What do we know about chrysidoid (Hymenoptera) relationships?

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The phylogeny of the superfamily Chrysidoidea is reviewed. Relationships among the families proposed by Carpenter (1986) were confirmed by Brothers and Carpenter (1993). The status of knowledge of phylogenetic relationships within families is assessed. Cladistic analyses have been undertaken only within Plumariidae (by Roig-Alsina 1996, a manual analysis of genera), Chrysididae (by Kimsey and Bohart 1991, a manual analysis of subfamilies and tribes, and genera within subfamilies) and Bethylidae (by Sorg 1988, a manual analysis of subfamilies, and genus groups within three of these; and by Polaszek and Krombein 1994, a quantitative cladistic analysis of the genera of Bethylinae). These analyeses are critically evaluated, and the current classifications within all the families examined cladistically. Generic relationships are investigated within Scolebythidae and Embolemidae; subfamily relationships are investigated within Sclerogibbidae and Dryinidae.

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Introduction

The stinging wasps, the Aculeata, are the most generally familiar Hymenoptera. Among the Aculeata, the superfamily Chrysidoidea is the least known. The Chrysididae are the only family familiar enough to have a common name — 'jewel' wasps, 'gold' wasps or 'cuckoo' wasps — but even the question of which taxa to include in the family has only been settled rather recently (Day 1979). Composition of less well known families has also fluctuated recently, and likewise at the subfamily level (Plumariidae: cf. Brothers 1974, 1975; and Day 1984). Of the generally recognized aculeate families (e.g., Gauld and Bolton 1988; Naumann 1991; Goulet and Huber 1993; Hanson and Gauld 1995), the most recently described is the Scolebythidae (Evans 1963), in the Chrysidoidea. The name applied to the superfamily has lately even changed (from Bethyloidea to Chrysidoidea; see Day 1997). Typically smaller size than aculeates in the superfamilies Apoidea and Vespoidea, fewer species, and, perhaps, parasitic behaviour, have combined to leave the group obscure.

Nevertheless, the group has been the object of phylogenetic research. The pioneering application of phylogenetic systematics to Hymenoptera by Oeser (1961) identified a synapomorphy in the sting for Bethylidae and Chrysididae, and suggested a sister-group relationship between this clade and the rest of Aculeata. The first application of numerical cladistic methods to Aculeata by Brothers (1975) confirmed a sister-group relationship between Chrysidoidea and Aculeata sensu stricto, and suggested that Plumariidae are basal within Chrysidoidea. The comprehesive cladistic analysis of chrysidoid families by Carpenter (1986) established the relationships shown in Fig. 1. This was the first analysis to include all chrysidoid families in the current sense, and upheld both a close relationship between Bethylidae and Chrysididae, and a basal position for Plumariidae within the superfamily. The relationships differed from those suggested in two studies subsequent to that of Brothers, namely the literature review by Königsmann (1978) and the non-cladistic narrative by Rasnitsyn (1980). Rasnitsyn (1988) subsequently modified his views to accept the distant relationship between Scolebythidae and Bethylidae + Chrysididae established by Carpenter (1986), but continued to argue that Embolemidae and Dryinidae are not sister-groups. As pointed out by Carpenter (1990), Rasnitsyn's paper contained several errors of fact and interpretation, and the conclusion of no close relationship of Embolemidae and Dryinidae was reached by discarding relevant characters. Brothers and Carpenter (1993), in a detailed reanalysis of Aculeata, upheld the relationships within Chrysidoidea proposed by Carpenter

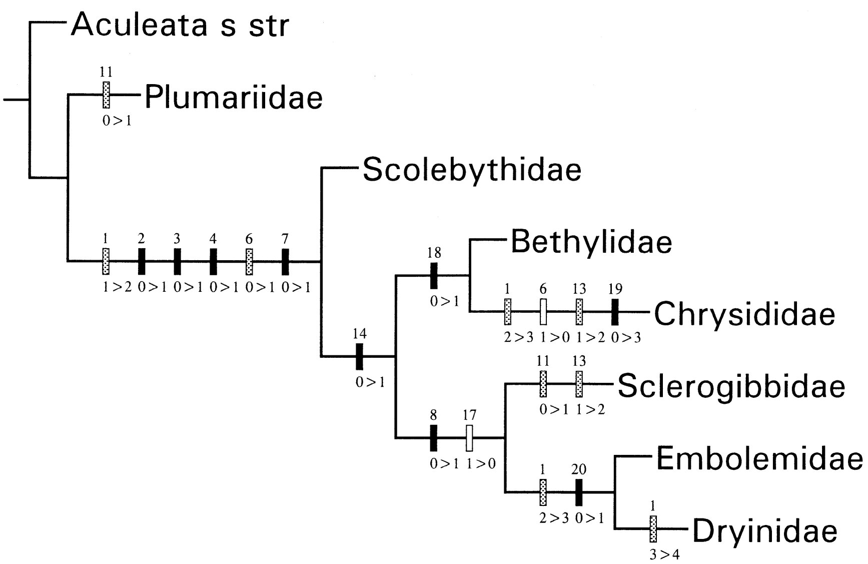

Fig. 1 Cladogram for families of Chrysidoidea. Characters have been optimized with the program Clados (Nixon 1998), plotting only unambiguous changes. Character numbers are above the hashmarks; state changes are shown below, with the respective primitive and derived conditions separated by a '>'. Filled hashmarks indicate a unique derivation, grayscale are convergent derivations, while open are reversals (unique or convergent).

(1986), in the context of a larger study, including all aculeate families with more characters. Those conclusions have since been accepted in general treatments of Hymenoptera (e.g., Goulet and Huber 1993; Hanson and Gauld 1995). Therefore, in this review I will concentrate on relationships within the families, rather than among them.

Phylogenetic relationships

Carpenter (1986) did not provide a character matrix for the families, only a phylogenetic diagnosis of the cladogram. To some extent, this lack is remedied by the matrices provided by Brothers and Carpenter (1993), Nevertheless, I take this opportunity to present a matrix for the characters treated by Carpenter (1986). The characters may thus be plotted on the cladogram (Fig. 1), giving a visual impression of the strength of support for each node. The matrix (Table 1) includes just the informative groundplan characters from Carpenter (1986), that is, no autapomorphies are listed as such. Autapomorphies for each family may be found in the diagnoses listed by Carpenter (1986) and Brothers and Carpenter (1993). There are also two corrections in Table 1 to the characters as treated by Carpenter (1986), discussed in Carpenter (1990). First, as pointed out by Rasnitsyn (1988), two midtibial spurs are present in various embolemids, and so reduction to one cannot be a synapomorphy with dryinids. This character is deleted. Second, as depicted in Carpenter (1986: fig. 16) but not discussed on p. 312, SC + R + RS is elongate in Embolemidae, possibly secondarily. This character is present in the matrix of Table 1, with a modified interpretation from Carpenter (1986).

When the characters from Table 1 are analyzed by the exact routines of either the program Hennig86 (Farris 1988) or Nona (Goloboff 1997a), a single cladogram results, that of Fig. 1. The length is 34 steps, with consistency index 0.82 and retention index 0.73. The optimization shown plots unambiguous changes only, that is, characters which could be optimized in more than one way are not plotted. The cladogram is stable to successive weighting with either program (Hennig 86 employs the rescaled consistency index of Farris 1989, as a weighting function, Nona the consistency index). The cladogram also results from implied weighting as implemented in the program Piwe (Goloboff 1997b).

Plumariidae

This family presently consists of five genera (Roig Alsina 1994). Three are found in arid regions of South America (viz., *Plumarius*, *Plumaroides* and *Maplurius*) and two in southern Africa (*Myrmecopterina* and *Myrmecopterinella*). Very few specimens of the wingless females have ever been collected, and the biology is unknown, but numerous males have been taken in Malaise traps. An ongoing revision by Argaman (unpublished) will doubtless add more species to the total known.

The phylogentic relationships among the genera were studied by Roig-Alsina (1994). He proved a list of 13 characters, polarized with reference to chrysidoid and aculeate

Table 1 Data on chrysidoid families from Carpenter (1986), with midtibial spurs deleted and SC + R + RS modified (Carpenter, 1990). A question mark denotes an unknown state. Multistate characters are treated as additive except as noted.

	1 5 10	15 20
Aculeata s.str	0000000000	0100001000
Plumariidae	1000000011	10101110??
Scolebythidae	2111011011	000011100?
Scerogibbidae	2111111111	1321110010
Embolemidae	3111011111	0211110021
Dryinidae	4111111111	0211110021
Bethylidae	2111011011	0011111100
Chrysididae	3111001011	0021111130

Character list

1. Forewing: 10 cells (0); eight (loss of m-cu2, r-m3) (1); seven (2); six (3); five (4).
2. RS2: present (0); absent (1).
3. Hindwing: with rs-m and cu-a (0); lost (1).
4. C: distally present (0); reduced (1).
5. SC + R + RS: present (0); reduced (1).
6. Costal cell: present (0); absent (1).
7. M + Cu: present (0); absent (1).
8. 1A: present (0); absent (1).
9. 2A and 3A: present (0); lost (1).
10. Jugal lobe: present (0); absent (1).
11. Females: winged (0); brachypterous (1).
12. Antennae: 13 articles (0); dimorphic (1); 10 articles (2); >14 articles (3) [non-additive].
13. Palpal formula: 6:4 (0); 6:3 (1); 5:3 (2).
14. Metapostnotum: present (0); constricted (1).
15. Metathoracic-propodeal suture: present ventrally (0); absent (1).
16. Sting: without postincision (0); articulation present (1).
17. Furcula: absent (0); present (1).
18. Second valvifer-sting articulation: present (0); absent (1).
19. Hosts: Coleoptera (0); Embiidina (1); Auchenorrhyncha (2); Tenthredinoidea or Phasmida (3) [non-additive].
20. Habits: ectoparasitic (0); endoparasitic then cyst (1).

