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Testing cladograms by fossil record: the ghost range test

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Abstract

A method of the ghost range calculation is proposed to assess the congruence between a cladogram and the fossil record and to compare cladograms on this basis. The method is tested on a set of cladograms developed recently to reveal the phylogeny of the hymenopterous insects (Order Vespida), and the results are discussed.

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Introduction

It is an ordinary condition in cladistic research that cladograms developed from different data for the same set of taxa often differ significantly from each other. This is crucial since the cladogram comparison is aimed at selecting the most correct one. There are a number of indices that have been developed to estimate statistical features that reflect deviation of the cladogram from the most parsimonious one (Quicke, 1996: 3.2.5). It is not so evident, however, that the evolutionary process does strictly observe the parsimony principle. That is why it seems reasonable to seek a method of assessment less dependent on particular evolutionary concepts.

The fossil record is a source of the evolutionary information that is not strictly dependent on our evolutionary hypotheses, and so in principle it may be used as an external standard in the comparison of cladograms. Of course, the fossil record is imperfect, but so are all our sources of evidence. This is true for cladistics as well, for the character set is never exhaustive, and transformation series composition and polarity are always hypothetical. That is why both sources of the evolutionary information, the fossil record and the cladograms, possess only degrees of 'perfection', but even so are worthy of comparison in testing phylogenies.

There are methods proposed to assess quality of the fossil record based on how it agrees with the cladogram of respective taxa (reviewed by Benton and Hitchin 1997). Unfortunately, these metrics do not fit the reverse task, that is, to test different cladograms of a particular taxon for their extent of congruence with the fossil record. Toward this end, I am proposing here a similar but slightly different approach. In its present form the method is rather rough, but whenever found appropriate, it may be easily improved for more precise calculation.

Material

Fossil record of the hymenopterous insects (Order Vespida = Hymenoptera) is selected to test the method for the following reasons. Incomplete like any fossil history, the hymenopteran record is rich enough to represent as many as 51 out of 54 ex-

tant families (e.g., Fig. 1; superfamily Chalcidoidea is used here as a single taxon because there is no cladogram available for it yet). As many as 38 of these families are recorded starting from the Mesozoic, a time wherein many high-level phylogenetic events occurred, and 20 more families are known to be extinct (mostly since the Mesozoic). A wealth of cladograms have been proposed recently for the family level phylogeny of the order, and this variety allows us to select enough of them to test. The examples are displayed in Figs. 1-6.

Fig. 1 is based on Rasnitsyn (1988), with several minor additions and modifications explained in the caption. Fig. 2 shows the results of the recent parsimony re-consideration of the concept by Rasnitsyn (1988) performed by Ronquist, Rasnitsyn, Roy, Eriksson and Lindgren (1999). Figs. 3-5 are re-drawn from the cladograms in Vilhelmsen (1997: fig. 2), Whitfield (1992: fig. 5), and Brothers and Carpenter (1993: fig. 11), respectively. Fig. 6 represents the apocritan molecular phylogeny performed by Dowton, Austin, Dillon and Bartowsky (1997: fig. 2), with the symphytan families, Orussidae and Stephanidae added after the work of Dowton and Austin (1994). All dendrograms are unified in their style, with the known duration of taxa being indicated by thick lines, relationships by horizontal thin lines, and the implied ghost ranges (see below) by vertical thin lines; the vertical thin line connecting two horizontal ones means nothing more than a connection of two parts of a horizontal line.

