

Cladistics of the Ichneumonoidea (Hymenoptera)

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Abstract.—We recognize only two extant families, Ichneumonidae and Braconidae, in the Ichneumonoidea. All other recent taxa that have been regarded as family-level taxa can be reasonably placed within one or the other family. We find no evidence to place Praeichneumonidae in the Ichneumonoidea and therefore consider it *incertae sedis* in the Apocrita. Likewise, though it is an ichneumonoid, there are no synapomorphies which suggest that *Tanychora* is an ichneumonoid. The cladograms of fossil and recent ichneumonoids support the monophyly of Eoichneumonidae and a sister-group relationship with Braconidae.

The purpose of this paper is to review and revise the family-level cladistics and classification of the Ichneumonoidea. The families comprising the Ichneumonoidea have fluctuated considerably over the years and recent classifications have included from two to seven extant families, i.e., from only Braconidae and Ichneumonidae, (e.g., Gauld and Bolton, 1988) to various combinations of the following: Agriotypidae (e.g., Mason 1971); Aphidiidae (e.g., Tobias 1989; Mackauer 1968; Mackauer and Stary 1967; Stary 1966; Conca 1973); Apozygidae, (Mason 1978); Braconidae; Ichneumonidae; Megalyridae (Pagliano and Scaramozzino, 1990); and Paxylommatidae (e.g., Achterberg 1976a; Mason 1981). We examine the validity of these familial concepts from a cladistic perspective and recognize a classification that consists of only two families, Braconidae and Ichneumonidae.

PLACEMENT OF THE ICHNEUMONOIDEA WITHIN HYMENOPTERA

Rasnitsyn (1988) suggested that Aculeata (his Vespomorpha) is the sister-group of Ichneumonoidea on the basis of the shared possession of an apomorphic condition of the propodeal foramen and the presence of valvilli in the ovipositor (Gauld 1976; originally referred to as hemmplättchen by Oeser 1961). The propodeal foramen, into which the metasoma is inserted (Fig. 1), is narrow and subdivided by a pair of tooth-like condyli (the "propodeal teeth").

Zessin (1985) suggested that the Ichneumonoidea is the sister-group of the remaining Apocrita. He based the monophyly of the Apocrita exclusive of the Ichneumonoidea on the loss of the anal veins, 2A and a, of the fore wing. In Zessin's phraseology, all traces of the lanceolate cell (anal) are lost. Within the Apocrita, traces of the lanceolate cell, in the form of 2A and crossvein a, are found only in some Braconidae. Although he did note that the veins must be convergently lost in the Ichneumonidae and the 'remainder of the Apocrita', Zessin did not consider the fact that they could be a reversal, an equally parsimonious interpretation.

A third hypothesis was presented by Rasnitsyn (1980) and supported by Johnson (1988). This is that Ichneumonoidea, Chalcidoidea, Cynipoidea, and Proctotrupeoidea s.l. (excluding Cerafronoidea) are a monophyletic group, the Ichneumonomorpha. Johnson supported the Ichneumonomorpha on the basis of the apomorphic condition of the midcoxal articulations, i.e., a reduced basicoxite, a deep coxal groove, and laterally displaced coxal cavities. According to Johnson, an identical character occurs in several lineages of Aculeata. A total of six steps accounts for the distribution of the character, with one derivation in Ichneumonomorpha, and four derivations and one reversal in Aculeata. If, however, one considers the Ichneumonoidea to be the sister-group of the Aculeata, the number of steps is the same for a clade consisting of Ichneumonoidea, Aculeata, Cynipoidea, Chalcidoidea, and Proctotrupeoidea (using the

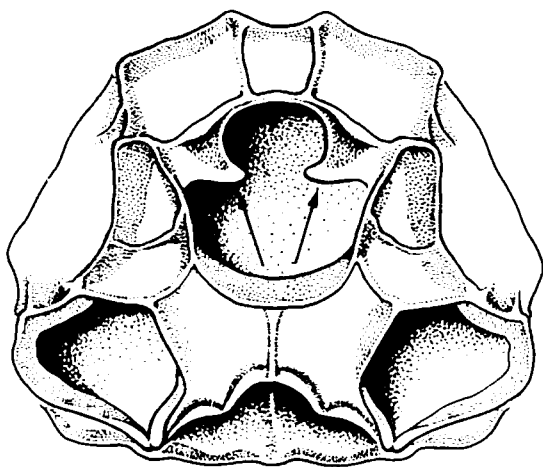


Fig. 1. *Alabagrus texanus*, posterior view of mesosoma with legs and metasoma removed. Arrow indicates the propodeal teeth in the propodeal foramen.

cladogram of Aculeate family relationships given in Johnson's figure 35).

Taking all the evidence into consideration, i.e. coxal articulations, wing venation, valvilli, and propodeal teeth, the sister-group relationship with the Aculeata is the most parsimonious hypothesis.