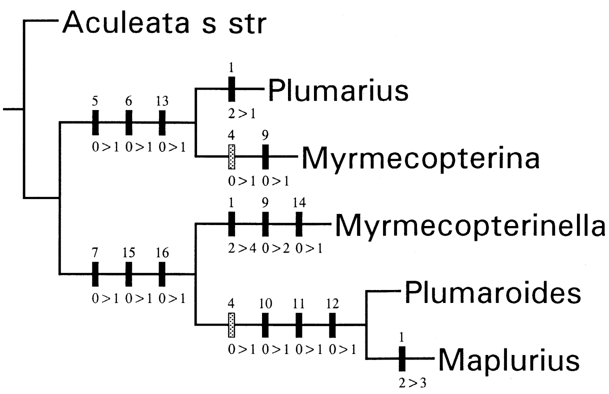

Fig. 2 Cladogram for genera of Plumariidae. Plotting conventions are as in Fig. 1.

Table 2 Data on plumariid genera, extracted primarily from Roig-Alsina (1994), with additions from Brothers (1974) and Day (1977). The asterisk denotes a polymorphism showing all applicable states. Multistate characters are treated as non-additive.

	1 5 10 15
Aculeata s.str.	00000000000000000
Plumarius	10201100000010000
Plumaroides	21010012011100111
Myremcopterina	2011110010001*000
Myrmecopterinella	42100011200001111
Maplurius	31210012011100110

Character list

1. Labial palpi: 4 (0); 3 (1); 2 (2); 1 (3); none (4).
2. Maxillary palpi: 6 (0); 5 (1); 3 (2).
3. Antennal setae: inconspicuous (0); conspicuous on flagellomeres (1); 4X width of flagellomeres, in rows (2).
4. Pronotal collar: present (0); absent (1).
5. Ventral angle of pronotum: round (0); pointed (1).
6. Propleura: dorsally separated by membrane (0); fused, forming tubular neck (1).
7. Epimeral area of propleuron: present (0); absent (1).
8. Prepectus: present (0); reduced, slender bar I1); reduced, narrow-filiform (2).
9. Forewing second submarginal cell: subpetiolate (0); reduced, petiolate (1); absent (2).
10. Anal lobe: slightly longer than submedian cell (0); more than twice length submedian cell (1).
11. Arolia of mid- & hindtarsi: present (0); absent (1).
12. Metasomal Sternum I: ecarinate (0); with median longitudinal carina (1).
13. Hindcoxa: ventrally glabrous (0); ventrally with specialized area of setae (1).
14. Hindwing costal cell: closed (0); open (1).
15. Clypeus: narrow (0); transverse (1).
16. Occipital carina: present (0); absent (1).
17. Metasomal Tergum VII: simple (0); with median carina & acute apex (1).

groundplans established by Carpenter (1986) and Brothers (1975), and through outgroup comparison to other families of Chrysidoidea. His phylogenetic tree was rooted with reference to these polarities, that is, the tree was pre-rooted in the terminology of Nixon and Carpenter (1993). The relationships depicted in his tree are shown in Fig. 2. The two African genera are each more closely related to American genera than to each other.

I have scored Roig-Alsina's characters in matrix form in Table 2. I have modified the interpretations of three of them and have also added four characters. Roig-Alsina (1994: 92) defined the apomorphous condition of the labial palpus to be 'less than three segments'; in Table 2 the number for both the labial and maxillary palpomeres is scored directly, and these characters treated non-additively. Although the states of the labial palpi (character no. 1) form a reduction series, those of the maxillary palpi (character no. 2) exhibit a gap, between five palpomeres and three. I have added a state to character no. 3, antennal setae, and characters no. 14–17 in Table 2 from the key by Brothers (1974), and those discussed by Day (1977). One of these characters, no. 14, whether the hindwing costal cell is open or closed, was discussed by Roig-Alsina (1994:

92), who stated: 'Brothers (1974, Fig. 3) presented a drawing of the hind wing of *Myrmecopterina filicornis* BISCHOFF with an incomplete costal vein. This feature was later mentioned by Day (1977) for *Myrmecopterinella*, suggesting that it associated the two African genera. The specimens of *Myrmecopterina* I have examined have a complete costal vein.' I have not studied specimens of *Myrmecopterina* (or *Maplurius*) myself, so I have scored that character as polymorphic for *Myrmecopterina* in Table 2. I have treated the multistate character no. 3, antennal setae, as non-additive, primarily because I am not confident that the first two states listed should be treated as distinct, that is, that there really is an intermediate state to the long setae seen in *Plumarius* and *Maplurius*. I have also treated multistate character no. 8, prepectus, as non-additive, because the reduced states are different in form. The outgroup represents the sister-group to the the Chrysidoidea, the Aculeata sensu stricto, used because Plumariidae are basal within Chrysidoidea.

Exact analysis of the data in table 2 with either Hennig86 (which requires that the polymorphism be treated as a missing value) or Nona results in one cladogram, that of Fig. 2. The length is 28 steps, with consistency index 0.85 and retention index 0.78; the cladogram is stable to successive weighting with either the rescaled consistency index or consistency index, and results from implied weighting. The relationships among the genera proposed by Roig-Alsina (1994) are upheld by this reanalysis.

It may be observed that no apomorphies are plotted for *Plumaroides* in Fig. 2. I have plotted only unambiguous optimizations on the cladogram. Character no. 17, metasomal Tergum VII carinate, could be optimized as a (convergent) step supporting that genus, but another optimization of this character is possible, thus the optimization is ambiguous and the 'support' by this character 'semistrict' in the terminology of Nixon and Carpenter (1996b). However, Roig-Alsina (1994: 94) listed several other characters as autapomorphies of *Plumaroides* relative to *Maplurius*. Each of the genera can thus be diagnosed by apomorphies, and phylogenetic work in the family can concentrate on relationships among the species (note that some of the genera are monotypic).

Scolebythidae

The family was for some time considered to consist of three extant genera (Nagy 1975). Two fossil species were described (Prentice *et al*. 1996), each in a new genus, and one of these genera has now been found to include an extant species (Avevedo, submitted). *Scolebythus* is found in Madagascar, *Clystopenella* in the neotropics and Australia, *Ycaploca* in South Africa and Australia, and *Dominibythus* in Brazil and Dominican amber. The other fossil genus, *Libanobythus*, was found in Lebanese amber. There is some evidence that these wasps are parasitoids of wood-boring Coleoptera, but it is circumstantial (see review by Gauld 1995). Each genus as described was monotypic, but *Dominibythus* now has two species, and Gauld (1995: 469) noted that several undescribed species of *Clystopsenella* are present in collections. I have seen one of these, from Costa Rica.

In their discussion of relationships of the fossil taxa, Prentice *et al*. (1996: 809) stated: 'The elongate pronotum that retains a pronotal collar in *Libanobythus milkii* suggests a sister-group relationship between this species and other known Scolebythidae ... This sister-group relationship would not be unexpected given the age of the fossil, but, if true, means the complete absence of vein R1 in both *L. milkii* and *D. inopinatus* is convergent.' They also suggested: '*Dominibythus inopinatus* appears to be most closely related to *Ycaploca evansi* as indicated by the presence in both taxa of a frontal prominence between the antennae that is marked laterally by two dorsally diverging carinae ... *Dominibythus inopinatus* also shares a well developed clypeal lobe, propodeal groove and evenly convex subgenital plate with *Ycaploca* but these features are also present in *Scolebythus*. An apparent tibial spur formula of 1-1-1 may be an additional character linking *D. inopinatus* with *Y. evansi* since *Scolebythus* and *Clystopsenella* have the ancestral tibial spur formula of 1-2-2.'

In order to test these suggestions, I have scored 14 characters for these genera in Table 3. The characters include those discussed by Prentice *et al*. (1996), as well some others that have been used to distinguish the genera by Evans (1963), Nagy (1975) and Evans *et al*. (1979), although I have phrased some of the characters differently. I have not seen the fossil taxa; for these, the characters are taken from the descriptions. The outgroup is the basal chrysidoid family Plumariidae. There are five multistate characters, all of which I have treated as non-additive. Two of these, no. 8, length of the malar space, and no. 10, notauli, are polymorphic in Plumariidae. Two of the others, no. 1, forewing marginal cell, and no. 2, forewing submarginal cell, include a state 'open,' which does not relate to any of the closed states in an obvious way. Also, no. 11, metapostnotum, includes a state 'not apparent' for *Dominibythus*, which leaves some ambiguity in mind concerning the circumscription of the states.

Exact analysis of the data in Table 3 with Nona results in one cladogram, that of Fig. 3. The length is 23 steps, with consistency index 0.82 and retention index 0.69; the cladogram is stable to successive weight-

Table 3 Data on scolebythid genera. A question mark denotes an unknown state. An asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism in Plumariidae. The subset polymorphisms are: character no. 8 [states 0 1] and no. 10 [states 1 2]. Multistate characters are treated as non-additive.

	1 5 10
Plumariidae	00*0000$*$0000
Ycaploca	11110000100110
Scolebythus	00101101101000
Clystopsenella	10001112101001
Libanobythus	2000000?02?11?
Dominibythus	2211000211211?