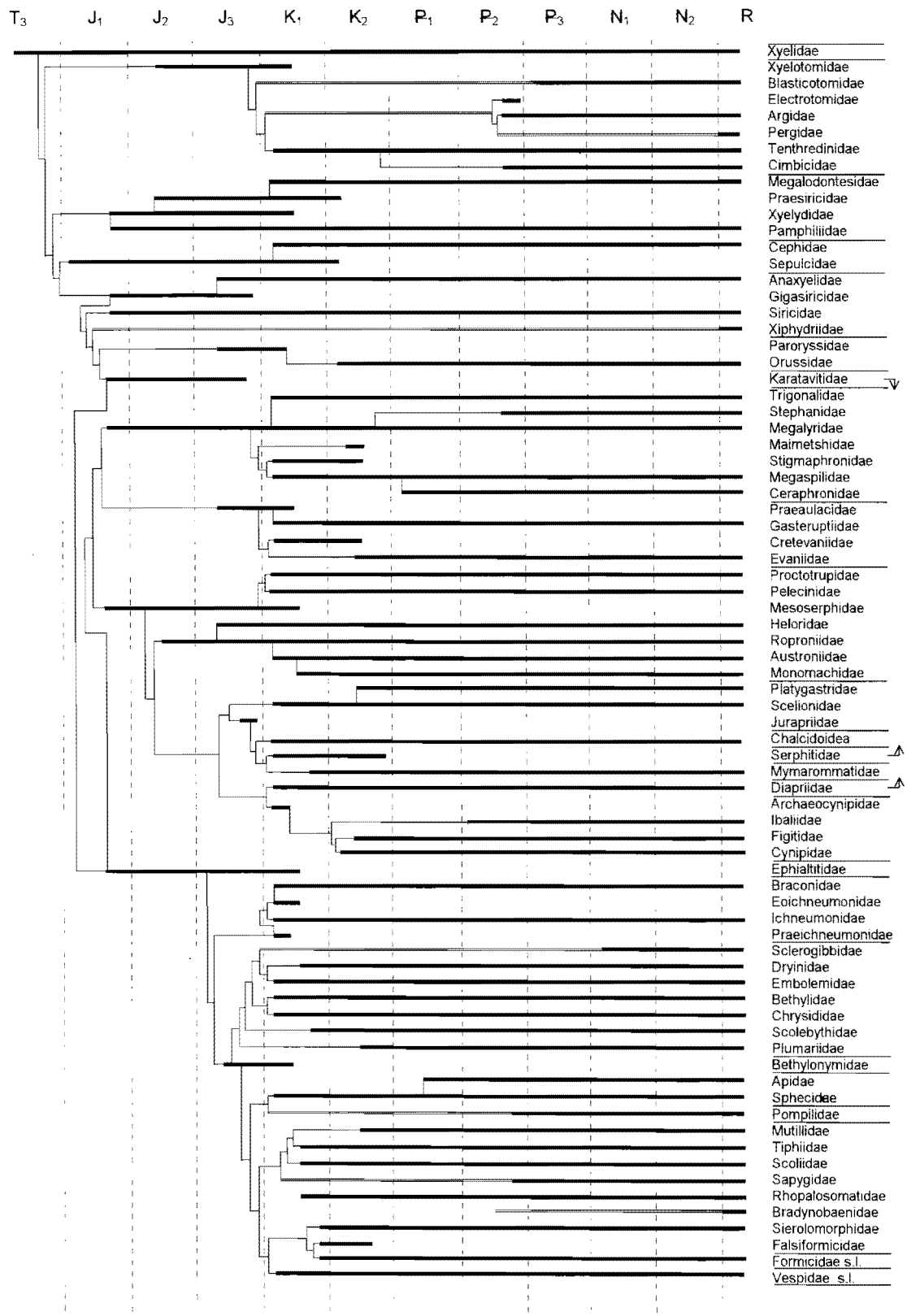
Methods

When we convert a cladogram into a phylogenetic tree, we fit the internode length to the paleontologically confirmed minimum duration of a particular subclade. In some cases we have to infer that a clade appears earlier than the fossil record would suggest (vertical thin lines in Figs. 1-6). These inferred cryptic intervals of existence were termed 'ghost ranges' (Norell, 1992). When more than one cladogram is developed for a particular set of taxa, they usually differ in their configuration as well as in the extension of ghost ranges displayed by the respective trees. It is apparent that the smaller these extensions, the better the cladogram fits the fossil record, i. e., the more parsimonious it is in that respect due to a lower degree of inference for the duration of taxa. This is a reason to try and use the ghost range concept for comparison and evaluation of competing cladograms.

