Strongylogaster*, *Selandria*, *Taxonus*, *Monophadnoides*, *Metallus*, *Hoplocampa*, *Nematinus*, *Cladius*, and *Diprion* were coded after Lorenz & Kraus (1957) for larval characters.

— *Xeris* and *Sceliphron* were coded after Quicke *et al.* (1994) for characters 210, 211, 214 and 215.

— *Selandria* and *Aglaostigma* were coded after Vilhelmsen (1996) for characters 6, 8, 10, 11, 28, 29, 34, 36 and 37.

— *Diprion* was coded after Vilhelmsen (1999) for character 17.

— *Diprion* and *Lophyrotoma* were coded after Vilhelmsen (2000a) for characters 52 and 95 and after Vilhelmsen (2000b) for characters 101–103, 112–115, 122, 124–127, 141–143, 148–152 and 156–157.

— *Aglaostigma*, *Diprion* and *Lophyrotoma* were coded after Vilhelmsen (2000c) for characters 193, 194, 196–210 and 212–213.

— *Acordulecera* was coded after Yuasa (1922) for larval characters.

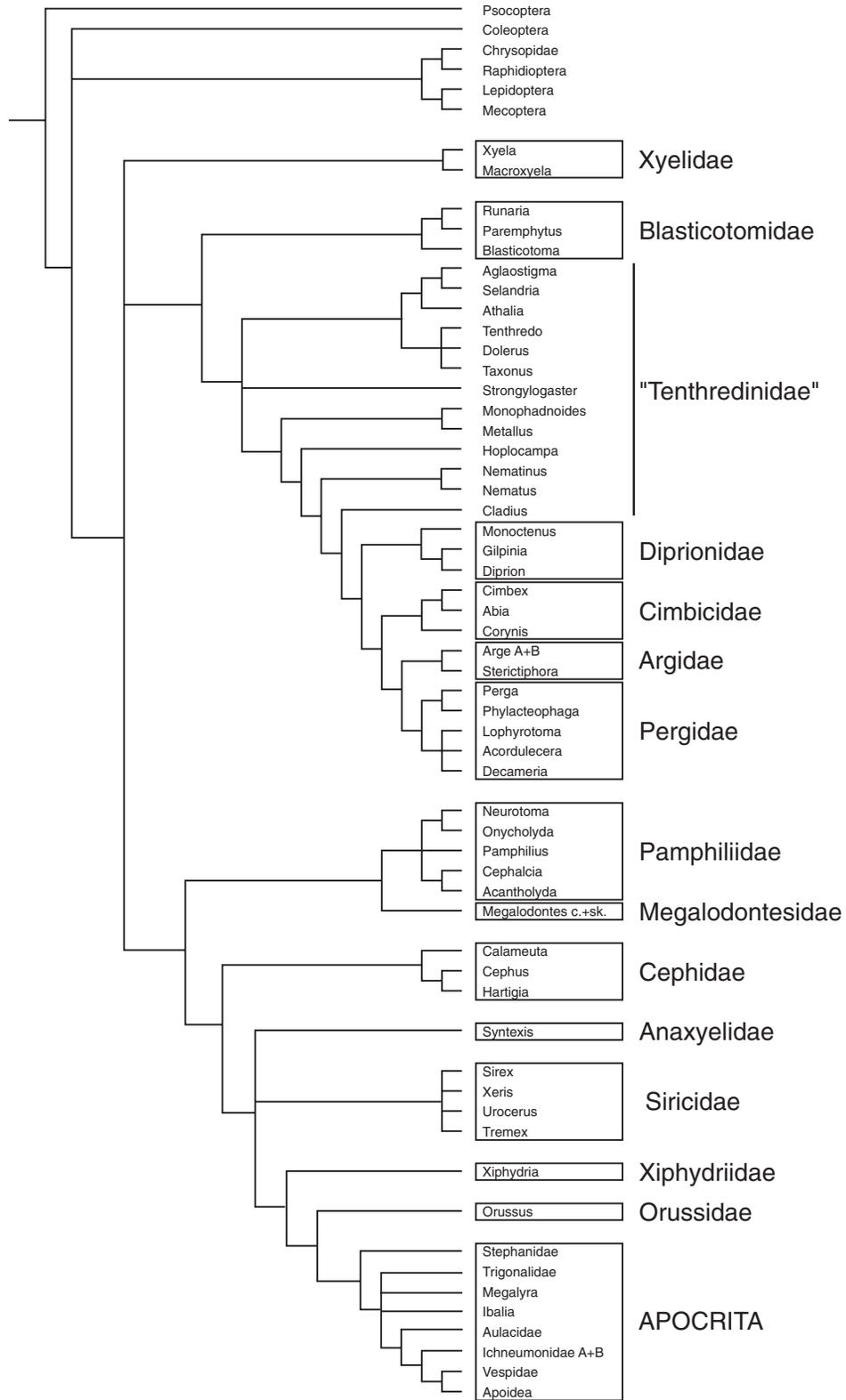
After adding the taxa mentioned above, this enlarged revised version of the data matrix of Vilhelmsen (2001) (Appendix 2) was analysed, treating some characters as ordered and excluding others, as outlined above. This analysis resulted in 38 most parsimonious trees of 934 steps. The strict consensus of these trees is depicted in Figure 4.

In comparison to the strict consensus of the trees resulting from the ordered analysis with the smaller taxon sample (Fig. 3), the result obtained with the large taxon sample (Fig. 4) shows an increased lack of resolution, associated with the added taxa. Nine tenthredinid genera were added to the matrix and the relationships among the tenthredinid taxa are now unresolved in two places. The relationships between the three new pergid taxa are ambiguous. Adding *Onycholyda* apparently leads to ambiguity in the placement of *Pamphilius* and the addition of *Xeris* results in a lack of resolution within Siricidae. The status of the families and the relationships among them, as implied by the smaller taxon sample, are unchanged except that the placement of *Syntexis* is ambiguous again (as in Fig. 1).

### ADDITIONAL CHARACTERS

In this section several characters are added to the characters of Vilhelmsen (2001). Some of these characters were used previously in the cladistic analyses of Ronquist *et al.* (1999), which are based on the study of Rasnitsyn (1988), and in the study of Sharkey & Roy (2002) (details on the characters are given below). In addition, some morphological characters are presented which have not been used in cladistic analyses previously (although some of these characters have been mentioned in morphological and taxonomical studies).

Interestingly, Vilhelmsen (1997b; 2001) did not use some of those characters that have long been listed as autapomorphies for certain families. This made some



**Figure 4.** Ordered analysis of the revised data matrix, including the additional taxa. The cladogram is a strict consensus of 38 trees of 934 steps.

sense in the earlier study in which these characters would have been parsimony-uninformative because entire families were used as terminal taxa. However, in studies using the exemplar approach, e.g. Vilhelmsen (2001), such characters should be included to contribute to the support of the monophyly of those families. They were hence included here. The codings for the new characters 237–266 are shown in Appendix 3.

#### Head

237. Number of articles in female antenna (Ronquist *et al.*, 1999: character 18): 0 = more than 15; 1 = 13–15; 2 = 12 or less. Ordered. The character state delineation was slightly changed compared to that of Ronquist *et al.* (1999) in order to optimize its usefulness for the taxon sample of this study.

238. Female antennae (Vilhelmsen *et al.*, 2001): 0 = not modified; 1 = modified into ‘hammers’.

239. Maxillary palp: 0 = thin, not leg-like; 1 = thick, leg-like, with a setae-bearing distal part.

240. Number of maxillary palp segments: 0 = one to five; 1 = six. (In *Xyela* and *Pleroneura*, the fourth segment is further subdivided into about four subsegments. This is counted here as one segment.) It seems that the reduction of the number of labial palp segments and the number of maxillary palp segments are dependent to some extent: they are often reduced in the same taxa (Table 1). It makes sense to assume that there is an adaptational pressure to shorten the palps which acts on both pairs of palps because they work in concert. However, in some taxa only one of the two is reduced, and the two characters in some cases are potential synapomorphies for different taxa. That the two pairs of palps do not always react simultaneously lies in the nature of evolution. Apparently, they are not completely dependent. Therefore I decided to code them as two separate but semi-independent characters. Because the number of both maxillary and labial palps is reduced in *Perga*, *Phylacteophaga* and *Decameria*, I decided to code the present character as inapplicable for these taxa, in order to prevent giving double weight to these reductions.

#### Thorax and wings

241. Forewing tegulae: 0 = absent; 1 = present, but small (and hidden under the pronotum in Hymenoptera); 2 = present, well-developed. Unordered. In *Syntexis*, the forewing tegulae are somewhat reduced in size and the front part is hidden under the pronotum, but the difference to the condition found in some Xiphidriidae is not significant. *Syntexis* was hence coded as having state 2. In Siricidae, the small remnants of the tegulae are completely hidden under the pronotum, so that they cannot be seen without lifting the pronotum.

**Table 1.** Number of maxillary and labial palp segments. In *Xyela* and in *Pleroneura*, but not in *Macroxyela* and *Xyelecia*, the fourth segment of the maxillary palp (counted from the base) is further divided into one long and three very short subsegments (cf. Jervis & Vilhelmsen, 2000: fig. 1C). This is counted here as one segment. The maximal numbers of 6 maxillary palp segments and 4 labial palp segments are highlighted by bold print to better visualize the evolution of these structures

	Maxillary palp	Labial palp
<i>Amphigerontia</i>	?	1
Raphidioptera sp.	5	3
Chrysopidae sp.	5	3
<i>Priacma</i>	4	3
<i>Micropterix</i>	5	2
<i>Panorpa</i>	5	2
<i>Macroxyela</i>	4	4
<i>Megaxyela</i>	?	4
<i>Xyelecia</i>	4	?
<i>Xyela</i>	4	4
<i>Pleroneura</i>	4	4
<i>Blasticotoma</i> , <i>Runaria</i>	<b>6</b>	4
Tenthredinidae	<b>6</b>	4
Diprionidae	<b>6</b>	4
Cimbicidae	<b>6</b>	4
Argidae	<b>6</b>	4
<i>Lophyrotoma</i>	<b>6</b>	4
<i>Perga</i>	4	3
<i>Phylacteophaga</i>	3	3
<i>Decameria</i>	3	1
<i>Acordulecera</i>	<b>6</b>	4
Pamphilioidea	<b>6</b>	4
Cephidae	<b>6</b>	4
<i>Syntexis</i>	<b>6</b>	3
<i>Sirex</i>	?	3
<i>Urocerus</i>	2	3
<i>Xeris</i>	2	3
<i>Tremex</i>	1	2
<i>Xiphidria</i>	4	3
<i>Orussus</i>	5	3
<i>Schlettererius</i>	<b>6</b>	4
<i>Stephanus</i>	<b>6</b>	4
<i>Megalyra</i>	4	3
Ichneumonidae ssp.	5	4
<i>Ibalia</i>	5	3
<i>Sceliphron</i>	<b>6</b>	4
<i>Dolichovespula</i>	<b>6</b>	4

242. Radial cell of forewing: 0 = closed distally (Fig. 2A–E); 1 = open distally (Fig. 2F).

243. Tip (and ‘appendix’) of radial cell of forewing: 0 = on the wing margin (Fig. 2A,C–E); 1 = away from the wing margin (Fig. 2B,F).

244. Structure of forewing tip (Benson, 1945a): 0 = smooth or coriaceous; 1 = corrugated (wrinkled).

Illustrated in Benson (1945a: figs 9,10). This character was included in the analysis particularly to provide information for the internal phylogeny of Pamphiliidae.

245. Crossvein in anal cell of forewing: 0 = oblique (Fig. 2A,C,D,F); 1 = at right angles to anal veins (Fig. 2E); 2 = absent even though anal cell is complete; — = not applicable because anal cell is incomplete (Fig. 2B). Unordered. This character has been used in various keys for the determination of Tenthredinidae.

246. Vein Sc + R of the hindwing: 0 = present, at a distance from C (Fig. 5A–D,F); 1 = present, running along the anterior wing margin, adjacent to C which is partly 'dissolved' (Fig. 5E); 2 = present, the basal half running along the wing margin, the distal half at some distance from the wing margin. Unordered.

247. Veins Cu and M of hindwing at the base of the wing (Sharkey & Roy, 2002: character 34): 0 = separate (Fig. 5A); 1 = completely fused (Fig. 5B–F). In eight out of nine hindwings of *Xyelecia* there were only traces left of the basal part of Cu, but it is clear that it was there. One of the nine hindwings had a clear basal part of Cu separate from M (H. Goulet, pers. comm.).

