The polyphyletic origin of endoparasitism in the cyclostome lineages of Braconidae (Hymenoptera): a reassessment

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A recent phylogenetic analysis of selected groups of cyclostome braconid wasps by Whitfield (1992) was used to investigate the evolution of biological characters associated with the transition from ecto- to endoparasitism. Incorrect methodology in character polarization and incorrect scoring of characters, and a failure to include other available data are shown by reanalysis of a corrected data matrix to compromise Whitfield's conclusion that endoparasitism evolved twice in his selected set of taxa. Greater rigor and the use of additional informative characters are advocated to obtain more robust phylogeny upon which conclusions regarding biological evolution can be more reliably based.

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Introduction

The Braconidae Nees, 1812, are a large family of parasitoid wasps with more than 40,000 species, of which fewer than half are described to date, distributed among some 40 or so subfamilies (Quicke & van Achterberg, 1990). Many species are economically important and the range of biologies they collectively display, including the spectrum from idiobiont ectoparasitoids to highly adapted koinobiont endoparasitoids, make them of considerable interest to evolutionary biologists. In the latter light, a recent paper by Whitfield (1992) joins a flurry of recent interest in the phylogeny of the group (van Achterberg, 1984a, 1988; Belokobyl'skij, 1987; Tobias, 1989; Quicke & van Achterberg, 1990; Wharton et al., 1992; van Achterberg & Quicke, 1992; Wharton, 1993) and significantly, attempts to answer the question of how many times endoparasitism has evolved within a particular lineage (or grade) of subfamilies. In particular, he attempts to investigate the origins and sequence of biological specializations leading to the evolution of endoparasitism in the Rogadinae Foerster, 1862, and in the Opiinae Foerster, 1862 + Alysiinae Stephens, 1829, two groups belonging to the cyclostome group of subfamilies, so-called because of the modified clypeus and labrum that give most members the appearance of having a nearly circular depression above the mandibles.

From parsimony analysis of Whitfield's data matrix comprising 16 taxa and 31 of his 36 characters, Whitfield concludes that endoparasitism evolved twice within his selected group of taxa, once in the line leading to the Rogadini (including *Clinocentrus* Haliday, 1833, and his *Stiropius* group) which attack Lepidoptera, and once in the line giving rise to the Opiinae+Alysiinae, which are parasitoids of Diptera possibly together with the Gnamptodontinae Fischer, 1970, though their biology is at present imperfectly known. Unfortunately, while Whitfield may well be right about this matter, reappraisal of the analysis he presents shows that his methodology and data set do not permit that conclusion.

Whitfield's general point about the polyphyletic origin of endoparasitism in these two groups of cyclostome braconids is in any case an over-simplification, as endoparasitism has also evolved separately within the Braconinae Nees, 1812, (the subtribe Aspidobraconina van Achterberg, 1984; van Achterberg, 1984b; Quicke, 1988) and apparently in the Doryctinae Foerster, 1862 (the genus*Sericobracon* Shaw & Edgerly, 1985; Shaw & Edgerly, 1985) though the subfamilial placement of the latter genus may need revising on further study. There is even the possibility that the Histeromerinae Fahringer, 1930, are endoparasitic though as emphasized by Shaw & Huddleston (1991) this is far from certain and on balance they seem most likely to be ectoparasitic.

Terminology follows van Achterberg (1979) as was used by Quicke & van Achterberg (1990); where this differs from Whitfield's use (e.g. character 23) both terminologies are provided.

Choice of taxa

The decision to represent the Exothecini Foerster, 1862, by inclusion of three separate genera, viz. *Colastes* Haliday, 1833, *Shawiana* van Achterberg, 1983, and *Xenarcha* Foerster, 1862, which differ from one another in only two of Whitfield's characters (6 & 20) and have identical biologies seems to reflect the fact that Shaw (1983) provided biological data for these particular genera. The effect on the analysis, however, is to hide additional variation displayed by other genera of the tribe, for example *Xenosternum* Muesebeck, 1935, which was examined by Whitfield and which has a complete occipital carina (van Achterberg, 1983a). If *Xenosternum* is a less derived exothecine then the implication is that the groundplan state for the tribe is likely to be possession of a complete occipital carina. Similarly, the choice of representing the Rhyssalini by the two genera *Oncophanes* Foerster, 1862 and *Rhyssalus* Haliday, 1833, also appears to originate in Shaw's study, and again this decision hides important variation within the tribe. For example, forewing vein m-cu is antefurcal in *Dolopsidea* Hincks, 1944. Similarly, selection of *Clinocentrus* to represent the Clinocentrini van Achterberg, 1991 (van Achterberg, 1991), misses variation such as the short hind tarsi of *Tebennotoma* Enderlein, 1912. Collectively these choices of taxa for analysis effectively invalidate a large part of the material examined section (table 1 in Whitfield, 1992) since the variation Whitfield must have observed in his studies is excluded from the analysis he presents.

In contrast, Whitfield chooses to combine the Opiinae with the Alysiinae for analysis purposes, despite the fact that the phylogenetic relationships of these in relation to the other endoparasitic cyclostomes is of crucial importance to Whitfield's argument concerning the multiple origin of endoparasitism within the cyclostome lineage. An important consequence of Whitfield's action is that their character states for 14 out of the 36 characters employed are coded as undefined, due largely to polymorphism within this combination. While both the Alysiinae and Opiinae are very large subfamilies in their own right and would if scored separately for characters have shown a fair proportion of polymorphisms, combining them has resulted in a further increase. Recently, Nixon & Davis (1991) have demonstrated that inclusion of polymorphic characters as unknowns can lead to incorrect phylogenies and have thus argued that when possible, partitioning of polymorphic taxa into smaller, monomorphic groups is the solution of choice. Even though Nixon & Davis's paper was published after Whitfield's work, it is surprising that he did not realize that by increasing the number of "unknowns" in his matrix he greatly reduced the chance of finding the correct relationships of the Alysiinae+Opiinae.

Choice of characters

Whitfield introduces several potentially useful new characters into the phylogenetic analysis of the Braconidae for the first time and also apparently provides some new information on previously known characters through his own observations on parasitoid biology and dissections of larval and adult material.

Of the 36 characters presented in Whitfield's data matrix only 31 were used for parsimony analysis (characters 31-35 inclusive being excluded) because he did not wish to bias the results by including characters that are directly related to whether or not the taxa are endoparasitic. Of the remaining 31, five (characters 7, 9, 11, 16 and 22), are completely uninformative. A further two (characters 8 and 24), are only informative about the sister group relationship between *Oncophanes* and *Rhyssalus*, both members of the Rhyssalinae Foerster, 1862, and a further six (characters 17, 25, 26, 27, 28, 29) are, as presented, only informative about the monophyly of, or the relationships within, the Rogadini (i.e. including *Clinocentrus* and his *Stiropius* group) though some of these become more informative if their states in the Opiinae+ Alysiinae are scored rather than being left unknown. As regards the last point, it should be noted that Whitfield states regarding his character 25 that, "I have not attempted to code this character for the diverse subfamilies Opiinae and Alysiinae", despite the fact that for the most part they are uniform for both this character and for larval characters 26, 27 and 28 that are also left unknown by Whitfield. Significantly, Čapek (1970), acknowledged as a source of most larval characters by Whitfield, does provide details of characters 26 and 27 for both Opiinae and Alysiinae and so these could presumably have been coded, unless of course, Whitfield was aware of additional intra-taxon variation that he did not mention. The result of all this is that Whitfield's conclusions about the relationship between the Rogadinae group, the Opiinae+Alysiinae, the Rhyssalinae, the Exothecinae and the seven other taxa included in his analysis are based on only 17 informative characters.