MONOPHYLY OF THE ICHNEUMONOIDEA

Character polarity for our cladistic analysis (Maddison et al., 1984) was based on the following sequential ordering of outgroups: Aculeata, other Apocrita, Orussidae, Xiphydriidae, other Symphyta (Gibson 1985, Rasnitsyn 1988). It is based on the distribution of character states in these outgroups that we suggest the following autapomorphies for the Ichneumonoidea.

1. Adult mandible with two teeth (Mason 1987). The plesiomorphic condition is three or perhaps four mandibular teeth, as in almost all Symphyta, and the vast majority of Apocrita. Some derived lineages of Chalcidoidea, Cynipoidea, Proctotrupoidea, and Scelionoidea have two teeth, but based on our surveys the ground plan of all of these taxa appears to be three or more teeth. Within the Ichneumonoidea, the teeth have been reduced to one in some lineages. In Alysinae, and some Opiinae the number has been increased to three or four. In Ichneumonidae the upper tooth has become

subdivided in Diplazontinae and certain Banchini.

2. Prepectus fused to posterior lateral (vertical) margin of the pronotum, mesothoracic spiracle positioned directly above prepectus, and external pit indicating origin of spiracular occlusor muscle lying near posterior pronotal margin (Gibson, 1985).

3. Sternum of first metasomal segment divided into heavily sclerotized anterior section and comparatively weakly sclerotized posterior section (Mason 1981, 1987). This character is found only in Ichneumonoidea.

4. Metasomal segments 1 and 2 articulated by a pair of dorsolateral condyles on the hind margin of tergum 1 and anterior margin of tergum 2. This character is found only in Ichneumonoidea (Mason 1987). The plesiomorphic condition is that metasomal segments 1 and 2 do not articulate on dorsolateral condyles so that they can telescope; such telescoping is not possible in ichneumonoids. In some other Apocrita this telescoping ability may be lost due to partial or complete fusion.

5. Costa and radius of fore wing adjacent/apressed, such that the width of the costal cell is narrower than the costal vein (Fig. 2). In many ichneumonoid taxa the costal cell is completely absent. Convergent appearances of this character are found in other Apocrita, most notably Rhopalosomatidae and miscellaneous Larridae.

6. Vein 2r-m of fore wing absent. The identity of the veins making up the apparent r-m cross veins of the fore wing has been a matter of some dispute. One interpretation is described by Tobias and Belokobylski (1984), with Braconidae possessing 2-Rs and 2r-m (3r-m is lost) and Ichneumonidae possessing 2r-m and 3r-m (2-Rs is lost). Much of the argument of these authors was based upon instances of aberrant venation in braconids. Rasnitsyn (1980) was of the opinion that 2r-m was lost (2-Rs and 3r-m retained) in an ancestral ichneumonoid and we have adopted this interpretation as it best accounts for venation in fossil taxa. For example, in the Cretaceous ichneumonoid *Tanychora* (Fig. 3) the outermost r-m crossvein is well distad 2m-cu, the usual position for 3r-m in Hymenoptera, and 2-Rs is in the plesiomorphic basal position. In the instances of 2m-cu occurring in braconids cited by Tobias and Belokobylski (Fig. 4), the outermost vein is in the same position. Rather than posit a migration of 2r-m from its usual position between 1m-cu and 2m-cu, Rasnitsyn's suggestion seems simpler. Rs is therefore considered to have migrated apically in

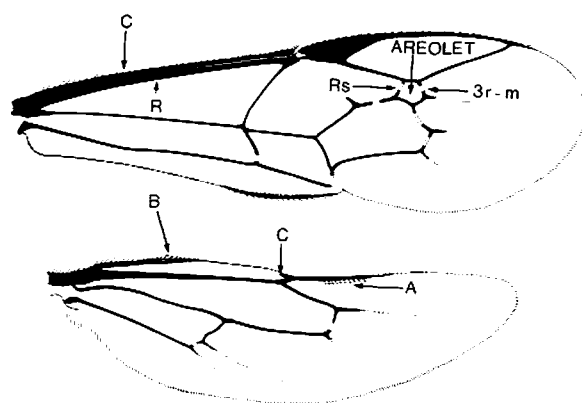
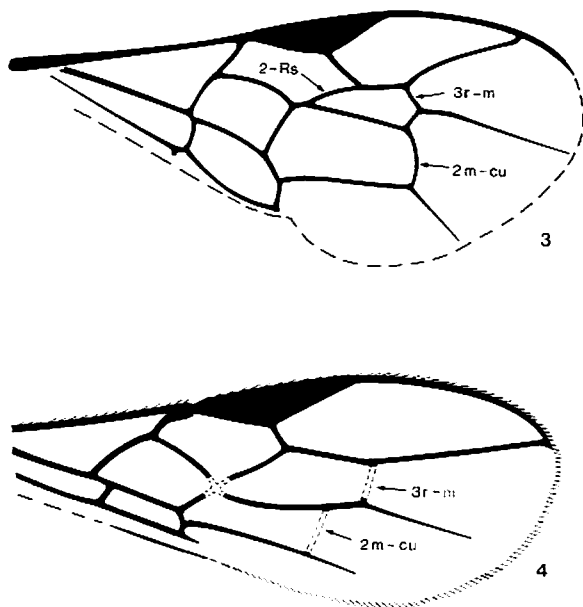