Thus we might suggest calculating the ghost ranges in million years, either as their total duration as expressed on the cladogram, or their average duration per node per terminal branch. However, the absolute duration of the geochronological units is still an extensively debatable issue, full

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Fig. 1. Relation and duration of the hymenopteran families (superfamily for Chalcidoidea) (modified from Rasnitsyn, 1988). Thick lines show known longevity, horizontal thin lines – relationship, vertical thin lines – ghost ranges, double thin lines – long ghost ranges (more than two geochronological epochs before entering fossil record). Periods: T – Triassic, J – Jurassic, K – Cretaceous, P – Paleogene, N – Neogene, R – contemporary (Holocene). Epochs are shown by subscript indices: $_1$ – Lower, $_2$ – Middle, $_3$ – Upper (in the Cenozoic, P_1 – Paleocene, P_2 – Eocene, P_3 – Oligocene, N_1 – Miocene, N_2 – Pliocene). Known ranges are modified for some taxa comparing Rasnitsyn (1988) basing on following sources. Argidae and Sapygidae are found in the Upper Eocene Baltic amber (old data by Brischke 1886, ignored by Rasnitsyn 1988), Megalodontesidae in the Lower Cretaceous of China (Ren et al., 1995; my identification of *Jibaissodes* Ren, Guo et Ji as a genus of Megalodontesidae), Evaniidae in the Burmese amber of disputably Upper Cretaceous amber (Bashibuyuk et al., 2000), Monomachidae in the Lower Cretaceous of Koonwarra, Australia (Jell and Duncan 1986: fig. 66 F; my identification), Scelionidae and Chalcidoidea (new family) in the lowermost Cretaceous of Mongolia (my identification), Platygastridae in the Upper Cretaceous amber of New Jersey (identified by L. Masner, personal communication by D.A. Grimaldi), Mymarommatidae in the Lower Cretaceous (Aptian) amber of Alava, Spain (my identification), Diapriidae and Bethylonymidae in the Lower Cretaceous of England (Rasnitsyn et al., 1998), Sclerogibbidae in the Miocene Dominican amber (my identification), Embolemidae in the Lower Cretaceous of Transbaicalia and Mongolia (Rasnitsyn 1996b), Scolebythidae in the Upper Eocene Baltic amber (Brothers and Janzen, 1999), Plumariidae in the Upper Cretaceous New Jersey amber (my identification), Rhopalosomatidae and Tiphiidae in the Lower Cretaceous of Brazil (Darling and Sharkey 1990), Sierolomorphidae in the Upper Cretaceous amber of New Jersey and Falsiformicidae in the Lower Cretaceous Lebanese amber (my identification), Formicidae in the Lower Cretaceous of East Siberia (Dlussky 1999). Superfamilies are outlined by boundary lines, except that sometimes members of one and the same superfamily (Karatavitidae and Ephialtitidae, Serphitidae and the rest of Platygastroidea, Diapriidae and other Proctotrupoidea) appear separated in the cladogram to simplify it visually. These "orphan" families are marked by a broken arrow.


T3
J1
J2
J3
K1
K2
P1
P2
P3
N1
N2
R
Xyelidae
Xyelotomidae
Blasticotomidae
Electrotomidae
Argidae
Pergidae
Tenthredinidae
Cimbicidae
Megalodontesidae
Praesiricidae
Xyelydidae
Pamphiliidae
Cephidae
Sepulcidae
Anaxyelidae
Gigasiricidae
Siricidae
Xiphydriidae
Paroryssidae
Orussidae
Karatavitidae
Trigonalidae
Stephanidae
Megalyridae
Maimetshidae
Stigmaphronidae
Megaspilidae
Ceraphronidae
Praeaulacidae
Gasteruptiidae
Cretevaniidae
Evaniidae
Proctotrupidae
Pelecinidae
Mesoserphidae
Heloridae
Roproniidae
Austroniidae
Monomachidae
Platygastridae
Scelionidae
Jurapriidae
Chalcidoidea
Serphitidae
Mymarommatidae
Diapriidae
Archaeocynipidae
Ibaliidae
Figitidae
Cynipidae
Ephialtitidae
Braconidae
Eoichneumonidae
Ichneumonidae
Praeichneumonidae
Sclerogibbidae
Dryinidae
Embolemidae
Bethylidae
Chrysididae
Scolebythidae
Plumariidae
Bethylonymidae
Apidae
Sphecidae
Pompilidae
Mutillidae
Tiphiidae
Scoliidae
Sapygidae
Rhopalosomatidae
Bradynobaenidae
Sierolomorphidae
Falsiformicidae
Formicidae s.l.
Vespidae s.l.