Character polarization and choice of outgroup

Whitfield constructs an hypothetical ancestor based predominantly on characters displayed by four outgroups, the braconid subfamilies Braconinae, Doryctinae and Histeromerinae, and the family Ichneumonidae. While there is little doubt that the Ichneumonidae Latreille, 1802, form the only extant sister group of the Braconidae as a whole (inclusive of the Apozyginae Mason, 1978, which are sometimes afforded separate family level status), Whitfield did not provide any evidence that the Histeromerinae, Doryctinae and Braconinae form an outgroup to the group of taxa his analysis concerns. Indeed, prompted in part by the publication of Quicke & van

Achterberg (1990) Whitfield obviously undertook a reanalysis of his data set including these three braconid subfamilies. Although he does not present the resulting trees, he describes them stating that the "Braconinae appeared as a basal lineage of the clade leading to the Exothecinae+Gnamptodontinae+Opiinae+ Alysiinae clade, while Doryctinae and Histeromerinae were basal to the whole assemblage except Rhyssalini". Thus, he demonstrates that his ingroup is apparently paraphyletic with respect to three of his outgroup taxa even though his character polarization was apparently still based on their use as an outgroup.

Even more surprising, is that Whitfield seems to be almost completely arbitrary in whether his character polarization decisions are based on his stated outgroups or not. Specifically, for his characters 2, 4, 5, 7, 8, 11, 15, 23, 24 and 27, the outgroups are collectively variable though Whitfield still polarizes the characters usually without any argument in favour of doing so. On the other hand, his outgroups are uniform as regards characters 6 and 10 but Whitfield does not polarize these.

Discussion of characters and data set

1. Occipital and hypostomal carinae reaching base of mandible separately (state 0) or meeting before jointly reaching mandibular base (state 1).

This character was not asigned a polarity a priori apparently on the grounds that both states are present in the Ichneumonidae. However, consideration of less derived ichneumonids (e.g. Labeninae, Rhyssinae and Xoridinae) strongly suggest that the plesiomorphous condition is state 1. Whitfield (table 3) codes the Doryctinae as having state 1 though they are in fact polymorphic for this character (Tobias & Potapova, 1982).

2. Occipital carina fully developed dorsally (state 0) or absent dorsally (state 1).

This is a widely used character (Quicke & van Achterberg, 1990; Wharton et al., 1992) but one which is subject to considerable homoplasy within the Braconidae as a whole. Within the group of taxa investigated by Whitfield it indicates a possible relationship between the Exothecini and the Gnamptodontini. However, a few Exothecini (*Xenosternum*) have a complete occipital carina and some Gnamptodontini also occasionally have a weak occipital carina, and if *Liparophleps* Enderlein, 1920, is included within that tribe, then some can have a complete occipital carina (van Achterberg, 1983b). Thus in both tribes the character is strictly speaking polymorphic and therefore ground states for each group should be discovered. It seems likely that in both cases the reductions in the occipital carina may be independent.

3. Malar suture distinct as a fine groove between the eye and mandibular base (state 0), or absent (state 1).

This character is coded as 0 for the *Stiropius* group rather than "?" even though *Polystenidea* Viereck, 1911, lacks the malar suture. This may be because in Whitfield's phylogenetic analysis of the *Stiropius* group, *Polystenidea* appears as one of the two most derived taxa, though Whitfield does not discuss this (Whitfield, 1990). More worrying is that this same character was used in Whitfield's analysis of relationships within the *Stiropius* group with the same polarization and therefore there is a risk that his analyses involve a circular argument. It is therefore suggested that the *Stiropius* group would be better coded as "?".

4. Hypoclypeal depression broad and round or oval, formed dorsally by a concave clypeal margin and a depressed, concave labrum (state 0), or more transverse, with a flatter labrum (state 1).

As recognized by Whitfield, this character could profitably be subdivided. In addition to the problem groups that he mentions (viz. the Hydrangeocolini Whitfield, 1992, and Gnamptodontini), the labrum is usually more or less flat and coriaceous in most Pambolini Marshall, 1885 (personal observation), and in some members of the *Stiropius* group (Wharton et al., 1992).

5. Prepectal carina present at least ventrally (state 0) or completely absent (state 1).

This is a widely employed character in braconid taxonomy though it appears to show considerable homoplasy (Wharton, 1988). In the set of taxa studied by Whitfield, this character appears as a synapomorphy for Exothecini, Gnamptodontini and Opiinae+Alysiinae. However, in the opiine *Ademon* Haliday, 1833, also studied by Whitfield, the prepectal carina is present ventrally and therefore it appears that Whitfield has employed the "common equals primitive" argument here. As *Ademon* shows several other plesiomorphous characters with respect to the remainder of the Opiinae s.s. then it seems best to consider that presence of a ventral part of the prepectal carina is part of the ground plan for the Opiinae. In the case of the Gnamptodontini, the situation is slightly more complicated in that while a prepectal carina is absent in all definite members of the subfamily, one is present in *Liparophleps* which was tentatively included within the Gnamptodontini by van Achterberg (1983b). Therefore, the possibility exists that this group should be coded as polymorphic; however, as the placement of *Liparophleps* is uncertain at present and this genus probably belongs ot the Doryctinae (van Achterberg, pers. comm.), I have not modified table 2 for purposes of reanalysis.

6. Pronope (sensu Achterberg, 1983a) absent (state 0) or present (state 1).

As for character 3 Whitfield states that "... a true pronope is represented in only a few taxonomically restricted groups ..." and his table 3 suggests that state 0 is displayed by all of his outgroups. It is not clear therefore, why he left this character unpolarized. More worrying is that Whitfield scores the Gnamptodontini as possessing a pronope whereas they actually lack one (van Achterberg, 1983b); this is corrected in the modified matrix presented here (table 2).

7. Metapostnotal-propodeal groove narrow, sulcus-like (state 0) or broad, crenulate (state 1).

This is an uninformative character for the group of taxa considered. A deep crenulate groove is also found in the braconid subfamily Apozyginae.

8. Propodeal areola "double", consisting of the area petiolaris and the areola sensu stricto, separated by a carina (state 0), or simple (apparently consisting of the true areola, possibly with a fused and reduced area petiolaris) (state 1), or absent (state 2).

This is a new character in the phylogenetic analysis of the Braconidae and particularly valuable is the distinction between different states of areolation. However, state 0 was treated as ancestral, citing for outgroup purposes, some Doryctinae and Ichneumonidae. Table 3 in Whitfield nevertheless shows that the Braconinae and Histeromerinae are not areolated (state 2) and the same is true for many Doryctinae. Thus while Whitfield's polarization may well be correct, his outgroup argument is at best flawed.

9. Propleural flange (see, e.g. van Achterberg, 1976) present and well developed (state 0) or essentially absent (state 1).

Whitfield leaves this character as unpolarized on the basis that it is variable among his outgroups, being absent in Braconinae and Histeromerinae, and variable in the Ichneumonidae. As he showed that the Braconinae and Histeromerinae may be ingroups the situation in the Ichneumonidae becomes critical for determining the polarization of this and other characters. Within the Ichneumonidae, a propleural flange is present in many members of the Xoridinae, Labeninae, Pimplinae and other putatively basal groups, and therefore it seems reasonable to conclude that its presence is part of the ground plan for the family.

