

**AN OUTLINE OF EVOLUTION OF THE HYMENOPTEROUS INSECTS
(ORDER VESPIDA)**

A. P. RASNITSYN

Paleontological Institute, Academy of Sciences of the USSR,
117868 Moscow, Profsoyuznaya 123, USSR

This paper is written to present the results of my research of evolution of the hymenopterous insects to English-reading entomologists, since these results have been published almost exclusively in Russian and are not easily available to many colleagues.

It is impossible to include all the results of 25 years of research in a journal paper. That is why I have confined myself here to strict phylogenetic data presented in the form of a cladogram accompanied by a list of apomorphies. The characters used and discussions as to their polarization have been discussed in full elsewhere and are only exceptionally mentioned here.

INTRODUCTORY REMARKS

Several notes should be given here to explain the author's position concerning current issues of controversy in phylogenetic systematics. The explanations are concise, being presented in full elsewhere.

On the whole I accept the Hennigian methodology of the phylogenetic analysis (Rasnitsyn, 1969, 1980, 1983; Ponomarenko & Rasnitsyn, 1971), except that the cladogram constructing is considered to be an iterative process. When facing with contradicting data, e.g. mutually inconsistent synapomorphies [homoplasy] or a contradiction between synapomorphies and paleontological succession of groups, I prefer to reconsider the situation in general by searching for new characters and re-evaluating the reliability of the evidence. I consider this procedure, though time-consuming and laborious, to be more effective than parsimony or other simple criteria in dealing with homoplasy.

It is the cladistics ("phylogenetic systematics") which I disagree with. The matter is that cladistics is not phylogenetic but genealogical systematics. Indeed, it is constructing the system based only on the succession of the events of divergence and, thus, excluding paraphyletic (ancestral) taxa. The resulting system is genealogical because it uses the same method as the old genealogy of noble families did. But genealogy is only part phylogeny, the other part being evaluation of anagenesis (the amount of differences acquired by a descendant comparing to an ancestor, or by sister groups comparing each other). The tempo of phylogeny is so variable that one of the descendants of, say, a Triassic xyelid sawfly is still a xyelid while another descendant has used the time elapsed to become an ant (see below). Cladists are ignoring the variability of the evolutionary tempo and insisting on the equal taxonomic ranking of the sister groups. They would either include all hymenop-

terans in Xyelidae or split xyelids despite their similarity. Similarly, they would place birds in Reptilia, the latter in Amphibia, this in turn in Pisces, and so on. Alternatively, each ancestral group would be split, giving equal rank to component clades, with no better result. While cladistic classifications are good in reflecting the topology of cladograms, the cladogram itself is best in that respect, thus allowing classifications to carry information other than just branching patterns. As to the functions of such classifications, they would be: 1) to efficiently summarize the relevant information; 2) to predict both the distribution of unknown characters among recognized taxa and characters of unknown taxa; 3) to serve as an interdisciplinary language [see Ponomarenko and Rasnitsyn (1971) or Rasnitsyn and Dlussky (1988) for details, and cf. Henning (1966)]

For the above reasons, I consider the paraphyletic (ancestral) taxon as a legitimate member of the natural system. I believe that it is sufficient if a taxon meets the requirements of the notion of a *monophyletic continuum*, where *continuum* denotes an uninterrupted chain, branched or not, of subtaxa, each of them being more similar to its every immediate neighbor in the chain than to members of any other continuum. Monophyly is taken here in its broader sense covering both holo- and paraphyly and is applicable to a taxon with its lower borderline (between this and ancestral taxa) crossed with a single phylogenetical line which is indivisible in the framework of the particular phylogenetic study independently of the taxonomic rank of the line, or, in other words: the taxon is monophyletic if the apomorphy characterizing the minimal clade covering the taxon has origin in the single first member of the taxon.

The last issue discussed here concerns the nomenclature of taxa above the family group level. I follow Rohdendorf (1977) in that only codification of all taxonomic names can reduce the arbitrariness and instability in their construction and use. As to doubts and reservations by Brothers (1983), all of them are equally applicable to names already codified and, thus, are irrelevant, with one exception. The codification will result in momentary, though massive, changes of familiar names and will affect many people. Nevertheless, I see no alternative with the only question being, to my mind, how long shall we be able to delay this painful but unavoidable step?

Concerning hymenopterans, the codification of the higher taxa names results in the application of only one name for the order itself, Vespida. The currently used name Hymenoptera may be permitted to persist as a vernacular name in a modified form as "hymenopterans" or "hymenopterous insects". As to the suborders, their new names should be treated as proposed for new taxa rather than as replacement names for old taxa. Similarly, the names of infraorders are names of new taxa and not replacement names for old taxa.

The body of the paper consists of a list of the evolutionary events (apomorphies) which took place at successive nodes of the cladogram shown in Figs. 1-4. The paragraph numbers in the list refer to the numbers of the corresponding nodes in the cladogram. When the paragraph number is followed by another number in parentheses, the latter is the number of an ancestral node; otherwise the preceding number is a number of the ancestral node. When an ancestry of the par-

ticular apomorphy (-ies) can be specified only within the interval covering several nodes, the apomorphy (-ies) is (are) listed under two numbers hyphenated and referred to the first and the last nodes within the interval.

As has been mentioned earlier, the evidence used in analysis and polarization of the transformation series of the characters is only exceptionally mentioned here, having been originally compiled by Rasnitsyn (1975, 1975a, 1980) and later completed and revised in part by Mason (1981-87), Gibson (1985, 1986), Naumann and Masner (1985) and Carpenter (1986). If necessary, additional information is presented in the notes to the respective nodes at the end of the paper; the node numbers are then marked with an asterisk. In some cases new information is included in the list of apomorphies itself.

The relevant paleontological information is compiled by Rasnitsyn (1969, 1975b, 1980) and later completed by Alexeyev and Rasnitsyn (1981), Rasnitsyn (1983 b,c,d.; 1986 a,b; 1988), Dlussky (1987) and Rasnitsyn and Kovalev (1988).

The classification of the order as it follows from the resulting cladogram is shown below.

Order VESPIDA Laicharting, 1781

Suborder Siricina Billbergh, 1820 (Latreille, 1802)

Infraorder Xyelomorpha Newman, 1834

Superfamily Xyeloidea Newman, 1834,

Family Xyelidae Newman, 1834

Infraorder Tenthredinomorpha Latreille, 1802

Superfamily Tenthredinoidea Latreille, 1802

Families Xyelotomidae Rasnitsyn, 1968, Blasticotomidae Thomson, 1871, Electrotomidae Rasnitsyn, 1977, Argidae Konow, 1890 (Newman, 1834), Pterygophoridae Cameron, 1878 (= Pergidae Ashmead, 1898), Tenthredinidae Latreille, 1802 (incl. Diprionidae Rohwer, 1911), Cimbicidae Leach, 1817.

Infraorder Siricomorpha Billbergh, 1820 (Latreille, 1802)

Superfamily Pamphilioidea Cameron, 1890 (Newman, 1834)

Families Xyelydidae Rasnitsyn, 1968, Pamphiliidae Cameron, 1890 (Newman, 1834), Praesiricidae Rasnitsyn, 1968, Megalodontidae Konow, 1897.

Superfamily Cephioidea Newman, 1834

Families Sepulcidae Rasnitsyn, 1968 (incl. Parapamphiliidae Rasnitsyn, 1968), Cephidae Newman, 1834.

Superfamily Siricoidea Billbergh, 1820 (Latreille, 1802)

Families Gigasiricidae Rasnitsyn, 1968, Anaxyelidae Martynov, 1925, Siricidae Billbergh, 1820 (Latreille, 1802) (incl. Myrmiciidae Maa 1949 = Pseudosiricidae Handlirch, 1906), Xiphydriidae Leach, 1815.

Suborder Vespina Laicharting, 1781

Infraorder Orussomorpha Newmann, 1834

Superfamily Orussoidea Newman, 1834

Families Paroryssidae Martynov, 1925, Orussidae Newman, 1834

Infraorder Ephialtitomorpha Handlirsch, 1906

Superfamily Ephialtitoidea Handlirsch, 1906

Families Karatavitidae Rasnitsyn, 1963, Ephialtitidae Handlirsch, 1906 (incl. Karataidae Rasnitsyn, 1977)

Infraorder Evaniomorpha Latreille, 1802

Superfamily Stephanoidea Leach, 1815

Families Megalyridae Schletterer, 1889, Stephanidae Leach, 1815, Trigonalidae Cresson, 1867 (incl. Ichneumononimidae Rasnitsyn, 1975), Maimetshidae Rasnitsyn, 1975, Stigmaphronidae Kozlov, 1975, Megaspilidae Ashmead, 1893, Ceraphronidae Haliday, 1833.