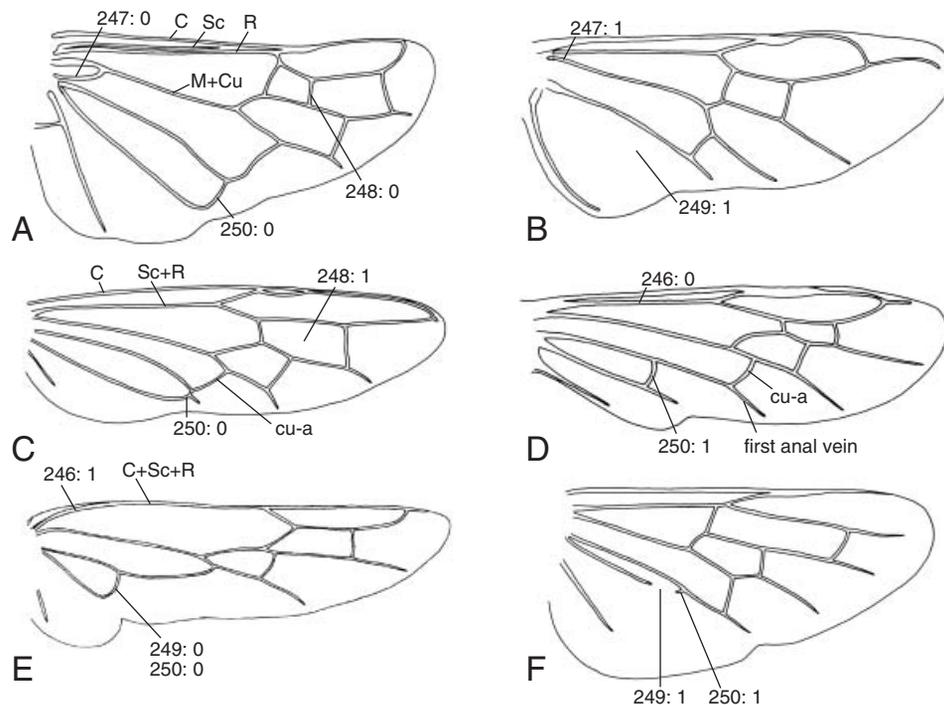
248. Crossvein 2r-m (= 2rs-m) in hindwing (Sharkey & Roy, 2002: character 35): 0 = present (Fig. 5A); 1 = absent (Fig. 5B–F).

249. Second anal vein of hindwing (Sharkey & Roy, 2002: character 36): 0 = present and complete (Fig.

5A,C–E); 1 = partly reduced or completely absent (Fig. 5B,F). There is some, but not complete, correlation of the absence of the second anal vein in the forewing and in the hindwing. The absence of the second anal vein in the forewing is often listed as a characteristic character of Pergidae; however, the vein does occur in some Pergidae. I specifically included a pergid (*Decameria*) in this study that has at least part of the second anal vein of the forewing (state 3 of the revised version of character 171). Contrary to the second anal vein in the forewing, the second anal vein of the hindwing is absent from all Pergidae. Outside of Tenthredinoidea *s.l.*, the second anal vein of the forewing is missing completely only from Apocrita, whereas the second anal vein of the hindwing is missing from *Xeris*, *Tremex*, *Urocerus* and *Vespina*.

250. Length of anal cell of hindwing: 0 = as long as cell 1Cu posteriorly, i.e. second anal vein joins first anal vein (almost) at the same point as cu-a (Fig. 5A,C,E); 1 = shorter than cell 1Cu, i.e. second anal vein joins first anal vein further proximal than cu-a and first anal vein extends beyond cu-a (Fig. 5D,F).

251. Mesopseudosternal sulci (Ronquist *et al.*, 1999: character 48): 0 = present, delimiting a pseudosternal area of the mesopectus; 1 = absent. Vilhelmsen (2001) distinguished between the presence and absence of internal ridges on the mesopseudosternum. The absence of internal ridges – with or without external



**Figure 5.** Hindwings of basal Hymenoptera. A. *Macroxyela ferruginea* (Xyelidae). B. *Decameria* sp. (Pergidae). C. *Tenthredo campestris* (Tenthredinidae). D. *Selandria serva* (Tenthredinidae). E. *Hartigia trimaculata* (Cephiidae). F. *Urocerus gigas* (Siricidae).

sulci – was found by Vilhelmsen (2001) in Tenthredinidae, Diprionidae, Cimbicidae, Blasticotomidae and *Phylacteophaga*, resulting in this character showing no unambiguous changes in the analysis of Vilhelmsen (2001). Rasnitsyn (1988) and Ronquist *et al.* (1999), on the other hand, distinguished between external pseudosternal sulci present – with or without internal ridges – or absent. In their analysis, the absence of the sulci is a synapomorphy of Tenthredinidae (including Diprionidae) and Cimbicidae. In order to better test Rasnitsyn's hypothesis of a monophyletic Tenthredinidae+Diprionidae+Cimbicidae, I add Ronquist *et al.*'s character 48 to the present data matrix.

#### Legs

252. Fore basitarsus of the female (Vilhelmsen *et al.*, 2001): 0 = not drawn out; 1 = distally drawn out into a kind of 'spur'.

253. Female foretibia (Vilhelmsen *et al.*, 2001): 0 = not divided; 1 = subdivided.

254. Mesotibial apical spurs: 0 = two, 1 = one, 2 = none. Unordered. State 0 is found in all sawflies except for the examined Siricidae, all of which have state 1. This character hence provides a potential synapomorphy for Siricidae. State 1 was also found in *Megalyra* in this study and state 2 was found in *Schlettererius cinctipes* and *Stephanus serrator*. Outside of the taxon sample used for this study, I found state 1 in one examined specimen of Torymidae (Chalcidoidea) and some species of Apoidea and Vespoidea and state 2 in one examined specimen of Chalcididae (Chalcidoidea). Brothers (1975: 523–524) mentions a number of aculeates that have state 1 and that state 2 is present in Bradynobaenidae and some Formicidae. According to Carpenter (1982: 20), the character shows considerable homoplasy within Vespoidea. State 2 could hence be a synapomorphy of Stephanidae.

255. Metatibial apical spurs: 0 = two spurs; 1 = one spur; 2 = no spurs. Unordered. State 0 occurs in all taxa included in this study except for *Xeris* and *Tremex*. I included this character in the analysis to provide information for the internal phylogeny of Siricidae. Outside of the taxon sample used for the analysis, I observed state 1 in Formicidae. According to Brothers (1975: 525), state 1 and 2 occur in some aculeates.

256. Plantulae (Schulmeister, 2003a): 0 = no plantulae; 1 = integrated; 2 = distal. Unordered. In Schulmeister (2003a: appendix 2), this character was coded in five states to maximize morphological information. However, as suggested by Schulmeister (2003a), it was coded in only three states for the cladistic analysis in the hope of obtaining unambiguously optimized changes.

257. Denticles on plantulae (Schulmeister, 2003a): 0 = no denticles on plantulae; 1 = denticles present somewhere on plantulae. The coding of this character differs from that in Schulmeister (2003a) in order to test the potential synapomorphy of state 1 for Tenthredinidae+Cimbicidae+Diprionidae.

258. Patch of bristle-shaped denticles on the ventral face of some or all plantulae (Schulmeister, 2003a): 0 = absent; 1 = present. Coding this character in more states would make it too variable to be of use in this analysis.

259. Secretion pores on plantulae (Schulmeister, 2003a): 0 = absent; 1 = present; — = not applicable due to lack of plantulae.

#### Abdomen

260. Structure of anterolateral apophyses of abdominal sternum three (Ronquist *et al.*, 1999: character 118): 0 = laterobasal corners of sternum slightly or not at all modified as apophyses; 1 = sternum with distinct horn-like or finger-like basal extensions directed forward or upward. The change in the coding of this character was adopted from a study by Basibuyuk *et al.* (2000). This and the next character were included to provide more information within Apocrita.

261. Structure of posterior margin of second abdominal sternum (Ronquist *et al.*, 1999: character 116; Brothers & Carpenter, 1993): 0 = distinctly overlapping anterior margin of third abdominal sternum; 1 = weakly or not overlapping third abdominal sternum.

262. Anterior margin of abdominal sternites: 0 = straight or smoothly curved or forming a slight angle; 1 = with median incision/angular notch. Character 117 of Ronquist *et al.* (1999) is similar to this character (anterior margin of third abdominal sternum angularly notched), but they incorrectly code Cephidae as having no notch. They observed this notch only in Dryinidae and Sclerogibbidae; maybe in these taxa the notch is really present only in the third sternite and is correlated with the petiolum. If this is the case, this could be coded as a third character state in a study that includes these taxa. The presence of a notch in the anterior margin of most abdominal sternites in Cephidae is probably correlated with the lateral compression of the abdomen in this group.

263. Tergite nine of the female: 0 = not elongated; 1 = distal part distinguished from basal part of the tergite, distal part elongated into a tip that extends beyond the cerci; 2 = as previous state, but the tip is further drawn out into a long, pointed, strongly sclerotized structure: the cornus. Ordered.

264. Ovipositor (Vilhelmsen *et al.*, 2001; L. Vilhelmsen pers. comm.): 0 = external; 1 = concealed (posterior part of the seventh sternite modified for gripping the ovipositor, median margins of the ninth tergite abut medially, hiding the third valvulae).

*Larvae*

265. Labrum of the larva (Schedl, 1991): 0 = symmetrical; 1 = asymmetrical. According to my own observations the larvae of *Cephus* and *Hartigia* have a symmetrical labrum. I did not find any explicit information for *Calameuta*. Larvae of *Xeris* and *Sirex* were observed to have an asymmetrical labrum (M. Jänicke, pers. comm.). The xyelid taxa were coded after Smith (1967), *Syntexis* after Middlekauff (1974). *Orussus* was coded after the figure of *O. occidentalis* by Rohwer & Cushman (1917). The other species were coded after Lorenz & Kraus (1957) and Yuasa (1922). 266. Larval abdominal legs (Lorenz & Kraus, 1957): 0 = present on abdominal segments 1–10; 1 = present on 2–8 and 10 (or only 2–8 (*Caliroa* and *Fenusa*); 2 = present on 2–7 and 10; 3 = present on 2–6 and 10. Ordered. All taxa were coded after Lorenz & Kraus (1957). Vilhelmsen (2001: character 231) coded the segmentation of the larval abdominal legs but not their distribution on the abdomen. However, this character constitutes potential synapomorphies not only for Nematinae, but also for Argidae+Pergidae.

*Male terminalia*

The characters of the terminal segments of the male abdomen, characters 267–353, were taken from Schulmeister (in press). A few changes were introduced to the matrix of the characters of the terminal segments of the male abdomen for the purpose of the cladistic analysis, as proposed by Schulmeister (in press). The modified matrix is presented in Appendix 4. In sum, the following changes were introduced into the matrix:

Characters 271 and 272 were coded as inapplicable for those taxa in which the cupula is absent or fused with the gonostipes ventrally, and characters 273 and 274 were coded as inapplicable for those taxa in which the cupula is absent; otherwise these dependent events would be given unproportionately high weight.

State 3 of character 288 was coded as inapplicable because this character deals with the configuration of muscle u, not with its presence or absence.

Character 290 (presence of gonomacula and muscle v) was coded as inapplicable for all taxa in which the harpe is missing.

Character 324 (position of the phallosome) was coded as inapplicable for those taxa which have a ventral sclerotized stylus to avoid giving double weight to these correlated transformations.

Character 336 (presence and configuration of the ventral sclerotized style) was coded only in two states (absence and presence of the style).

States 4 and 5 of character 343 were coded as state 1 because the narrowness of the eighth sternite is also a kind of constriction. Form of abdominal sternum eight in males: 0 = not constricted, almost rectangu-

lar, but in some cases distal margin concave; 1 = somewhat constricted medially or very narrow overall; 2 = strongly constricted, with scleritous bridge in the middle; 3 = separated into two sclerites connected only by membrane. Ordered.