10. Transverse sulcus of pronotum complete and well developed (usually crenulate) (state 0) or absent (state 1).

I have to admit that I am not entirely sure what Whitfield means by this character, whether a groove medio-anteriorly (in the same position as the pronope) or around the sides. However, from Whitfield's citation of van Achterberg (1983a) it may be the former. If that is so, then it is strange that Whitfield scores all three exothecine genera the same (i.e. state 0) when van Achterberg used absence of a crenulate transverse groove as a key character for *Shawiana* and *Xenarcha*. If Whitfield means the more lateral groove, then even greater variation is present (see van Achterberg, 1983a). As the presence of a medio-anterior crenulate pronotal groove is excluded by the presence of a true pronope (see character 6) its value is questionable. Because of the uncertainty in Whitfield's meaning, I have not modified table 2 for the purpose of reanalysis.

11. Dorsope (sensu van Achterberg, 1974) distinct, well delineated by dorsal carinae (state 0) or obsolescent (in this case the dorsal surface of tergum 1 is relatively flattened) (state 1).

Whitfield states that "state 0 is clearly ancestral" but from his table 3 it is clear that both states 0 and 1 occur in his outgroups. No justification is given for his selection of state 0 as plesiomorphous.

12. Ovipositor sheaths long, at least a third length of metastoma (state 0) or very short, usually shorter than basitarsus (state 1).

While I believe Whitfield's polarization to be correct, he does not specify which basal lineages of Ichneumonidae are referred to for his outgroup analysis of this character; the list he provides as putative basal taxa (table 2, loc. cit.) includes the Ichneumoninae which have short ovipositors making it appear that he used a "common equals primitive" argument rather than rigorously deriving a groundplan. Reference could have been made to Gauld (1988) who discussed at length the evolutionary significance of concealed hosts for ichneumonoid evolution. Whitfield codes the Gnamptodontini as "?" for this character though the great majority of species have a very short ovipositor indeed.

13. Dorsal carine (sensu van Achterberg, 1974) long, remaining well separated posteriorly (state 0) or converging to meet or nearly so (state 1).

This character was scored as 0 for the Histeromerinae in Whitfield's table 3 though in this subfamily the dorsal carinae are absent (van Achterberg, 1992).

14. Reservoir of venom apparatus entire (state 0) or subdivided (state 1).

This useful character is based on the results of Edson & Vinson (1979) which Whitfield states as being supplemented by some of his own original dissections though he does not specify what genera he himself examined. Comparison of his data matrix with Edson & Vinson's results suggests that Whitfield must have examined Gnamptodontini, Hormiini (as Edson & Vinson noted that their preparation was poor and consequently did not score all characters), *Shawiana* and *Xenarcha* (as the generic placement of Edson & Vinson's *Phanomeris* spec. is questionable). However, *Rhysipolis* Foerster, 1862, is scored as 0 (i.e. undivided) by Whitfield whereas Edson & Vinson score it as divided into two or more parts, and Whitfield scores Gnamptodontini as having a divided reservoir whereas Quicke & van Achterberg illustrate the venom apparatus of *Gnamptodon* as undivided. Whitfield does not comment on these conflicting data. Recent studies by Quicke et al. (1992) support Whitfield's finding for *Rhysipolis* in that the reservoir is undivided though the primary venom duct is strongly swollen in this genus. However, the same is not true for Whitfield's scoring of Gnamptodontini and Hormiini. In order to help resolve this, I have dissected a specimen of another species of *Gnamptodon* Haliday, 1833, (viz. *G. decorus* Foerster, 1862) and have again found the reservoir to be undivided as in the undescribed Australian species illustrated by Quicke & van Achterberg. Therefore it seems best to score the reservoir in *Gnamptodontini* as undivided. Similarly, recent studies by Quicke et al. (1992), based on several genera including *Hormius* Nees, 1818, and *Parahormius* Nixon, 1940, show that the reservoir in these Hormiini is undivided and consequently this change has been made for the modified data matrix presented below (table 2).

Whitfield did not polarize this character presumably because in his table of outgroup character states the Ichneumonidae are coded as being variable. This together with his scoring for the Doryctinae as state 0 appears to be in error. Firstly, Edson & Vinson (1979) clearly score all of the Doryctinae they examined as having subdivided venom reservoirs. Secondly, as far as is known, the reservoir is not subdivided in any Ichneumonidae (e.g. Togashi, 1963; Robertson, 1968). As Whitfield's own analysis showed his 'outgroups', Doryctinae and Braconinae, as likely to be ingroups, it is proposed that this character should be polarized on the basis of its condition within the Ichneumonidae.

15. Spiracles of metasoma tergum 2 placed laterally on epipleuron (state 0) or near lateral edge of dorsal face of tergum.

As stated by Whitfield, the character state distribution among the four 'outgroup' taxa he employed is equivocal, but nevertheless he argues that state 0 is plesiomorphous (and uses this polarity in his analysis) on the grounds that it is displayed by the Rhyssalini and Hydrangeocolini (ingroups!) and by the 'helconoid' and 'microgastroid' complexes, two groups whose relationship with the taxa under investigation have not been proven and were not discussed. Whitfield notes that this polarity is not the same as used by Quicke & van Achterberg and then continues that if the alternative polarity were accepted then the "... only effect ... will be to provide a synapomorphy for Rhyssalini & Hydrangeocolini". This statement ignores the possibility that a change in polarization might also change the point at which the outgroup "Ancestor" taxon attaches to the cladogram.

Whitfield scores this character as state 1 for the Opiinae + Alysiinae but it is variable in both subfamilies (Quicke & van Achterberg, 1990). Although Whitfield's coding may be correct if *Ademon* is taken as a basal member of the Opiinae (Wharton, 1988) and the Alysiinae are considered to be derived from the Opiinae, Whitfield provides no justification for his decision. If the relationships of the Opiinae and Alysiinae are not to be pre-judged, it would probably be better to code this character as variable.

16. Anterior portion of second metasomal tergite unmodified (state 0) or raised into a roughly semicircular transverse region (state 1).

As presented by Whitfield this character is uninformative, the apomorphous state only being displayed by the Gnamptodontini.

17. First [sic] metasomal tergite without longitudinal medial carina (state 0) or with one (state 1).

From the order the characters are presented in, the fact that an otherwise similar character is employed in character 13 and the accompanying discussion it appears that this should read as the *second metasomal tergite*. While Whitfield is almost certainly correct in his assessment of the polarity of this character, he states that "Occasional species of Hormiini and Lysitermini Tobias, 1968, appear to have a medial carina, but ... this appears to be non-homologous with that in the Rogadini". Consequently, he did not code these two as having the character (or more correctly as being polymorphic for it) but unfortunately, Whitfield did not explain why these were apparently non-homologous and my examination of many hundreds of specimens in all groups has failed to show me why the carinae of rogadines and some lysitermines are not homologous, indeed in some they appear virtually identical and likewise very similar to those of many Betylobraconinae Tobias, 1979.

18. Epipleura of metasomal terga 2 and 3 not clearly set off by sharp fold (state 0) or sharply set off by fold.

This is a new character in cyclostome systematics but from Whitfield's data matrix its value appears limited because both states 0 and 1 are displayed by groups of taxa unlikely to form monophyletic units. However, even if fairly homoplaseous it may still carry some useful phylogenetic information.

19. True Hagen's glands opening on ninth metasomal tergum of male absent (state 0) or present (state 1).

Whitfield states that data for this character are from Buckingham & Sharkey (1988) though he provides data for all of the taxa in his data matrix. Of the taxa included in Whitfield's study, Buckingham and Sharkey only provided data on Alysiinae, Braconinae, *Oncophanes*, *Rhysipolis*, Gnamptodontini, Opiinae and Rogadini sensu stricto (i.e. *Aleiodes* Wesmael, 1838). Unless Whitfield omitted to say that he had prepared additional material (something he did for characters 14 and 25) then it appears that even if his codings proved to be correct some at least have been included by mistake. In any case, if Whitfield's data do come from original dissections then it would be important to know which genera of for example, Hormiini, Hydrangeocolini, Lysitermini, Pambolini, Rhyssalini, and the *Stiropius* group he prepared.