Superfamily Evanioidea Latreille, 1802

Families Praeaulacidae Rasnitsyn, 1972 (including Anomopterellidae Rasnitsyn, 1975), Gasteruptiidae Ashmead, 1900 (Kirby, 1837) (= Aulacidae Schuckard, 1841) (incl. Baissidae Rasnitsyn, 1975, Kotujellidae Rasnitsyn, 1975), Cretevaniidae Rasnitsyn, 1975, Evaniidae Latreille, 1802.

Infraorder Proctotrupomorpha Latreille, 1802.

Superfamily Proctotrupeoidea Latreille, 1802 (incl. Diaprioidea Haliday, 1833)

Families Mesoserphidae Kozlov, 1970, Pelecinidae Haliday, 1840, Proctotrupidae Latreille, 1802 (incl. Vanhorniidae Crawford, 1909), Heloridae Foerster, 1856 (incl. Peradeniidae Naumann & Masner, 1985), Roproniidae Viereck, 1916, Austroniidae Kozlov, 1975 (including Trupochalcididae Kozlov, 1975), Monomachidae Szepligeti, 1889, Diapriidae Haliday, 1833, Jurapriidae Rasnitsyn, 1983, Scelionidae Haliday, 1839, Platygastriidae Westwood, 1840, Serphitidae Brues, 1937 and possibly Mymarommatidae Debauche, 1948.

Superfamily Cynipoidea Latreille, 1802

Families Archaeocynipidae Rasnitsyn & Kovalev, 1988, Figitidae Hartig, 1840 (incl. Eucoilidae Thomson, 1862, Charipidae Dalla Torre & Kieffer, 1910), Cynipidae Latreille, 1802, Ibalidae Thomson, 1862 (incl. Liopteridae Ashmead, 1895).

Superfamily Chalcidoidea Spinola, 1811 (including Mymaridae Haliday, 1833 and possibly Mymarommatidae Debauche, 1948). (Not further treated here).

Infraorder Ichneumonomorpha Latreille, 1802

Superfamily Ichneumonoidea Latreille, 1802

Families Praeichneumonidae Rasnitsyn, 1983, Ichneumonidae Latreille, 1802 (including Paxylommatidae Foerster, 1862 = Hybrizonidae Marshall 1872), Braconidae Nees, 1814 (incl. Aphidiidae Haliday, 1833, Apozygidae Mason, 1978).

Infraorder Vespomorpha Laicharting, 1781**Superfamily Bethylonymoidea Rasnitsyn, 1975****Family Bethylonymidae Rasnitsyn, 1975****Superfamily Chrysidoidea Latreille, 1802 (= Bethyloidea Haliday, 1839)**

Families Plumariidae Bischoff, 1920 (Andre, 1913), Scolebythidae Evans, 1963, Dryinidae Haliday, 1833, Sclerogibbidae Ashmead, 1902, Embolemidae Foerster, 1856, Bethylidae Haliday, 1839, Chrysididae Latreille, 1802.

Superfamily Sphecoidea Latreille, 1802

Families ?Baissodidae Rasnitsyn, 1975, Sphecidae Latreille, 1802, Apidae Latreille, 1802.

Superfamily Pompiloidea Latreille, 1804

Families Pompilidae Latreille, 1804, Rhopalosomatidae Ashmead, 1896.

Superfamily Scoliidea Latreille, 1802

Families Sapygidae Latreille, 1810, Tiphiidae Leach, 1815, Mutillidae Latreille, 1802, Scoliidae Latreille, 1802, Bradynobaenidae Saussure, 1892, Sierolomorphidae Krombein, 1951, Falsiformicidae Rasnitsyn, 1975.

Superfamily Formicoidea Latreille, 1802. (Not further treated here).

Superfamily Vespoidea Laicharting, 1781. (Not further treated here).

Description of the hymenopteran cladogram (Figs.1-4)***1. Xyelidae**

Flight functionally dipterous, with wing pairs and respective segments differing strongly both in size and structure.

Wing venation of Xyelid type.

Possibly (unless inherited from ancestral Permosialids, which are known only from wings):

Male haploid (female diploid).

Basal flagellar segments fused in thick and long composite "3rd" segment followed by normal segments.

Inner (fore) fore tibial spur modified in calcar.

Wings fixed at rest with area aspera (housed in loop of anal vein in a fore wing) catching on metanotal cenchrus.

Larval eye composite in origin but covered with single lens.

Larva feeding on pollens in Gymnosperm male cone and protecting itself with silk produced by labial glands.

1a. Macroxyelinae

Fore wing with R joining C before pterostigma. Ovipositor short (saw-like).

1b(1). Xyelinae

Larval eye below level of antenna.

*2(1a). Xyelotomidae

Flagellar segments thick, reduced in number.

Fore wing with RS bifurcation displaced far beyond 2r-m (and further lost) with 2r-rs meeting pterostigmal apex (anteriorly) and RS far beyond 2r-m (posteriorly), with 1st abscissa of RS very short, and with cell 1m-cu large.

2-3. Mesopseudosternum (sensu Shcherbakov, 1980; "mesosternum" of authors) reaching fore margin of segment.

Spinisternum attached to fore mesothoracal margin ventromesally.

Mesotergo-mesotrochanteral muscle lost.

Meso- and metafurca with lateral arm thick (hollow) and directed lateral, and with fore arm short.

Male gonostylus with gonomaculum (apical membranous disc) lost.

Larva with subanal appendage segmented.

3. Possibly (unless inherited from ancestral xyelotomid subtaxon):

Pronotum short medially

Fore wing with SC lost except fore branch crossing costal space.

4. Blasticotomidae

Single (or no) flagellomere beyond composite one.

Fore wing with RS lost between submarginal cells.

Larva boring fern stem, with caudal structure modified.

5(3). Spinisternum incorporated in mesothoracal venter anteromesally.

Male genitalia rotated at 180.

Larva with eye and antenna distant and with mandible lacking incisive molar flange.

6. Larva with subspiracular and suprapedal lobes merged in one lobe and with antenna 3-segmented.

6-8. Mesofurca with fore arms reduced.

Mesopseudosternum (cf. node 2) wide on fore mesothoracal margin.

Fore wing lacking 2r-rs

7. Electrotomidae

Larval legs reduced in segmentation.

8(6). Larva free-living with antenna 1-segmented, with subanal appendage lacking segmentation or lost, and with secondary ducts in salivary glands.

9. Argidae

Antenna with 3 segments.

Larval leg secondary two-clawed with posterior claw modified.

10(8). Pterygophoridae

Antenna with 3rd segment reduced, subequal to following ones in size.

Hind wing lacking m-cu crossvein.

11(5). Tenthredinidae

Antenna with 3rd segment reduced, subequal to following ones in size.

Pseudosternal (cf. node 2) sulci lost.

Preapical tibial spurs lost.

Male with 8th sternum hardly visible, strongly excised apically.

- Larva free living, with prolegs two-segmented, with subanal appendage lost, and with ductus of salivary gland margined with 2 rows of glandular cells.
12. Cimbicidae
Antenna clavate.
Fore wing lacking RS between submarginal cells, with pterostigma long and narrow.
Larva with antenna 1-segmented and with the 1st to 9th abdominal segments bearing 7 annulets.
- 13(1b). Siricomorpha
Head capsule closed with hypostomae fused between oral cavity and occipital foramen.
Tentorium issuing anterior arms below level of tentorial bridge.
Propleurae contiguous ventromedially.
Fore wing with RS simple, not furcate.
Male gonostylus with gonomacula subapical.
Larval abdominal sterna with prolegs, longitudinal and oblique sulci lost.
Larval salivary gland with common envelope and with duct quadrangular in section.
Larval subanal appendage segmented and displaced to base of anal slit.
14. Xyelydidae
Ovipositor small, claw-like.
- 14-15. Head capsule with mandibular and oral cavities isolated.
Mandible of cutting type instead of chewing, with cutting edge twisted into a moving plane.
Larva exophytic (still silk-protected), with all appendages setiform, and with antenna distant from eye.
15. Antenna with 3rd (compound) segment reduced, subequal to the following segments, at least in width.
- *16. Pamphiliidae
Lower tentorial bridge intervening between hypostomae and replacing them in closing head capsule between oral cavity and occipital foramen.
Fore wing with M+Cu angulate (with or without supernumery cu-a cross vein).
- 17(15). Praesiricidae
Mesopseudosternum long, praepisterna hardly or not at all touching each other.
Both wings lacking SC.
18. Megalodontidae
Antenna pectinate.
Fore wing with R and Cu (M+Cu) straight from wing base till pterostigma and 1m-cu, respectively, with basal abscissae of RS and M making smooth basal vein, and with A₂₊₃ running behind area aspera without arching.