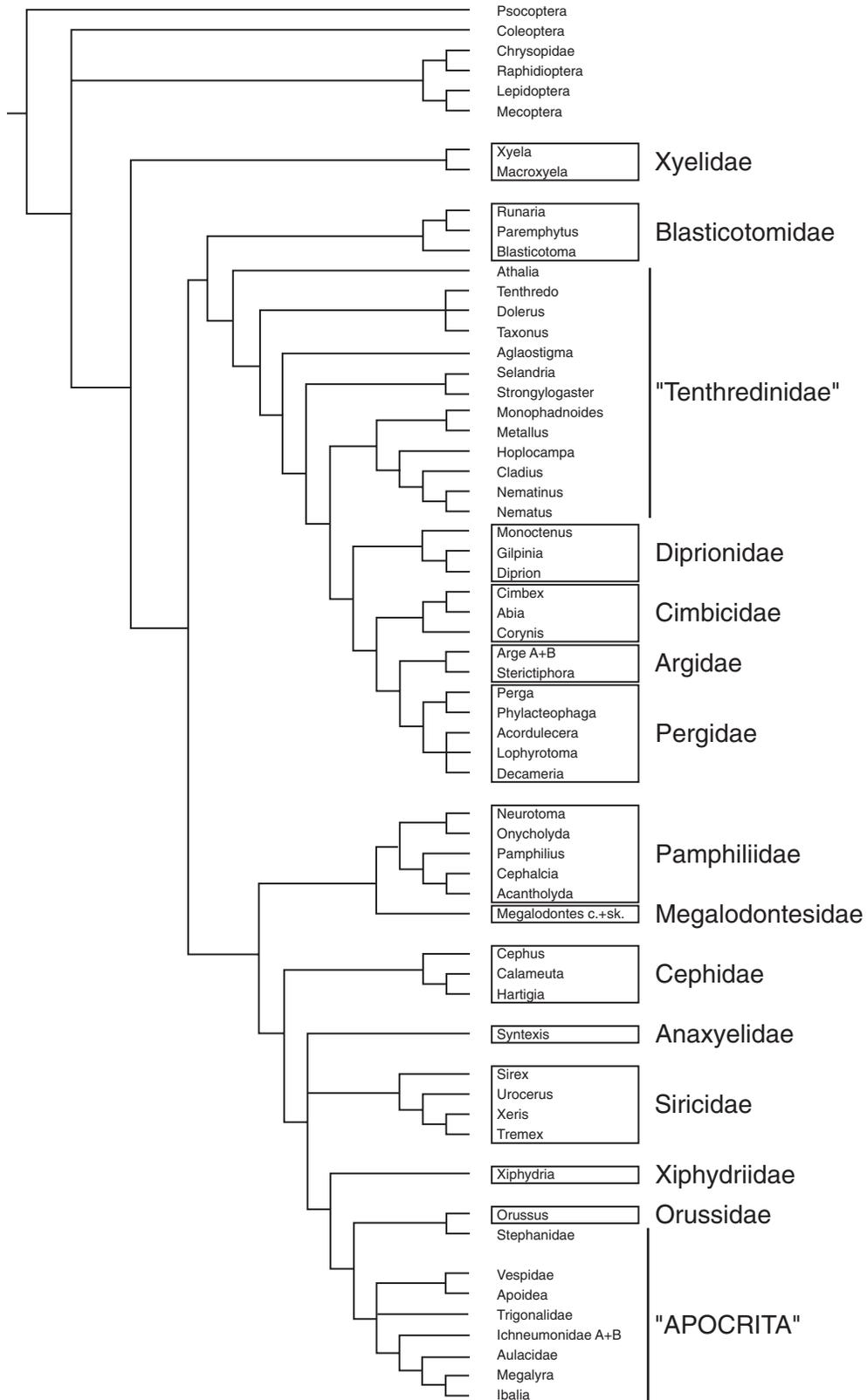
## UNORDERED ANALYSIS

In order to examine whether the additional multistate characters should be treated as unordered or ordered, an unordered analysis of all data was made. The revised matrix (Appendix 2) of the data of Vilhelmsen (2001), the matrix of new characters (Appendix 3) and the modified matrix of the male terminal segments (Appendix 4) were analysed simultaneously, using the complete taxon sample. All characters were treated as unordered. The characters 43, 45, 136, 190, and 212 were excluded from the analysis for reasons given above. The characters 216–220 were excluded from the analysis because they correspond to characters 294, 299, 287, 290, and 325 from Schulmeister (in press)/Appendix 4. The total number of characters included in the analysis is hence 343. The analysis resulted in 24 trees of 1411 steps. The strict consensus of the 24 trees is shown in Figure 6.

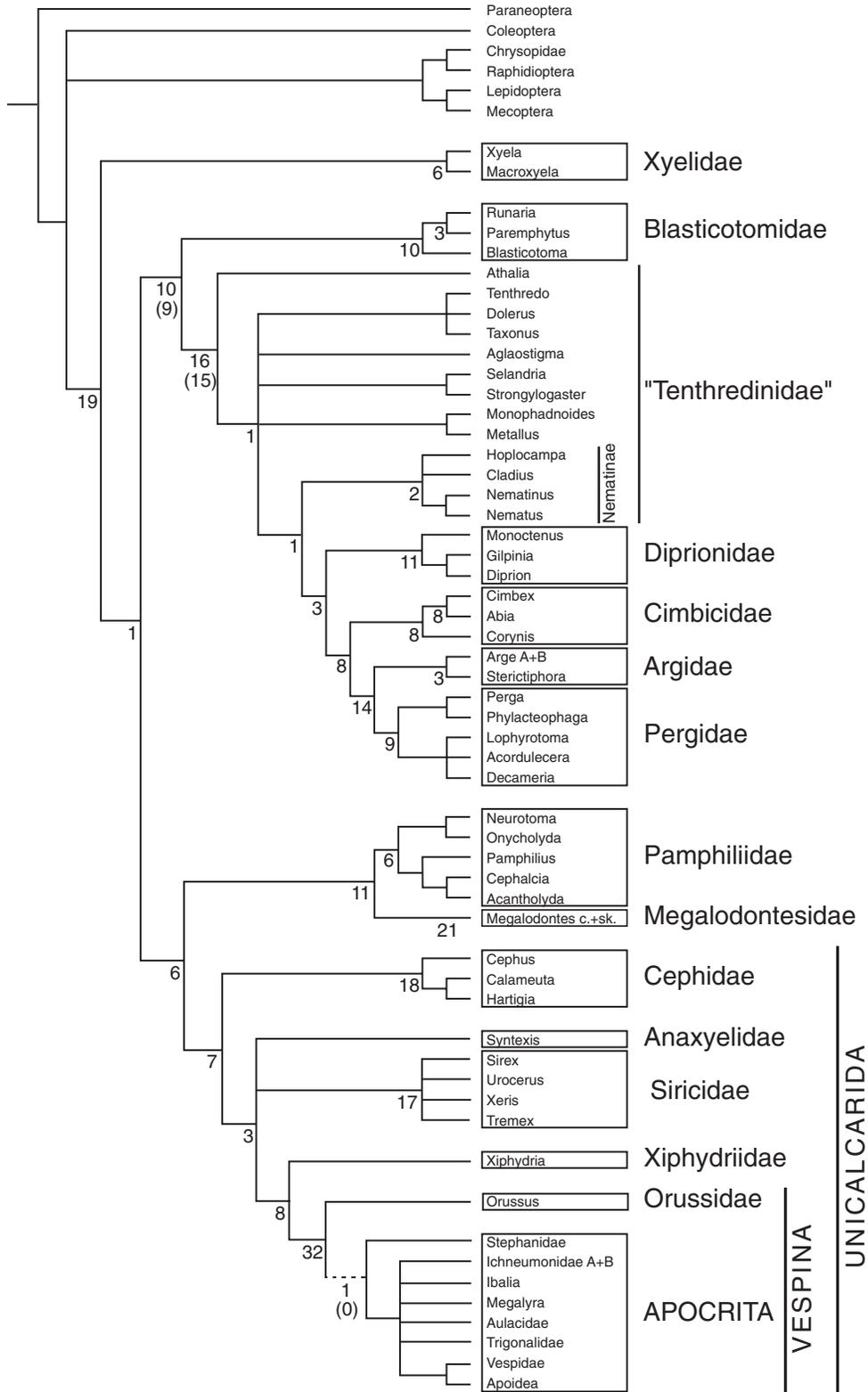
Above it was stated that it could not be determined from Figure 1 whether state 1 of character 94 was plesiomorphic or apomorphic with respect to state 2. Now, with a larger taxon sample, it must be concluded that, at least within Tenthredinoidea, state 2 is plesiomorphic relative to state 1. Within Xiphydriidae+Vespina, the optimization is still ambiguous. Hence, the character should be ordered as 0–2–1 instead of as 0–1–2, as done by Vilhelmsen (2001), that is if it should be ordered at all. Because ordering is not necessary in order to obtain the optimization within Tenthredinoidea, and I cannot see any reason why either state should be more plesiomorphic, I continue to treat the character as unordered.

## ORDERED ANALYSIS

All three data matrices (Appendices 2–4) were analysed simultaneously. The characters 20, 23, 27, 30, 35, 36, 41, 42, 46, 48, 59, 65, 78, 79, 99, 112, 117, 134, 146, 157, 171, 188, 191, 192, 193, 224, 228 and 229 of Appendix 2, the characters 237, 263 and 266 of Appendix 3, and the characters 288, 296, 299, 304, 343, 347 and 349 of Appendix 4 were treated as ordered. The characters 43, 45, 136, 190, 212 and 216–220 were excluded from the analysis. This ordered analysis resulted in 210 most parsimonious trees of 1451 steps. The strict consensus of all trees is shown in Figure 7. The analysis was repeated with character 65 treated as unordered (see discussion below) and the differences to the previous analysis are noted in Figure 7.



**Figure 6.** Unordered analysis of the revised data matrix, including the additional characters and taxa. The cladogram is a strict consensus of 24 trees of 1411 steps.



**Figure 7.** Ordered analysis of the revised data matrix including the additional taxa and characters. The cladogram is a strict consensus of 210 (282) trees of 1451 (1450) steps (numbers in parentheses refer to the same analysis with character 65 treated as unordered). Numbers denote Bremer support values. In the strict consensus of the trees resulting from this analysis, the relationships among *Orussus*, Stephanidae, and the remaining Vespina are unresolved.

The analysis was also repeated without excluding the characters 43, 45, 136, 190 and 212. The strict consensus of the resulting trees is identical to that in Figure 7 except for an increased lack of resolution within Apocrita and for Tenthredinidae.

The most notable difference of the strict consensus (Fig. 7) to the results of the ordered analyses without the additional characters (Figs 3, 4) is that Xyelidae are now resolved as the basalmost sawfly lineage as in the final hypothesis of Vilhelmsen (2001). This is caused by the addition of the characters 240 and 247 which provide putative synapomorphies for the non-xyelid hymenopteran lineages. Surprisingly, the relationships among the tenthredinid taxa show an increased lack of resolution. Apart from that, *Athalia* is now the sister-group of all other Tenthredinoidea s.s., and Nematinae are monophyletic. The relationships within Pamphiliidae are now resolved with Pamphiliinae being paraphyletic. The relationships within Cephidae have changed.

#### INTERNAL PHYLOGENY OF XYELIDAE

Schulmeister (2003a: fig. 10) proposed a tentative phylogeny of extant xyelid genera, based on a mental analysis: ((*Macroxyela Megaxyela*) (*Xyelecia* (*Xyela Pleroneura*))). In order to provide a better test for the monophyly of Xyelidae, and to reexamine the phylogeny of Schulmeister (2003a), I coded as many characters as possible for *Xyelecia nearctica* Ross 1932 and *Pleroneura bruneicornis* Rohwer 1910. For coding the characters, two museum specimens were used, which could not be dissected. Additional information was obtained from the literature (see Appendix 5). Codings for *Megaxyela* were obtained exclusively from the literature.

Because only relatively few characters could be coded for these three xyelid taxa, the data are presented separately from those of the other taxa (in Appendix 5), and a separate analysis was performed with the inclusion of the three additional xyelids. For this analysis one character was slightly changed. One potential synapomorphy of *Xyela* and *Pleroneura* is the subdivision of the fourth maxillary palp segment into subsegments. In order to add this information to the analysis with the additional xyelid taxa, I recoded character 240 slightly for the analysis: number of maxillary palp segments: 0 = one to five; 1 = six; 2 = four segments, but the fourth divided into subsegments (unordered).