20. Origin of r on distal half of stigma, near middle (state 0) or in proximal 0.4 of stigma (state 1).

As with character 3 this character is coded as 0 for the *Stiropius* group rather than "?" even though in *Choreborogas* Whitfield, 1990, displays state 1 (Whitfield, 1990). It appears that Whitfield is assuming that in this genus the position of vein r (which is said to result from a distal elongation of the pterostigma as in Hydrangeocolini) is not a basal character within the *Stiropius* group. While this may well be true, Whitfield does not discuss this and again there is an element of circularity in his argument since in his 1990 paper he polarized the character by reference to his assumed outgroups Rogadini and Rhysipolini.

21. Hindwing M+Cu subequal in length with or longer than 1-M (state 0) or clearly shorter than 1-M (state 1).

Whitfield correctly notes that this is a highly variable character within some groups (viz. Hormiini, Rogadinae, Alysiinae and Opiinae) but he also codes it as "?" for *Clinocentrus* and Lysitermini which display state 0. This character is not polarized either here or by Whitfield though an argument could be made for regarding state 0 as plesiomorphic.

22. Stigma of normal proportions, or up to 5 times as long as broad (state 0) or reduced in width and elongated to a slightly thickened vein along costal margin (state 1).

This character although not rigorously defined is nevertheless fairly easy to code. However, only in the case of the Hydrangeocolini does any group display this character consistently. It is therefore uninformative for the purpose of Whitfield's analysis.

23. Forewing vein m-cu postfurcal - meeting M distal to 1Rs junction (state 0), or antefurcal - meeting M proximal to 1Rs junction (state 1). [N.B. Exact venational homologies between Ichneumonidae and Braconidae concerning the 2nd submarginal cell/areolet are equivocal, but do not affect the discussion presented below; the veins that Whitfield refers to as 1Rs and M are referred to by Quicke & van Achterberg, 1990 as 2-SR and 2-M respectively.]

Although I fully agree with Whitfield's polarization of this character (see Quicke & van Achterberg, 1990 versus Wharton et al., 1992), Whitfield clearly misunderstood Quicke & van Achterberg (1990) and makes no sense regarding this character and the Ichneumonidae. Firstly he suggests that his character is expressed by Quicke & van Achterberg as a ratio of vein lengths (citing character 34 loc. cit.) but nothing could be further from the truth as Quicke & van Achterberg's character 34 (a vein length ratio) has nothing to do with the position of vein m-cu (equivalent to vein 1m-cu in the Ichneumonidae). Rather, the equivalent character in Quicke & van Achterberg is number 30 (loc. cit.) and is expressed in terms of whether vein 2-SR+M (=2-Rs+M in Whitfield's terminology) appears transverse or longitudinal.

Secondly, Whitfield suggests that vein 1m-cu is postfurcal in the Ichneumonidae, implying that in this family, 1m-cu must meet M distal to its junction with 1Rs. Two alternative interpretations of venation in the ichneumonid forewing lead to different conclusions about the character state displayed by 1m-cu. If the areolet (second submarginal cell) of ichneumonids is interpreted as being closed basally by vein 2-SR (= 1Rs) as is believed to be the case in the Braconidae, and as is implied by Whitfield's venation terminology, then the following argument refutes Whitfield's conclusion that m-cu is postfurcal in the Ichneumonidae. Thus, as vein 1-SR+M is generally absent in ichneumonids it is seldom possible to know for certain whether that vein would join 1m-cu directly (giving an antefurcal state) or join 2-SR (giving the postfurcal state). However, in many ichneumonid genera (e.g. *Exyston*Schiødte, 1839, *Monoblastus* Hartig, 1837, *Protarchus* Foerster, 1868, and *Xylophrurus* Foerster, 1868) what appears to be a stub of vein 1-SR+M (= Rs+M) the so-called ramulus, is present on the combined 1m-cu (+) 2-SR+M. That this is likely to be a remnant of 1-

SR+M is indicated by the not uncommon occurrence of teratological specimens in which a complete vein is present from 1m-cu to the parastigma (M.G. Fitton, pers. comm.). Given that the position of the ramulus in the Ichneumonidae indicates that 1-SR+M would originate directly from the anterior end of 1m-cu and not on 2-SR, this model implies that in the Ichneumonidae, vein 1m-cu is actually antefurcal (i.e. Whitfield's state 1).

If, however, the venation of the Ichneumonidae were interpreted as having the proximal side of the areolet formed by vein 2r-m (= 2rs-m) instead of 2-SR (Rs) (i.e. if vein 2-SR is assumed to have been lost in the Ichneumonidae) then consideration would have to be given to the course that this vein would have taken in the ancestors to the Ichneumonidae. Reference to potential outgroups possessing more complete venations (i.e. groups with 2-SR (= 1Rs) and both transverse r-m (= rs-m) veins present), such as the less derived Aculeata, or the Trigonalyidae Cresson, 1867, Orussidae Newman, 1834, and Xiphidriidae Leach, 1815, is equivocal but most groups indicate that 2-SR would have joined the ramulus. This interpretation therefore better supports Whitfield's and Quicke & van Achterberg's polarity decisions.

24. Hind tarsi subequal in length to the hind tibiae (state 0) or clearly shorter (state 1).

This is a new and potentially useful character but it is not rigorously defined and perhaps as a consequence I do not agree with some of Whitfield's assessments of character states. Certainly from my measurements and others kindly supplied to me by van Achterberg (Leiden), the ratio of tibial to tarsal length is continuously variable and so any division of this into two states must be arbitrary. As presented in Whitfield's table 3, only the Rhyssalini have the apomorphous state, and while Whitfield also mentions that shorter hind tarsi do occur in some other groups he simply states that they then appear to be autapomorphies of particular genera, without providing any further evidence that this is the case. Whitfield does not mention the genus *Yelicones* Cameron, 1887 (a basal member of the Rogadinae s.s.), the Betylobraconinae, nor the Apozyginae all of which have very short hind tarsi. Further, our measurements of the ratio of hind tarsal to hind tibial length indicate that several other groups included in Whitfield's data set ought to be coded differently. Most members of the Rhyssalini (genera examined by Whitfield) have values ranging from 0.75 to 0.88 (though two genera not mentioned by Whitfield, *Pseudavga* Tobias, 1964, and *Noserus* Foerster, 1862, can have larger values up to 1.05 and 0.9 respectively). Taking 0.89 as an upper cut-off value that defines *Rhyssalus* and *Oncophanes* as having state 1, then *Cantharoctonus* Viereck, 1912, with values ranging from 0.86 to 0.93 should be scored as "?", similarly Lysitermini with values from 0.78 to 0.94 should be scored as "?", the Pambolinae ranging from approximately 1.0 in *Pambolus* Haliday, 1836, to approximately 0.83 in *Notiopambolus* van Achterberg & Quicke, 1990, and 0.63 in *Chremylus* Haliday, 1833, should be coded as "?", and Hydrangeocolini with values from 0.86 to 0.89 ought to be scored as 1.