- Larva feeding on herbaceous angiosperm plants.
- 19(13). Outer (hind) fore tibial spur reduced and further lost.
Mesofurca with fore arms long, fused for some distance.
Larva xylophagous in living plant tissues, with supra-anal horn, with appendages reduced both in size and segmentation, and with salivary gland not capable to produce silk.
20. Sepulcidae
SC lacking fore branch in fore wing, with stock appressed to and then fused with R.
- 20-21. Upper tentorial bridge bearing corpotendon.
Lower tentorial bridge present in addition to the upper one.
Male gonostylus fused with gonocoxa and lacking gonomacula.
Aedeagus tubular.
21. Cephidae
Fore wing with 1r-rs longer than 2r-rs and much longer than both adjacent RS abscissae, with the 1st abscissa of RS very short, with cell 1m-cu large, almost reaching R, with Cu (M+Cu) straight from wing base till 1m-cu, and with area aspera lost along with respective arching of A_{2+3} .
Metanotum with cenchri lost.
Abdomen compressed, with rocking between the 1st and the 2nd segments enhanced.
Larva boring in angiosperm plants (unless inherited from some cretaceous Sepulcidae)
- 22(19). Gigasiricidae
Costal space moderately narrow.
(The following character states are inferred as synapomorphy of living descendants):
Tibiae with preapical spurs lost
Ovipositor needle-like (subcircular in section)
Larva feeding on dead wood conditioned with symbiotic fungi
Larval morphology strongly reduced, with eyes lost, legs lacking segmentation, intersegmental annulation of body lost, etc.
23. Anaxyelidae
Fore and hind wing each with single r-m
- 24(22). Antenna with compound 3rd segment reduced in size and subequal to the following ones.
Head capsule with postgenae subcontiguous, divided with very narrow hypostomal bridge.
Mesoscutum with transscutal line.
Prepectus concealed under posterolateral edge of pronotum.
- *25. Siricidae
Head capsule with postgenae contiguous.
Prospinal muscles lost.

Mesoscutum with transscutal suture bent forward laterally (unless *Sinosirex* is really plesiomorphic in that respect; see Rasnitsyn, 1980: 53-54 for details).

Fore wing with basal abscissa of RS subvertical to reclined.

- 26(24). Incipient lateral scutal lines ("parapsides" as usually applied for Apocritans but not parapsides of other insects) present.

Fore wing with SC lost except fore branch crossing costal space, and with Cu (M+Cu) straight between wing base and 1m-cu.

- *27. Xiphydriidae

Pronotum with dorsal (not sloping) part very short except laterally.

Propleurae elongated in long "neck".

Larva feeding on angiosperm wood.

- *28. Vespina

Head with postgenae in contact between oral cavity and occipital foramen.

Tentorium with upper bridge narrow and stripe-like, n-like bent, with corpotendon issuing mesally, and with incipient lower bridge present.

Pronotum with spiracular lobes present.

Postspiracular sclerite lost (probably fused with basalare), basalare long.

Lateral scutal lines ("parapsides", cf. node 26) well developed.

Mesopseudosternum (cf. node 2) wide on fore mesothoracal margin but not clearly margined laterally.

Fore wing with SC lost, with costal space of almost constant moderate width from wing base to pterostigma (R straight) and with 1r-rs longer than 2r-rs and much longer than both adjacent abscissae of RS.

1st abdominal tergum with halves merged in single plate-propodeum, and abutting with metapostnotum.

Rocking mobility enhanced between 1st and 2nd abdominal segments.

Male gonostylus lacking gonomacula.

Larva parasitizing wood-boring, probably horntail larva, with morphology simplified.

29. Paroryssidae.

Size small.

Fore wing with 1r-rs, 3r-m, 2m-cu and A_{2+3} before a_1 - a_2 lost.

Hind wing with all crossveins lost.

- 29-30. Spinisternum with muscles lost.

30. Orussidae

Head with teeth in ring around fore ocellus.

Female profurca with arms sessile and apart to house internal loop of ovipositor.

Ovipositor internal, bent in long loop reaching prothorax.

- 31(28). Karatavitidae

Metanotum with cenchri lost.

Propodeum sloping backward making metasomal articulating foramen low (though still wide).

- Fore wing with area aspera and respective anal loop or arching lost. (cf. nos. 18, 21)
- 31-32. Tentorial bridge thin rod-like.
Spinisternum incorporated in mesothoracal venter anteromesally.
32. Ephialtitidae
Fore wing with 1r-rs interrupted near pterostigma (often lost), and with the 1st abscissa of RS subvertical to reclined.
Hind wing with jugal lobe dedifferentiated and incorporated into vannus.
- *33. Fore wing with A_{2+3} and a_1-a_2 lost.
1st to 6th metasomal spiracles lost.
Possibly: Toruli not in contact with clypeus (supposing toruli in contact with clypeus in Scelionidae and related families to be secondarily so).
Possibly: Propodeum with metasomal articulating foramen moderately narrow (unless inherited from ancestral group within Ephialtitidae).
- *34. Evaniomorpha
Mesopostepisternum overlaying mid coxa to articulate with its surface instead of its basal margin.
- *35. Megaliridae
Hind wing with A lost beyond cu-a, seemingly replaced with Cu (though Cu still running before and not behind anal fold).
- *36. Stephanidae
Head with teeth in ring around fore ocellus.
Hind femur with lower margin dentate.
Fore wing with 2-3r-m and 2m-cu lost.
Hind wing with m-cu and basal abscissa of RS lost.
1st metasomal segment long, tube-like.
- 37(35). Trigonalidae
Left mandible with 3, right with 4 teeth (not proved for Ichneumonimiminae).
Median mesoscutal sulcus (not line) and respective internal apodeme lost.
Metasomal sterna hard, convex.
Metasomal spiracles lost.
Ovipositor internal, reduced (reduction not proved for Ichneumonimiminae).
- 38(35). Maimetshidae
Antenna with 16 segments.
Fore wing with cell 1m-cu small, distant from cell 2rm, and with 3r-m lost, 2m-cu weak.
1st metasomal segment small, ring-like.
- 38-41. 1st spiracle with ocluser muscle originating very low on pronotum.
Mesonoto-mesotrochanteral muscle lost.
Metasomal spiracles lost.
Larva parasitizing on other hosts than xylophilous insect larva.
39. Antenna with 11 segments.

- Fore wing lacking costal space and all tubular veins except C, R, 2r-rs, RS beyond 2r-rs, and pterostigma.
Hind wing lacking all tubular veins but R.
Mesosoma with metasomal articulating foramen isolated from coxal articulating foramens.
2nd metasomal segment enlarged.
Ovipositor internal.
40. Stigmaphronidae
Hind ocellus almost touching eye.
Vertex acute.
Hind leg saltatorial, with coxa larger than femur, very wide, femur thick, tibia short, subequal to basitarsus and to longer tibial spur.
- 41(39). Megaspilidae
Fore tibia with 2 spurs.
Metasoma with Waterstone organ.
42. Ceraphronidae
Female antenna with 10 (male one with 11) segments.
Middle tibia with 1 spur.
Metasoma with Waterstone organ lost.
- *43(34). Praeaulacidae
Mesosoma with metasomal articulating foramen small and displaced far above coxal articulating foramens.
- 43-44. Mesotergo-mesotrochanteral muscle lost.
44. Antenna with 14 segments.
Pronotum short medially, rigidly connected with mesopleuron.
Mesonotum with median sulcus and respective internal apodeme lost.
Hind wing with all tubular veins lost except R and (M+)Cu.
- 44-48. Prepectus extending dorsally behind and above mesospiracle and fused with hind pronotal margin as interior pronotal inflection (in homoplasy with Stephanoidea other than Stephanidae, and by implication, Megalyrid subfamily Cleistogastrinae).
45. Gasteruptiidae
Pterostigma semicircular (secondary modified in some Cenozoic forms).
Possibly (unknown for Mesozoic members):
Male antenna with 13 segments.
Prepectus lost leaving 1st spiracle lying free in membrane between pro- and mesonotum and mesopleuron.
- 46(44). Antenna with 13 segments.
Head large, tightly appressed to mesosoma, only weakly movable.
Mesosoma short and high, strongly sclerotized.
Metathoracic venter projecting anteromesally between middle coxae.
Metasoma short, compressed, with 1st segment long and tubular.
Ovipositor short, not exerted.
- 46-48. Larva developing in roach ootheca.
47. Cretevaniidae

Antenna with 12 segments.