The analysis resulted in 25 most parsimonious trees of 1456 steps. The strict consensus (not shown) agrees with the one in Figure 7, except that the relationships of the tenthredinid taxa and Apocrita are slightly more resolved. Xyelidae are monophyletic in all trees. The internal phylogeny of Xyelidae in these trees is:

((*Macroxyela Megaxyela*) *Xyelecia* (*Xyela Pleroneura*)), with either *Xyelecia* or *Macroxyela+Megaxyela* as the sister-group of *Xyela+Pleroneura* in the constituent trees. A synapomorphy for the group *Xyelecia+Xyela+Pleroneura* is the maxillary palp being leg-like (239: 1), and the alternative group, *Macroxyela+Megaxyela+Xyela+Pleroneura*, is supported by the presence of integrated plantulae (256: 1). Synapomorphies for *Xyela* and *Pleroneura* are the presence of an opening for the tendon of the mesoscutello-metanotal muscle (87: 1), the presence of unsclerotized lines between the dorsal and lateral regions of the abdominal tergites (188: 2), the larval eyes being ventrally of the antennae (223: 1), the division of the fourth maxillary palp segment into subsegments (240: 2) and the strophandry of the male genitalia (294: 1).

However, the fact that this analysis results in an unresolved phylogeny for Xyelidae does not mean that the mental analysis of Schulmeister (2003a: fig. 10) was wrong, because the characters concerning the plantulae were excluded from that analysis. If the analysis of the present data matrix with *Xyelecia* and *Pleroneura* is repeated with the exclusion of the characters concerning the plantulae (256–259), all 281 resulting trees (1444 steps) show the phylogeny ((*Macroxyela Megaxyela*) (*Xyelecia* (*Xyela Pleroneura*))), corresponding to that of Schulmeister (2003a). (Character 248 (vein 2r-m of the hindwing) does not, however, constitute a synapomorphy of *Xyelecia+Xyela+Pleroneura*, as suggested by Schulmeister.)

#### PHYLOGENY OF BASAL HYMENOPTERA

The purpose of the present paper is to bring together and revise all the morphological characters that have been gathered for a phylogenetically broad sample of basal Hymenoptera and to add some characters that had so far not been used in phylogenetic analysis. In a follow-up paper, this morphological information is analysed together with a large molecular data set to yield the most comprehensive simultaneous analysis of the basal lineages of Hymenoptera to date (Schulmeister, 2003b). Because many clades are found both in the morphological tree (Fig. 7), and in the tree resulting from the simultaneous analysis, synapomorphies will be mentioned in the present paper only for those groups that are not found in the simultaneous analysis.

The most interesting effect of the revision of the data matrix of Vilhelmsen (2001) was the fact that the relationships at the base of Hymenoptera were unresolved (Figs 3, 4), with either Xyelidae or Tenthredinoidea s.l. being the basalmost sawfly lineage. However, this was not very surprising because non-xyelid Hymenoptera were only very weakly supported

in the ordered analysis of Vilhelmsen's (2001) original data matrix (Bremer support: 1, bootstrap: 0.56), and in the strict consensus of the trees resulting from his unordered analysis (Vilhelmsen, 2001: fig. 9), the basal node was even unresolved.

In the course of this study, the number of taxa was increased by more than 50%, and the number of characters by 47%. The status of and relationships among the families as proposed by Vilhelmsen (2001) are confirmed in the final hypothesis of this paper (Fig. 7), with the exception that the relationships among *Syntexis*, Siricidae and *Xiphydria*+Vespina are now unresolved. Apocrita are not convincingly supported: if character 65 at the base of Apocrita is treated as unordered, Apocrita are collapsed in the strict consensus.

Of the 112 new characters that were added in this study, two contained potential synapomorphies for non-xyelid Hymenoptera – the maxillary palp being composed of six segments (240) and veins Cu and M being completely fused at the base of the hindwing (247) – so that this group was, once again, found to be monophyletic in the final hypothesis of this paper, i.e. Xyelidae is the most basal sawfly lineage. However, non-xyelid Hymenoptera are still very weakly supported, with a Bremer support value of 1.

Rasnitsyn (1988) and Ronquist *et al.* (1999) had proposed that Xyelidae were paraphyletic. Vilhelmsen (2001) and Schulmeister, Wheeler & Carepenter (2002), on the other hand, found evidence that this family is monophyletic. In this analysis, the latter hypothesis is confirmed and has a Bremer support of 6.

Tenthredinoidea *s.l.* and *s.s.* are monophyletic and well supported. In this study, the number of exemplars of Tenthredinidae was more than tripled. Even with this enlarged taxon sample, Tenthredinidae are still indicated as a paraphyletic grade, with respect to the remaining Tenthredinoidea *s.s.* (Fig. 7). The sister-group relationship of **Nematinae and Diprionidae+Cimbicidae+Argidae+Pergidae** is supported by the cenchri being at least twice as broad as long (117: 1), the absence of the crossvein 2r in the forewing (166: 1), and the reduction of the larval antennae to four segments (224: 3). The relationships within the sistergroup of Nematinae are the same as those proposed by Vilhelmsen (2001). The monophyly of **Diprionidae+Cimbicidae+Argidae+Pergidae** is supported by the cenchri being at least three times as broad as long (117: 2), the cenchri not being inflected (118: 1), the absence of anapleural sclerites (135: 1), the reduction of the larval antennae to no more than three segments (224: 4) and the absence of a patch of bristle-shaped denticles on the ventral face of all plantulae (258: 0). The sister-group relationship of **Cimbicidae and Argidae+Pergidae** is supported by the absence of metafurco-mesospinal muscles (103: 1),

the absence of metanoto-metabasalar muscles (124: 1), the absence of a division of the first abdominal tergite (129: 1), the absence of metapleural muscles between the first tergite and second sternite (131: 1), the fusion of the first abdominal tergite and the metepimera (139: 3), the absence the posterior metapleuro-metafurcal muscles and their apodemes (143: 1), the absence of metabasalar-metacoxal muscles (152: 1), the absence of the anterior branches of the subcosta of the forewing (160: 1), the absence of secondary hamuli (176: 1), the reduction of the larval antennae to no more than two segments (224: 5), the presence of muscle n (281: 3), the parapenis not being set off from the rest of the gonostipes (304: 1), the parapenis being more or less parallel to the median axis of the genitalia (309: 0) and the harpe of the male genitalia being rather straight instead of triangular (314: 0). The monophyly of Argidae still has very little support. Diprionidae and Argidae+Pergidae are the best supported groups within Tenthredinoidea *s.s.*

Rasnitsyn (1988) proposed that Tenthredinidae *sensu* Rasnitsyn (= Tenthredinidae including Diprionidae) are the sister-group of Cimbicidae, which together would be the sister taxon to Argidae+Pergidae. He suggested the following synapomorphies for Tenthredinidae *sensu* Rasnitsyn and Cimbicidae: 1. third segment of antenna reduced in size, 2. mesopseudosternal sulci lost, 3. preapical tibial spurs lost, 4. eighth sternum of male strongly excised apically. Rasnitsyn's (1988) hypothesis was further supported by the analysis of Ronquist *et al.* (1999) which included the four characters mentioned above. Vilhelmsen (2001) did not include the fourth character in his analysis and recoded the second character in such a way that it could not support the hypothesis of Rasnitsyn (1988). In my opinion, neither of these changes were justified. Moreover, by making these changes, the power of the test of the hypothesis of Rasnitsyn (1988) and Ronquist *et al.* (1999) was severely reduced, because significant evidence in favour of this hypothesis is excluded from the test. I added the characters of Ronquist *et al.* (1999) concerning the mesopseudosternal sulci and the male eighth sternum back into the analysis in order to provide a 'fair' test to the hypothesis of Rasnitsyn (1988). But in spite of these changes, the hypothesis of the monophyly of Tenthredinidae+Diprionidae+Cimbicidae was rejected. (However, cf. Schulmeister, 2003b.)

Pamphilioidea are the sister-group to Unicalcarida (= Cephidae, Anaxyelidae, Siricidae, Xiphydriidae and Vespina; Schulmeister *et al.* (2002)), which is satisfactorily supported. Within Unicalcarida, the relationships are (Cephidae (Anaxyelidae Siricidae (Xiphydriidae (Orussidae Apocrita))). Schulmeister *et al.* (2002) proposed that *Syntexis* is the sister-group of Siricidae. For the original data matrix of Vilhelmsen

(2001), this hypothesis is three steps longer than the most parsimonious tree in which Siricidae is the sister-group to Xiphydriidae+Vespina (Vilhelmsen, 2001: 435). This relationship is still found in the results from the ordered analysis of the revised data matrix (Fig. 3). In this study, five characters were added that support the monophyly of Siricoidea: extension of the female ninth tergite (263: 1), asymmetry of the larval labrum (265: 1), presence of muscle n in the male genitalia (281: 3), presence of muscle si in addition to s (286: 2), and basal orientation of the foramen genitale (296: 1). Two characters that support Siricidae+Xiphydriidae+Vespina (less than six maxillary palp segments (240: 0 and mesopseudosternal sulci absent (251: 1)) were also added so that the relationships of *Syntexis* and the Siricidae are unresolved in the final hypothesis (Fig. 7).

One reviewer asked to discuss the phylogenetic results of the unordered analysis, saying that 'it can be argued that this is the only analysis one should consider using parsimony criteria' because 'an unordered analysis does not impose 'human induced' constraints on character evolution'. I cannot agree with this. The moment we code a morphological character into different states, ordered or not, we are introducing human constraints. The same effect of ordering a multistate character can be achieved by coding it as two unordered binary characters; the constraint is the same. Treating the multistate character as unordered can have an effect equivalent to excluding one of the two binary characters from the analysis. So why should I discard information (by treating the multistate character as unordered) simply because I happened to code the information as an ordered multistate character instead of as two unordered binary characters? For this reason I have been discussing only the results of the ordered analysis as the final hypothesis of this paper.

Even so, the unordered analysis still gives some interesting information. As discussed above for character 65, treating a multistate character is not always without problems. While the ordering might be necessary and justified in one area of the tree, in which state 1 and state 2 are found in two sistergroups, the ordering of this character can lead to a transition from state 0 to state 2 in another area of the tree (where the intermediate state is not found) being counted as two steps. Looking through the ordered multistate characters, and focusing on the groups found in Figure 7, one can find instances of this, for example, in characters 23 (giving extra support to Argidae), 36 (Vespina), 42 (Cimbicinae+Abiinae), 65 (Apocrita), 112 (Argidae+Pergidae), 117 (Diprionidae+Cimbicidae+Argidae+Pergidae), 171 (*Monophadnoides*+*Metallus* and Vespina), and 224 (Hymenoptera). If the group is also found in the

results of the unordered analysis, or if at least the Bremer support value for this group (in the ordered analysis) exceeds the amount of extra support for this group, this extra support is not a problem as there is enough support from other sources. However, if the group disappears without this extra support this is a case worth discussing. All groups found in the results from the ordered analysis (Fig. 7) are also found in the results from the unordered analysis (Fig. 6) with one exception: Apocrita. In the ordered analysis, Apocrita has a Bremer support value of only one step. If the analysis is repeated with character 65 being treated as unordered (all else being the same), the relationships between the orussid, the stephanid and the remaining Vespina are unresolved. This means that the hypothesis of the monophyly of Apocrita depends on whether a transformation from state 0 to state 2 of character 65 is counted as one or as two steps. In the light of this result, I find it difficult to defend counting the transformation as two steps, and conclude that Apocrita is not convincingly supported as monophyletic by this analysis. More research is obviously required in this area.

#### ACKNOWLEDGEMENTS

I thank Ewald Altenhofer, Stephan Blank, Mark Dowton, Henri Goulet, Paul Hanson, Thomas Hörnschemeyer, Malte Jänicke, Niels Peder Kristensen, Stefan Schmidt, David R. Smith, Andreas Taeger, and Lars Vilhelmsen for providing valuable specimens and/or helpful information. I want to thank Rainer Willmann, James M. Carpenter, Donald Quicke, and two anonymous reviewers for reading earlier versions of the manuscript and making extensive comments which helped to improve the paper.

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## APPENDIX 1

Species examined by Vilhelmsen (2001) and in this study for coding the characters in Appendices 2 and 3. For full scientific species names (with author and year of description) of the taxa used by Vilhelmsen (2001) refer to his publication. Higher taxa are separated by long lines, OTUs by shorter lines. For a list of the species used to generate the data in Appendix 4, see Schulmeister (in press).