25. Larval epistomal arch essentially complete (state 0) or incomplete to completely reduced (state 1).

Whitfield states that much data from Čapek (1970) is supplemented by several new dissections but he does not specify of what. Compairing his table 3 with Čapek it would appear that data presented for *Cantharoctonus, Rhysipolis* and *Xenarcha* may be new, and the same would seem likely to be true for characters 26 and 27 also. Since Whitfield derived most of his data from Čapek's survey, it is surprizing that he does not code characters 25 to 28 for Lysitermini since Čapek states that he examined a larval exuvium from *Aulosaphes* Muesebeck, 1935, a genus that Whitfield includes in his concept of the Lysitermini. Whitfield states that he has not attempted to code this character for the Opiinae+Alysiinae though from Čapek it appears that in all Opiinae he examined, the epistomal arch is incomplete, while in the Alysiinae it is incomplete except in *Aspilota* Foerster, 1862, and *Synaldis* Foerster, 1862 (= *Dinotrema* Foerster, 1862). Separate coding for these two subfamilies might therefore have provided extra information.

26. Larval mandibles robust and toothed (state 0) or slender and toothless (state 1).

This is in fact two separate characters rather than one since Čapek's survey shows that many braconids have slender and toothed mandibles (Čapek, 1970; Quicke & van Achterberg, 1990). Surprisingly, Whitfield did not code this character for the Opiinae+Alysiinae though according to Čapek, none of these have toothed mandibles; perhaps this omission is because in these subfamilies, the mandible while being toothless can also be robust. Failure to code this character for Opiinae+ Alysiinae in fact reduces the chance of these linking to the Rogadinae complex in Whitfield's analysis. Therefore in my reanalysis, this character is redefined so to just include the toothed versus toothless component. Apart from enabling the Opiinae+ Alysiinae to be scored this decision does not affect any of Whitfield's other scorings. Whilst robustness does vary greatly in the Braconidae as a whole (Quicke & van Achterberg, 1990) Whitfield does not rigorously define it here. Further, variation in this aspect within the group of taxa investigated here is comparatively small. As for character 25, Čapek provides enough detail to permit scoring for the Lysitermini and accordingly this has been entered into the revised data matrix (table 2).

27. Larval antennae long and prominent, papilliform (state 0) or flat and reduced (state 1).

This character seems generally well correlated with the ecto- versus endoparasitic way of life though that does not make it an inappropriate character for analysis. Whitfield however, codes the Opiinae+Alysiinae as having state 0 whereas from Čapek (1970) it appears that the antennae are extremely reduced in these and are not papilliform even in *Ademon*, arguably the least derived member of the opiine lineage (Wharton, 1988). As Whitfield does not provide any explanation about this anomaly, it seems likely to be a mistake in his matrix and one which would effectively reduce the likelihood of the Opiinae+Alysiinae appearing next to the Rogadinae in his analysis.

28. Larval skin spiny (state 0) or smooth (state 1).

This character while new for braconid systematics is not clearly defined and character states are not illustrated nor illustrations referred to. Larval skins of virtually all braconids are at least minutely spiculate and thus spiny most probably refers to a relative condition of having fewer and larger spicules as opposed to more and smaller. Within some subfamilies the condition is variable between instars (O'Donnell, 1987 - re Aphidiinae; M. Shaw, pers. comm. - re Rogadinae).

29. Host stage attacked either late instar (state 0) or early instar (state 1).

This is a new character for phylogenetic analysis of the Braconidae. As stated by Whitfield, outgroup analysis based on Doryctinae, Braconinae and Ichneumonidae clearly suggests that state 0 is plesiomorphous for the taxa investigated. It is not clear therefore why Whitfield did not polarize this character.

30. After the host is stung, but before the parasitoid egg is laid, the female either leaves (state 0) or remains with host (state 1).

This character appears to be based largely or entirely on the observations of Shaw (1983) since data are presented only for taxa whose stinging and oviposition behaviour was described by Shaw. However, I am uncertain as to exactly what aspect of the parasitoid's biology Whitfield was referring. The character as used by Whitfield seems to be the same as states 0 and 1+2 of character 32, i.e. it appears to refer to whether or not the parasitoid's egg is laid away from the host or on (or in) the host. If this is so then the inclusion of this character in the parsimony analysis presupposes that there is no correlation between where the egg is laid and endoparasitism. While it is true that this character varies among ectoparasitoids, eg. Exothecini vs *Oncophanes* and *Rhysipolis*, and may therefore be informative about their relationships, it seems inevitable that endoparasitoids will show state 1. If Whitfield is not simply referring to movement of the wasp just to enable it to deposit its egg away from the host in the latter's retreat, then the scoring for *Oncophanes* seems strange since Shaw (1983) reports that in *O. laevigatus* (Ratzeburg, 1852), the host is stung through the leaf but then the parasitoid walks around the edge of the leaf roll before entering it in order to host feed and ultimately oviposit on the host. Thus in the case of *Oncophanes*, the wasp does leave the host, albeit to return. It would probably have been more meaningful to have left the endoparasitoid taxa uncoded thus avoiding bias due to correlation with endoparasitism.

36. Larvae (of parasitoid) essentially always solitary (state 0) or often or always gregarious (state 1).

This character as defined effectively applies the common equals primitive argument to decide which state is primitive for which taxon. As this particular biological character was used in the formation of Whitfield's cladogram it would have been far better to try to determine which state was primitive for each taxon. Whitfield did not attempt to polarize this character and did not include it in his outgroup character state table.

Characters 31 to 35 (inclusive) were not included in Whitfield's parsimony analysis but were fitted to his most parsimonious tree afterwards.

31. Egg placement either loose in host mine, shelter or other retreat, rather than directly on or in host (state 0), or directly on host (state 1), or inserted into host (state 2).

32. Venom paralysis allowing only partial or no recovery or host activity (state 0) or full recovery at least of ability to locomote and feed (state 1).

33. Host condition at the time of feeding of the parasitoid larva either dead or moribund (state 0), or active and capable of spinning cocoon but not of pupating (state 1) or active and capable of developing beyond the stage attacked but not capable of spinning cocoon (state 2) or active and capable of developing further and pupating (state 3).

34. Larva (of parasitoid) feeds from an external position on host (state 0) or internally, within the host, at least for most of its development (state 1).

35. Cocoon formation away from the host remains (state 0) or closely associated with the host remains (state 1) or within mummified host larva or prepupa (state 2) or pupation (primarily without cocoon spinning) within host puparium (state 3).

Reanalysis

The data matrix published by Whitfield (table 1 here) was reanalysed, in accordance with his stated methodology, using the branch-and-bound algorithm PAUP version 3.0 (Swofford, 1991) followed by construction of strict and semi-strict consensus trees. The results obtained (75 trees of length 42) were identical with those of Whitfield (fig. 1) thus confirming that the matrix employed was the same as the one he used.

A second data matrix constructed on the basis of the arguments presented above is presented in table 2. In this, those character states that have been recoded are indicated in bold. Specifically this means that characters 1, 6, 9, 14 and 29 were polarized, the polarization of character 15 was reversed, character 27 is redefined to just include the toothed versus toothless component and it is scored for the Opiinae+Alysiinae, character 3 coded as variable (i.e. "?") for *Stiropius* group, character 6 is scored as 0 for the Gnamptodontini, character 14 coded as 0 for Gnamptodontini and Hormiini, character 15 is coded as variable for the Opiinae+ Alysiinae, character 17 is coded as variable for the Hormiini and Lysitermini, character 24 is coded as variable for *Cantharoctonus*, the Pambolini and the Lysitermini and as 1 for the Hydrangeocolini, character 25 is coded as 0 for the Lysitermini, characters 26 and 27 are both scored as 0 for the Lysitermini and 1 for the Opiinae+Alysiinae, and character 28 is scored as 0 for the Opiinae+Alysiinae. This matrix (excluding characters 31-35 inclusive) was analysed using the branch-and-bound algorithm as described above.

The reanalysis of table 2 yielded 216 trees of length 45 and consistency index 0.71, the strict and semistrict consensus trees of which (fig. 2), although broadly

Table 1. Data matrix used by Whitfield (1992).