Fore wing venation strongly modified and partly lost (both m-cu crossveins present).

Hind wing very short, with tubular venation lost except R(+C?).

Legs thick with hind tibia clavate.

Metasomal articulating foramen displaced forward almost to reach metanotum.

48(46). Evaniidae

Venation reduced with fore wing retaining single r-m and single m-cu.

Distal wing membrane corrugated.

Both wings with jugal lobe divided from vannus by notch.

*49(33). Mesoserphidae

Head with lower tentorial bridge intervening between postgenae to reach occipital foramen and to replace postgenal bridge (Unlike Ichneumonoidea the cardinal condyli are far apart).

Prepectus extending behind and above the 1st spiracle (cf. paragraph "44-48").

Mesonotum with medial scutal sulcus (or line) lost.

Fore wing with cell r long triangular, with 2-3r-m and 2m-cu lost (speculating that 2r-m restored again as complete cross-vein in Cynipoidea and as secondary "RS₂" in Pelecinoidea), and with (M+)Cu straight (Cu angulated at cu-a and 1m-cu in *Ropronia* as secondary modification).

Hind wing with RS enclosing minute cell r (further lost), with r-m long, oblique, meeting extreme base of RS near hamuli-bearing end of R, with hamuli reduced in number (probably to 2 or 3, secondarily up to 8 in the largest forms), and with A lost beyond cu-a being seemingly replaced with Cu (in homoplasy with Stephanioidea).

Mesotergal-mesotrochanteral muscle lost (secondarily regained by higher Diapriids and by Chalcidoidea).

Possibly: Male genitalia with volsellae associated to aedeagus rather than to paramere (data not complete enough as yet).

Larva temporarily endoparasitic (when young) or facultatively (supposing fully ectoparasitic development in some Chalcidoidea as secondary).

50. Pelecinoidea

Pronotum annular, short dorsomedially, rigidly connected with mesopleuron.

Prepectus fused with pronotum forming internal pronotal inflection.

Mesopleuro-mesotrochanteral muscle present.

Fore wing with RS₂-like 2r-m present.

Middle and hind trochantelli lost.

Metasoma elongate moderately, penetrating soil during oviposition, closed at rest apically, with apical tergum and sternum weakly movable, and with ovipositor internal.

Male genitalia with cuspides lost.

- Larva parasitizing ground-dwelling beetle larva.
- *51. Proctotrupidae
Antenna with 13 segments.
Metasoma short but extendable in length.
Ovipositor exerted secondarily with sheaths transformed to help penetration rather than protection.
- *52(49). Roproniidae
Antenna with 14 or 15 segments (data insufficient for fossils).
First metasomal segment at least incipiently modified as articulating tube (petiole).
53. Heloridae
Fore wing with 1m-cu very short, making cell 1mcu triangular (or very narrow), and with crossvein cu-a long, subequal to or longer than basal vein.
Metasomal apex closed at rest, with apical tergum and sternum weakly movable.
Ovipositor internal.
Male genitalia lacking cuspides.
- 54(52). Austroniidae
Antenna sexually dimorphic in segment numbers.
Fore wing with RS+M lost as tubular or nebulous vein, and with 1m-cu displaced basad up to near M-Cu fork.
Hind wing with r-m joining R far basad from distal group of hamuli.
- 54-55. Male genitalia lacking cuspides.
Larva endoparasitic in larval Diptera.
55. Hind wing narrow sub-basally, with maximum width beyond anal region.
56. Monomachidae
Scape long.
Metasoma with 1st segment very long, tubular.
Female metasoma strongly elongate to penetrate soil during oviposition, with apex closed at rest.
- 57(55). Basal flagellar segments modified in male.
Pronotum short medially, immovably connected with mesopleuron.
Prepectus fused with pronotum forming internal pronotal inflection.
Fore wing lacking tubular veins except those closing costal, basal and radial cells (pterostigma present).
Hind wing lacking tubular veins except those closing basal cell and also R beyond basal cell, with M(+Cu) and r-m concave from above.
58. Diapriidae
Antenna weakly geniculate.
Metasomal apex closed at rest (still weakly so in Ismarinae).
- 59(57). Archaeocynipidae
Medial scutal line (not sulcus furnished with internal apodeme) re-established.

- Fore wing with RS+M and 2r-m re-established as nebulose veins from spectral precursors. (Precursors of those veins exist as spectral ones: Rs+M in *Ismarus*, 2r-m in *Monomachus* and, as rudiment, in *Belita*). 2r-m complete, C lost, and pterostigma reduced in size.
- 59-60. (Unknown for Archaeocynipidae)
Flagellomeres with multiporous plate sensillae.
60. Pterostigma lost.
61. Figitidae
Fore wing with RS+M lost (central cell reaching Cu).
Possibly: 3rd metasomal (2nd post-petiolal) tergum enlarged, subequal to or longer than preceding one (providing that the seemingly plesiomorph condition in Anacharitinae is secondary, the small "3rd" tergum in Eucoilinae and Pycnostigmatinae is morphologically 4th in female, 5th in male).
- 62(60). Fore wing with 1m-cu lost (central cell not reaching Cu).
Larva parasitizing wood-inhabiting insect larva.
63. Cynipidae
Larva phytophagous (possibly gall forming).
- 64(62). Ibaliidae
Fore wing with RS+M issuing from near (or, further, above) midpoint of basalis.
One of subapical metasomal terga enlarged.
- 65(49). Jurapriidae
Antenna with 15 segments, strongly geniculate, subclavate in female, with scape moderately long.
Fore wing with RS+M, and also M and Cu beyond 1m-cu, lost as tubular veins.
Hind wing with RS lost, r-m subvertical, meeting R far basad from hamuli, possibly also A and cu-a lost as tubular veins.
Possibly (unknown for Jurapriidae): male genitalia tubular, with both volsella and parameres fused with adeagus, with parameres reduced and cuspides lost.
66. Chalcidoidea
Antenna with multiporous plate sensillae, with 13 segments (a rudimentary 14th segment found by Dzhanokmen, 1979, to be secondarily detached).
Prepectus secondarily exposed.
Mesospiracle displaced up to lateral mesonotal margin.
Mesonotum with axillar phragma developing to give origin of restored tergotrochanteral muscle.
Mesopleuro-mesotrochanteral muscle lost.
Wings with pterostigma and all tubular veins lost, except R and, in fore wing only, 2r-rs and abscissa of basalis.
Metasoma with 1st segment tube-like (secondarily ring-like).
Male genitalia with basal ring lost.

- 67(65). Antenna with 14 segments and with a very long scape, in female bent twice and strongly clavate.
Toruli continuous (secondarily) with clypeus.
Pronotum short medially, rigidly connected with mesopleuron, with prepectus reduced and fused with pronotum internally as posterior pronotal inflection (not confirmed in Serphitidae), and possibly externally as netrion.
Mesofurcal-mesotrochanteral muscle modified in pleuro-trochanteral (not confirmed in Serphitidae).
Hind wing narrow subbasally, with maximum width beyond vannus.
Metasomal spiracles lost.
Ovipositor internal.
Larva developing in host eggs.
68. Basal flagellomeres modified in male.
Pronotum annular.
Metasoma closed apically at rest, with apical tergum and sternum weakly movable.
69. Scelionidae
Praescutellar excavation reduced to narrow sulcus or transverse line.
Trochantelli lost.
- 70(68). Platygastriidae
Antenna with 10 segments.
Mesopleuro-mesotrochanteral muscle lost (as observed on *Isocibus* sp.).
Fore wing with single tubular vein (R) not reaching wing margin.
2nd metasomal segment enlarged.
Cerci lost.
- 71(67). Serphitidae
Antenna with 10 segments in female and 9 in male.
Prescutellar excavation reduced to crenulate sulcus.
Fore wing with pterostigma enlarged.
1st and 2nd metasomal segments both thin and tube-like.
- 72(66? 71?). Mymarommatidae.
(Ancestry uncertain, for details see Gibson, 1986).
- 73(32). Propodeum with metasomal articulating foramen narrow, subdivided with a pair of tooth-like condyli (cf. note to node 49).
74. Praeichneumonidae.
Pronotum short medially, rigidly connected with mesopleuron.
Medial mesoscutal sulcus (not line) and respective internal apodeme lost.
Fore wing with costal space narrow.
Hind wing with M almost straight between Cu and r-m.
- 74-75. Toruli distant from clypeus.
Lower tentorial bridge long with cardinal (=articulating with cardo, 1st sclerite of maxilla) condyli close to each other at its distal margin.
Prepectus much reduced and fused with hind pronotal margin below mesospiracle.