Taxa	Species used by Vilhelmsen (2001)	Species used in the present study	Names of OTUs
Psocoptera	<i>Amphigerontia bifasciata</i>	–	Psocoptera
Chrysopidae	<i>Chrysopa perla</i>	Chrysopidae sp.	Chrysopidae
Raphidioptera	<i>Raphidia xanthostigma</i>	Raphidioptera sp.	Raphidioptera
Coleoptera	<i>Priacma serrata</i>	<i>Priacma serrata</i> Leconte 1861	Coleoptera
Lepidoptera	<i>Micropterix calthella</i>	<i>Micropterix calthella</i> (Linnaeus 1761)	Lepidoptera
Mecoptera	<i>Panorpa communis</i>	<i>Panorpa</i> sp.	Mecoptera
Xyelidae	<i>Xyela julii</i>	<i>Xyela</i> sp.	Xyela
	<i>Macroxyela ferruginea</i>	<i>Macroxyela ferruginea</i> (Say 1824)	Macroxyela
Blasticotomidae	<i>Runaria reducta</i>	<i>Runaria reducta</i> (Malaise 1931)	Runaria
	<i>Paremplytus flavipes</i>	<i>Paremplytus flavipes</i> (Takeuchi 1939)	Paremplytus
	<i>Blasticotoma filiceti</i>	<i>Blasticotoma nipponica</i> Takeuchi	Blasticotoma
Tenthredinidae	<i>Tenthredo arcuata</i> + <i>Tenthredo</i> sp.	<i>Tenthredo campestris</i> Linnaeus 1758	Tenthredo
	–	<i>Aglaostigma lichtwardti</i> (Konow 1892)	Aglaostigma
	<i>Dolerus niger</i> + <i>Dolerus</i> sp.	<i>Dolerus</i> sp.	Dolerus
	–	<i>Selandria serva</i> (Fabricius 1793)	Selandria
	–	<i>Strongylogaster multifasciata</i> (Geoffroy 1785)	Strongylogaster
	–	<i>Monophadnoides</i> sp.	Monophadnoides
	–	<i>Metallus</i> sp.	Metallus
	<i>Athalia</i> sp.	<i>Athalia rosae</i> (Linnaeus 1758)	Athalia
	–	<i>Taxonus agrorum</i> (Fallén 1808)	Taxonus
	–	<i>Hoplocampa fulvicornis</i> (Panzer 1801)	Hoplocampa
	–	<i>Nematinus luteus</i> (Panzer 1804)	Nematinus
	<i>Nematus</i> sp.	<i>Nematus</i> spp.	Nematus
	–	<i>Cladius pectinicornis</i> (Geoffroy 1785)	Cladius
Diprionidae	<i>Monoctenus juniperi</i> + <i>Monoctenus</i> sp.	<i>Monoctenus juniperi</i> (Linnaeus 1758)	Monoctenus
	<i>Gilpinia</i> sp.	<i>Gilpinia</i> sp.	Gilpinia
	–	<i>Diprion</i> sp. ( <i>pini</i> or <i>similis</i> )	Diprion
Cimbicidae	<i>Cimbex</i> sp.	<i>Cimbex</i> sp.	Cimbicinae
	<i>Abia fasciata</i> + <i>Abia</i> sp.	<i>Abia fasciata</i> (Linnaeus 1758) + <i>A. sericea</i> (Linnaeus 1767)	Abia
	<i>Corynis</i> sp.	<i>Corynis crassicornis</i> (Rossi 1790)	Corynis

Argidae	<i>Arge nigripes</i> + <i>A. gracilicornis</i> + <i>A. pullata</i>	– – <i>Arge cyanocrocea</i> (Forster 1771) <i>Sterictiphora furcata</i> (Villers 1789)	Arge A Arge B Sterictiphora
Pergidae	<i>Perga condei</i> <i>Phylacteophaga froggatti</i>	<i>Perga</i> sp. <i>Phylacteophaga froggatti</i> (Riek 1955)	Perga
		<i>Lophyrotoma analis</i> (Costa)	Phylacteophaga
		<i>Acordulecera</i> sp.	Lophyrotoma
		<i>Decameria</i> sp.	Acordulecera
		<i>Neurotoma nemoralis</i>	Decameria
Pamphiliidae		<i>Neurotoma fasciata</i> (Norton 1862)	Neurotoma
		<i>Onycholyda amplexa</i> (Fabricius 1804)	Onycholyda
	<i>Pamphilius sylvaticus</i> + <i>Pamphilius</i> sp.	<i>Pamphilius middlekauffi</i> Shinohara & Smith 1983 + <i>Pamphilius hortorum</i> (Klug 1808)	Pamphilius
	<i>Cephalcia arvensis</i>	<i>Cephalcia</i> sp. ( <i>abietis</i> or <i>arvensis</i> )	Cephalcia
	<i>Acantholyda erythrocephala</i> + <i>A.</i> sp.	<i>Acantholyda</i> sp. ( <i>erythrocephala</i> or <i>flavipes</i> )	Acantholyda
Megalodontesidae		<i>Megalodontes cephalotes</i>	Megalodontes
		<i>Megalodontes skorniakowii</i> (Freyruth 1870)	Megalodontes
	<i>Cephus cultratus</i> + <i>C. nigrinus</i>	<i>Cephus pygmeus</i> (Linnaeus 1767)	Cephus
		<i>Cephus spinipes</i> (Panzer 1801) (for char. 265)	Cephus
	<i>Calameuta filiformis</i> + <i>C. pallipes</i>	<i>Calameuta filiformis</i> (Eversmann 1847)	Calameuta
	<i>Hartigia linearis</i> + <i>H. xanthostoma</i>	<i>Hartigia trimaculata</i> (Say 1824)	Hartigia
		<i>Hartigia xanthostoma</i> (Eversm. 1847) (for char. 265)	Hartigia
Anaxyelidae	<i>Syntexis libocedrii</i>	<i>Syntexis libocedrii</i> (Rohwer 1915)	Syntexis
Siricidae	<i>Sirex juvencus</i>	<i>Sirex juvencus</i> (Linnaeus 1758) (in Boulangé 1924) + <i>Sirex</i> sp.	Sirex
		<i>Xeris spectrum</i> (Linnaeus 1758)	Xeris
	<i>Urocerus gigas</i>	<i>Urocerus gigas</i> (Linnaeus 1758)	Urocerus
	<i>Tremex columba</i>	<i>Tremex columba</i> (Linnaeus 1763)	Tremex
Xiphydriidae	<i>Xiphydria camelus</i>	<i>Xiphydria camelus</i> (Linnaeus 1758)	Xiphydria
Orussidae	<i>Orussus abietinus</i> + <i>O. occidentalis</i>	<i>Orussus abietinus</i> (Scopoli 1763)	Orussus
Stephanidae	<i>Schlettererius cinctipes</i>	<i>Stephanus serrator</i> (Fabricius)	Stephanidae
Megalyridae	<i>Megalyra fasciipennis</i>	<i>Megalyra fasciipennis</i> Westwood 1832	Megalyra
Trigonaidae	<i>Orthogonalys pulchellus</i>	<i>Orthogonalys pulchellus</i> (Cresson 1867)	Trigonaidae
Aulacidae	<i>Aulacus striatus</i>	<i>Pristaulacus erythrocephalus</i> (Cameron)	Aulacidae
Ichneumonidae		Ichneumonidae sp.1	IchneumonidaeA
		Ichneumonidae sp.2	IchneumonidaeB
Ibaliidae	<i>Ibalia rufipes</i>	<i>Ibalia rufipes</i> Cresson 1879	Ibalia
Apoidea		<i>Sceliphron caementarium</i> (Drury 1773)	Sceliphron
Vespidae	<i>Vespula rufa</i>	<i>Dolichovespula adulterina</i> (du Buysson 1905) (= <i>D. arctica</i> Rohwer 1916)	Vespidae

## APPENDIX 2

Revised version of the data matrix of Vilhelmsen (2001), including additional taxa.

	000000001 1234567890	111111112 1234567890	222222223 1234567890	333333 123456	3334 7890	444444444 1234567890
Psocoptera	000001000	0000100-10	0000?110?0	?1-230	??00	00?- -0-010
Chrysopidae	000000000	0?00010010	0000?00000	01-110	?100	00?010-000
Raphidioptera	000000000	000011?001	?000?00000	01-210	?100	001000-000
Priacma	0010011000	0??011001?	?000?00010	?1-11?	??00	00?- - - -00
Micropterix	0000001100	0010000-10	0000?11010	100022	0000	00?000-00?
Panorpa	0000-00000	0010010011	0000?01000	11-320	0?00	012000-0?0
Xyela	0010000100	0010000-00	0010111010	000101	0000	0010010110
Macroxyela	0010000100	0010000-00	0010011010	01-001	0000	00100101??
Runaria	0010000010	0100000-00	002-001000	00010?	0010	1120020110
Paremphtus	0010000010	0?00000-00	002-?0100?	?0010?	?010	11?0021???
Blasticotoma	0010000010	0?00000-??	?010?01000	?00101	?010	112002?1??
Tenthredo	0010000000	0000000-00	0000001000	?00100	0010	11200202??
Aglaostigma	001000?0?0	0000000-00	?00000100?	?00100	0010	12?001?2??
Dolerus	0010000000	0?00000-00	0000001000	?00100	0010	11200202??
Selandria	001000?0?0	0000000-00	?00000100?	?00100	0010	121012?2??
Strongylogas	00100?????	?000000-00	0000001???	?00?00	?010	111002?2??
Monophadnoides	00100?????	?000000-?0	?000001???	?00?00	?010	112002?2??
Metallus	00100?????	?000000-?0	0000001???	?00?0?	?010	111012?2??
Athalia	0010000000	0010000-01	0000?01000	000100	0010	1100020211
Taxonus	00100?????	?000000-00	?000001???	?00100	?010	112002?2??
Holocampa	00100?????	?000000-?1	?000001???	?00?0?	?010	110002?2??
Nematinus	00100?????	?000000-?1	?000001???	?00100	?010	110002?2??
Nematus	0010000000	0?00000-01	0000001000	?00100	?010	11200202??
Cladius	00100?????	?010000-?1	?100001???	?00100	?010	111012?2??
Monoctenus	0010000000	0?00000-00	010000100?	?00100	?010	110002?2??
Gilpinia	0010000000	0110000-00	0100001000	000100	0010	1100020211
Diprion	00100?????	?010000-?0	?100001???	?00?00	?010	110002?2??
Cimbicinae	0010100000	0?00001-00	0001001000	?00100	?010	13000202??
Abia	0010000000	0010100-01	0001?01000	000100	0010	1100020211
Corynis	00100000?0	0?00010002	0001?01000	?0010?	?010	11000102??
ArgeA	0010000000	0000000-00	002-001000	000100	0010	1210021211
ArgeB	??????????	??????????	??????????	??????	????	??????????
Sterictiphora	0010000000	0?00000-00	002-?01000	?00100	?010	12100212??
Perga	0010000000	0?00001-00	0001?01000	?00210	?010	12100212??
Phylacteophaga	0010000000	0000000-00	0000001000	000110	?010	1200021211
Lophyrotoma	00100?????	?110000-?0	?200001???	?00100	?010	220001?2??
Acordulecera	00100?????	??00000-?0	?000?0?0??	?00?0?	?010	120002?2??
Decameria	00100?????	?110000-?0	?000001???	?1-230	?010	120002?2??
Neurotoma	0011000000	0?01010002	0000?2200?	?00101	?100	01?002?2??
Onycholyda	00110?????	?0110100?2	0000?22???	?00101	?100	011002?2??
Pamphilius	0011000000	0?01010000	0000022000	?0010{0,1}	?000	01100212??
Cephalcia	0011000000	0011010001	0000022000	100101	0000	0110021210
Acantholyda	0011000000	0?01010000	0000022000	?00101	?000	011002?2??
Megalodontesc	0011100000	0011010002	1200022000	000101	?000	0110121211
Megalodontesk	00111?????	?1110100?2	1200?22???	?00?01	?000	011012?2??
Cephus	0011010020	0110011000	1000?01000	000102	0000	0010020210
Calameuta	0011010020	0110011000	1000001000	?00102	?000	001002?2??
Hartigia	0011010020	0110011000	?000001000	?00102	?000	001002?2??
Syntexis	0011110021	0110011000	0000101000	001112	0000	0001021210
Sirex	0111110020	0110010100	0000?01000	000312	0111	00?00202?1
Xeris	011?0000??	?1100101?0	?000001?0?	?00312	?111	001002?2??
Urocerus	0111110020	0110010100	0000001000	?00312	?111	0010021211
Tremex	0111110020	0?00010100	0000001000	?00322	?111	001002?2??
Xiphidria	0111110001	0110110000	0000001000	000112	0010	1100021211
Orussus	1111110001	1110110112	1000101000	001210	1110	2100120210
Schlettererius	1111110001	1?01101012	1000?01101	?01200	?010	210212?2??
Megalynra	011- - -0021	0?????1?1?	?000101102	?01210	1?10	310212?2??
Orthogonalys	00111?0021	0?01101012	1000001101	?00110	?110	210212?2??
Aulacus	00110100?1	0?011?102	0?001010??	?01200	??10	210212?2??
IchneumonidaeA	00?00?????	?110110102	?000101?0?	?01200	?110	110012?2??
IchneumonidaeB	00100?????	?1101101?2	?000101?0?	?01200	?010	110212?2??
Ibalia	00110?00?1	0?0110002	1000101002	?01210	1010	110212?2??
Sceliphron	00110?????	?11111?1??	?000002???	?01100	?000	210212?2??
Vespa	00111100?1	011011?112	1000101102	?01100	1110	2102121211