Ancestor	?0?00?00??	000?000?00	?0000000??	??????
Rhyssalus	1010000000	000?000000	000100000?	?00001
Xenarcha	0100110100	0011100100	1010000000	000000
Shawiana	0100110100	0011100101	1010000000	000000
Colastes	0100100100	0011100101	1010000000	000000
Oncophanes	1010000000	000?000100	0001000001	100001
Rhysipolis	0000000100	001010?100	1010000001	111010
Cantharoctonus	1000001101	011?10?100	101000000?	??1010
Hormiini	0000000100	0?01100100	?000000?0?	?00001
Pambolini	1010000100	000?100000	00?000000?	000001
Clinocentrus	1000000100	0010101100	?010111101	211120
Rogadini	?000000200	0110101100	?010111111	212120
Gnamptodontini	?111110?11	1?11110110	1010000???	?11?10
Stiropius group	0000000100	011?101100	101011111?	211120
Hydrangeocolini	0000000?00	0?0?000001	0100??????	???0??
Lysitermini	00?0000100	0?0?100100	?000????0?	?00001
Opiinae+Alysiinae	0?011?010?	001?10001?	???0??0???	21313?

Table 2. Data matrix of Whitfield (1992) modified for reasons described in the text. Changed character states compared with Whitfield's original matrix (see table 1) are indicated in bold type.

Ancestor	10?00**0**00**0**?	000**01**00?00	?0000000**0**?	??????
Rhyssalus	1010000000	000?000000	000100000?	?00001
Xenarcha	0100110100	0011100100	1010000000	000000
Shawiana	0100110100	0011100101	1010000000	000000
Colastes	0100100100	0011100101	1010000000	000000
Oncophanes	1010000000	000?000100	0001000001	100001
Rhysipolis	0000000100	001010?100	1010000001	111010
Cantharoctonus	1000001101	011?10?100	101**?**00000?	??1010
Hormiini	0000000100	0?0**0**10**?**100	?000000?0?	?00001
Pambolini	1010000100	000?100000	00?**?**00000?	000001
Clinocentrus	1000000100	0010101100	?010111101	211120
Rogadini	?000000200	0110101100	?010111111	212120
Gnamptodontini	?1111**0**0?11	1?1**0**110110	1010000???	?11?10
Stiropius group	00**?**0000100	011?101100	101011111?	211120
Hydrangeocolini	0000000?00	0?0?000001	010**1**??????	???0??
Lysitermini	00?0000100	0?0?10**?**100	?00**?000**?0?	?00001
Opiinae+Alysiinae	0?011?010?	001?**?**0001?	???0?**110**??	21313?

similar to those obtained by Whitfield, also differ in several respects from the results of his analyses. In particular, the Exothecini appear as an unresolved monophyletic group rather than as a potentially paraphyletic one and the two genera of Rhyssalini (*Rhyssalus* and *Oncophanes*) are unresolved with respect to the Pambolini and Hydrangeocolini. Unfortunately, the character set employed still does not permit basal resolution of the clade comprising *Rhysipolis*, *Cantharoctonus*, Rogadinae sensu stricto, Exothecini, Gnamptodontini and Opiinae+Alysiinae.

In an attempt to improve on the resolution of this set of cladograms, table 2 was further analyzed using the iterative weighting procedure of Carpenter (1988) with the rescaled consistency index used as the weighting function (Farris, 1989). The results, which are shown in fig. 3, include increased resolution of the basal grade with Rhyssalini+Hydrangeocolini appearing as a monophyletic clade and it also shows the relationships within the Exothecini as resolved. However, the major area of interest from the point of view of the evolution of endoparasitism, the relationships of the Rogadinae, Exothecinae, *Rhysipolis*, *Cantharoctonus*, Gnamptodontini and Opiinae +Alysiinae remain unresolved.

Interpretation and conclusions

Having obtained the consensus cladogram (fig. 1) Whitfield used the programme MACCLADE (Maddison & Maddison, 1987) to optimize character state changes for biological characters to the tree topology. This potentially powerful method, however, is compromised by the lack of resolution in the critical part of Whitfield's cladogram. In his discussion on the use of MACCLADE, Whitfield states that "Some minor alterations in the results were made to account for multifurcations in the consensus trees" but unfortunately he does not state precisely what these assumptions actually

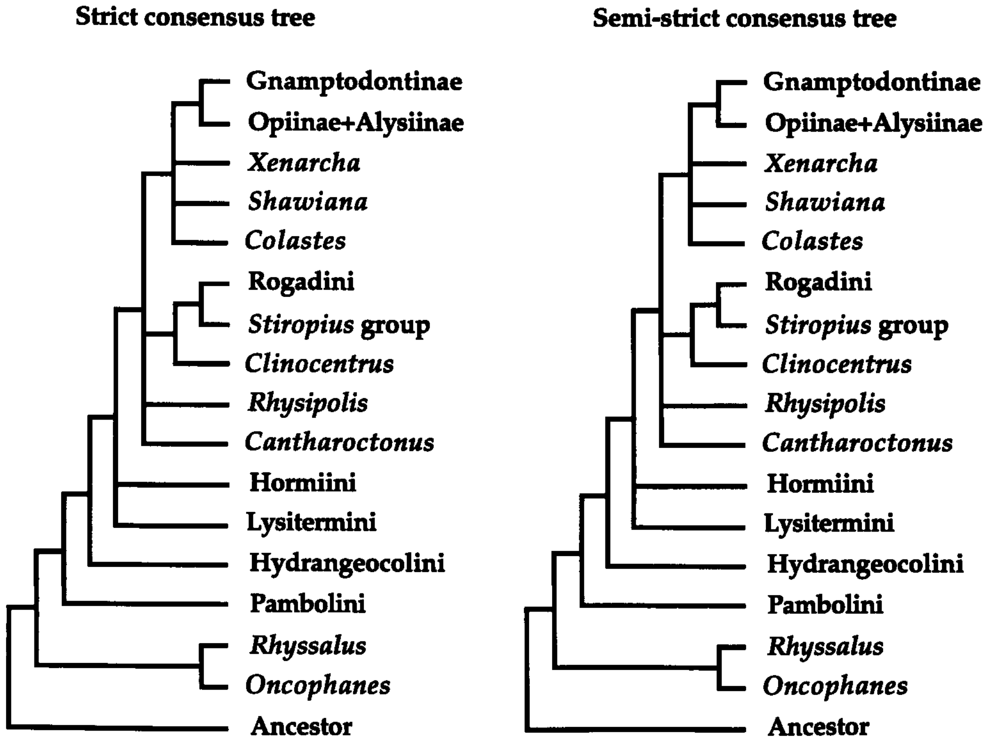
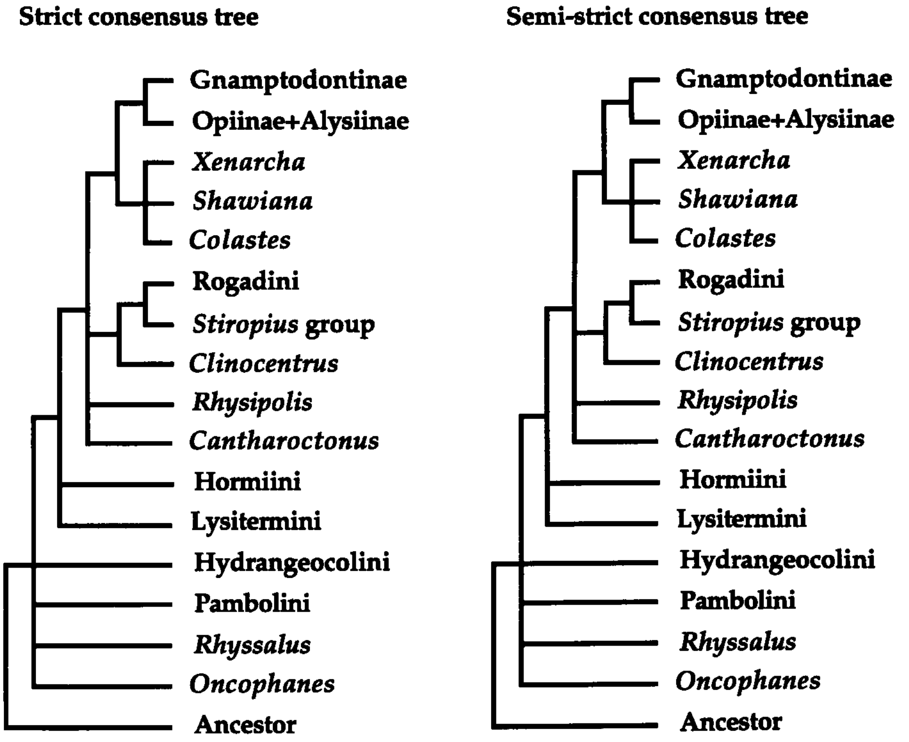