- Mesotergal-mesotrochanteral muscle lost.
75. Fore wing with costal space and 2r-m (not 3r-m!) lost.
- *76. Ichneumonidae
Fore wing with RS + M weak and further lost.
- *77(75). Braconidae
Hind wing with r-m oblique, meeting R or the very base of RS.
2nd and 3rd metasomal terga fused.
- *78(73). Bethylnymidae
General appearance Bethylinid-like.
Antenna with 13 segments.
Ovipositor short, weakly exerting.
Female supposedly hunting on beetle larva in rotten wood and/or soil.
(May be dwelling within rotten wood and/or soil in search for beetle larva as prey).
- 78-79. Metasomal sterna hard (convex when dry) in female.
- *79. Aculeata
Ovipositor fully internal, modified in sting (see Rasnitsyn, 1980: 100-101, for details).
- *80. Chrysidoidea
Fore tentorial arm thin, rod-like.
Profurca proclined.
Medial scutal sulcus (not line!) and respective internal apodeme lost.
2nd valvifer bipartite, intra-articulated.
Possibly: fore wing with crossveins 2r-m and 2m-cu lost (assuming r-m in Embolemidae to be 3r-m secondarily displaced basally comparing with 2m-cu; further assuming 2m-cu secondarily regained by Embolemidae as small rudiment and by Epyrine and Pristocerine Bethilids as spectral vein).
81. Plumariidae
Female apterous, strongly dissimilar from male, with pronotal collar reduced, fore coxa produced apically, metathoracic venter projected anteromesally, and general form of mesosoma modified.
Prosternum reduced externally.
Metapleural-propodeal borderline (metapleural suture) lost below endophragmal pit.
Fore wing with RS bent, Z-like, with secondary RS present and with cell 2+3rm short.
Hind wing with 2r-m shifted basad approximately at the level of RS base.
- 82(80). Trochantelli lost.
Fore wing with RS base reclined and with 1mcu cell small.
Hind wing with crossveins lost and with hamuli reduced in number.
- *83. Scolebythidae
Pronotal collar reduced.
Metapostnotum triangular (short laterally; clearly seen from inside in *Clistopsenella*).

Prosternum very large externally.

Fore coxae contiguous apically, trochanters originating basally.

Fore wing with RS lost between submarginal cells.

Hind wing with tubular veins lost except basal portion of R.

Arboreal.

84(82). Prepecti in broad contact or, usually, fused medially.

*85. Hind wing lacking tubular veins except basal portion of R.

2nd metasomal sternum excised angularly, anteromesally, with antecosta widest mesally.

Larva developing on active hemimetabolous host.

Possibly: Ovipositor with furcula fused with 2nd valvulae as their basal process (unless plesiomorphy; cf. node 89).

*86. Dryinidae

10 antennomeres only.

Fore wing with 3r-m lost, with adventitious vein closing cell cua_2 posteriorly in front of cubital furrow.

Larva in capsule built of egg shell and previous larval skins, parasitizing Homoptera Auchenorrhyncha.

Possibly: Antenna geniculate, female fore tarsus chelate, female femora clavate.

87(85). Sclerogibbidae

Female apterous, strongly dissimilar from male, with general appearance strongly modified.

Antenna originating from below frontal process, with more than 14 segments.

Prosternum almost lost externally.

Fore wing with RS lost between submarginal cells.

Larva feeding on embiids.

88(84). Mesothoracic venter produced caudally between middle coxae (lost in many Chrysididae but not in Amiseginae).

Metathoracic venter projected between middle coxae as bicarinate plate, varying from subtriangular (Emboleminae, Bethylinae: *Bethylus*) to elongate (Chrysididae: *Cleptes*), with its posterolateral angles elongated and elevated (secondarily reduced to double or Y-shaped keel in most Chrysidids, probably due to not burrowing or digging habits; further developed in most Bethylinae).

1st metasomal sternum weakly or not overlapping 2nd except secondarily overlapping with modified bilobate margin in Cleptinae and Chrysidinae).

2nd metasomal sternum with fore margin straight (secondarily modified in Chrysididae other than Amiseginae), with invaginated finger-like apophyses (instead of elongated anterolateral corners) and with desclerotized patches behind apophyses (modified in Chrysididae but only weakly so in Amiseginae).

*89. Embolemidae

Antenna far distant from clypeus, with 10 segments, not geniculate though scape strongly elongate. Head capsule roughly triangular in profile, with a pair of sutures connecting toruli and clypeus.

Prosternum lost externally.

Synprepectus fused laterally with inner pronotal surface making pronotum annular.

Fore wing with RS lost between submarginal cells, with adventitious vein (homoplasious with Dryinidae and a few Bethylidae and Chrysidae).

Hind wing with C lost (R percurrent, costal membrane present).

Larva in xylophilous nymphs of Achilidae, possibly endoparasitic.

Possibly: Fore wing with 2m-cu rudiment regained and furcula fused with bases of 2nd valvulae in ovipositor (unless plesiomorphies).

*90(88). Loss of articulation of 2nd valvula with proximal sclerite of the 2nd valvifer.

Possibly: Hind wing with C and R lost as tubular veins except basally (supposing percurrent C in *Parnopes* and R in *Chrysis* to be regained due to enlarged size).

91. Bethylidae

Head with eyes small, clypeus with median longitudinal carina, postgenal bridge long.

Metapostnotum apparently absent due to loss of posterior borderline and also reduced in length.

92(90). Chrysididae

Antenna geniculate.

Metapostnotum lost except laterally (metanotum reaching propodeum).

Fore wing with 3r-m lost.

Apical metasomal segments modified into a telescopic tube.

Female ovipositing through a hole cut with mandible (in host cocoon, or secondarily, in walking stick egg resulting in endoparasitic development).

*93(79) ?Baissodidae

12 antennomeres in female, 13 in male.

Mandible of cutting type, with cutting (toothed) edge twisted in moving plane of mandible.

Hind wing with jugal lobe redifferentiated.

Female with the 7th metasomal tergum internal, desclerotized medially except for antecosta, bearing hypertrophied spiracles.

Sting with 1st valvula with lamellate valva bearing 2 lamellae on common base.

Cercus lost in female.

94 ?Baissodidae

Spiracular pronotal lobes inflated.

Female hunting for prey other than cryptobiotic larva of Holometabola, probably for free-living or subcryptobiotic insect nymphs.

- *95. Sphecidae (?including Baissodidae)
Metapostnotum strongly enlarged.
Possibly: Inner hind tibial spur modified in calcar (assuming that the spur in *Astata* is secondarily simple).
96. Apidae
Hairs branched.
Hind leg with basitarsus widened and combing apparatus lost.
7th metasomal tergum with halves detached in female. (The halves lost the connecting chitin stripe and became completely independent).
Female storing pollens in nest to feed larvae.
- 97(94). Pompiloidea
Midcoxal base narrow, tubular.
98. Pompilidae
Sting lacking lamellate valve from the 1st valvula.
Female preying on spiders.
- 99(97). Rhopalosomatidae
Wing venation reduced and modified.
Female tarsi widened.
Metapostnotum narrow.
Mesopleuron lacking oblique suture.
Larva external parasites on active cricket in sack made of skins of egg and earlier larval stages (as in Dryinidae).
- 100(93). Scolioidea
Hypopharyngeal pubescence lost.
Medial mesoscutal sulcus (not line[^]) and respective internal apodeme lost.
Metapostnotum narrow.
Tarsi with arolium and orbicula small.
1st metasomal sternum thick apically, hardly overlapping the base of 2nd sternum.
101. Middle and hind tibia with outer surface covered with strong (fossorial) spines.
6th metasomal sternum depressed (weakly convex) below in female. The laterosternites large and detached with an apical incision and ranging from contiguous to medially overlapping while the body of the sternite is depressed and weakly convex from below. The sting exit slit-like.
102. Sapygidae
Fossorial tibial spines reduced.
6th metasomal sternum secondarily conical, with laterosternites widely overlapping and having lateral incisions reduced, and with sting exit narrow and subcircular.
Female ovipositing in aculeate nests.
- 103(101). Middle coxa medially overlapped by mesopleural lamella.
Metathoracical venter elevated between middle and hind coxae.