	000000000	000000000	000000000	000000000	000000001
	5555555556	6666666667	7777777778	8888888889	9999999990
	1234567890	1234567890	1234567890	1234567890	1234567890
Psocoptera	1100000??1	00000?0000	000000000?	1--0?0003	?000?1-000
Chrysopidae	?000000??1	011000?0??	-2-00?000?	011000000?	?0-0?1-000
Raphidioptera	10000-0??1	011000??1	-2-00?100?	00--000000	-0-0?1-000
Priacma	111100-001	0000021001	00000?0000	1--1000-3	?0?0?1-000
Micropterix	0000000001	01?001????	-00000000?	0?????000?	?0??1-001
Panorpa	0000101??1	0100--1101	00000?1000	00--000003	?0?0?1-000
Xyela	0001100010	0200000000	0100010000	0100011000	0000000100
Macroxyela	?101101010	0200000000	010001000?	0100010000	?000?00100
Runaria	1100100020	02101000100	110001000?	0?????0?03	2102110???
Paremphtus	?100100020	02101001?0	01000?000?	0100?10003	?102?1?101
Blasticotoma	?100100020	0210100????	010001000?	0100010003	?102?1?001
Tenthredo	?100111031	02102001?1	0100000001	0100010001	?102111001
Aglaostigma	??001001-1	0????2?????	010000000?	?????????1	2102111???
Dolerus	?100111031	02102001?0	0100000001	0100010001	?102?11001
Selandria	??00100031	02102001?0	0100000001	0?????0??3	?102?11000
Strongylogas	??0010?031	0????2??1??	0100000001	010001?003	?102?1?00?
Monophadnoides	??00100031	0????2?????	010000000?	?????????3	?121?1????
Metallus	??00100031	0????2?????	000000000?	?????????3	?102?11???
Athalia	1000100031	0210210110	00000?000?	00--0?0001	0102111001
Taxonus	??00111031	02?02001??	0100000001	0????0????1	?102?1100?
Hoplocampa	??0010?031	0????2?????	0?0???0001	?????????3	?101?1????
Nematinus	??00100031	0????2?????	0?0000000?	?????????1	?101?1????
Nematus	?000101031	02102001?0	010000000?	00--0?0001	0101?11001
Cladius	??00101031	0????2?????	000000000?	?????????3	?101?11???
Monoctenus	?100100031	02102001?0	001000000?	0100010001	0101?11001
Gilpinia	1100100031	0210200110	00100?0001	0100010002	0101111001
Diprion	?100100030	0?102001??	001000000?	010001?003	?101?1100?
Cimbicinae	?1011001-1	1210210110	001000000?	0101030003	?10111?001
Abia	11011001-1	1210210110	00100?000?	0101030003	210111?001
Corynis	?100100021	0210210???	00000?100?	1--0?0002	0102?11001
ArgeA	1100110031	0210210111	0000000001	0100010003	2101101001
ArgeB	???????????	???????????	???????????	???????????	???????????
Sterictiphora	?100110031	0210200111	000000000?	0100010003	?101?01001
Perga	?0011111-0	02102001?1	00000?000?	00--1?0003	2111101001
Phylacteophaga	10001111-0	0210200111	100000000?	00--1?0003	2102110001
Lophyrotoma	?0001001-1	0?10200???	000000000?	?????????3	?201101???
Acordulecera	??001001-1	0????2??1??	0000000001	1?001?0003	2201?1100?
Decameria	??001001-1	02102001?1	0000000001	1???1????3	?20?01001
Neurotoma	?101111011	021020?????	010001000?	01000?0003	?100?1?100
Onycholyda	??01111011	021000?0??	0100010000	0????0????3	?100?10100
Pamphilus	?101111011	02100000?0	0100010000	0100010003	1100010100
Cephalcia	1101111010	0210000000	011001000?	0100010003	1100010100
Acantholyda	?101111010	021000?0??	0110010000	0100010003	?100?10101
Megalodontesc	1001111011	0210000110	010002000?	01000?0001	2100001100
Megalodontessk	??01111011	?210?0????	010002??0?	0????0?????	?????0110?
Cephus	1001111010	0210021100	1101110000	0100010113	1100000110
Calameuta	?001111010	021002?????	110111000?	01000?0113	?100?00110
Hartigia	?001111010	021002?1??	110111000?	0100010110	?100?00110
Syntexis	1001111010	0200021000	1100120000	0100011010	0100000120
Sirex	1101110020	0200021100	110001101?	0???0?0?110	?10001?120
Xeris	??011110?0	0?????????	110001101?	?????????0	?100?11???
Urocerus	1101111020	0200021100	1100011010	0100020110	0100?1?121
Tremex	?101111020	020002?1??	1100011010	0???020110	?200?1?120
Xiphydria	1001110010	0201001100	1100020120	01100121-2	010101?121
Orussus	10111101-0	0201021100	1101221220	1--1?20-2	021201-121
Schlettererius	?011110011	021020?????	11012?0220	0101?020-2	?212?1?121
Megalyra	?0111111-1	020120?1?0	1101200020	0101?021-3	?20?1?121
Orthogonalys	?0111111-1	020120?????	1101201221	01011321-3	?201?1?021
Aulacus	?011111010	021020?????	1101201221	0101?021-3	220?1?021
IchneumonidaeA	??111111-1	021020?????	1101201211	01???1?2-3	?202?1?121
IchneumonidaeB	??111111-1	0????2?????	110120121?	?????????2-3	?202?1????
Ibalia	?0111111-1	0201?211?0	1101201221	01100321-3	2202?1?121
Sceliphron	???1111???	??01?2?????	1101201?2?	01?11?2?-3	-20?1?121
Vespula	1011111011	0210221110	1101211221	01011321-3	220011?121

	1111111111 0000000001 1234567890	1111111111 1111111112 1234567890	1111111111 2222222223 1234567890	1111111111 3333333334 1234567890	1111111111 4444444445 1234567890
Psocoptera	?20010000?	0?00?0--00	?0??010010	?000100101	?0101--0?0
Chrysopidae	121000000?	0-00?0--00	0010000100	?000?00000	?100102000
Raphidioptera	?2?0000???	0-00?0--00	001?010100	0000100031	01001010?0
Priacma	0200100000	0?0000--00	0010000010	0100100001	?001102000
Micropterix	?2?0000???	0?01?0--00	10???111100	1000?00101	00?01--001
Panorpa	?21000010?	0-00?0--00	10000110?0	?000100001	0100102001
Xyela	0002100000	1000010000	00?0010000	0100100000	0000000100
Macroxyela	0002100???	1000010000	?00?010000	?100000000	00000001??
Runaria	000?1??110	101?11?010	0000000000	1100000021	110?1?210
Paremphtus	?002100???	101011?01?	?000000000	?100000021	?1001122??
Blasticotoma	0002100???	101??1001?	?00?000000	?10000?021	?1?01122??
Tenthredo	0002100110	1011?10010	?00?000000	?100011001	?1001012??
Aglaostigma	????1?????	1????100??	??????0000	??00011021	???0101???
Dolerus	0002100110	1011110011	?000000000	?100000001	?1?01012??
Selandria	?01?1??1??	1?1??11011	???010?000	??00011001	???0101???
Strongylogas	????1?????	1????100??	??0???0000	??00?1?001	???0101???
Monophadnoides	????1?????	1????100??	?0????0000	??0001?001	???0101???
Metallus	????1?????	1????100??	??????0000	??00010001	???0100???
Athalia	0212100???	1011110011	0000000000	0100100001	1100101201
Taxonus	?00?1?????	1?1??1001?	??0?00?000	??000?0001	???0101???
Hoplocampa	????1?????	1????110??	??0???0000	??0000104-	???0101???
Nematinus	????1?????	1????110??	??0???0000	??000?0001	???0101???
Nematus	0002100???	1011111011	?00?000000	?200001001	?1001012??
Cladius	????1?????	1????110??	??0???0000	??000?104-	???0101???
Monoctenus	0002100?00	1011112111	?00?000000	0100101000	?1?01012??
Gilpinia	0002100110	1011112111	0000000000	0100110000	1100101211
Diprion	?0?1??????	10111121??	?00?000000	??00?0?000	?1001012??
Cimbicinae	0012100?00	1210112101	0101011010	1100101-3-	1110101211
Abia	2012100???	1110012101	?101011010	1100101-3-	1110101211
Corynis	?212100???	1010111100	?00?011010	?200111-3-	?1101012??
ArgeA	0212100110	1211112111	0001000000	11010103-	1110101211
ArgeB	???????????	???????????	???????????	???????????	???????????
Sterictiphora	?212100???	1211?1211?	?00?000010	??10?0103-	?1101012??
Perga	1212100???	121111?111	?00?000010	020010103-	?1101012?0
Phylacteophaga	221210011?	1211112111	00?1000010	120010103-	1110101210
Lophyrotoma	12??1?????	12111111??	?0?0000010	??0010003-	?0101012??
Acordulecera	????1?????	1????111??	??????0010	??00??003-	???0101???
Decameria	?21?1?????	1?1??11111	??0?00?010	??0010?03-	???0101???
Neurotoma	?002100???	1000?1000?	?00?010000	?100100000	?0000010??
Onycholyda	?00?1?????	1?0??10000	??0?01?000	??00100000	???0010???
Pamphilus	?002100100	1000010000	?000010000	?100100000	?0000010?0
Cephalcia	0002100???	1000010000	0000010000	1100100000	1000010110
Acantholyda	?0?2100???	1?00?10000	?00?010000	?100100000	?0000010??
Megalodontesc	0002100???	1000012000	0001000010	1100100000	1100110200
Megalodontessk	?0?1??????	1????12000	??0???0010	??00???????	???01?0???
Cephus	1001100000	101100--00	0001110100	0200100011	1100120100
Calameuta	10?2100???	101100--0?	?00?110100	?200100011	?1001201??
Hartigia	?0?1100000	10?1?0--0?	?00?110100	?200100011	?1001201??
Syntexis	0002100???	1010011000	0000110100	1100100100	1000110110
Sirex	0102100???	1000010020	0001000100	0100110000	1000102100
Xeris	????1?????	1????100??	??0???100?	??00??0000	???0102???
Urocerus	0102100000	1000?10020	0001000100	0100110000	?0001021??
Tremex	?1?2100000	1000?100??	?00?00?100	?100110000	?0001021??
Xiphydria	0002100100	1-00010020	0011000100	0100100100	1110110210
Orussus	1002110111	1000010001	0011010010	0201100101	1111101210
Schlettererius	?0?2110???	1000?0--??	?01?01?010	?20211013-	?1111012??
Megalyna	?2?2111111	1000?0--??	?01?01?010	??0211?13-	?1111012??
Orthogonalys	2212111111	1000?0--0?	?01?01?010	?20211?13-	?1111?2???
Aulacus	?2?2111???	1000?0--0?	?01?00?011	??0211013-	?1?11012??
IchneumonidaeA	?21?1??1??	1?0??0--??	??1?00?011	??02??013-	???1101???
IchneumonidaeB	????1?????	1????0--??	??1???0011	??02??013-	???1???????
Ibalia	2212110111	1000?0--0?	?01?000011	?20210013-	?1111012??
Sceliphron	?21?1?????	1????0--??	??1?01?011	??02??013-	???1???????
Vespa	2212110111	100000--01	0011011-10	120211013-	1111101211