Character list

1. Forewing marginal cell: apex on margin of wing (0); apex curving away from margin of wing (1); open (2).
2. First submarginal cell: short (0); elongate (1); open (2).
3. Clypeal apex: short (0); produced (1).
4. Frontal prominence: absent (0); present (1).
5. Facial depression: flat laterad of antennal sockets (0); depressed laterad of antennal sockets (1).
6. Ocellar triangle: equilateral (0); obtuse (1).
7. Occipital carina: present (0); absent (1).
8. Malar space: very short (0); one third width mandibular base (1); one half width mandibular base (2).
9. Pronatal collar: present (0); absent (1).
10. Notauli: present (0); reduced posteriorly (1); absent (2).
11. Metapostnotum: distinct (0); partly obliterated (1); not apparent (2).
12. Midtibial spurs: 2 (0); 1 (1).
13. Hindtibial spurs: 2 (0); 1 (1).
14. Female Sternum VI: simple (0); with polished area & setae (1).

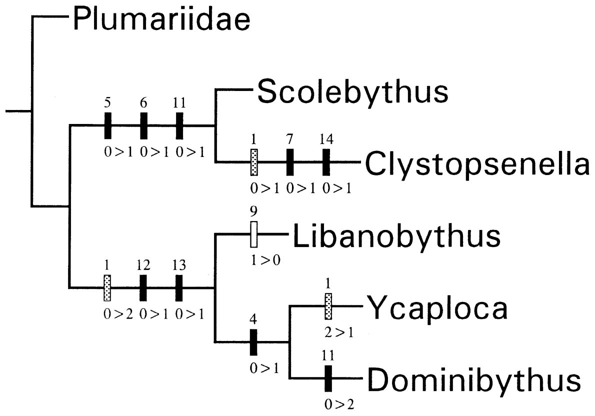

Fig. 3 Cladogram for genera of Scolebythidae. Plotting conventions are as in Fig. 1.

ing with the consistency index, and results from implied weighting.

Unexpectedly, rather than sister-group to the remaining Scolebythidae, *Libanobythus* is placed as the sister-group to *Ycaploca* + *Dominibythus*. This is due primarily to the tibial spur formula, which was described as 'apparently 1-1-1' by Prentice *et al.* (1996: 807) in *Libanobythus* as well as *Dominibythus*. The pronotal collar, character no. 9, is thus treated as a reversal in *Libanobythus*.

Note that no apomorphies are plotted for *Scolebythus* in Fig. 3. Character no. 3, produced clypeal apex, and no. 8, broadened malar space, could be optimized as (convergent) steps supporting that genus, but that apomorphy is semistrict. Although each genus currently has only a single described species, and the concept of monophyly is not applicable at the species level (Hennig 1966; Nixon and Wheeler 1990), I attempted to determine at least one autapomorphy for each taxon. As noted above, *Clystopsenella* is already known to contain other, undescribed species, and an extant species of *Dominibythus* is being described by Azevedo (submitted). Other species may be discovered in *Scolebythus* and *Ycaploca*. As long as it remains monotypic, the lack of an autapomorphy for *Scolebythus* presents no problem, but the addition of other species may result in a paraphyletic genus. Elimination of a paraphyletic *Scolebythus* by, say, synonymy with *Clystopsenella*, would result in use of the latter name, which has priority. Under our present rules of nomenclature the family group name Scolebythidae would nevertheless be conserved.

Prentice *et al.* (1996: 810) averred: 'The addition of two new monotypic fossil scolebythid genera to the three extant monotypic genera might seem to unnecessarily clutter this small family with genera. However, on phenetic grounds, the recognition of five genera is justified.' Instead, from the results presented here, it seems that the generic classification of the family deserves reconsideration, in the context of a phylogenetic investigation including additional characters — and the new species.

Sclerogibbidae

These wasps are parasitoids of Embiidina, and the known fauna is a handful of species worldwide. Richards (1939) recognized two genera, *Probethylus* and *Sclerogibba*, the latter with five generic synonyms. *Probethylus* had three species, while *Sclerogibba* had six recognizable species, with several other names in tentative synonymy. Richards (1958) later added another species, *Sclerogibba longiceps*, which was later redescribed several times (see Argaman 1988b)[1], and under one of these names became the type of a new genus, *Caenosclerogibba* (Yasumatsu 1958). Argaman (1988b) revised the family, recognizing 10 species, establishing the synonymy of numerous species described subsequent to the revision by Richards (1939). These 10 species were arranged in no fewer than seven genera, with four of

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[1] Argaman (1988b: 182) stated that 'Richards described *longiceps* in January 1958, and as first reviser, I select the name *longceps* as valid for this species.' This is an error; priority establishes *longceps* as the senior synonym.

the synonyms of *Sclerogibba* revived (one with a replacement name). In fact, all but one of the genera recognized by Argaman was monotypic. Later, Argaman (1993), revived the last generic synonym, *Prosclerogibba*, transferring one species from synonymy to this genus and describing a new one,[2] and added another new genus, monotypic for a new species. Thus, 13 species were arranged in no fewer than nine genera.

Argaman (1988b) additionally proposed subfamilies and tribes within the Sclerogibbidae. The family had not previously been so classified, and of these categories Finnamore and Brothers (1993: 139) stated 'the appropriateness of which awaits evaluation of further material.' The subfamilies were Caenosclerogibbinae (monobasic for *Caenoclerogibba*, itself monotypic), Probelthylinae (monobasic for *Probethylus*), and Sclerogibbinae. Sclerogibbinae was in turn subdivided into tribes. Tanynotini (monobasic for the monotypic *Tanynotus*), Parasclerogibbini (monobasic for the monotypic *Parasclerogibba*), and Sclerogibbini (with three, monotypic, genera).

It is scarcely necessary to examine material to evaluate this classification. The point of taxonomy is efficient diagnosis: the names in a classification convey inclusion relationships, with the names only useful if they refer to characters that allow description to be made concise, by concentrating just on the features by which taxa are distinguished within a named group (Farris 1979). Redundant names add nothing to efficient diagnosis. Our rules of nomenclature require generic epithets in a species name, but families need not be subdivided into subfamilies and tribes. Argaman's classification contained four entirely redundant higher categories, out of a total of six. That classification is thus mostly superfluous: the subfamily/tribal names and generic names refer mostly to the same characters (as for that matter do the species epithets). The classification should be rejected on those grounds alone.

To be sure, Argaman's higher taxa did convey two inclusion relationships: that five genera were contained in Sclerogibbinae, and three of these within Sclerogibbini. This last relationship, at least, could have been conveyed more efficiently by including those three monotypic genera in one genus[3]. The same might be said about the fact that five (monotypic) genera were contained within Sclerogibbinae, but a more pertinent question about that taxon is whether it is monophyletic. And the answer is: probably not. Sclerogibbinae was diagnosed by the female metanotum present but reduced, and divided in dorsal view by the scutellum, eyes 'rather large,' midtibial spurs 'normal,' male with 'submarginal vein petiolate on marginal' (by which Argaman meant 1r-rs perpendicular on RS in the forewing) and [male] notauli complete. The latter four of these states are plesiomorphic within Aculeata. As to the condition of the female metanotum, the state contrasted with the metanotum not so divided in dorsal view in Caenosclerogibbinae, and absent in Probethylinae. Argaman's (1988b: fig. 11) depiction of the state in *Caenosclerogibba longiceps* contrasts with that of Richards (1958: fig. 1, and see also the description on p. 17), but that aside, at best Sclerogibbinae are less derived than Probethylinae in this character. Sclerogibbinae as construed by Argaman is thus evidently a paraphyletic group. At present, it is uncertain whether the subfamily is paraphyletic with respect to just one or both of the other subfamilies. This is because Caenosclerogibbinae might be considered similar to Probethylinae in one respect: it has one midtibial spur shortened, while one spur is absent in Probethylinae. Caenosclerogibbinae is known only from the female, and if the male proved to be similar to males of Probethylinae in having 1r-rs oblique on RS, then *Caenosclerogibba longiceps* might be the sister-group of *Probethylus*. Sclerogibbanae would thus be doubly paraphyletic.

Argaman's subfamilies and tribes should therefore not be recognized. The same conclusion applies to most of the genera. To the extent that most are monotypic, they add nothing to efficient diagnosis, phylogenetic or otherwise. *Probethylus*, with three species the only genus not monotypic in the 1988 revision, is evidently a monophyletic group, as shown by the reduction of the metanotum in the femal and oblique 2rs-m in the male, But it is not clear which of the remaining genera might be its sister-group. On the other hand, it seems clear that the remaining genera do not together constitute a monophyletic group. Therefore it is unclear whether more than one genus should be recognized in the Sclerogibbidae. Future research should be directed toward clarifying the phylogenetic relationships among the species of this family. The generic classification can then be revised on a cladistic basis — which need not entail the proliferation of higher categories (for example, by the use of phyletic sequencing; see Wiley 1979).

Embolemidae

There are just two genera in this family, *Embolemus* and *Ampulicomorpha*, both cosmopolitan. This is another group of which our knowledge has been greatly augmented by the use of the Malaise trap: the recent revision by Olmi (1996a) more than doubled the described fauna, to 16 extant species, with a couple of additional fossil species known. Olmi (1998) added 13 more species. Ongoing

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[2] However, he did not state whether he ws restoring the type species of the genus from synonymy. He did not examine this species.