104. Tiphidae
Larva with 2nd (metathoracic) spiracle lost.
105. Mutillidae
Female apterous, dissimilar to male.
Thoracic venter with supracoxal lamelli and intercoxal elevated plate reduced or lost.
Fossorial tibial spines reduced.
6th metasomal sternum with laterosternites small and with lateral incisions reduced, making sting exit narrow and subcircular.
Larva parasitizing sphecoid (s.l.) larva (secondarily on other insects).
- 106(103). Scoliidae
Pronotum moderately short medially, rigidly connected with mesopleuron.
Prepectus reduced, fused with mesopleuron.
Middle and hind coxae at level with thoracic venter, with each pair widely separated mesally.
Wings with venation modified, with 2r-m lost and with wide apical part free of veins.
- 107(?104, ?108). Bradynobaenidae
Female apterous, dissimilar to male.
Hind wing with m-cu meeting M+Cu (instead of Cu).
Metasoma with a pair of stridulators.
2nd metasomal tergum with felt lines.
(Relationships obscure; see Rasnitsyn, 1980: 124-128 for details).
- 108(100). 1st and 2nd metasomal segments with articulation permitting both rocking and rotatory movements (see Rasnitsyn, 1980: 121-124).
(Mandibles with a tendency to reverse to chewing type with cutting edge rotated subvertically to moving plane of mandible, as seen in Cenozoic Formicoidea, in Polistinae and to lesser extent, in Sierolomorphidae).
- 108-110. Female first prepares nest and lays eggs, only then hunting and storing several prey per larva (habits unknown for Sierolomorphidae).
109. Sierolomorphidae
Middle coxal base narrow, tubular.
Fore wing with 3r-m and 2m-cu lost.
Hind wing with both free Cu and jugal lobe lost.
- 110(108). Inner (posterior) hind tibial spur modified in calcar.
111. Falsiformicidae.
Prepectus reduced and fused with mesopleuron.
Middle coxal base narrow and tubular.
Female with 1st metasomal segment modified as petiole.
112. Formicoidea
Antenna geniculate (scape not very long initially).
Metapleural gland present.
Fore wing with 3r-m and 2m-cu lost.
Both sexes with 1st metasomal segment modified as a petiole.

Incipient eusociality present (lacking nursing manipulation with eggs and larvae).

Possibly: Female dimorphic, with reproductive and worker casts (not proved for Sphecomyrminidae and Armaniidae).

(See Dlussky and Fedoseeva, 1988 for further information on evolution of ants).

113(110). Vespoidea

Hind head surface with subocular furrow (two trough on posterior side of head dorsolaterally of the occipital foramen).

Pronotum mesally short, rigidly connected with mesopleuron, elongated beyond spiracular lobe in acute process overlaying tegula.

Prepectus fused with pronotum and reduced.

1st and 2nd metasomal segments hinged, with rotatory mobility lost in articulation.

Sting with 1st valvula lacking lamellate valve.

Prey transported in air to nest.

(For further Vespoid evolution see Richards, 1962, and Carpenter, 1982).

NOTES TO THE RESPECTIVE NODES OF THE CLADOGRAM

1. Order Vespida is supposed here to have originated from the extinct order Palaeomanteida (= Miomoptera) and particularly from the family Permosialidae (= Permonkidae) known from Late Permian--Early Jurassic; for details see Rasnitsyn (1980).
2. Contrary to Gibson (1985), a free postspiracular sclerite is inherited from Xyelidae (cf. Rasnitsyn, 1969, fig. 59) and not a synapomorphy of Tenthredinomorpha and Siricomorpha.
16. Contrary to Rasnitsyn (1969), an angulate M+Cu with a supernumery cu-a crossvein is considered here as apomorphic character state. Considering the straight or weakly arcuate M+Cu lacking supernumerary cu-a in all Siricina except Pamphiliidae and, partly, Siricidae and Sepulcidae, as an automorphy would result in too many cases of homoplasy connected with this character.
25. Myrmiciidae (= Pseudosiricidae) are synonymized with Siricidae based upon recently found fossils [from Mid Cretaceous (Albian) near Okhotsk, Soviet Far East] showing myrmiciid wings with a typical siricid thorax. "Myrmiciidae" of Eocene age including *Formicium* belong to Formicidae (Lutz, 1986).
27. Contrary to Rasnitsyn (1969), spinisternal muscles are present in Xiphydriidae.
28. I agree with Gibson (1985) concerning the monophyly of Apocrita + Siricoidea rather than Apocrita + Cephoidea. The alternative hypothesis accepted in Rasnitsyn (1980) is abandoned.
- 33 and 34. Both these nodes are purely hypothetical, because the respective insects are hardly identifiable in impression fossils of Ephialtitidae.
35. A medially shortened pronotum which is rigidly connected with the mesopleuron is not a synapomorphy of Stephanoidea because the wide

pronotum is retained by Stephanidae and by at least some Cleistogastrinae (Megalyridae). The same is true for the free prepectus present in Stephanidae and, by implication, probably also in Cleistogastrinae. This possibly also applies to the metasomal articulating foramen, which is only moderately narrow in Stephanidae and in some Cleistogastrinae.

36. Dr. Gibson has kindly informed me that Stephanidae are synapomorphous with Evaniomorpha in structure of the metacoxal articulation and thus are members of that infraorder. Stephanidae are further synapomorphous with Megalyrids and their descendants in having the hind wing with A reduced apically and almost replaced with Cu, which is bent backward and then outward along the anal furrow, as is seen in *Schlettererius cinctipes* Cresson. That is why Stephanidae are here transferred to the superfamily Stephanoidea (formerly Ceraphronoidea), while the rest of the previous superfamily Stephanoidea is renamed Ephialtitoidea.
43. Besides the Jurassic Anomopterellidae, the Lower Cretaceous genus *Cretocleistogaster* Rasnitsyn, 1975, described in Megalyridae and later transferred to Aulacidae (Rasnitsyn, 1986: 156-157), is here included in Praeaulacidae. This is based upon the presence of antenna with more than 14 segments, a medially long pronotum, mesonotum with the medial scutal sulcus and respective internal apodeme present, and hind wing with basal cell closed with tubular veins.
49. I abandon here a hypothesis of the sister-group relationship of infraorder Proctotrupomorpha (formerly Microhymenoptera) to Ichneumonoidea, as proposed by Rasnitsyn (1975a, 1980), for the following reasons: The suggested synapomorphies of the former infraorder Ichneumonomorpha (s.l.) are either doubtful or even erroneous. Each "dentiform" propodeal condylus in Proctotrupidae and Heloridae resembles a locally produced margin rather than the really dentiform process in Ichneumonoidea and Vespomorpha. Indeed, its base is relatively wide, and its surface is concave or flat basally and has elements of the propodeal sculpture. On the contrary, the condyli of Ichneumonoidea and Vespomorpha are basally thin, with a convex outer surface, and are sharply delimited from the rest of propodeum by an elevated band surrounding the articulating foramen. *Sparasion* within the Scelionidae has propodeal condyli a little more ichneumonoid-like, but it a derived group within the proctotrupoid complex. Because of it, I consider this similarity between Proctotrupoidea s.l. and Ichneumonoidea to most likely be parallelism.

Concerning the hind cephalic structure, Proctotrupomorpha are similar to Ichneumonomorpha s. str. only in the lower tentorial bridge intervening between postgenae from the oral cavity up to the occipital foramen, not in the adjacent position of the cardinal (=articulating with cardo, 1st sclerite of maxilla) condyli (contrary to Rasnitsyn, 1980: 77). It is not a true synapomorphy but represents a common tendency, as some primitive Ichneumonidae still retain the plesiomorphic condition of having the postgenal bridge not completely replaced with the lower tentorial one.

Alternative synapomorphies shared by Proctotrupomorpha with Evaniomorpha as listed at node 33 are not very reliable as well. Nevertheless, I

believe that they are true synapomorphies, because unlike the previous hypothesis this one is in agreement with the paleontological data which indicates an early origin of Proctotrupomorpha relative to the Ichneumonoidea.

I also abandon here Diaprioidea as a superfamily distinct from Proctotrupeoidea, based on the data by Gibson (1985, 1986) and Naumann and Masner (1985), and also on new paleontological findings (still unpublished) which fill a large part of the gap between Roproniidae and Austroniidae.