	1111111111 555555556 1234567890	1111111111 666666667 1234567890	1111111111 777777778 1234567890	1111111111 888888889 1234567890	1111111112 999999990 1234567890
Psocoptera	?0??0001?1	?010-1-111	011--10101	111100-000	000-020110
Chrysopidae	00??010100	00?0??????	011--100??	???1000000	010--?----
Raphidioptera	???0011100	000000????	011--100??	??01000000	010-02000-
Priacma	00000001--	?-----	-11--110??	000000000?	0?????????
Micropterix	0??0010-00	0??0??????	?11--111??	???1000000	02-----
Panorpa	000?010100	0??0??????	011--100??	??01010000	02-----
Xyela	0011100010	0000000000	1000000000	0000010200	001010000-
Macroxyela	????100000	0000000000	1000000000	00000101?0	001010000-
Runaria	100110?120	1-11001000	1100000100	0000010210	00?????0010
Paremphtus	????101120	1-11001000	1100000100	0000010210	00?????0010
Blasticotoma	???1101120	1?11001000	1100000100	0000010210	0010100010
Tenthredo	????111121	0-01001000	11000?0100	00000101?0	0010101010
Aglaostigma	???????120	0-010?1000	1100000100	00000101?0	0010?01010
Dolerus	????111120	0-0100-100	1100000100	00000101?0	0010101010
Selandria	???1111120	0-01001000	1100000100	00000101??	00????????
Strongylogas	???????120	0-01001000	1100000100	00000101?0	0010?01?10
Monophadnoides	???????120	0-01001000	310?010101	10000101??	00????????
Metallus	???????121	0-11001000	310???0101	10000101??	00????????
Athalia	0011111121	0-01001000	1100000100	00000101?0	0010101010
Taxonus	????111120	0-01001000	110?010100	00000101??	00????????
Hoplocampa	???????120	0-11001000	2100000100	00000101?0	00????????
Nematus	???????120	0-1101-000	3100000100	00000101?0	00????????
Nematus	???1111120	0-1101-{0,1}00	3100000100	00000101?0	0010101010
Cladius	???????120	0-1101-000	2100010100	00000101?0	00?????1?10
Monoctenus	???1111120	0-1101-000	21000?0100	00000101?0	001010100-
Gilpinia	1011111120	0-1101-000	11000?0100	00000101?0	001010100-
Diprion	?????11121	0-1101-000	1100000100	00000101?0	?010?0100-
Cimbicinae	111?111121	0-11001000	1100010100	0000010200	0010101010
Abia	1111111121	0-11001000	2100010100	0000010200	0010101010
Corynis	???1111121	0-11001000	21000?0100	0000010200	0010101010
ArgeA	1101111020	0-0101-000	2100010100	00000101?0	0010101010
ArgeB	??????????	??????????	??????????	??????????	??????????
Sterictiphora	???1111121	0-1101-110	21000?0100	00000101?0	0010101010
Perga	?0?0111021	0-0101-000	4101010100	10000101?0	0010101010
Phylacteophaga	0110111021	0-0101-000	4101010100	10000101?0	0010101010
Lophyrotoma	?????11120	0-0101-100	4101010100	10000101??	0021?01010
Acordulecera	???????021	0-1101-000	4101110100	10000101?0	00????????
Decameria	????111121	0-0101-000	3101010100	10000101??	00????????
Neurotoma	???1100001	0001000000	1001000000	0000011200	0010111110
Onycholyda	???100000	0001000000	1001000000	0000011200	00101111?1
Pamphilus	???100000	0001000000	1001000000	0000011200	0010110110
Cephalcia	0011100000	0001000000	1001000000	0000011200	0010110110
Acantholyda	???1010100	0001000000	1000000000	0000011200	0010110110
Megalodontesc	1111100021	0101000000	1101010100	00000101?0	0010110110
Megalodontesk	???100021	0101000000	1101010100	00000101?0	00????????
Cephus	1011100021	0001100000	1101000100	00001101?0	0010100010
Calameuta	???100021	0001100000	1101000100	00001101?0	0010100010
Hartigia	???100021	0001100000	1101000100	00001101?0	0010100010
Syntexis	0011100121	000110-100	1101000101	10000101?0	0021100011
Sirex	0111100101	0101000000	1100010100	00000101?0	0021100011
Xeris	???????100	0101000000	11000?0101	10000101??	00????????
Urocerus	???100100	0101000000	1100010100	00000101?0	0021100011
Tremex	???100100	010100-100	1100010100	00000101?0	0021100011
Xiphydria	1111101120	0001000000	1001010100	0000010200	0020100011
Orussus	0111101121	0-11200011	3101101111	10000101?1	202110000-
Schlettererius	???100121	010120-111	4101011111	10111101?1	2020100011
Megalyra	???112121	011120-111	4101101111	11111101?1	100-10000-
Orthogonalys	???112121	0101200000	4101001111	???11101??	20????????
Aulacus	????112121	010120-110	4101111111	11111101?1	1010100011
IchneumonidaeA	???11?121	0111200?00	4101011101	10011101??	00????????
IchneumonidaeB	???????121	0111200?00	41010011??	??011101??	00????????
Ibalia	???1111121	-11120-011	4101111111	11111101?1	102010000-
Sceliphron	???112121	-111200000	4101000110	10001101??	00????????
Vespula	1110112121	0101200000	4101010110	10011101?0	000-000011

	222222222 000000001 1234567890	222222222 111111112 1234567890	222222222 222222223 1234567890	22222 333333 123456
Psocoptera	000--1?-0	?00?00100	-----	-----
Chrysopidae	--1--0?0-	----?????	0014010002	-0001-
Raphidioptera	--01--101-	--?00000	0004001002	-0001-
Priacma	??????????	?????010?	??????????	??????
Micropterix	-----	----00100	001401?010	0?001-
Panorpa	-----	----00000	0004000010	00001-
Xyela	-000000010	0000011011	0111000011	00001-
Macroxyela	--00000000	0000101011	0101000011	000000
Runaria	0000????0?	?00?01001	??????????	??????
Paremphtus	000?000?0?	?0?0?01001	??????????	??????
Blasticotoma	0000000?00	0100001001	0101000012	-00001
Tenthredo	1000110?00	?10?11001	0102000010	10001-
Aglaostigma	1010110100	?10?11001	0?02000?10	10????
Dolerus	1100110?00	?10?11001	0102000010	10001-
Selandria	??????????	?????11001	???2??0?10	??????
Strongylogas	?????????00	?????11001	0?02000?10	10????
Monophadnoides	??????????	?????11001	???2?0?10	10????
Metallus	??????????	?????11001	???2?0?10	00????
Athalia	1000110100	?10?11001	0102000010	10001-
Taxonus	??????????	?????11001	0?02000010	10????
Hoplocampa	?????????0?	?????11001	0?03000010	1?????
Nematinus	??????????	?????11001	0?03000?10	1?????
Nematus	1100110?01	?00?11001	01031?0010	10001-
Cladius	?????????0?	?????11001	???3??0?10	1?????
Monoctenus	-010010?00	?01?11001	0104100010	1?001-
Gilpinia	-010010100	?01?11001	0104100010	10001-
Diprion	-010010?00	?01?11001	???41?0?10	1?????
Cimbicinae	0100110100	?01?11001	0105000010	11001-
Abia	1100110100	?01?11001	0105000010	11001-
Corynis	1100110?00	?00?11001	???5?0?0?	?1????
ArgeA	11010-0001	0000011001	0106000010	00001-
ArgeB	??????????	??????????	??????????	??????
Sterictiphora	11010-0?01	?00?11001	0106?00010	0??00?
Perga	11010-0101	?00?10001	0?0??0010	0??01-
Phylacteophaga	10010-0?01	?10?10001	??????????	??????
Lophyrotoma	10010-0?01	?00?10001	??????????	??????
Acordulecera	??????????	?????10001	0?06?000?2	-??0??
Decameria	??????????	?????10001	??????????	??????
Neurotoma	0000-11?11	?00?01011	0?10000?22	-?1001
Onycholyda	??00??0?1?	?0??01011	??????????	??????
Pamphilus	0000-11011	0001001011	0110000122	-01001
Cephalcia	0000-11011	0101001011	0110000122	-01001
Acantholyda	0000-11?11	?10?01011	0?10000122	-??001
Megalodontesc	0000-01011	?00?01011	0?10000?22	-?1001
Megalodontessk	??????????	?????01011	??????????	??????
Cephus	0000000000	01011011-1	0?03000222	-?0100
Calameuta	0000000?00	?10?011-1	??????????	??????
Hartigia	0010000000	01011011-1	0?03000222	-?0100
Syntexis	0000000000	0100001001	1--4011222	-?011-
Sirex	0000000?00	0101001011	1--?011222	-0011-
Xeris	?????????0?	0?0?01011	??????????	??????
Urocerus	0000000000	0101001011	??????????	??????
Tremex	0000000?00	?10?01011	1--5011222	-0011-
Xiphydria	0000010100	0100101011	1--4011222	-?011-
Orussus	-000000?01	01001011-1	1--60?13-2	-?01-
Schlettererius	??00010?01	?10?011-1	1--60?13-2	-??0??
Megalynra	-?00010?01	11001?11-1	??????????	??????
Orthogonalys	?????????1	0??1001201	??????????	??????
Aulacus	??00?1??01	?10?011-1	??????????	??????
IchneumonidaeA	??????????	?????011-1	??????????	??????
IchneumonidaeB	??????????	?????011-1	??????????	??????
Ibalia	-?010-0?01	11011011-1	1--?113-2	-??0??
Sceliphron	?????????1	0??21011-1	??????????	??????
Vespa	000000?01	?00?011-1	1--61013-2	-0001-

## APPENDIX 3

Additional characters presented in the present paper.

	2222	2222222222	2222222222	222222
	3334	4444444445	5555555556	666666
	7890	1234567890	1234567890	123456
Psocoptera	????	??????????	??????????	??????
Chrysopidae	?000	1????00???	?00?0---?	??00??
Raphidioptera	0000	1????00???	1??000---0	-0????
Coleoptera	2000	0??????0?	??000---?	?0????
Lepidoptera	0010	1????00???	?00?0---?	?00???
Mecoptera	0000	1????0000?	100000---0	0000??
Xyela	2010	2000000100	0000010000	000000
Macroxyela	2000	2000000000	0000010000	000000
Runaria	2001	2001001101	0??002000?	0000??
Paremphytus	200?	?001001101	??????????	??00??
Blasticotoma	2001	2001001101	0??002???	??000-
Tenthredo	2001	200010??00	1000021100	000001
Aglaostigma	2001	2000101101	1000021000	000001
Dolerus	2001	200000??00	1000021000	000011
Selandria	2001	200020??01	1??0021100	000001
Strongylogaster	2001	200020??00	1000021100	000001
Monophadnoides	2001	2000-01101	1000021100	0000?1
Metallus	2001	2000-01101	100002???	010001
Athalia	2001	2000001101	1000020000	0000?1
Taxonus	2001	2000001100	1000021000	000001
Hoplocampa	2001	2000-01101	1000021100	000002
Nematinus	2001	2000-01101	000002???	000002
Nematus	2001	2000-01101	0000021100	0000?2
Cladius	2001	2000-01101	0000021100	000002
Monoctenus	0001	2000-01101	1000021000	000001
Gilpinia	0001	2000101101	1000021000	0000?1
Diprion	0001	2000101101	1000021000	0000?1
Cimbicinae	2001	2001101101	100002100?	0000?1
Abia	2001	2001-01101	1000021{01}00	000001
Corynis	2001	2001-01101	1000021000	0000?1
ArgeA	????	??????????	??????????	??????
ArgeB	2001	2010-01101	0000020000	000003
Sterictiphora	2001	2100-01101	0000020000	000002
Perga	200-	20?1-???	0??002000?	0?00??
Phylacteophaga	200-	2000-0111-	1??0020000	0000??
Lophyrotoma	?001	2011-0111-	0??0020000	0000??
Acordulecera	2001	2000-0111-	100002???	0000?2
Decameria	?00-	2010-0111-	0??0020000	0000??
Neurotoma	0001	2001001101	100001???	?0000-
Onycholyda	0001	2001001101	1000010000	0000?-
Pamphilus	0001	2001001101	000001000?	?0000-
Cephalcia	0001	2000001101	0000010000	00000-
Acantholyda	0001	2000001101	0??0010000	00000-
Megalodontesc	0001	2001001101	0000010000	00000-
Megalodontessk	0001	2001001101	0??0010000	?0000-
Cephus	0001	2000111101	0000021000	01000-
Calameuta	0001	2000111100	0000021000	0100?-
Hartigia	0001	2000111100	0000020000	01000-
Syntexis	0001	2100001101	000000---?	01101-
Sirex	0000	1111001101	?00101001?	00201-
Xeris	0000	111100111-	1??110---0	00201-
Urocerus	0000	1111001111	?001010010	0020?-
Tremex	1000	111100111-	100111001?	00201-
Xiphydria	0000	2001001101	1000020000	00000-
Orussus	2100	21-0-0111-	111000---0	00010-
Stephanidae	0001	2100-0111-	10?200---?	1000?-
Megalyra	1000	2?00-2111-	1??100---?	0????-
Trigonalidae	0001	2000-2111-	??002???	0????-
Aulacidae	1001	2000-0111-	1??000---?	0????-
IchneumonidaeA	0000	2000-0111-	100000---0	1000?-
IchneumonidaeB	0000	2000-0111-	1??000---0	1000?-
Ibalia	1000	2001-0111-	??0000---0	0?00?-
Sceliphron	1001	2000-0111-	1000020001	000?0-
Dolichovespula	1001	2000-0111-	100000---1	100?0-

## APPENDIX 4

The characters of the terminal abdominal segments of male Hymenoptera (Schulmeister, in press), slightly modified for phylogenetic analysis (see text).