of gaps and traps for a non-expert user. To avoid these traps, the calculation should be preceded by special efforts to evaluate the absolute time ranges of the involved taxa. However, this sophistication of approach does not seem necessary now, when the matter of issue is a testing of the method itself rather than fine tuning a particular phylogeny. Indeed, if the method is found workable in its simplest form, it will be the more so even after reasonable complication.

The simple metrics applied here is the sum of the 'long ghost ranges' per cladogram. This means counting the cases when a terminal taxon or a subclade is inferred to originate prior to its first fossil appearance for more than a particular time unit. For the present, to satisfy the definition of the "long" ghost range, the time interval should be equal to, or longer than, two geochronological epochs (two steps of the time grid as displayed in Figs. 1-6). Thus, all ghost ranges are shown there by thin vertical lines, while long ghost ranges are represented by double thin lines. The dashed double lines that appears in figs 2-6 indicate the long ghost ranges absent in Fig. 1.

Results and discussion

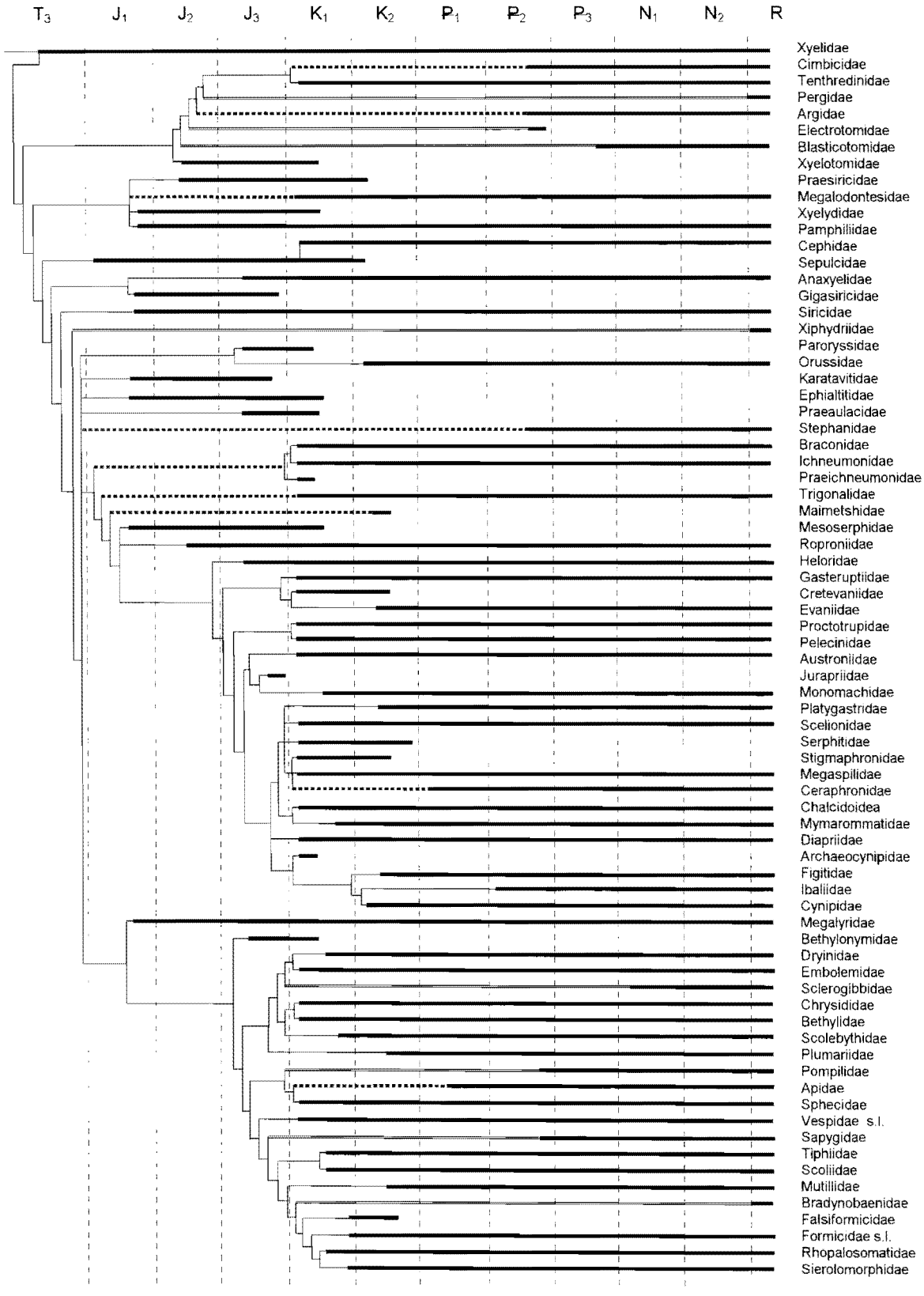
Figs. 1-6 show considerable differences between the cladograms in regards to the occurrence of the long ghost ranges. Fig. 1 depicts the tree with 76 terminal taxa and eight long ghost ranges that concern three families lacking fossil record (Pergidae, Xiphydriidae and Bradynobaenidae), and five others (Blasticotomidae, clade Electrotomidae + Argidae + Pergidae, Sclerogibbidae, Pompilidae, and Sapygidae) that enter the fossil record in the Late Eocene (e. g., as inclusions in the Baltic amber) or later. These individual cases may be found in all other trees tested, whenever they consider these taxa. Furthermore, I shall only discuss the "long" ghost ranges that appear in addition to these eight. The cladogram from Ronquist et al. (Fig. 2) produces a tree with 75 terminal taxa and eight additional long ghost ranges (Cimbicidae, Argidae, Stephanidae, Ichneumonoidea, Trigonalidae, Maimetshidae, Ceraphronidae, and Apidae) above those seen in Fig. 1. Vilhelmsen's cladogram (Fig. 3) considers only the lower hymenopterans (13 terminal