Fig. 2. Ichneumonidae sp., fore and hind wing. B = basal hamuli, A = apical hamuli C = costa



Figs. 3, 4. 3, *Tanychora petiolata*, fore wing. 4, *Ontsira rara*, fore wing.

Ichneumonidae to form the family's characteristic areolet (Fig. 2).

7. Larva with hypostomal spur. Ichneumonoid larvae possess an extensive system of sclerotized bands around the mouthparts. The hypostoma is a sclerotized band running posteriorly along the subgenal margin of the cranium; a spur projects ventrally from the hypostoma across the stipes (Fig. 5). The hypostomal spur is found only in

Ichneumonoidea and apparently functions to help brace the labium during cocoon construction. It has been lost on several occasions in braconids and ichneumonids, usually in taxa that do not spin cocoons (Short, 1978).

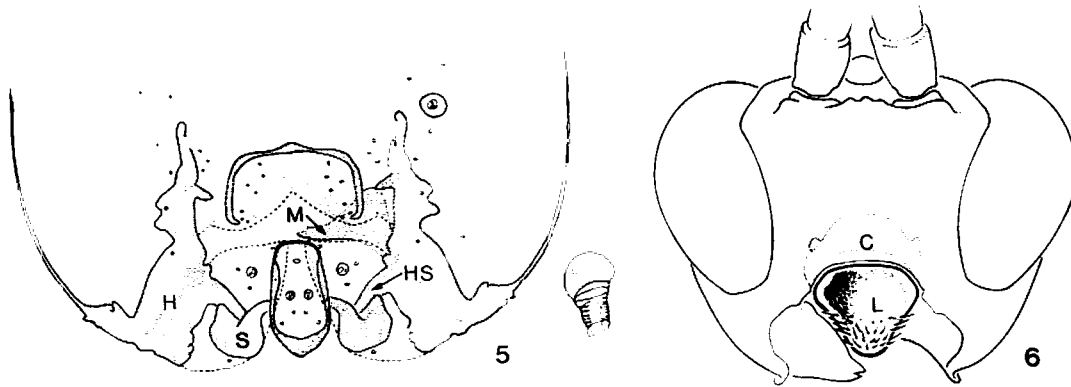
TAXA THAT HAVE BEEN RECOGNIZED AS FAMILIES OF ICHNEUMONOIDEA

Agriotypus

This group is usually recognized as an ichneumonid subfamily by ichneumonid researchers e.g., Townes (1969). *Agriotypus* shares the two known autapomorphies of Ichneumonidae, the apical displacement of vein 2-Rs of the fore wing with the resulting formation of the characteristic ichneumonid areolet, and loss of vein 1-Rs+M of the fore wing. We keep *Agriotypus* within Ichneumonidae.

Aphidiinae

It is now fairly well accepted that Aphidiinae are derived braconids sharing all of the braconid synapomorphies (detailed below). The character that has caused some confusion in the group's placement is the presence of an apparent suture between metasomal terga 2 and 3. When examined carefully, this is found to be a weakness in the fused terga rather than a true suture. Therefore, the braconid synapomorphy of fused terga 2 and 3 is valid even with the inclusion of Aphidiinae. Some specialists, particularly Tobias (1968, 1989) and Tobias and Starý (in the 1988 edition of the newsletter *Ichnews*) maintain that Aphidiinae should have familial status. Tobias (1989) stated that there are two well established lineages within the Braconidae, the cyclostomes (Apozyginae, Alysiinae, Braconinae, Doryctinae, Gnampodontinae, Opiinae and Rogadinae s.l.) and the clade of endoparasitoids representing all other braconids. To date there has been no compelling evidence to associate the Aphidiinae with either of these lineages, and on the basis of this negative evidence, Tobias (1968, 1989) argued that Aphidiinae should be considered the sister-group of the braconids. In our view, this is faulty logic. If, as Tobias and Starý appear to believe, the cyclostome braconids, the Aphidiinae and the non-cyclostome braconids form an unresolved trichotomy, the Aphidiinae could represent the sister-group of either or both of the two other taxa. There are synapomorphies defining the Braconidae



Figs. 5-6. 5, *Grotea* sp., head capsule. H = hypostoma, HS = hypostomal spur, M = mandible, S = stipital sclerite. 6, *Aleiodes terminalis*, head. C = clypeus, L = labrum

including the Aphidiinae, but when one excludes the Aphidiinae there is none. This is sufficient reason to classify the Aphidiinae within the Braconidae.