	2222	2222222222	2222222222	2222222223
	6667	7777777778	8888888889	9999999990
	7890	1234567890	1234567890	1234567890
Psocoptera	????	---??????	?????????1	??0?????2?
Chrysopidae	????	??????????	??????????	??????????
Raphidioptera	????	---??????	?????????1	??0?????2?
Priacma	????	??????????	??????????	??00?????
Micropterix	????	---??????	?????????1	??0?????2?
Panorpa	????	---??????	?????????1	??0?????2?
Xyela	0-00	?000000000	2000000100	0001010000
Macroxyela	0-00	0000000000	2000000100	0000010000
Runaria	0-00	0000000201	4010020211	0000010000
Paremphtus	0-00	0000000211	1010000211	0000000000
Blasticotoma	????	??????????	?????????1	??00000000
Tenthredo	2000	2001000101	3000000211	0001000000
Aglaostigma	2000	2001000001	3010000211	0001000000
Dolerus	2000	--11100101	3010000--1	0001000002
Selandria	2000	2001200101	1010000211	0001000000
Strongylogaster	2000	2000000101	1010000211	0001000000
Monophadnoides	2000	--01100001	3000000211	0001000001
Metallus	2000	--11200101	1010000--1	0001000011
Athalia	2000	2000000101	1000000--1	0001000000
Taxonus	2000	2001000101	2000000211	0001000000
Hoplocampa	2000	2100000101	1010000211	0001020000
Nematinus	2000	2000000101	1010000211	0001000000
Nematus	2000	2000000101	0010000211	0001000000
Cladius	2000	2000200201	1000000--1	0001000000
Monoctenus	2010	2011000101	1010000--1	0001000000
Gilpinia	2010	2001000001	1010032--1	0001000100
Diprion	2110	2001000101	101003?--1	0001000100
Cimbicinae	2110	2001100101	3000002201	0001000000
Abia	2110	2001000101	3000000--1	0001000000
Corynis	2000	2001200101	3000020201	0001000000
ArgeA	0-00	--11000001	3110010201	0001000011
ArgeB	0-00	--11000001	3110010201	0001000011
Sterictiphora	0-00	--01000011	3000010201	0001010001
Perga	??00	---00000?1	?210??0?1	00010-002-
Phylacteophaga	??00	---0000?1	1010010--1	00010-002-
Lophyrotoma	0-00	---200001	1200010201	00010-002-
Acordulecera	1-00	---000001	3200010201	00010-002-
Decameria	1-00	---000001	3200010201	00010-002-
Neurotoma	1-00	?10?000?00	3020??0100	0000000000
Onycholyda	1-00	0100000000	3000000100	0000010000
Pamphilius	1-00	?100000?00	302000?1?0	0000010000
Cephalcia	2-00	0100000100	3020020100	0000010000
Acantholyda	??0?	??0??00?00	30?00?01?0	0000010000
Megalodontesc	1-00	0100000011	3021100100	0000000010
Megalodontess	??00	01??000211	3021100?0?	0000000010
Cephus	1-00	2000000201	1020111---	0010000000
Calameuta	1-00	2001000211	1020111---	0010000000
Hartigia	1-00	1000100201	1020111---	0010000000
Syntexis	????	001100000?	3000?20--1	0000010000
Sirex	1-0?	00?0100000	30200?0000	00?0010000
Xeris	1-00	0000100000	3020000000	0010010000
Urocerus	1-00	0000110000	3020020000	0010010000
Tremex	1-00	0?001000?0	3020000010	0000000000
Xiphydria	1-00	1000000001	1000010000	0000000000
Orussus	1-01	100010000?	?000031---	0000100000
Stephanus	1-20	1001100201	1000011---	0000100000
Megalyra	????	??????????	??????1---	?????00?0?
Orthogonalys	1-20	200000000?	3000??2--1	?000020000
Pristaulacus	????	??????????	??????1---	??0?010000
IchneumonidaeA	0-00	1000100211	3000001---	0100100010
IchneumonidaeB	1-00	1000000011	3000001---	0100100000
Ibalia	????	??????????	??????1---	?????10000
Sceliphron	1-00	2000000201	1000131---	0000021000
Dolichovespula	1-00	1010000101	1000031---	1000011010

	333333	3	333	3333333333	3	3	33333333	3333333333	33	3	3333333	333
	000000	0	001	1111111112	2	2	22222223	3333333334	44	4	4444445	555
	123456	7	890	1234567890	1	2	34567890	1234567890	12	3	4567890	123
Psocoptera	??????	?	???	??????????	?	?	?0????	????????000	??	?	???????	???
Chrysopidae	??????	?	???	??????????	?	?	????????	??????????	??	?	???????	???
Raphidioptera	??????	?	???	????????0??	?	?	?0????	??????????	??	?	???????	???
Priacma	??????	?	???	????????0?0	?	?	?0????	??????????	??	0	0?0????	0??
Micropterix	??????	?	???	??????????	?	?	?0????	??????????	??	?	???????	???
Panorpa	??????	?	???	????????0?0	?	?	?0????	????????0??	??	0	0?0????	010
Xyela	000100	0	101	0000000100	0	1	00100000	0000000000	00	2	0000010	000
Macroxyela	000100	0	101	0000000100	0	1	00100000	0000000000	00	1	0000010	000
Runaria	000101	0	00?	0-?0001010	0	1	00100010	0000000000	00	0	0020010	000
Paremphytus	000101	0	000	0-10001010	0	1	10100010	00010000?0	0?	0	0020010	000
Blasticotoma	000100	?	000	0-?0001010	0	?	?1?001?	?000000000	00	0	0?0????	000
Tenthredo	000300	0	101	0-?1000000	0	0	00100010	0000000020	00	2	0001020	100
Aglaostigma	000300	0	211	0-11000000	0	2	?0100010	0000000010	10	1	0001010	000
Dolerus	000310	0	101	0-?1000000	0	0	10100010	0000000000	00	2	0001020	000
Selandria	000300	0	100	0-11000000	0	2	00100010	0000000040	00	1	0001020	000
Strongylogaster	000300	0	110	0-11000000	1	2	00100010	0000000030	00	1	0001020	000
Monophadnoides	000300	0	111	0-11000000	0	1	00100010	0000000000	2-	2	0001010	000
Metallus	000300	0	111	0-110000?0	0	1	10100010	0000000000	2-	1	0001013	000
Athalia	000200	0	201	0-11000000	0	0	00100010	0000000000	00	3	0101010	000
Taxonus	000300	1	101	0-11000000	0	2	00100010	0000000000	00	2	0001020	000
Hoplocampa	000300	0	111	0-11000010	0	1	10100010	0000000000	00	2	0001020	000
Nematinus	000300	0	110	0-11000011	0	2	00100010	0000000000	00	1	0001021	000
Nematus	000300	{01}	110	0-11000001	0	{12}	10100010	0000000000	00	{12}	0001024	000
Cladius	000200	1	101	0-?1000010	0	1	10100010	0000000030	00	1	0001011	000
Monoctenus	000300	0	11?	0-11000000	1	2	00110010	0000000000	00	3	0001020	000
Gilpinia	000300	1	111	0-11000000	1	3	10110010	0000000020	00	3	0200010	000
Diprion	000300	0	11?	0-11000000	1	0	10110010	0000000020	00	3	0100010	???
Cimbicinae	000200	0	101	0-10000000	0	2	00101010	0000000030	00	2	0000030	000
Abia	000200	0	101	0-10000000	0	2	10111010	0000000000	00	{13}	0000030	000
Corynis	000100	0	101	0-?0000100	0	2	00111010	?000000000	00	3	0001032	???
ArgeA	100100	0	001	0-10100000	0	2	11100010	0000100130	??	0	0301010	000
ArgeB	100100	0	001	0-10100000	0	2	11100010	0000100130	?1	0	0001010	000
Sterictiphora	101100	0	001	0-10100000	0	0	01100010	0000100130	01	0	0001020	000
Perga	--0100	0	101	0-?0000000	0	?	?110001?	?000100???	??	?	?3?01?	???
Phylacteophaga	--0110	0	?0?	0-10000000	?	2	0110001?	?000000000	2-	0	0331010	001
Lophyrotoma	--0100	0	101	0-10000000	0	3	01101010	0000100000	01	0	0301010	100
Acordulecera	--0100	0	100	0-10000000	0	2	01100010	0000100000	??	0	000?010	021
Decameria	--0100	0	001	0-10000000	0	2	11100010	0000100000	01	0	0301010	001
Neurotoma	000000	?	?00	01?0011000	0	?	?010001?	?000000000	00	0	0200010	000
Onycholyda	000000	0	101	0110011000	0	3	00100010	0000000000	00	0	0200010	000
Pamphilius	000000	?	?00	01?0011000	0	?	?010011?	?00000000?	0?	0	0200010	000
Cephalcia	000000	0	101	0110011000	0	3	00100110	0000000000	00	0	0200010	000
Acantholyda	000000	?	?01	01?00?1000	0	?	?0100110	0000000000	?0	0	020?01?	000
Megalodontesc	000000	1	101	0110010000	0	4	10110010	0000000040	00	1	0201021	000
Megalodontess	000000	1	101	01?0010000	0	4	10110010	?00000???	??	1	0201021	???
Cephus	000100	0	000	0-----1000	0	2	0-100110	0000010000	2-	0	0300010	000
Calameuta	000100	0	000	0-----1000	0	2	0-100110	0000010000	2-	0	0300000	000
Hartigia	000100	0	000	0-----0000	0	2	0-100110	0000010000	2-	0	030000?	000
Syntexis	000100	1	001	0-10001000	0	3	0010001?	?000?00???	??	?	0?0????	???
Sirex	001100	0	?0?	01?000?000	0	?	?-100?1?	?000?10?0?	??	?	?3110??	000
Xeris	001100	0	10?	0110001000	0	1	0-100111	?000010000	00	1	0311011	000
Urocerus	001100	0	10?	01?0001000	0	1	0-100011	0000010000	00	1	0311010	000
Tremex	001100	0	100	01?0001000	0	?	1-120011	?000?10???	??	1	0310011	001
Xiphydria	010100	1	101	0110001000	0	2	00100010	0000000000	00	0	0020010	000
Orussus	000100	0	101	0-----1000	0	3	00100000	0011000030	?0	0	0001112	200
Stephanus	010000	0	301	0-----1000	0	2	10101001	0001001001	??	1	0102000	020
Megalalya	011100	?	?0?	0-----?000	0	?	??11001?	??00?00???	??	0	0102002	020
Orthogonalys	010100	1	?00	0-1-000000	0	?	1011001?	?00000000?	??	0	0102010	210
Pristaulacus	010100	1	?00	0-----?000	0	?	?01?000?	?00000??0?	??	0	0100010	200
IchneumonidaeA	110100	0	000	0-----1000	0	2	00100010	0000000?00	2-	0	0031000	200
IchneumonidaeB	010100	0	100	0-----1000	0	2	0?100100	0000000000	2-	0	0001001	020
Ibalia	000100	?	?0?	0-----?000	0	?	0?10011?	?000?00???	??	0	?--1--2	001
Sceliphron	010000	0	300	0-----0000	1	?	01100010	0100001001	20	0	0201011	211
Dolichovespula	010000	1	201	1-----1000	0	0	0?110001	0000001050	20	1	1102011	211