taxa) and yields two additional long ghost ranges (Cimbicidae and Cephidae). Whitfield's cladogram deals mostly with superfamilies; his tree (Fig. 4) also includes 13 terminal taxa and six long ghost ranges, all additional to those seen in Fig. 1. The cladogram from Brothers and Carpenter (Fig. 5) concerns only aculeate wasps. It produces a tree with 19 terminal taxa and four long ghost ranges, all being the same as in Fig. 1 (the long ghost ranges of Pompilidae and Sapygidae are longer here than in Fig. 1, while in the case of the Bradynobaenidae the opposite may be true). The tree based on the composite molecular cladograms from Dowton with co-authors (Fig. 6) considers 24 terminal taxa and produces eight long ghost ranges, seven of which do not repeat those in Fig. 1.

The above results indicate that the cladograms by Rasnitsyn (1988) and Brothers and Carpenter (1993) are more congruent with the fossil record than the others. This follows from the observation that these two cladograms (each within its own scope) infer the minimum number of ghost ranges when corresponding sections of the considered cladograms are compared. The results deserve some additional discussion, however.

The high score gained by my cladogram is not peculiar. My cladogram acknowledges presence of ancestral taxa (those lacking autapomorphic character states). The other cladograms follow the strict cladistic concept that ancestors can never be identified as such. Therefore, only sister group relationships are available for these cladograms. Unlike mother-and-daughter taxa, the sister groups always have equal age. So when we take a daughter for a sister, we infer it to have an earlier origin and therefore a longer ghost range. I have discussed at length elsewhere the reasons why it is necessary to acknowledge phylogenetic ancestors (Rasnitsyn, 1996). In fact, in Ronquist's cladogram (Fig. 2), four long ghost ranges (cases of Cimbicidae, Megalodontesidae, Ceraphronidae, and Apidae) appear

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Fig. 2. Relation of the hymenopteran taxa as calculated by Ronquist et al. (1999: figs. 2, 5 and 9, combined), formatted after Fig. 1. Dashed double line – long ghost ranges additional to those seen in Fig. 1.