Apozyx

Apozyx is represented by one species known only from Chile. Mason (1978) described the species and proposed family rank in the Ichneumonoidea. It has also been included as a subfamily of the Braconidae (e.g., Quicke and Achterberg, 1990)

Apozyx shares all four synapomorphies of the Braconidae, i.e., migration of vein 1r-m to or basal to the separation of veins R1 and Rs in the hind wing, loss of functional basal hamuli, loss of stub of vein C of the hind wing basad the distal hamuli, and fusion of metasomal terga 2 and 3.

In our view, *Apozyx* is a cyclostome braconid. The most telling synapomorphy supporting this hypothesis is that the labrum is the typical cyclostome type: concave, triangular, smooth, and mostly glabrous (cf. Fig. 6) and the ventral margin of the clypeus is concave (Fig. 6).

Apozyx may be the sister-group of the remaining cyclostomes, all of which have lost the second abscissa of vein Cu (2-Cu) of the hind wing (Fig. 8). The only character which argues against this placement is the apparently plesiomorphic presence of vein 2m-cu in the fore wing of *Apozyx* (Fig. 8). This vein is present in the Ichneumonidae and other outgroups but present in no other Braconidae except some freak specimens, e.g. *Ontsira rara* (Fig. 4) (Tobias and Belokobylskij, 1984). It is more parsimonious to hypothesize a recurrence of 2m-cu in *Apozyx* than treat the cyclostome characters as convergences.

Braconidae (including Aphidiinae and *Apozyx*)

This is one of the two families we recognize in Ichneumonoidea. The family is supported by four autapomorphies.

The first autapomorphy, the fusion of metasomal terga 2 and 3, is found without exception in all known braconids. It is also found convergently in derived lineages of Ichneumonidae and Aculeata, but, based on its distribution within these taxa, the plesiomorphic condition of mutually articulating terga must be considered to be part of the ichneumonoid and aculeate ground plan.

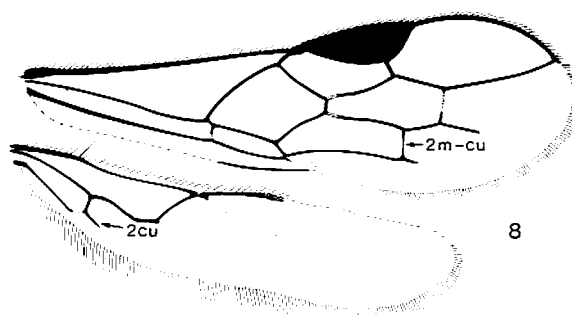
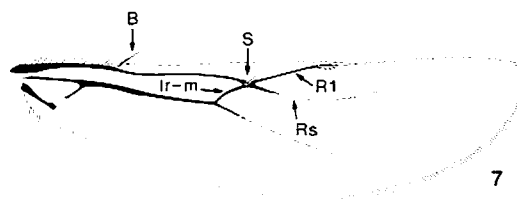
The second autapomorphy is the loss of functional basal hamuli on vein C of the hind wing. Functional basal hamuli are hooked and are found near the point where veins C and R of the hind wing diverge (Fig. 2). Basal hamuli are found in some members of the Braconidae, e.g., Braconinae (Fig. 7), but they do not form hooks and do not appear to function as wing couplers. Functional basal hamuli are widespread in Ichneumonidae (Fig. 2), Aculeata, Trigonalidae and the symphytan superfamilies, but are unknown in the Braconidae. It is worth noting here that the convergent loss of functional basal hamuli in the Apocrita exclusive of the Ichneumonoidea, Aculeata and Trigonalidae, may be a synapomorphy for this assemblage. This suggestion is supported by several venational characters such as the loss of the second closed Rs cell in the fore wing and the loss of a closed Cu cell in the hind wing.

A third autapomorphy of Braconidae is the loss of an independent stub of vein C of the hind wing, basad the distal hamuli (Fig. 7). Vein C is complete in some Aculeata and presumably the ground plan for the group (Brothers, 1975). Many aculeate taxa have some indication of vein C basad the point

where R or R1 meets the anterior wing margin. Although vein C of the hind wing is incomplete in all Ichneumonoidea, most Ichneumonidae have retained a small stub of vein C basad the point where R1 meets the anterior margin (Fig. 2) and this is the most parsimonious assignment for the ground plan.