Fig. 1. Strict (and semi-strict) consensus tree from 75 maximally parsimonious trees obtained by analysis of data matrix given in table 1. Data and results identical with those of Whitfield.

were, and therefore the following discussion is necessarily conservative. The problem is that the unresolved relationships (fig. 1) between the (Exothecini+Gnamptodontini+Opiinae+Alysiinae), the Rogadini sensu stricto (i.e. including *Clinocentrus* and the *Stiropius* group) and *Rhysipolis* and *Cantharoctonus* leave open the possibility that the Rogadini sensu stricto are a sister group of the Exothecini+ Gnamptodontini +Opiinae+Alysiinae. If that were the case, then whether or not endoparasitism seems more likely to have evolved twice (i.e. on separate occasions leading to the Rogadini sensu stricto and to the Opiinae+Alysiinae) rather than just once depends critically on the biology of the Gnamptodontini. If the latter are ectoparasitoids, then it would be reasonable to assume separate origins of endoparasitism since, for example, the presence of true Hagen's glands (character 19) in Gnamptodontini and in many Opiinae and Alysiinae seems to provide strong evidence of monophyly of this group of subfamilies. However, if the Gnamptodontini are in fact endoparasitoids, then there would be no a priori reason on the basis of the data presented by Whitfield to prefer a dual origin of endoparasitism over a single origin combined with a reversal at the base of the Exothecini lineage. It may also be worth noting that Buckingham & Sharkey (1988) found male metasomal glands rather similar to the Hagen's glands of the Opiinae group in *Rhysipolis*, and if these are indeed homologous then further interpretation of relationships might be necessary.


Strict consensus tree

Semi-strict consensus tree

Fig. 2. Strict (and semi-strict) consensus tree from 216 maximally parsimonious trees obtained by analysis of modified data matrix given in table 2.

Whitfield did explicitly consider the possibility that the Opiinae+Alysiinae + Gnamptodontini could be the sister group of the Rogadini but he discounted this because all trees with these as a monophyletic clade were at least 4 steps longer than his most parsimionious trees. However, from his consensus cladogram, this possibility would seem unikely because the Opiinae+Alysiinae+Gnamptodontini appear in a monophyletic clade together with the three genera of Exothecini, and could thus either be the sister group of the Exothecini (i.e. Exothecini monophyletic) or derived from within it (i.e. Exothecini paraphyletic). Thus it would have been more sensible (on the basis of his data) to consider a possible sister group relationship between the Rogadini and the Opiinae+Alysiinae+Gnamptodontini+ Exothecini, even though this could leave open the possibility of a single origin of endoparasitism coupled with a reversal.

It is not my intention here to suggest that the cladograms presented in fig. 2 or fig. 3 are better hypotheses of the ancestry of the present set of cyclostome braconid taxa than Whitfield's (fig. 1). Nor is it my intention to suggest that Whitfield's conclusions regarding two origins of endoparasitism are incorrect. It is, however, my intention to indicate that the relationships among the cyclostome taxa are still equivocal, and that (i) before confident statements concerning the origins of endoparasitism can be made, more resolved and secure estimates of phylogeny need to be obtained, and (ii) that in order to achieve this resolution, it will undoubtedly be

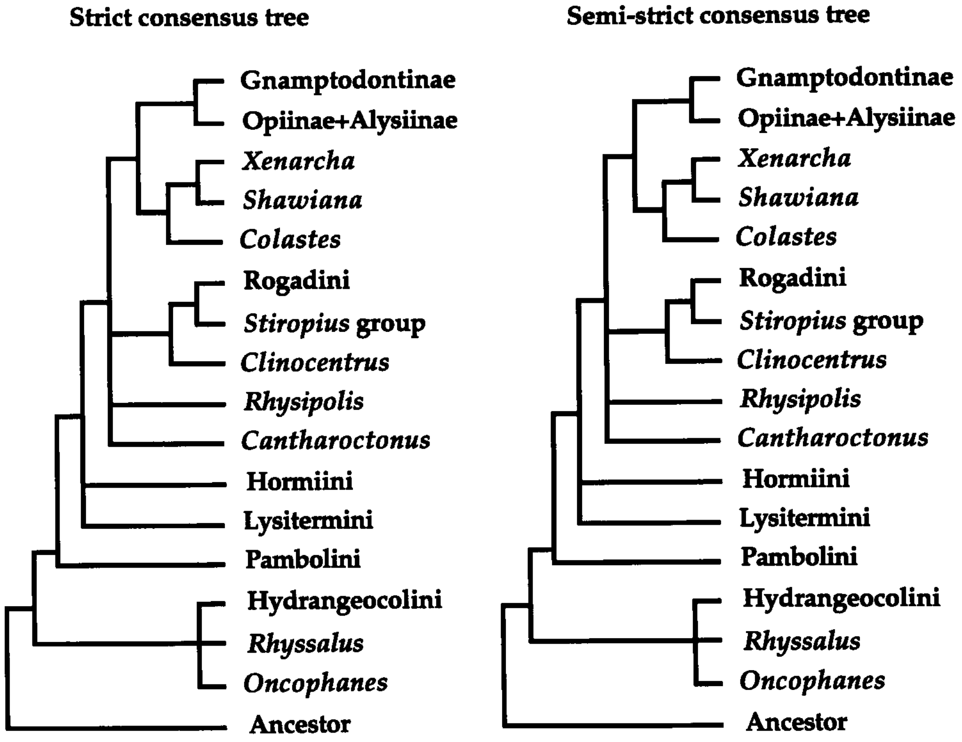


Fig. 3. Strict (and semistrict) consensus tree from 84 maximally parsimonious trees obtained by reanalysis of modified data matrix given in table 2 using iterative, differential character weighting based on the rescaled consistency index for characters in the 216 trees represented in fig. 2.

necessary to analyse a more comprehensive data set than that presented by Whitfield and also to apply considerably more rigour in both character coding and polarization. In this particular instance, it should also be noted that the interpretation of biological changes seems to hang critically on the biology of the Gnamptodontini, and it is to be hoped that this hiatus in our knowledge will not last for too long.