[3] Assuming, of course, that the characters diagnosing it were apomorphic, but they evidently were not, consisting merely of the absences of the derived characters of the other tribes in the subfamily.

work by Olmi and others will add still further species. The biology of only one species has been determined, and it is a parasitoid of nymphs of the fulgoroid family Achilidae (Bridwell 1958; Wharton 1989). The use of Homoptera as hosts, and the initially endoparasitic larva, are traits shared with Dryinidae, and are evidently synapomorpies (Carpenter 1986).

For just two genera, the phylogenetic question that may be asked is: are both genera monophyletic? *Embolemus* has several evident autapomorphies. The females are brachypterous or micropterous, while the females of *Ampulicomorpha* are fully winged. The first subdiscal cell of the forewing is closed in *Ampulicomorpha* (albeit only by nebulous veins), but open in males of *Embolemus*. However, *Ampulicomorpha* is evidently monophyletic as well. The pronotum is elongate in *Ampulicomorpha*, with a pronounced longitudinal median groove (except males of a few species; see Olmi 1996a), and with the hind margin transverse. In *Embolemus* the pronotum is short, without a pronounced median groove (although traces may be present, Olmi 1996a), and the hind margin is strongly concave. Both of the latter conditions are found also in Dryinidae, thus the states in *Ampulicomorpha* are derived. Phylogenetic research in the Embolemidae may thus be oriented toward elucidating the relationships among species.

Dryinidae

The Dryinidae are a sizable family: the revision by Olmi (1984) recognized more than 800 species worldwide. These wasps are parasitoids — and predators — of Auchenorrhyncha (Homoptera), and some species are of economic importance, although attempts to introduce them for biological control have been unsuccessful. The chelate foretarsi of most females are a striking morphological feature, used in capturing prey.

Olmi (1984) arranged 26 genera into 10 subfamilies, five of the latter newly described. Olmi (1987) subsequently described another subfamily, and then (Olmi 1993b) sank one of the subfamilies, and Olmi (1996b) another, for a total of nine extant subfamilies presently recognized. Olmi (1989) described another subfamily for a fossil species from Baltic amber.

Little has been done in the way of phylogenetic research in Dryinidae. Olmi (1994: 30–31) stated:

> 1 we can discuss female affinities, because the females show clear and different evolutionary levels;
> 2 we can discuss male affinities, but with great difficulty since males are very uniform and their differential morphological characteristics are usually very slight;
> 3 we cannot discuss species affinities, because evolution has followed completely different paths in males and females, and female affinities are completely different from male affinities.

That last conclusion, of course, does not follow, even if the first two propositions are accepted. Olmi (1994: 32) referred to: 'A cladogram[4] (Table 2) is given to show the possible phylogenetic relationships among the females of Fennoscandian and Danish Dryinidae and Embolemidae' which if taken literally, implies different phylogenetic relationships among females and males of the same species! In reality, this is nothing more than a confusion between relationships implied by different data sources and 'true' relationships. Data from the different data sets may be in conflict, but that does not mean a species has multiple phylogenies, just as homoplasy within a data set does not simply imply multiple character 'phylogenies.'[5] Conflict within data sets is arbitrated by parsimony – just as conflict among data sets is properly arbitrated by parsimony, through simultaneous analysis (Nixon and Carpenter 1996a).

To demonstrate this point, data from both females and males are combined in Table 4. There are 32 variables, with different variables sometimes being used for the same character in the two sexes. I have not studied specimens of five of the subfamilies (viz., the small subfamilies Conganteoninae, Transdryininae, Apodryininae and Plesiodryininae, and the fossil Laberitinae). The characters are those used to distinguish among the subfamilies in the keys and descriptions by Olmi (1984, 1987, 1989), with the subfamily composition as modified by Olmi (1993a, b, 1996b). Many of the subfamilies are polymorphic for the key characters distinguishing these taxa: the matrix of Table 4 has about 16% polymorphic cells, and another 12% are missing observations. All of the polymorphic multistate characters are treated as non-additive; if treated as additive, a subset polymorphism would have to be interpreted as having the full range of values in the polymorphism. The outgroup is the Embolemidae, sister-group of Dryinidae.

Exact analysis of the data in Table 4 with Nona results in four cladograms, with length 45 steps, consistency index 0.75 and retention index 0.70. The consensus tree is shown in Fig. 4. The clade concordance index (Nixon and Carpenter 1996b), *CC*, is 0.58, with the consensus length $CL = 52$ and summed greatest lengths of each character $\Sigma GL_n = 48$. The intermediate value of the clade concordance index means that some grouping information remains in the characters in the groups collapsed in the consensus, but that almost half the possible group/charac-

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[4] How this cladogram was derived was not specified.

[5] Although fuzzy thinking of precisely this sort has led to the notion of a cladogram as a 'fuzzy and cloudlike' (Maddison, 1997: 534).

Table 4 Data on subfamilies of Dryinidae. A question mark denotes an unknown state, while a dash denotes an inapplicable character. An asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism. All characters that are polymorphic are treated as non-additive; multistate characters are otherwise additive. The subset polymorphisms are as follows: Embolemidae, character no. 1 [states 0 1], 15 [0 1 2 3], 16 [0 1], 17 [0 1 2], 18 [0 1], 20 [0 1], 30 [0 1]; Aphelopinae, no. 1 [states 2 3], no. 13 [1 2], no. 15 [0 1], no. 16 [0 1], 18 [0 1]; Anteoninae, no. 10 [0 2]; Bocchinae, no. 6 [0 1], 10 [0 1], 13 [1 2 3 4], 14 [1 2 3 4]; Dryininae, no. 7 [0 1], 10 [1 2], 14 [0 2], 28 [0 1]; Gonatopodinae, no. 6 [1 2], 7 [1 2], 10 [0 2]; Apodryininae, no. 14 [1 2], 15 [1 2], 19 [1 2].

	1				5					10					15					20					25					30		
Embolemidae	$	0	0	*	0	0	0	1	1	0	0	1	0	0	$	$	$	$	0	$	0	0	0	0	0	0	0	–	0	$	0	0
Aphelopinae	$	0	*	0	0	0	0	*	*	0	0	0	$	2	$	$	1	$	0	0	0	0	0	0	0	0	0	–	0	1	0	0
Conganteoninae	2	0	*	0	0	0	0	1	1	0	0	*	1	1	$	0	$	0	0	0	0	0	1	0	1	1	1	2	1	1	0	0
Anteoninae	1	1	*	0	0	0	0	*	0	$	*	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	2	1	0	0
Bocchinae	1	0	*	0	0	$	0	1	1	$	0	0	$	$	0	0	0	0	0	1	1	1	1	0	1	1	1	2	1	1	*	0
Dryininae	1	0	*	0	*	*	$	*	1	$	*	0	0	$	0	0	0	0	0	2	1	0	1	1	1	2	1	$	1	1	*	0
Transdryininae	1	0	0	0	1	2	?	1	?	1	?	0	4	?	0	0	?	?	0	2	1	0	1	1	1	2	1	0	2	2	1	?
Gonatopodinae	1	0	*	0	*	$	$	1	1	$	*	1	0	2	*	*	*	*	0	2	0	0	1	1	1	*	1	0	1	2	*	1
Apodryininae	1	0	0	1	1	2	0	1	1	0	0	1	0	$	$	0	0	0	$	1	0	1	1	0	1	2	1	1	1	1	*	?
Plesiodryininae	?	?	1	1	2	?	1	?	0	?	1	0	?	0	0	?	?	1	1	0	1	1	0	1	2	1	0	1	1	1	?	1
Laberitinae	1	1	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	0	0	?

Character list

1. Forewing: four cells closed by tubular veins (0); three closed by tubular veins (1); two closed by tubular veins (2); one closed by tubular veins (3) [non-additive].
2. Forewing R1: abscissa beyond pterostigma long (0); abscissa beyond pterostigma short (1).
3. Forewing RS: long (0); short (1).
4. Female ocelli: present (0); absent (1).
5. Female rhinaria: absent (0); present (1).
6. Female occipital carina: present (0); incomplete (1); absent (2) [non-additive].
7. Male occipital carina: present (0); incomplete (1); absent (2) [non-additive].
8. Female frontoclypeal suture: close to antennal sockets (0); separated (1).
9. Male frontoclypeal suture: close to antennal sockets (0); separated (1).
10. Female clypeus: rounded (0); emarginate (1); bidentate (2) [non-additive].
11. Male clypeus: rounded (0); emarginate (1).
12. Female subocular sulcus: present (0); absent (1).
13. Female mandible: quadridentate (0); quadridentate, one reduced (1); tridentate (2); bidentate (3); unidentate (4) [non-additive].
14. Male mandible: quadridentate (0); quadridentate, one smaller (1); tridentate (2); bidentate (3); unidentate (4) [non-additive]
15. Female maxillary palpomeres: 6 (0); 5 (1); 4 (2); 3 (3); 2 (4) [non-additive].
16. Female labial palpomeres: 3 (0); 2 (1); 1 (2) [non-additive].
17. Male maxillary palpomeres: 6 (0); 5 (1); 4 (2); 3 (3); 2 (4) [non-additive].
18. Male labial palpomeres: 3 (0); 2 (1); 1 (2) [non-additive].
19. Female mesosoma: segments separate (0); only pronotum mobile (1); mostly fused (2) [non-additive].
20. Female pronotum: short in dorsal view (0); visible (1); elongate (2) [non-additive].
21. Pronotal turbercles: absent (0); present (1).
22. Epicnemium: visible (0); absent (1).
23. Female forecoxae: short (0); elongate (1).
24. female trochanters: short (0); elongate (1).
25. Female foretarsi: not chelate (0); chelate (1).
26. Female foredistitarsus: without lamellae (0); one lamella (1); lamellae (2) [non-additive].
27. Female foreleg first claw: small (0); enlarged (1).
28. Enlarged claw teeth: absent (0); one (1); median & distal row (2) [non-additive].
29. Female foreleg second claw: present (0); rudimentary (1); absent (2).
30. Midtibial spurs: two (0); one (1); none (2) [non-additive].
31. Hindtibial spurs: two (0); one (1).
32. Male paramere: without dorsal process (0); with dorsal process (1).

ter conflict occurs in the four cladograms underlying the consensus. Successive weighting with the consistency index stabilizes on three cladograms from the initial set of four, the consensus of which is more resolved by showing Dryininae, Transdryininae and Gonatopodinae together as a clade. Implied weighting resulted in three cladograms, the consensus of which is the same as that from successive weighting.