T3
J1
J2
J3
K1
K2
P1
P2
P3
N1
N2
R
Xyelidae
Cimbicidae
Tenthredinidae
Pergidae
Argidae
Electrotomidae
Blasticotomidae
Xyelotomidae
Praesiricidae
Megalodontesidae
Xyelydidae
Pamphiliidae
Cephidae
Sepulcidae
Anaxyelidae
Gigasiricidae
Siricidae
Xiphydriidae
Paroryssidae
Orussidae
Karatavitidae
Ephialtitidae
Praeaulacidae
Stephanidae
Braconidae
Ichneumonidae
Praeichneumonidae
Trigonalidae
Maimetshidae
Mesoserphidae
Roproniidae
Heloridae
Gasteruptiidae
Cretevaniidae
Evaniidae
Proctotrupidae
Pelecinidae
Austroniidae
Jurapriidae
Monomachidae
Platygastridae
Scelionidae
Serphitidae
Stigmaphronidae
Megaspilidae
Ceraphronidae
Chalcidoidea
Mymarommatidae
Diapriidae
Archaeocynipidae
Figitidae
Ibaliidae
Cynipidae
Megalyridae
Bethylonymidae
Dryinidae
Embolemidae
Sclerogibbidae
Chrysididae
Bethylidae
Scolebythidae
Plumariidae
Pompilidae
Apidae
Sphecidae
Vespidae s.l.
Sapygidae
Tiphiidae
Scoliidae
Mutillidae
Bradynobaenidae
Falsiformicidae
Formicidae s.l.
Rhopalosomatidae
Sierolomorphidae

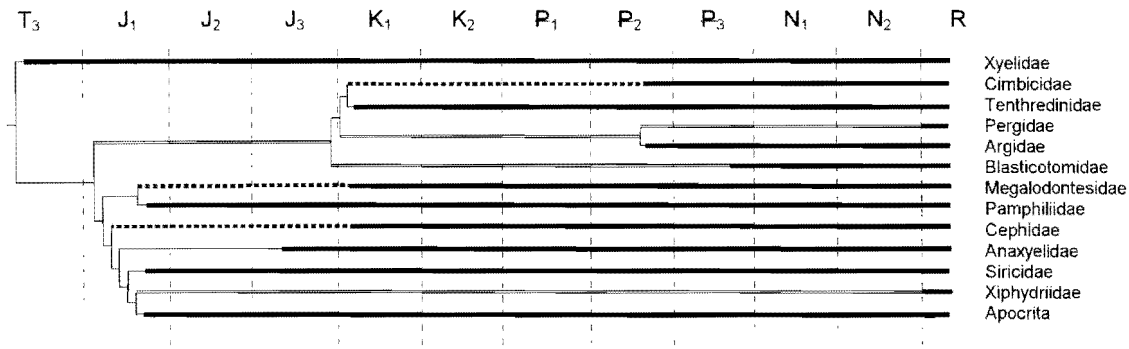


Fig. 3. Relation of the symphytan taxa as calculated by Vilhelmsen (1997: fig. 2), formatted after Figs. 1, 2.