The fourth braconid autapomorphy is the basal migration of vein 1r-m of the hind wing, to or basal to the separation of veins R1 and Rs (Fig. 7); the plesiomorphic condition is for 1r-m to be apical the separation. Ichneumonidae, Aculeata, other Apocrita, e.g. Trigonalidae, and most Symphyta have this plesiomorphic state. In at least one ichneumonid taxon (*Neorhacodes*) 1r-m is opposite the R1-Rs separation, but never basad. There are several braconid taxa such as *Trachypetus* and *Rhamphobarcon* where reversals have occurred.

Mason (1981) discussed the various positions of the r-m crossveins in ichneumonoids. He posited the ancestral ichneumonoid to have two r-m crossveins with Ichneumonidae having lost 1r-m and Braconidae having lost 2r-m. We reject Mason's arguments because explicit outgroup analysis exposes them as unsupported. With rather convincing support, Gibson (1985) postulated the following pattern of relationships: (Siricidae (Xiphydriidae (Orussidae + Apocrita))). We are unaware of any Apocrita with two r-m crossveins, with the exception of some braconids. Furthermore, the one crossvein present in apocritans is always opposite or distad the point of separation of R1 and Rs, with the aforementioned exception of braconids (Gauld, 1984). Orussids have only one crossvein, which is distad of the separation by about the length of the crossvein. Xiphydriids have three crossveins: r-m and 3r-m are tubular, 2r-m is spectral. It is noteworthy that 1r-m is well distad of the R1 and Rs separation and in the same position as the 1r-m crossvein of ichneumonids and aculeates. There are two r-m crossveins in the siricid hind wing: the most basal varies from basad to distad the separation, and the outermost one is in the position of 3r-m of xiphydriids and the Jurassic siricoid *Protosirex* (Mason, 1981: Fig. 5). No trace of a crossvein can be seen between the two existing crossveins. We therefore conclude that the most parsimonious solution to the question of hind wing r-m homologies is to consider: (1) 2r-m and 3r-m to be lost in the common ancestor of Apocrita + Orussidae, (2) 1r-m to be shifted in braconids to a position basad the separation of R1 and Rs, and (3) the second r-m crossvein of some braconid



Figs. 7-8. 7, *Coeloides rufovarigatum*, hind wing. B = basal hamuli, S = elongate setae. 8, *Apozyx penyai*, fore and hind wing.

subfamilies to be the product of one or more reversals. The preceding hypothesis prevents the wildly unparsimonious scenario of multiple 2r-m losses.

Ichneumonidae (including *Agriotypus* and *Paxylomatinae*)

Ichneumonids are usually recognized by having 1-Rs+M absent and metasomal terga 2 and 3 articulating. The former character is apomorphic though it is also found in widely scattered groups of braconids; the latter is plesiomorphic. What other apomorphies distinguish the family? Mason believed that ichneumonids lack 1r-m in the hind wing; our objections to that hypothesis are detailed above in the discussion of Braconidae. Tobias and Belokobylski (1984) argued that the areolet in braconids and ichneumonids is formed by different veins (2-Rs and 2r-m in braconids, 2r-m and 3r-m in ichneumonids). Again, our objections to that idea are presented in the section dealing with ichneumonoid autapomorphies. Ichneumonidae have a very characteristic, small, areolet (Fig. 2). If our hypotheses on fore wing vein homologies are correct, then the apical displacement of vein 2-Rs is

necessary to account for the small areolet. A precursor condition to this may be the long and slanting vein 2-Rs of *Tanychora* (Fig. 3), but this is quite speculative. In summary, we put forward the loss of fore wing vein 1-Rs+M, and the apical displacement of fore wing vein 2-Rs as autapomorphies of the Ichneumonidae.

Megalyridae

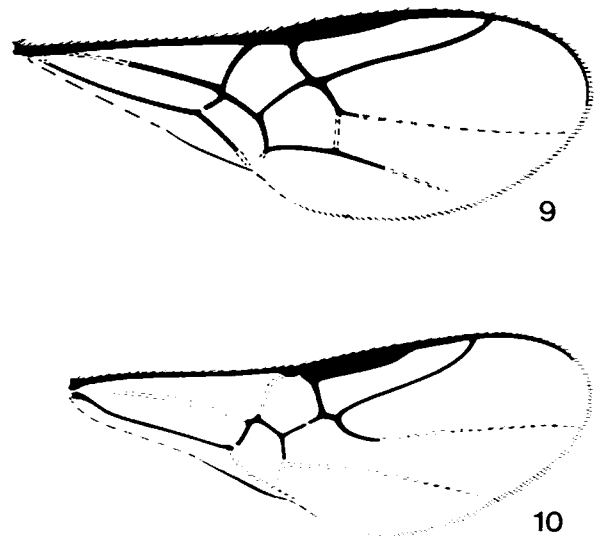
Pagliano and Scaramozzino (1990) include this family in the Ichneumonoidea in their catalog of hymenopteran generic names. This is a rather novel hypothesis which we reject since megalyrids lack the ichneumonoid synapomorphies discussed previously.