51. Observations by Mason (1983) do not falsify the hypothesis about synapomorphy of *Vanhornia* and Proctotrupidae in having the ovipositor sheaths modified to penetrate (but not to drill) substrate during oviposition. Neither do they falsify completely the hypothesis that Vanhorniinae are descendants of some ancient Proctotrupidae, because only Cenozoic representatives are known to have autapomorphy in structure of the metasomal base. Mason is possibly correct in insisting that Vanhorniidae (excluding *Heloriserphus*) merits a rank of family. Nevertheless, I prefer to follow Townes & Townes (1981) in lumping Vanhorniidae and Proctotrupidae so that the classification is not burdened with small groups of higher ranks.
52. The diagnosis of Roproniidae is expanded here to cover undescribed Mesozoic fossils differing from Mesoserphidae only in having the 1st metasomal segment modified more or less as an articulating tube. The gap between Mesozoic Roproniids and *Ropronia* is partly filled by a living representative from the Soviet Far East (now under study by M. Kozlov in Leningrad).
76. Contrary to Mason (1981), I consider r-m crossvein in Ichneumonid and Braconid hind wing as one and the same vein. Otherwise we come to deeply diphyletic Ichneumonoidea, with the assumed ancestral lines of Ichneumonidae and Braconidae (marked with 2r-m and 2r-m, respectively) meeting only at the phylogenetic level of Ephialtitidae or, rather Karatavitidae (because the only Ephialtitid with two r-m is huge *Leptephialtites gigas* Rasn. which could secondarily acquire a supernumerary vein). As to the two r-m veins in Braconidae, the distal of them is similar in shape and occurrence to another extra vein crossing r cell in Braconid hind wing (Mason, 1981, fig. 6). The latter vein is clearly a secondary one (or restoration of an old, probably pre-hymenopteran vein). The same is most probably true for the extra r-m vein.
Early Cretaceous *Eoichneumon* (Jell and Duncan, 1986) has not been adequately described to infer its true relationship within Ichneumonoidea.
77. Apozygidae are here lumped with Braconidae because of their essentially Braconid structure (Mason, 1987), with the only autplesiomorphy comparing to other described Braconidae being 2m-cu crossvein (contrary to Mason, 1981 the sclerotized metasomal sterna of *Apozyx* are an apomorphy). This vein is present in a group of Early Cretaceous Braconidae (now under study by M. Sharkey and myself). *Apozyx* is possibly the last and aberrant representative of that group.
78. *Arthrogaster* and *Leptogastrella*, described as members of Bethyloynymidae (Rasnitsyn, 1975b), probably belong elsewhere. The taxonomic position of the former is unknown, while the latter belongs to Praeaulacidae.

79. Contrary to Gibson (1985), Baissodidae have retained a medial scutal sulcus together with the respective internal apodeme (W. Pulawski, personal communication, 1986).
80. Cladograms for Chrysidoidea proposed by Rasnitsyn (1980) and Carpenter (1986) are conflicting and both are burdened with errors and weak synapomorphies (common tendencies instead of true synapomorphies in Rasnitsyn's cladogram, similarity due to simple reduction in Carpenter's). If for a moment we set aside all such characters, we will be left only with the following putative synapomorphies in the conflicting part of the cladogram:
- (a) 2nd metasomal sternum modified basally as described at node 85; (b) larva developing externally on active host--both characterizing Dryinidae + Sclerogibbidae; (c) alternative modification of the 1st and 2nd metasomal sterna as described at node 88; (d) posteromedial projection of mesothoracic and median one of metathoracic venter between middle coxae (digging and burrowing adaptation), for Embolemidae + (Bethylidae + Chrysididae); (e) parasitism of Homoptera Auchenorrhyncha, characterizing Dryinidae + Embolemidae; (f) furcula fused with the base of the 2nd valvulae in ovipositor, characterizing Dryinidae + Embolemidae + Sclerogibbidae (unless symplesiomorphy). No sound cladogram can be constructed on such a foundation, of course, but with the data at hand the cladogram accepted here includes clades characterized each with two strong synapomorphies (a+b and c+d, respectively) while in Carpenter's cladogram clades Sclerogibbidae + (Embolemidae + Dryinidae) and Embolemidae + Dryinidae are characterized each with a single strong synapomorphy (f and e, respectively), if we may consider the synapomorphy (f) as strong.
- Contrary to Carpenter (1986), a prosternum upcurved before fore coxa and thus partly invisible externally, is universal for hymenopterans beginning with Xyelidae. The same is true for a lack of a differentiated intercoxal projection on the metathoracic venter. Such a projection is found, as far as I know, only in Evaniidae, Cretevaniidae and various aculeates.
- 83, 90. Upper Cretaceous *Cretobythus* does not belong to Scolebythidae. Additional preparation and study of the holotype shows the structure of its basal metasomal sterna to be similar to that of *Bethylus* or *Goniozus* (Bethylidae), except that the finger-like apodemes are not seen in the fossil. Further, the metathoracic venter is weakly produced medially (similar though weaker than in *Bethylus*). Taking into consideration a clypeus with median keel, large eye, short postgenal bridge and an evident metapostnotum, *Cretobythus* should be treated as a member of the group ancestral to Bethylidae or, possibly, for all the clade Bethylidae + Chrysididae.
86. Contrary to Carpenter (1986), the dryinid groundplan includes long metapostnotum with a clear hind margin (cf. Olmi, 1984, Figs. 2, 397, 401, etc.) and all developmental stages external (Ponomarenko, 1975, and personal communication, 1986). The antenna is hypothesized as geniculate in the groundplan, based on Early Cretaceous fossils with such antenna (unpublished) and assuming that some living members secondarily acquired non-geniculate an-

tenna. Similarly, the groundplan of the female fore leg is hypothesized as chelate and with a clavate femur based on Early Cretaceous fossils (unpublished) with clavate femora (fore tarsus is unfortunately not seen in Early Cretaceous female). This supposes that the Aphelopinae s.l. with their reduced morphology and late (probably post-Eocene) origin have the female fore leg secondarily male-like.

89. Contrary to Carpenter (1986), the metapostnotum is well developed and the middle tibia is with two spurs in all winged Embolemids studied (males of *Embolemus* spp. and both sexes of *Ampulicomorpha confusa* Ashmead; middle tibial spurs are rudimentary in females of the latter species).

Biological observations on Embolemids are confusing. The description by Bridwell (1956) can be understood as indicating the larva developed endoparasitically, while R. A. Wharton (in litt., 1986) observed the larva enclosed in an external sac. Unfortunately, the nature of the sac has not been studied.

90. (See also note on node 83). Unlike Mason (1986), I failed to find an adventitious vein closing cua_2 cell in front of cubital furrow in more than occasional Bethylids (*Pristocera* spp.) and Chrysidids (*Omalus* spp., *Notosus* spp.). That is why I doubt whether this character state is a part of the groundplan of Bethylidae + Chrysididae.
93. Fossil Baissodidae are not sufficiently known to allow their placement on the cladogram within the interval of nodes 93-95.
95. Widely separated middle coxae is hardly a character state of the Sphecoid groundplan because the coxae are contiguous in *Heterogyna* Nagy and subcontiguous in *Mellinus* F. The same is true for the annular pronotum, which is not annular in *Dolichurus* Latr. or *Heterogyna*.

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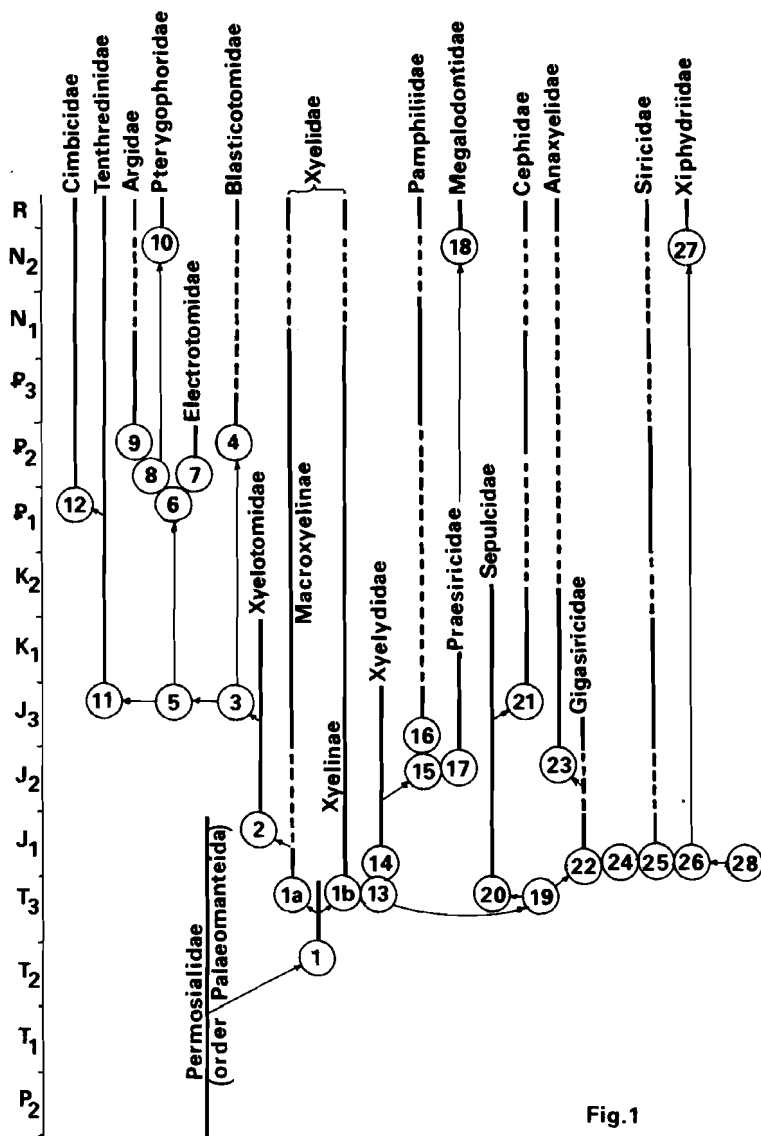