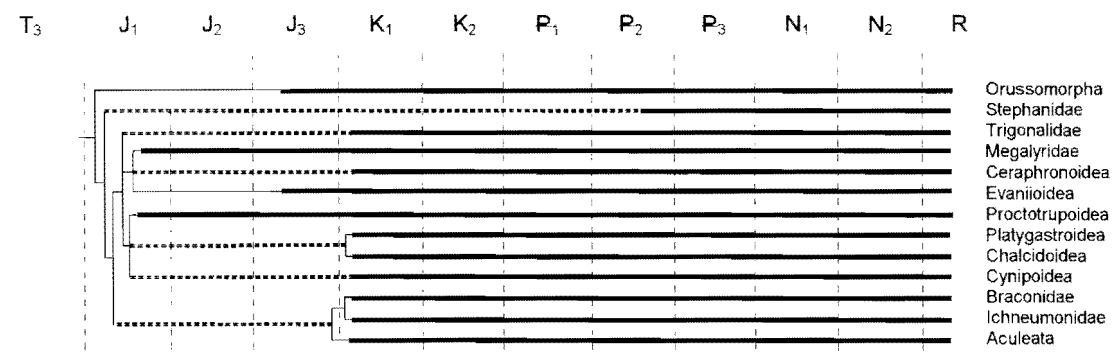


Fig. 4. Relation of the parasitic taxa as presented by Whitfield (1992: fig. 5), formatted after Figs. 1, 2.

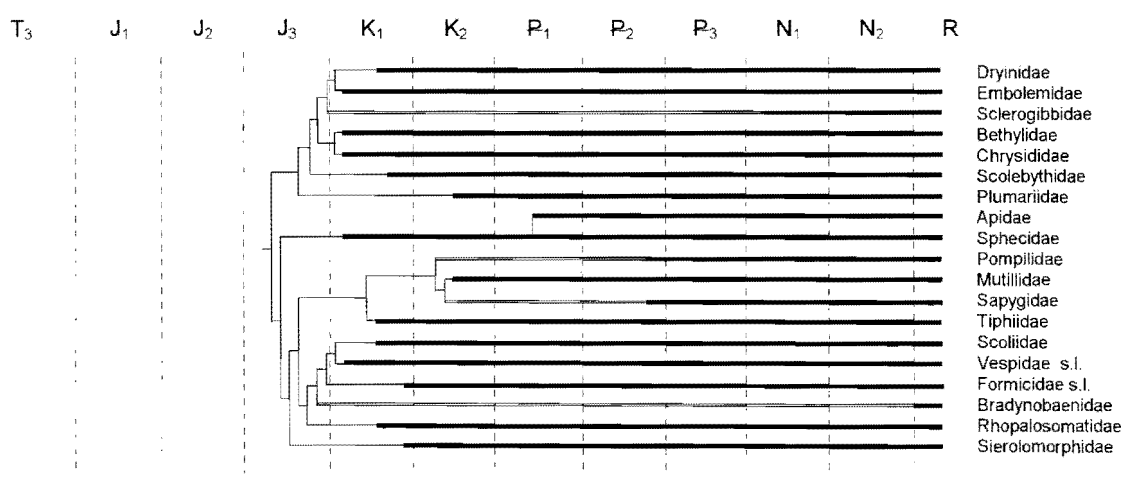


Fig. 5. Relation of the aculeate taxa as calculated by Brothers and Carpenter (1993: fig. 11), formatted after Figs. 1, 2.