Paxylommatinae

This taxon consists of two extant genera, *Hybrizon* Fallén and *Ghilaromma* Tobias. Paxylommatinae has been treated as a subfamily of Braconidae (Shenefelt 1969; Achterberg 1976 a,b), a separate family (Tobias 1968; Marsh 1971, 1979; Mason 1981; Achterberg 1984), and a subfamily of Ichneumonidae (Rasnitsyn 1980; Gauld 1984; Gauld and Bolton, 1988).

Paxylommatinae has been placed in the Braconidae on the basis of the absence of vein 2m-cu in the fore wing. The large number of autapomorphies has led to its recognition as an independent family. Mason (1981) was the first to examine *Hybrizon's* relationship to Ichneumonidae and Braconidae from a phylogenetic perspective. He demonstrated that metasomal terga 2 and 3 are not fused, thus excluding *Hybrizon* from the Braconidae. Further evidence of this is that 2m-cu of the fore wing appears to be part of the paxylommatine ground plan, as demonstrated by the fossil paxylommatine *Tobiasites striatus* from Baltic amber (Fig. 9) (Kasparyan 1988). On the basis of his ideas on hind wing r-m homologies, Mason (1981) suggested that the r-m crossvein of *Hybrizon* is 1r-m and eliminated the genus from membership in the Ichneumonidae. As discussed earlier under the section on Ichneumonidae, we reject this interpretation.

Achterberg (1984) hypothesized Paxylommatinae to be the sister-group of Ichneumonidae, citing as evidence the absence of vein 1-Rs+M in the fore wing, and loss of vein 1r-m in the hind wing. In turn, this assemblage was considered to be the sister-group of Braconidae. We agree that Paxylommatinae and Ichneumonidae are closely related, although we disagree with the interpretation of hind wing venation for reasons



Figs. 9-10. 9, *Tobiasites striatus*, fore wing. 10, *Hybrizon flavocinctum*, fore wing.

presented above. Achterberg gives four autapomorphies supporting the monophyly of Paxylommatinae but only one character for Ichneumonidae exclusive of Paxylommatinae — the presence of an accessory longitudinal tracheal commissure. This may be a good autapomorphy for ichneumonids, although more taxa need to be surveyed. The main criticism of his use of the character is that the larval stages of members of Paxylommatinae have never been described. How can one differentiate between two groups when the critical character for one of them is unknown? Achterberg's argument for the sister-group relationship of Paxylommatinae and Ichneumonidae appears unsupported.

Members of Paxylommatinae (Fig. 10) lack vein 1-Rs+M, as do all ichneumonids. At present, this is the strongest direct evidence placing it in the Ichneumonidae although the reliability of the character is somewhat vitiated by its multiple losses in Braconidae. As mentioned earlier, Rasnitsyn pointed out the similarity of *Hybrizon's* venation to that of *Neorhacodes*. Members of both genera parasitize aculeate Hymenoptera, and they may well be sister-groups.

Stephanidae

The Stephanidae have often been included within Ichneumonoidea (Townes 1969; Carlson 1979). Townes (1969) based the superfamily Ichneumonoidea on: a) distinct vein C of the fore wing, b) veins C and R of the fore wing adjacent or

fused so there is no costal cell between them, c) antenna with more than 14 flagellomeres, and d) adult mandible with two teeth.

We reject these arguments for the following reasons. Vein C is absent in Stephanidae, and even if it were present the presence of vein C is plesiomorphic. Contrary to ichneumonoids, stephanids possess a narrow but distinct costal cell anterad vein R. The polarity of the character state, antenna with more than 14 flagellomeres, is uncertain and quite possibly plesiomorphic. Finally, stephanid adults have only one apical mandibular tooth not two. Within the context of the characters analyzed here, the propodeal teeth and valvilli discussed in section one are absent in stephanids and they possess only one of the ichneumonoid apomorphies discussed earlier, the loss of vein 2r-m of the fore wing. This convergent loss is found in all of the larger apocritan lineages and therefore is not particularly convincing. Thus, there appears to be little evidence to support the placement of the Stephanidae in the Ichneumonoidea.

FOSSIL ICHNEUMONOIDEA

Rasnitsyn (1983) described *Praeichneumon townesi* as a new family (Praeichneumonidae) in Ichneumonoidea; the specimen is from Lower Cretaceous deposits in Mongolia. Placement in the Ichneumonoidea was based on a narrow costal cell of the fore wing, an external ovipositor, and an antenna with more than 13 flagellomeres (Rasnitsyn 1983; Rasnitsyn and Sharkey 1988). Examination of Rasnitsyn's figures (Rasnitsyn, *ibid.*) reveals a distinct costal cell, unlike the condition in other ichneumonoids where the costal cell is narrower than the costal vein. An external ovipositor is a plesiomorphic character state for the Apocrita and of no value for determining relationships at this level of investigation. Numerous flagellomeres might be a ground plan character state for the Apocrita because it is present in several taxa that appear to be basal in the Apocrita based on characters such as venation, e.g., Trigonalidae, Stephanidae. Finally, *Praeichneumon* has vein 2r-m present in the fore wing, a vein that all ichneumonoids have lost (see above discussion). The lack of the critical ichneumonoid synapomorphies listed at the beginning of this essay leads us to remove this species from Ichneumonoidea and consider it *incertae sedis* within the Apocrita.