It is seen that both female and male characters support terminals (subfamilies) and clades, hence female and male characters can indeed be combined and species 'affinities' investigated. However, the resolution of the consensus tree is not very satisfactory. As might be expected, the subfamilies wherein the female has chelate foretarsi form a clade; this modification is an outstanding synapomorphy. The fossil Laberitinae, for which the females are unknown, is placed as the sister-group of Anteoninae because of the short forewing R1 (character no. 2), and the fact that scores for female characters are missing values. The taxon is plesiomorphic in its tibial spur formula, thus its placement in Fig. 4 might well be an artifact of lack of information, specifically the 79% missing values scored for it in Table 4. The inclusion of such fragmentary fossils in an analysis is not at all straightforward (Nixon, 1996), but in this case deletion of the taxon does not change the consensus otherwise. Dryininae, Transdryininae, Gonatopodinae and Apodryininae + Plesiodryininae form a clade, based largely on female modifications. Apodryininae + Plesiodryininae with wingless females, are sister-groups. Thus, what grouping information is retained in the consensus tree resides primarily in female characters. However, most of the characters, female or male, are in conflict. Most of the steps plotted on the consensus tree in Fig. 4 are convergent, but this is also true of all of the underlying cladograms. Most of the characters are polymorphic, and all of the subfamilies have either polymorphisms or missing values, or both. This calls into question the characters that are used to distinguish these subfamilies: if the characters are polymorphic, then the taxa 'distinguished' by the characters are less useful, as the names do not efficiently convey the character information. The whole subfamily classification should be reconsidered. This should be done in the context of a comprehensive cladistic analysis of the genera of Dryinidae. Prior to the revision by Olmi (1984), just four subfamilies were generally recognized within Dryinidae: Aphelopinae, Anteoninae, Dryininae and Gonatopodinae. Based on the results summarized in Fig. 4, there could be no return to that system: Olmi's other subfamilies could not be accomodated within those four traditional subfamiles by simple synonymy, for example. Analysis at the level of genera would divide taxa (subfamilies) that are variable for informative characters into

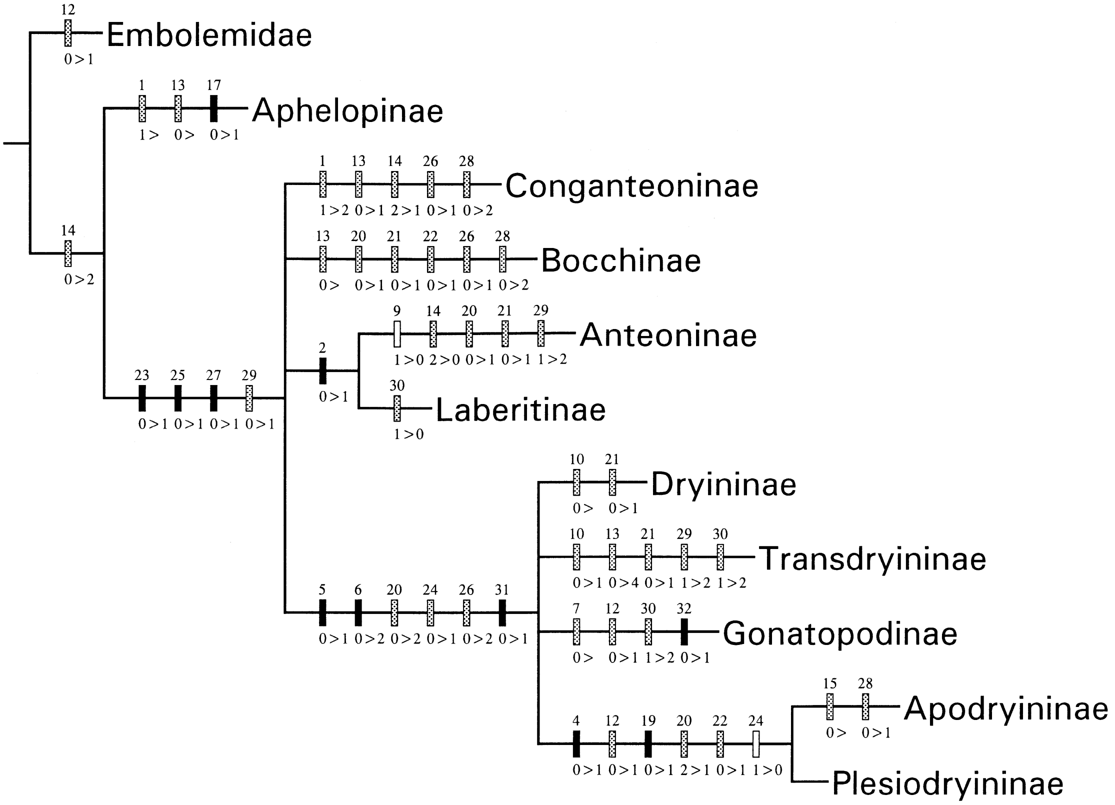

Fig. 4 Consensus tree for subfamilies of Dryinidae. Plotting conventions are as in Fig. 1, but note that steps within polymorphic terminals are usually not plotted. Where there must be a change from the ancestral condition, this is indicated simply by a '>' following the primitive state.

groups (genera) in which more of the pertinent states were of constant distribution, at least potentially improving the interpretability of the results (Nixon and Davis 1991). A cladistic analysis at the generic level is necessary for a reclassification.

The results of such an analysis are also necessary for testing Olmi's (1994: 29–32) scenario for the evolution of female characteristics as adaptations to host capture. A cladogram is necessary for establishing polarity, which tests adaptation, and establishing relative phylogenetic origin of features, which tests causal relationships among those features (for recent general review see Grandcolas *et al.* 1994, 1997).

A cladogram is likewise necessary for critical investigation of the historical biogeography of the Dryinidae, and for much the same reasons (see review by Humphries and Parenti 1986). Distributional data, when expressed cladistically as area cladograms, may be interpreted when compared to similarly organized, but independent, geological data. Such approaches as regression analysis of species number on distances among islands and continents (Olmi 1990) may give some insight into the ecology of those species, but mere similarity of the species fauna from one island to another obviously says less about the evolution of their distributions than would partitioning that similarity into primitive and derived.

Bethylidae

The Bethylidae are one of the largest families in Chrysidoidea, with more than 1800 species worldwide listed in the catalog by Gordh and Moczar (1990). These wasps are parasitoids of Coleoptera and Microlepidoptera, and rarely even Hymenoptera. The host may be repositioned, and some species even construct a primitive nest. Many species are gregarious, and female brood care and cooperation in subduing prey have been observed. Several species have been used in biological control.

There has been some study of the phylogeny of the family (Evans 1964: fig. 1; Sorg 1988), and Polaszek and Krombein (1994) published a numerical cladistic analysis of genera in the subfamily Bethylinae, the first such study in the Chrysidoidea. Four subfamilies are usually recognized, following Evans (1964): Bethylinae, Mesitiinae, Pristocerinae and Epyrinae, the latter divided into three tribes (viz., Epyrini, Sclerodermini and Cephalonomiini). Nagy (1974) proposed two other subfamilies, one fossil and one monotypic, and Argaman (1988a) proposed another monotypic subfamily. These taxa were recognized by Gordh and Moczar (1990), but of them Finnamore and Brothers (1993: 136) stated 'which we consider to fall within the range of those recognized above.' All recent general treatments of Hymenoptera have recognized just four subfamilies (Gauld and Bolton 1988; Naumann 1991; Goulet and Huber 1993; Hanson and Gauld 1995), as did the phylogenetic analysis by Sorg (1988), and that classification is therefore followed here. The subfamilies proposed by Nagy (1974) and Argaman (1988a) are all considered to be Pristocerinae. The female of Nagy's Galodoxinae is winged, unlike other Pristocerinae, but this merely entails a slight change to the diagnosis of the subfamily.

An analysis including all of the subfamilies was presented by Sorg (1988). He studied representatives of all the higher taxa of Bethylidae, and each of the families of Chrysidoidea. He polarized 45 character systems, and presented a cladogram (his fig. 12), pre-rooted with reference to these polarities, and with each component diagnosed by apomorphies (Sorg, 1988: 47–49). The relationships among the subfamilies were those shown in Fig. 5. In addition, Sorg discussed relationships among genus groups in three of the subfamilies, including the tribes within Epyrinae.