Fig.1

Fig. 1. Cladogram of the suborder Siricina. Numbers in the circle represent corresponding nodes of the cladogram, solid lines show the occurrence confirmed by the fossil records, dashed lines - supposed occurrence. Ancestor-descendant connections are shown either with arrows or with touching circles, the circle with the lower number representing the ancestral node. Left is the simplified geochronological scale, where P₂ is the Late Permian, T₁₋₃ Early Middle and Late Triassic, respectively, J₁₋₃ - Early, Middle and Late Jurassic, K₁₋₂ - Early and Late Cretaceous, P - Paleogene (P₁ - Paleocene, P₂ - Eocene, P₃ - Oligocene), N - Neogene (N₁ - Miocene, N₂ - Pliocene), R - Anthropogene including the Present Time.

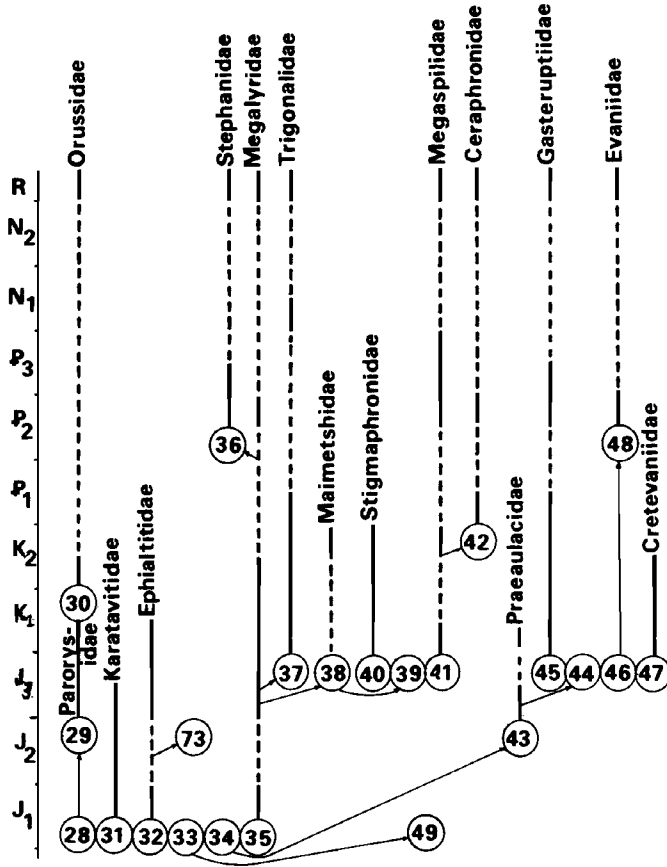


Fig.2

Fig. 2. Cladogram of the lower Vespina. For the cladograms subtended with the nodes 49 and 73, see Figs. 3 and 4, respectively, for other explanations - Fig.1.

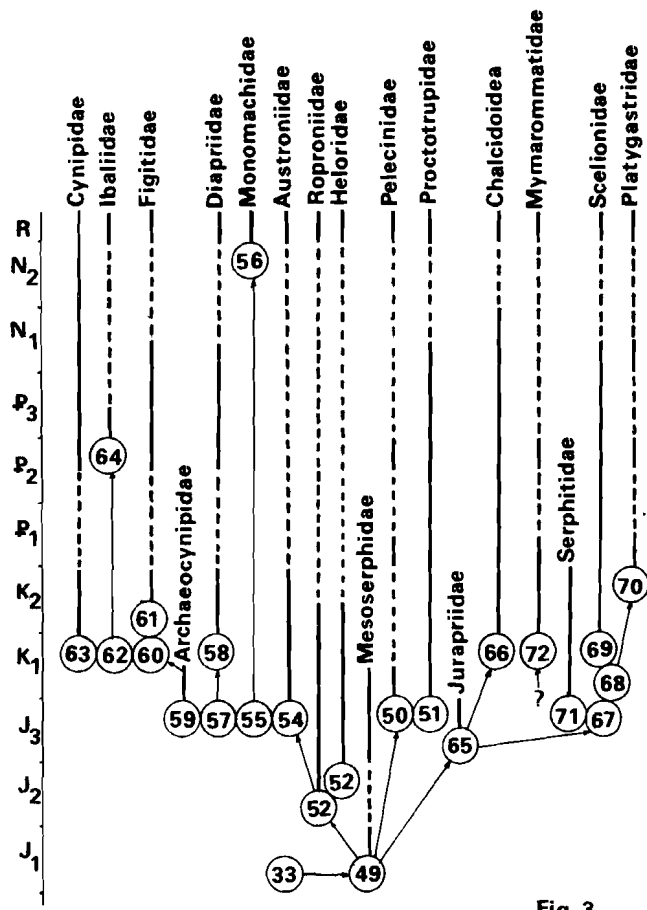


Fig. 3

Fig. 3. Cladogram of the infraorder Proctotrupomorpha. For explanations see Fig. 1.

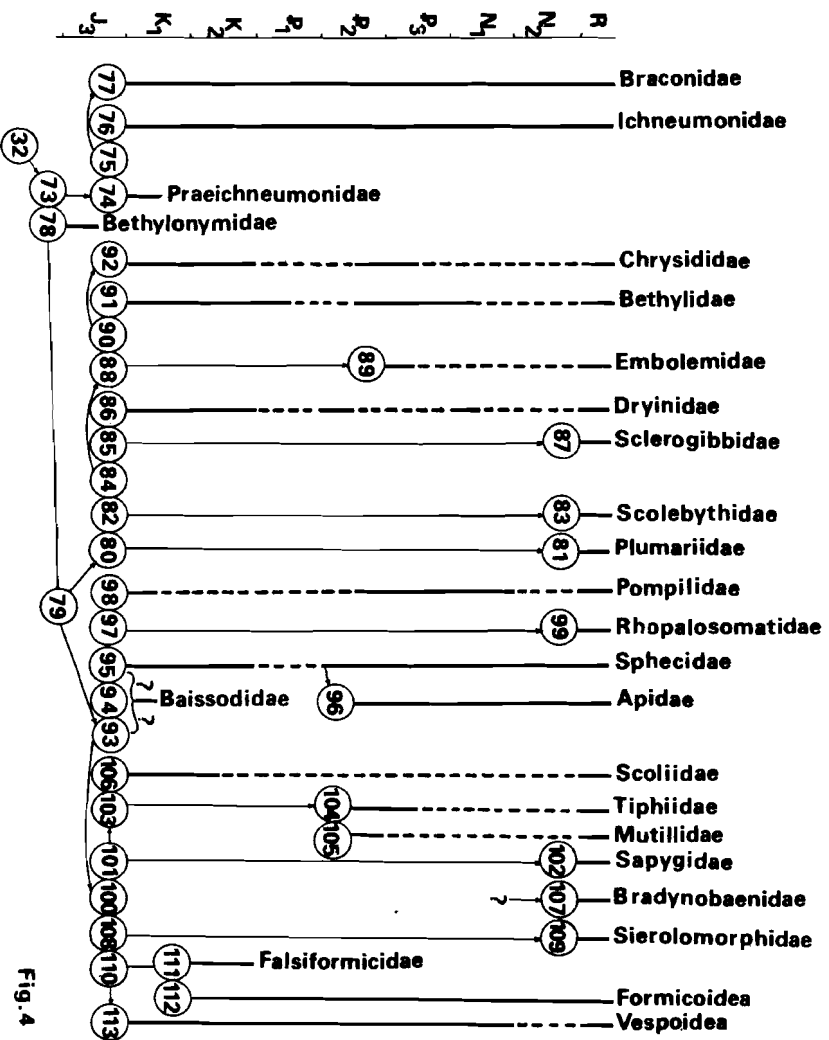


Fig. 4

Fig. 4. Cladogram of the infraorders Ichneumononomorpha and Vespomorpha. For explanations see Fig. 1.