Several other fossil Hymenoptera are of interest. Townes (1973) described *Tanychora* from the lower Cretaceous of Transbaikalia. He placed it in the Ichneumonidae, stating that the genus could be "ancestral to all of the modern Ichneumonidae, it could represent an extinct phyletic line, or it could be a primitive representative of 1 of the modern subfamilies. There is not sufficient evidence to eliminate any of these 3 possibilities." Rasnitsyn (1980) placed *Tanychora* in its own subfamily (Tanychorinae) in the Ichneumonidae.

Eoichneumon was described from a specimen of the early Cretaceous of Australia (Jell and Duncan 1986) and the family Eoichneumonidae was proposed for the genus. Rasnitsyn and Sharkey (1988) described an additional three genera and 14 species (*Baissobracon* (1 species), *Cretobraconus* (7 species), *Archobraconus* (6 species)) in Eoichneumonidae. These species are from the early Cretaceous of Siberia and Mongolia.

The above fossil genera were defined by combinations of plesiomorphic and apomorphic characters, and hence their status and relationships are uncertain. We have compiled a data matrix using Townes (1973) and Rasnitsyn and Sharkey (1988) as sources of characters. The set of available characters is quite small since few characters are visible in fossil impressions. Ovipositor length and length of 1-Rs of the fore wing were used by Rasnitsyn and Sharkey, but these characters are not employed here because of their variable nature, lack of polarity, and our inability to code the ground plan for the Ichneumonidae and Braconidae.

The characters, polarized using the same outgroups as those used to support the monophyly of the Ichneumonoidea, are as follows; the data matrix is given in Table 1.

1. Fore wing vein 1-Rs+M
 - 0: present
 - 1: absent.
2. Fore wing vein 1cu-a
 - 0: apicad vein 1-M
 - 1: basad vein 1-M.
3. Fore wing vein 2-Rs
 - 0: basal position (basad apex of stigma)
 - 1: apical position (apicad apex of stigma).
4. Fore wing vein 3r-m
 - 0: tubular
 - 1: spectral/absent.
5. Fore wing vein 2m-cu.
 - 0: tubular
 - 1: spectral/absent.
6. Hind wing vein 1r-m.
 - 0: apicad separation of veins Rs and R1

- 1: at or basal to separation of Rs and R1. (The hind wing is missing in *Eoichneumon*.)
7. Notauli of mesoscutum.
0: separated for their entire length
1: converging before scutellum. (The mesoscutal surface cannot be seen in *Baissobracon*.)
8. Surface of propodeum.
0: areolate
1: finely reticulate.
9. Metasomal terga 2-3.
0: articulated
1: fused.
10. Metasomal terga 1-2.
0: without prominent longitudinal striae.
1: with prominent longitudinal striae.

The relationships among Ichneumonidae, Braconidae, *Tanychora*, *Eoichneumon*, *Baissobracon*, *Cretobraconus*, and *Archobraconus* were analyzed using the Hennig86 cladistics program (version 1.5) of Farris (1988). The ie (implicit enumeration) option resulted in four cladograms. One of the cladograms was supported only by an ambiguous optimization and was rejected (Platnick et al. 1991). The remaining cladograms (Fig. 11) had a length of 11 steps, a consistency index of 0.83 (excluding autapomorphies), and a retention index of 0.85. Some characters used in the analysis, especially loss or weakness in veins, may be difficult to determine in fossil specimens due to poor preservation or variable impression. Therefore, some of the conclusions that follow, particularly those concerning the monophyly of the Eoichneumonidae, are rather speculative.

Our conclusions are: 1) The cladograms support the monophyly of the Eoichneumonidae based on the reduction or absence of fore wing crossvein 3r-m. 2) The clade Eoichneumonidae plus Braconidae is supported by the loss or reduction of fore wing crossvein 2m-cu. 3) The inclusion of *Tanychora* in the Ichneumonidae or any other family may not be inferred from the data and therefore we consider it as a plesion in the Ichneumonoidea.

Wiley (1981) discusses the problems of classifying fossil taxa of uncertain placement, using the convention of *incertae sedis* and the plesion concept. Wiley defines the latter (p. 205), modified from the original concept of Patterson and Rosen (1977), as "a name of variable rank accorded a fossil species . . . when classified with one or more Recent species or groups." Wiley goes on to say (p. 219) that "the use of 'plesion' is a conservative means of classifying fossils with Recent taxa . . . no matter how many times the plesion's phylogenetic position may change in relation to its Recent relatives."