Table 5 is a data matrix for the subfamilies and tribes extracted mainly from the diagnosis given by Sorg (1988). I have phrased a few characters differently, and I have not included a few that appeared to represent trends, not definite character differences. An example is scape-flagellum articulation at least weakly bent ('zumindest schwach gewinkelt') and antennae subject to sexual dimorphism ('die Antennen unterliegen dem Sexualdimorphismus'), diagnosing the clade Pristocerinae + (Mesitiinae + Epyrinae). The outgroup is Chrysididae, the sister-group of Bethylidae. The characters are all binary, with the exception of no. 10, the clypeal carina, which is treated as non-additive because it is polymorphic. There is substantial polymorphism in the binary characters as well: more than 16% of the cells in the data matrix of Table 5 are polymorphic.

Table 5 Data on subfamilies of Bethylidae, scored primarily from Sorg (1988). An asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism in Epyrinae (character no. 10 [states 0 1]). That character is treated as non-additive.

	1				5					10					15	
Chrysididae	*	*	1	*	*	0	0	0	0	0	0	0	0	*	*	*
Bethylinae	*	0	*	*	0	0	1	0	0	2	0	0	0	0	1	0
Mesitiinae	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1
Pristocerinae	1	1	1	1	1	1	0	1	1	1	0	1	0	0	0	0
Epyrinae	1	1	1	1	*	0	0	0	0	$	0	0	1	0	*	0

Character list

1. Marginal cell: closed (0); open (1).
2. Forewing RS + M: present or angled where meeting (0); absent (1).
3. First submarginal cell: present (0); absent (1).
4. Forewing 1m-cu: present (0); absent (1).
5. Female wings: present (0); absent (1).
6. Female scape: cylindrical (0); flattened (1).
7. Antennal articulations: close (0); lateral (1).
8. Female eyes: elongate (0); reduced (1).
9. Female ocelli: present (0); absent (1).
10. Clypeal carina: absent (0); present (1); extending onto frons (2).
11. Prontum: short (0); elongate (1).
12. Female tegula: present (0); absent (1).
13. Male metanotum: present (0); reduced medially (1).
14. Sculpture: light (0); heavy (1).
15. Claws: toothed or simple (0); bifid (1).
16. Tergum II: length subequal to other terga (0); elongate (1).

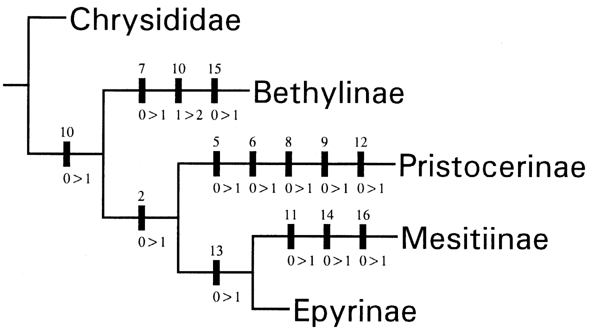

Fig. 5 Cladogram for subfamilies and tribes of Bethylidae. The optimization shown is the 'slow' or delayed transformation option of Clados; plotting conventions are otherwise as in Fig. 1.

Exact analysis of the data in Table 5 with Nona results on one cladogram. The length is 14 steps, with consistency index 1.0 and retention index 1.0; the cladogram is stable to successive weighting with the consistency index, and results from implied weighting. The characters fit the cladogram perfectly, because the homoplastic steps occur in polymorphic characters, and steps occurring in polymorphic characters in terminal taxa are not plotted by Clados.

Fig. 5 shows the cladogram with characters plotted according to the 'slow' or delayed transformation optimization routine of Clados. The relationships depicted accord with those suggested by Sorg (1988). However, Fig. 5 is not strictly supported. The optimization supporting the clade Pristocerinae + (Mesitiinae + Epyrinae) is ambiguous: character no. 2, forewing RS+M absent, could be optimized as ancestral in Bethylidae, because it is polymorphic in the outgroup Chrysididae. Inclusion of other outgroups, or breaking up Chrysididae into components that are constant for this character could lead to strict (unambiguous) support for Pristocerinae + (Mesitiinae + Epyrinae). But the other characters cited by Sorg as supporting this clade, namely reduction in forewing wing veins and an open marginal cell, are all characteristic of Chrysididae as well. That is, the support for Pristocerinae + (Mesitiinae + Epyrinae) is more ambiguous than might at first appear.

No apomorphic steps are plotted for Epyrinae in Fig. 5. Sorg (1988: 49) was unable to cite any apomorphy for this group, stating only: '? (keine Befunde).' Paraphyly of this subfamily is a real possibility, evidently in terms of Mesitiinae, as discussed by Sorg (1988). Sorg (1988: 60–62, fig. 17) treated relationships among the tribes and genera of Epyrinae, and concluded that although the tribes Cephalonomiinia and Sclerodermini could be diagnosed apomorphically, the Epyrini could not, and moreover this tribe includes a number of genera that are evidently paraphyletic, taxonomic wastebaskets ('Sammelgruppierungen'), namely *Epyris* and *Rhabdepyris*. The subfamily and tribal classification of the Bethylidae should therefore be reconsidered, based on a cladistic analysis of all the genera simultaneously.

Chrysididae

The last family of the Chrysidoidea is the jewel, the Chrysididae. Best known of the chrysidoid families, it is also the largest: the revision by Kimsey and Bohart (1991) recorded about 3000 described species. These wasps are parasitoids or cleptoparasites, feeding on the larval provisions of the host. Hosts range from walking stick eggs (Amiseginae and Loboscelidiinae) to sawfly prepupae (Cleptinae) to aculeate wasp and bee larvae (most Chrysidinae) and moth prepupae (Chrysidinae: *Praestochrysis*).

The phylogenetic relationships within Chrysididae are also generally better known than in other chrysidoid families. Bohart and Kimsey (1982), Kimsey (1986) and Kimsey and Bohart (1991) all proposed phylogenetic trees, with characters mapped, for the subfamilies (and tribes, in the latter publication, and they also investigated genera within the higher taxa). Character lists were provided, with primitive and derived state either stated explicitly (Bohart and Kimsey 1982; Kimsey and Bohart 1991) or implied (Kimsey 1986). The trees were prerooted, with reference to these character polarities. Bohart and Kimsey (1982: 9–10) stated of their character list 'Using the above list of characteristics, it is possible to derive a hypothetical ancestor for Chrysididae.' They then went on to do just that, then concluded 'No existing family exhibits all or nearly all of the primitive states listed above. However, more of them are found with the Bethylidae than any other family we have studied.' Their fig. 1 depicted the root as 'Bethylidae Dryinidae.'

There were some differences in the relationships resulting from these three studies (cf. Figs. 6, 8–9). Bohart and Kimsey (1982) recognized seven subfamilies, and treated Allocoeliinae and Chrysidinae as sister-groups, with Parnopinae in turn sister-group to this clade (Fig. 6). Kimsey (1986) corrected one of the characters used by Bohart and Kimsey (1982), pointing out that Allocoeliinae have dentate tarsal claws, like Elampinae, and thus the sole character grouping Parnopinae + (Allocoeliinae + Chrysidinae), claws with more than one tooth or edentate, was invalid. Kimsey (1986) proposed instead that Chrysidinae and Parnopinae are sister-groups, with Allocoeliinae in turn sister-group to this clade (Fig. 8). This scheme of relationships was also concluded by Kimsey and Bohart (1991), however they considered these taxa as tribes with an expanded subfamily Chrysidinae (Fig. 9).

In order to evaluate these studies critically, I have scored the characters in matrix form (Tables 6–8). The root is a hypothetical ancestor, thus prerooting the cladograms, as done in the previous studies.

Bohart and Kimsey (1982: 9) listed 22 characters, with polarity of the states. Their fig. 1 mapped the character states, except that their character 1, number of antennal articles, was not mapped at all (it is invariant in chrysidids), and state 5a, three labial palpomeres, was not mapped (this is ancestral for Chrysididae). I have scored the character matrix of Table 6 from Bohart and Kimsey (1982: 9 and fig. 1), filling in the omissions from fig. 1. The first analysis treated most of the multistate characters as additive, as that seemed to be the implication of the character mapping provided by Bohart and Kimsey (1982: fig. 1). Character nos 4 and 5, which are reduction in the maxillary and labial palpomeres, respectively, were treated as non-additive, because there is a gap in the reduction series.

Exact analysis of the data in Table 6 with either Hennig86 or Nona results in one cladogram, that of Fig. 7. The length is 30 steps, with consistency index 0.93 and retention index 0.93; the cladogram is stable to successive weighting with either the rescaled consistency index or consistency index, and results from implied weighting.