In conclusion, Whitfield (1992) has made an interesting start at trying to interpret shifts in biology within the cyclostome group of braconid wasps, and his separate treatment of a number of taxa previously often lumped together on the grounds of adult morphology (e.g. the Rhyssalini, *Cantharoctonus* and *Rhysipolis*) should signpost the way for future studies. However, from the data that Whitfield was able to assemble and analyse, his conclusion that two separate origins of endoparasitism have taken place should be treated with caution until relationships within the cyclostome group are better known. Further, particular care ought to be exercised when dealing with consensus trees that show unresolved polychotomies. In these cases there are two possible evolutionary explanations involving dichotomous splits; either one group can be paraphyletic with respect to another, or the polychotomy can be resolved in terms of two monophyletic groupings. Such situations are often treated as demonstrating paraphyly when an alternative solution exists, and therefore it would be better to term such groups defined by polychotomies as metataxa so as to emphasise their inherent ambiguity.

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References

Achterberg, C. van, 1974. The features of the petiolar segment in some Braconidae (Hymenoptera).— Ent. Ber., Amst. 34: 213-214, figs. 1-4.

Achterberg, C. van, 1979. A revision of the subfamily Zelinae auct. (Hymenoptera, Braconidae).— Tijdschr. Ent. 122: 241-479.

Achterberg, C. van, 1983a. Revisionary notes on the Palaearctic genera and species of the tribe Exothecini Foerster (Hymenoptera: Braconidae).— Zool. Med. Leiden 57: 339-355.

Achterberg, C. van, 1983b. Revisionary notes on the subfamily Gnamptodontinae, with description of eleven new species (Hymenoptera, Braconidae).— Tijdschr. Ent. 126: 25-57.

Achterberg, C. van, 1984a. Essay on the phylogeny of Braconidae (Hymenoptera).— Ent. Tidskr. 105: 41-58.

Achterberg, C. van, 1984b. Revision of the genera of Braconini with the first and second metasomal tergites immovably joined (Hymenoptera: Braconidae).— Tijdschr. Ent. 127: 137-164.

Achterberg, C. van, 1988. Parallelisms in the Braconidae (Hymenoptera) with special reference to the biology. In: Gupta V.K. (ed.). Advances in Parasitic Hymenoptera Research: 85-115.— Leiden.

Achterberg, C. van, 1990. Illustrated key to the subfamilies of Holarctic Braconidae (Hymenoptera: Ichneumonidae).— Zool.Med. Leiden 64: 1-20.

Achterberg, C. van, 1991. Revision of the genera of the Afrotropical and W. Palaearctic Rogadinae Foerster (Hymenoptera: Braconidae).— Zool. Verh. Leiden 273: 1-102.

Achterberg, C. van, 1992. Revision of the genus *Histeromerus* Wesmael (Hymenoptera: Braconidae).— Zool. Med. Leiden 66: 189-196.

Achterberg, C. van & Quicke, D.L.J., 1992. Phylogeny of the subfamilies of the family Braconidae: a reassessment assessed.— Cladistics 8: 237-264.

Belokobyl'skij, S.A., 1987. [Structure of the genitalia of male braconids of the subfamily Doryctinae (Hymenoptera, Braconidae): their evolution and utility for classification of groups.].— Morphological Foundations and Philosophy Insects, Nauka: 209-219 [in Russian].

Buckingham, G.R. & Sharkey, M.J., 1988. Abdominal exocrine glands in Braconidae (Hymenoptera).In: Gupta V.K. (ed.). Advances in Parasitic Hymenoptera Research: 199-242..— Leiden.

Čapek, M., 1970. A new classification of the Braconidae (Hymenoptera) based on the cephalic structures of the final instar larva and biological evidence.— Can. Ent: 102: 846-875.

Carpenter, J.M., 1988. Choosing among multiple equally parsimonious cladograms.— Cladistics 4: 291-296.

Edson, K.M. & Vinson, S.B., 1979. A comparative morphology of the venom apparatus of the female braconids (Hymenoptera: Braconidae).— Can. Ent. 111: 1013-1024.

Farris, J.S., 1989. The retention index and the rescaled consistency index.— Cladistics 5: 417-419.

Gauld, I.D., 1988. Evolutionary patterns of host utilization by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae).— Biol. J. Linn. Soc. 35: 351-377.

Maddison, W. & Maddison, D., 1987. MACCLADE. Version 2.1. A phylogenetics computer package for the MacIntosh computer.— Distributed by the authors.

Nixon, K.C. & Davis, J.I., 1991. Polymorphic taxa, missing values and cladistic analysis.— Cladistics 7: 233-241.

O'Donnell, D.J., 1987. Larval development and determination of the number of instars in aphid parasitoids (Hymenoptera: Aphidiidae).— Int. J. Insect Morphol. & Embryol. 16: 3-15.

Quicke, D.L.J., 1988. Higher classification, biogeography and biology of the Braconinae (Hymenoptera: Braconidae). In: Gupta V.K. (ed.). Advances in Parasitic Hymenoptera Research: 117-138.— Leiden.

Quicke, D.L.J. & Achterberg, C. van, 1990. Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea).— Zool. Verh. Leiden 258: 1-95.

Quicke, D.L.J., Tunstead, J., Falco, J. V. & Marsh, P.M., 1992. Venom gland apparatus in cyclostome braconid wasps with special reference to the subfamily Doryctinae (Insecta, Hymenoptera, Braconidae).— Zool. Scr. 21: 403-416.

Robertson, P. L., 1968. A morphological and functional study of the venom apparatus in representatives of some major groups of Hymenoptera.— Aust. J. Zool. 16: 133-166.

Shaw, M.R., 1983. On[e] evolution of endoparasitism: the biology of some genera of Rogadinae (Hymenoptera: Braconidae).— Contr. Am. ent. Inst. 20: 307-328.

Shaw, M.R. & Huddleston, T., 1991. Classification and biology of the braconid wasps (Hymenoptera: Braconidae).— Handbk Ident. Br. Insects 7 (11): 1-26.

Shaw, S.R. & Edgerly, J.S., 1985. A new braconid genus (Hymenoptera) parasitizing web-spinners (Embiidina) in Trinidad.— Psyche 92: 505-511.

Swofford, D.L., 1990. PAUP-Phylogenetic Analysis Using Parsimony, version 3.0.— Computer program distributed by the Illinois Natural History Survey.

Tobias, V.I., 1989. On use of the method of the phylogenetic analysis of W. Hennig for construction of phylogenetic tree of family Braconidae (Hymenoptera).— Proc. Zool. Leningrad 202: 67-86. [In Russian].

Tobias, V.I. and Potapova, Y.S., 1982. Morphological characteristics of the head capsule of braconids (Hymenoptera, Braconidae) and the main trends in their evolution.— Ent. Rev. 61: 34-47.

Togashi, I., 1963. A comparative morphology of the poison glands in the adults of ichneumon-flies (Hymenoptera, Ichneumonidae).— Kontyu 31: 297-304.

Wharton, R.A., 1988. Classification of the braconid subfamily Opiinae (Hymenoptera).— Can. Ent. 120: 333-360.

Wharton, R.A., 1993. Review of the Hormiini (Hymenoptera: Braconidae) with description of new taxa.— J. Nat. Hist. 27: 107-171.

Wharton, R.A., Shaw, S.R. Sharkey, M.J., Wahl, D.B., Wooley, J.B., Whitfield, J.B., Marsh, P.M. & Johnson, J.W., 1992. Phylogeny of the subfamily of the family Braconidae (Hymenoptera: Ichneumonidae): a reassesment.— Cladistics 8: 199-235.

Whitfield, J.B., 1990. Phylogenetic review of the *Stiropius* group of genera (Hymenoptera: Braconidae, Rogadinae) with description of a new Neotropical genus.— Proc. ent. Soc. Wash. 92: 36-43.

Whitfield, J.B., 1992. The polyphyletic origin of endoparasitism in the cyclostome lineages of Braconidae (Hymenoptera).— Syst. Ent. 17: 273-286.

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