Table 1. Data set of extinct and extant ichneumonoid taxa (characters described in the text).

Taxa	Characters									
	1	2	3	4	5	6	7	8	9	10
outgroup	0	0	0	0	0	0	0	0	0	0
Ichneumonidae	1	0	1	0	0	0	0	0	0	0
<i>Tanychora</i>	0	0	0	0	0	0	0	0	0	0
<i>Baissobracon</i>	0	1	0	1	1	0	?	1	0	1
<i>Cretobraconus</i>	0	0	0	1	1	0	1	0	0	0
<i>Eoichneumon</i>	0	0	0	1	1	?	0	0	0	0
<i>Archobraconus</i>	0	0	0	1	1	1	1	0	0	0
Braconidae	0	0	0	0	1	1	0	0	1	0

Thus, applying Wiley's sequencing convention, a classification of extant and fossil taxa that are considered Ichneumonoidea is as follows:

Superfamily Ichneumonoidea *incertae sedis*:

- Plesion *Tanychora*
- Family Ichneumonidae
- Family Braconidae
- Family Eoichneumonidae

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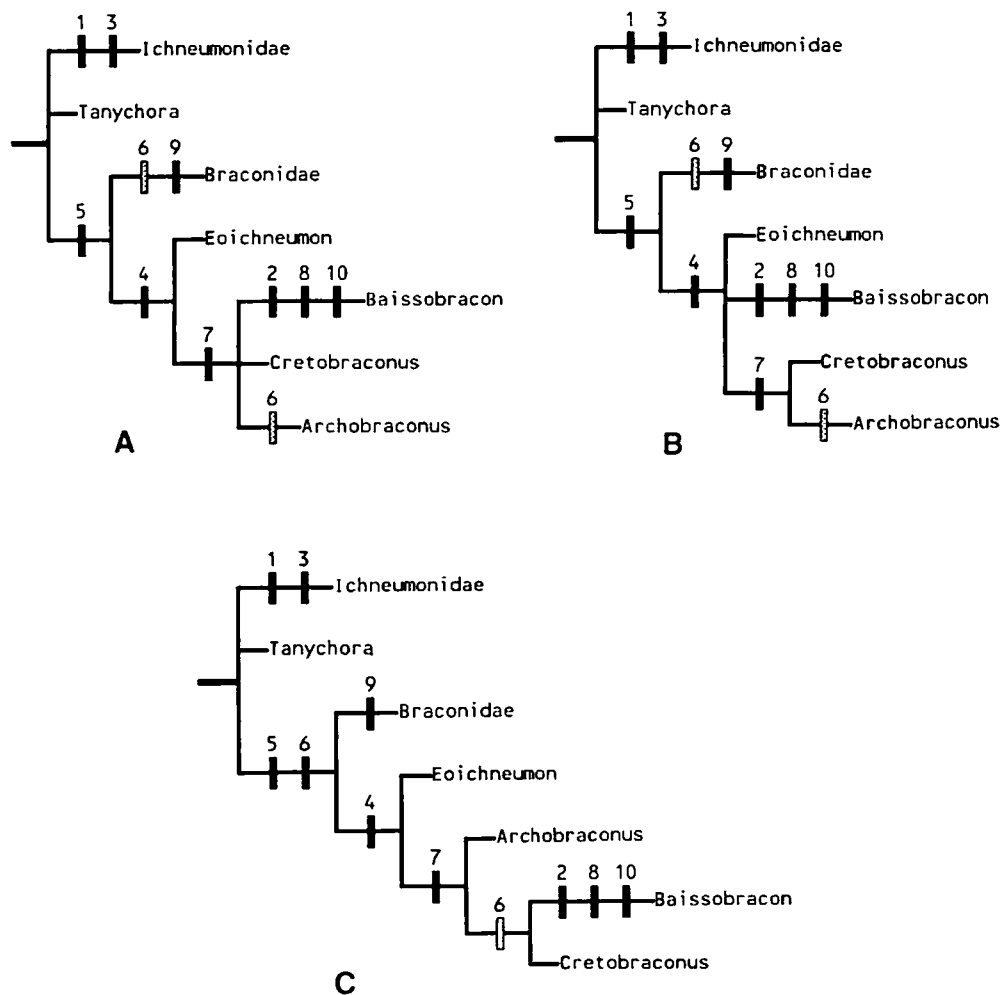


Fig. 11. A-C are the three minimum length cladograms from the data set of extinct and recent ichneumonoid taxa (Table 1), character descriptions are presented in the text. Black bars = apomorphies, grey bars = parallelisms, white bars = reversals

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