That cladogram differs from that of Bohart and Kimsey (1982: fig. 1, and here as Fig. 6). Elampinae, not Parnopinae, are the sister-group of Allocoeliinae + Chrysidinae. The cladogram of Fig. 6 is one step longer. However, this result is due to the method of coding followed by Bohart and Kimsey (1982). Their character no. 14, whether or not there is sexual dimorphism in the number of metasomal segments, is not independent of characters 15 (number of metasomal segments in female) or 16 (number of metaso-

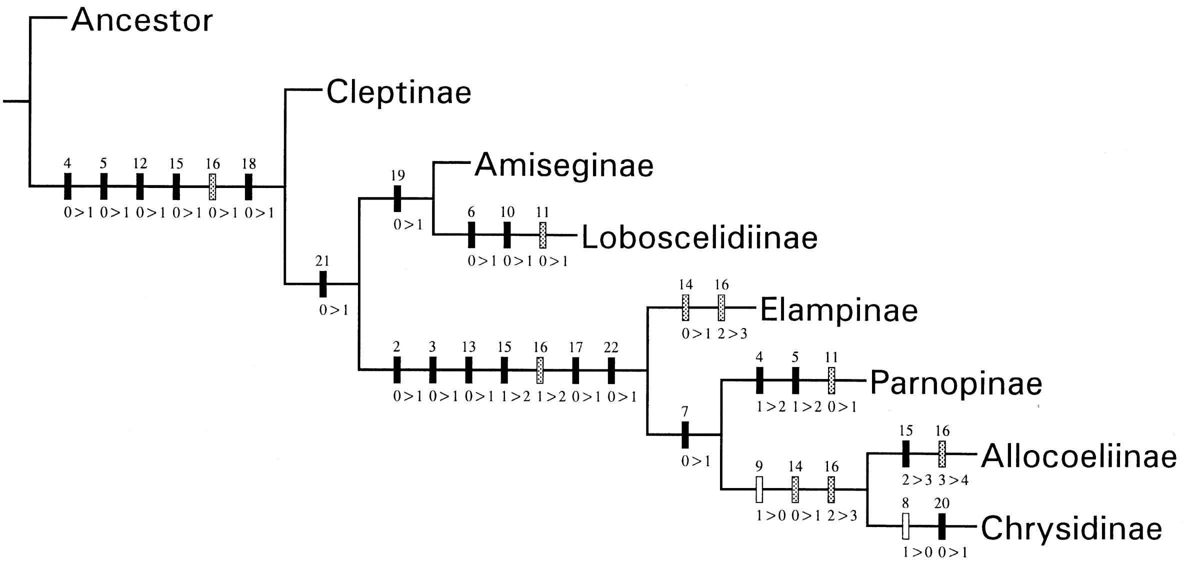

Fig. 6 Cladogram for subfamilies of Chrysididae, redrawn from Bohart and Kimsey (1982), with characters plotted as discussed in the text. Plotting conventions are as in Fig. 5.

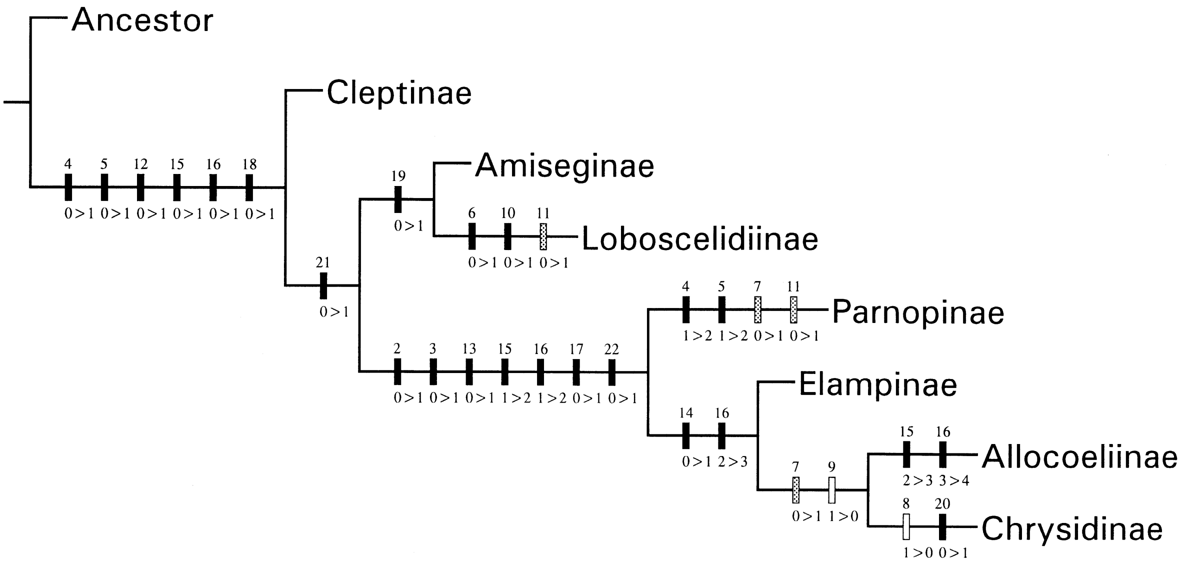

Fig. 7 Cladogram for subfamilies of Chrysididae, based on analysis of characters in Table 6. Plotting conventions are as in Fig. 5.

mal segments in male). If that redundant variable is deleted, and the analyses redone, then the cladogram of Fig. 6 results (length 29 steps, consistency index 0.93, retention index 0.93). The cladograms of both Figs 6 and Fig. 7 result if characters 15–16 are treated as non-additive (length 30 steps, consistency index 0.93, retention index 0.92). Ignoring the nesting of similarity in the reduction series thus results in increased ambiguity – a common outcome of the rather widespread practice of blindly treating all multistate characters as non-additive. However, if these characters are treated as non-additive and character 14 deleted, then just the cladogram of Fig. 6 results. It is clearly the redundant variable that is responsible for the result shown in Fig. 7. Other aspects of the coding presented by Bohart and Kimsey (1982), for example, had the effect of lumping distinct conditions into one state, but the inclusion of the non-independent variable most obviously affected the result. Because Kimsey (1986) and Kimsey and Bohart (1991) corrected and augmented the characters, recoding of Bohart and Kimsey's (1982) list is

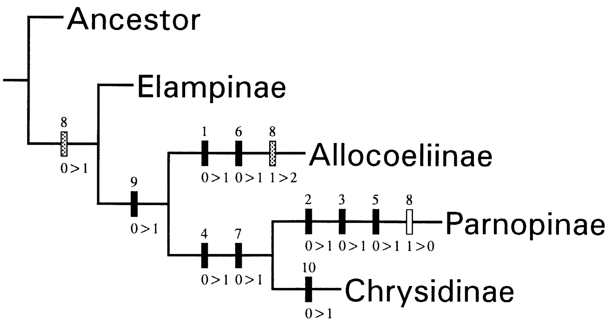

Fig. 8 Cladogram for higher subfamilies of Chrysididae, redrawn from Kimsey (1986), with characters plotted as scored in Table 7. Plotting conventions are as in Fig. 5.

not pursued here (the interested reader should see the discussion in Pogue and Mickevich 1990).

Kimsey (1986: table 1) listed derived states for 12 binary characters, which were mapped on her fig. 20. The characters were some of the same ones used by Bohart and Kimsey (1982), but there were some additions, and the states of the claws were corrected, as noted above. These characters are scored in Table 7. Kimsey's characters nos 8–10 are combined in Table 7; they were respectively whether the external metasomal terga were four in males and three in females, three in both sexes, or two in both sexes. These variables are not independent of one another, as implied by Kimsey's nonadditive binary coding (see discussion in Pogue and Mickevich 1990).

Exact analysis of the data in Table 7 with either Hennig86 or Nona results in one cladogram, that of Fig. 8. The length is 12 steps, with consistency index 0.91 and retention index 0.75; the cladogram is stable to successive weighting with either the rescaled consistency index or consistency index, and results from implied weighting. Kimsey's revised placement of Allocoeliinae is upheld by this reanalysis.

Kimsey & Bohart (1991: 45–50) provided a phylogenetic discussion of 43 characters, which were mapped on their fig. 10. The characters were some of the same ones used by Bohart & Kimsey (1982) and Kimsey (1986), with a number of additions, and some of the characters used by Bohart & Kimsey (1982) were excluded. Kimsey and Bohart's (1991) characters are scored in Table 8. Several characters are combined in Table 8: their characters nos 18–20 (states of the tegula), 25–26 (claw dentition), 29–31 (metasomal segments), 35–36 (rim of metasomal Tergum III), 38–39 (states of the digitus) and 41–43 (host). In each case, non-additive binary coding implied independence of what are clearly non-independent character states. The recoding reduced to 34 characters in Table 8. All of the polymorphic multistate characters are treated as non-additive.

Exact analysis of the data in Table 8 with Nona results in one cladogram, that of Fig. 9. The length is 50 steps, with consistency index 0.94 and retention index 0.91; the cladogram is stable to successive weighting with the consistency index, and results from implied weighting. The cladogram also results from analysis with Hennig86, with

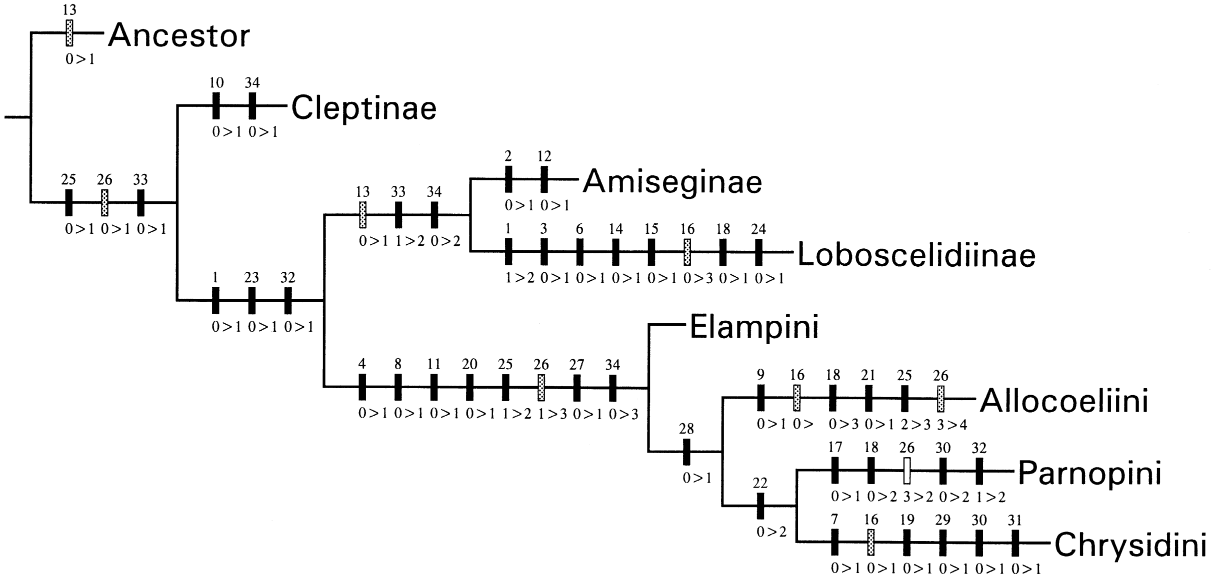

Fig. 9 Cladogram for subfamilies and tribes of Chrysididae, with characters from Kimsey and Bohart (1990) plotted as scored in Table 8. Plotting conventions are as in Fig. 5.