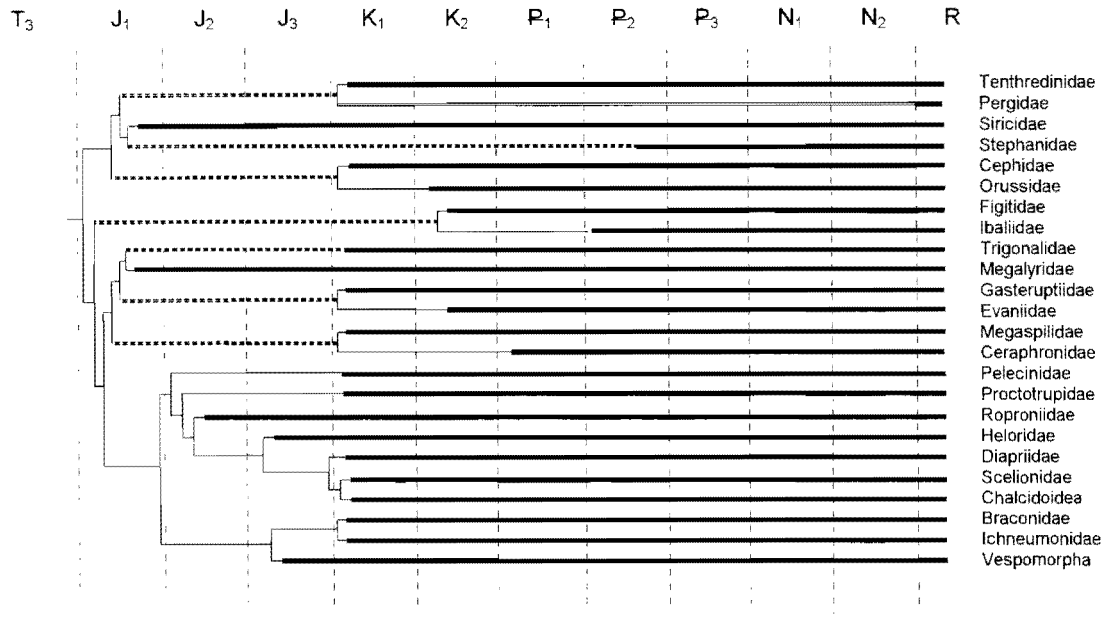


Fig. 6. Molecular phylogeny of hymenopteran taxa as calculated by Dowton and Austin (1994: fig. 3), for symphytan families, Orussidae and Stephanidae, and by Dowton et al. (1997: fig. 2) for the apocritans, formatted after Figs. 1, 2.

solely because they are considered to be sister and not daughter groups of Tenthredinidae, Praesiricidae, Megaspilidae, and Sphecidae, respectively. The same is true for three cases (Cimbicidae, Megalodontesidae and Cephidae) in Vilhelmsen's cladogram (Fig. 3); in my cladogram Cephidae is the daughter taxon of Sepulcidae. Of six long ghost ranges in Whitfield's tree (Fig. 4), five are absent in my cladogram because Trigonalidae and Ceraphronoidea (s.str.) are suggested there to descend directly from Megalyridae, Platygastroidea + Chalcidoidea and Cynipoidea – from the ancestral proctotrupoid family Mesoserphidae, and Ichneumonoidea + Aculeata from Ephialtitidae. In Dowton and Austin's cladogram (Fig. 6), there are seven additional long ghost ranges comparing to Fig. 1. Four of them result from the same causes: in my cladogram, Tenthredinoidea originate directly from Xyelidae, Cephidae from Sepulcidae, Trigonalidae from Megalyridae, and Evaniidae + Gasteruptiidae from Praeaulacidae.

The reasons why other long ghost ranges appear in Figs. 2, 3, 4 and 6 in addition to those seen in the Fig. 1, are not so evident. Possibly they are relevant to the phylogeny of Hymenoptera rather than to methodology of phylogenetics, and so they will be considered elsewhere.

Conclusion

The above observations indicate that the total amount of ghost ranges displayed by different phylogenetic trees for the same set of taxa does allow us to compare and evaluate the cladograms forming the background of these trees. Moreover, the results of application of the method are understandable and possible to explain, at least in part. That the cladogram from Rasnitsyn (1988) fits better to the fossil record than the majority of others, depends at least partially on the appreciation of mother and daughter groups in additional to the sister groups, these latter being the only legitimate ones in cladistics. At the same time, testing of the cladogram by Brothers and Carpenter (1993) indicates that the high score received by Rasnitsyn's (1988) cladogram from the present test is not a straightforward result of the method used there, i.e., the making of a cladogram by the method of Hennig ("paper and pencil" approach) instead of the automatic parsimony calculation, and an appreciation of the ancestor and descendant taxa.

Several ways to further development of the ghost range method may be proposed. The most evident one is the calculation of the length rather than the simple count of ghost ranges: this would make the

method more precise. However, there is yet another possibility. As proposed, the ghost range method is designed to test competing cladograms in regards to their congruence with the fossil record. Instead, it might be found useful to use the geochronological data directly in the parsimony calculation, to include the information from fossil record into the cladistic procedure. However, even it its simplest form, the ghost range method might be a useful test for cladograms.

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