Table 6 Data on subfamilies of Chrysididae, scored from Bohart and Kimsey (1982: 9 and fig. 1). Multistate characters are treated as additive except as noted, and see text for discussion.

	1 5 10 15 20
Ancester	0000000110000000000000
Cleptinae	0001100110010011010000
Amiseginae	0001100110010011011010
Loboscelidiinae	0001110111110011011010
Elampinae	0111100110011123110011
Parnopinae	0112201110111022110011
Allocoeliinae	0111101100011134110011
Chrysidinae	0111101000011123110111

Character list

1. Antenna: 13 articles (0); fewer (1).
2. Tongue: lying flat in oral fossa (0); with basal angle or fold (1).
3. Cardo: small strip (0); elongate rod or plate (1).
4. Maxillary palpomeres: 6 (0); 5 (1); 1 (2) [non-additive].
5. Labial palpomeres: 4 (0); 3 (1); absent (2) [non-additive].
6. Prothorax: freely moveable (0); fused to mesothorax (1).
7. Claws: unidentate (0); more than one tooth or edentate (1).
8. Forewing discal cell: complete (0); incomplete (1).
9. Forewing marginal cell: closed, or RS extending half cell length (0); RS less than half cell length (1).
10. Pterostigma: present (0); absent (1).
11. Tegula: covering forewing base (0); covering both wing bases (1).
12. Metanotum: laterally rounded (0); laterally carinate or dentate (1).
13. Propodeum: dorsally elongate (0); shortened, subtriangular (1).
14. Metasomal terga number: sexually dimorphic (0); equal in the sexes (1).
15. Female terga 6 (0); 4 (1); 3 (2); 2 (3).
16. Male terga: 7 (0); 5 (1); 4 (2); 3 (3); 2 (4).
17. Metasomal sterna: convex (0); flat or concave (1).
18. Sting: present (0); reduced, lancets and sheath in ovipositor tube (1).
19. Ovipositor tube: large & robust (0); slender & needlelike (1).
20. Tergum III: evenly curved (0); with subapical pit row or groove (1).
21. Digitus: lobate (0); elongate or absent (1).
22. Hosts: harmless (0); harmful (1).

Table 7 Data on higher subfamilies of Chrysididae, scored from Kimsey (1986: table 1 and fig. 20). The multistate character is treated as additive.

	1 5 10
Ancestor	0000000000
Elampinae	0000000100
Allocoeliinae	1000010210
Parnopinae	0111101010
Chrysidinae	0001001111

Character list

1. Tingue length: equal in the sexes (0); sexually dimorphic (1).
2. Maxillary palpomeres: 5 (0); fewer (1).
3. Labial palpomeres: 3 (0); fewer (1).
4. Metanotum: without lateral teeth (0); laterally dentate (1).
5. Tegula: covering forewing base (0); covering both wing bases (1).
6. Tegula size: large (0); reduced (1).
7. Claws: dentate (0); edentate (1).
8. Metasomal terga: four in males, three in females (0); three in both sexes (1); two in both sexes (2).
9. Spiracles of Terga II-V: not on laterotergite (0); on laterotergite (1).
10. Tergum III: apically smooth (0); with subapical pit row (1).

Table 8 Data on subfamilies and tribes of Chrysididae, scored from Kimsey and Bohart (1990: 45–50). An asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism. All multistate characters that are polymorphic are treated as non-additive; multistate characters are otherwise additive except as noted. The subset polymorphisms are as follows: Cleptinae, character no. 16 [states 0 3]; Amiseginae, 16 [0 3]; Elampini, 22 [0 1]; Allocoeliini, 16 [2 3].

	1 5 10 15 20 25 30
Ancester	0000000000001000000000000000000000
Cleptinae	000000000100000$000000001100000011
Amiseginae	110000000001100$000000101100000122
Loboscelidiinae	2010010000001113010000111100000122
Elampini	100100010010000000*10$102310000113
Allocoeliini	100100011010000$030110103411000113
Parnopini	1001000100100000120102102211020213
Chrysidini	1001*011001000010011021023111111113

Character list

1. Scapal basin: absent (0); present (1); frontal projection (2).
2. Malar sulcus: absent (0); present (1).
3. Antennal position: inserting low on face (0); inserting midface (1).
4. Genal carina: absent (0); present (1).
5. Transfrontal carina: absent (0); present (1).
6. Cervical projection: absent (0); present (1).
7. Preoccipital carina: absent (0); present (1).
8. Tongue: flat short (0); protruding, long & slender (1).
9. Tongue dimorphism: absent (0); present (1).
10. Pronotum: quadrate, short collar (0); narrowed, broad collar (1).
11. Pronotal lobe: adjacent to tegula (0); separated (1).
12. Pronotal pit: absent (0); present (1).
13. Prosternum: exposed (0); obscured by propleura (1).
14. Prothorax: freely moveable (0); fused to mesothorax (1).
15. Tegular clip: absent (0); present (1).
16. Scrobal sulcus: short, shallow, oblique (0); broad, horizontal (1); broad pit (2); absent (3) [non-additive].
17. Epimeral plate: absent (0); present (1).
18. Tegula: covering forewing base (0); covering both wing bases, enlarged (1); covering both wing bases, subovoid (2); reduced (3) [non-additive].
19. Scutellar lobe: absent (0); present (1).
20. Metapleural carina; absent (0); present (1).
21. Propodeal angles: horizontal (0); oblique, broad or lobulate (1).
22. Claws: unidentate (0); more than one tooth (1); edentate (2) [non-additive].
23. Forewing RS + M: originating nearer base of M (0); originating near apex of M (1).
24. Wing venation reduction: not extreme (0); pterostigma, C, cu-a & hindwing veins absent (1).
25. Female terga: 6 (0); 4 (1); 3 (2); 2 (3).
26. Male terga: 7 (0); 5 (1); 4 (2); 3 (3); 2 (4).
27. Metasomal sterna: convex (0); flat or concave (1).
28. Metasomal spiracles: not on laterotergites (0); on laterotergites (1).
29. Tergum III: evenly curved (0); with subapical pit row or traces (1).
30. Tergum III rim: smooth (0); dentate or angulate (1); thickened, with denticles & foveae (2) [non-additive].
31. Sternum II spots: absent (0); present (1).
32. Digitus: lobate (0); elongate (1); absent (2) [non-additive]
33. Ovipositor tube: absent (0); large & robust (1); slender & needlelike (2).
34. Hosts: Lepidoptera or Coleoptera prepupae (0); Symphyta prepupae (1); Phasmida eggs (2); Aculeata (3) [non-additive].

the polymorphisms treated as missing values, and is stable to successive weighting with the rescaled consistency index.

Kimsey and Bohart's (1991) scheme of relationships is upheld by this reanalysis. But note that, of all the higher taxa, Elampini have no apomorphic steps plotted in Fig. 9. Kimsey and Bohart's (1991: fig. 10) did not plot two apomorphies as supporting Elampini, but these were their characters no. 26, claw dentition, and 31, metasomal segment number. Neither was independent of other characters, and tarsal claws in any event are polymorphic within Elampini, while Elampini and Chrysidini have the same number of metasomal segments. All of the other subfamilies and tribes are evidently monophyletic, but Elampini may be paraphyletic. Phylogenetic relationships within Chrysidinae should therefore be reinvestigated, by means of a cladistic analysis of all the genera in the subfamily, to settle the status of the tribes, which may require reclassification. Kimsey and Bohart (1991) discussed generic relationships within each tribe, and this could be extended by combining all these genera into a single, simultaneous analysis.

In this context, the description by Antropov (1995) of a new tribe, Kimseyini, monobasic for a new monotypic genus, is dubious. This tribe is distinguished from Elampini by having reduced forewing venation, loss of propodeal teeth, simple claws, and being covered with long hairs while lacking metallic sheen. All of these characters are derived (and the claws and metallic sheen variable in Elampini), thus, Elampini are distinguished solely by the absences of the derived characters of Kimseyini. If the monophyly of the tribe was questionable before, recognition of Kimseyini does not seem to resolve the matter favorably. Kimsey and Bohart (1991: 153–158 and fig. 51) provided a phylogenetic discussion and tree for genera of Elampini, and this should be extended to include *Kimseya* as well. But as noted above, it would be desirable to do so in the course of an analysis of all genera of Chrysidinae.

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