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Phylogeny and classification of the Signiphoridae (Hymenoptera: Chalcidoidea)

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ABSTRACT. A data set consisting of twenty-eight anatomical characters scored for twenty-eight terminal taxa representing the world fauna of Signiphoridae was analysed using parsimony and compatibility methods. The Coccophaginae (Aphelinidae) and the Azotinae (Aphelinidae) were used as outgroups to establish polarity of character state changes. Relationships of Signiphoridae to other Chalcidoidea are discussed. Several multistate characters were treated in the parsimony analyses either as unordered or as ordered into transformation series using additive binary coding, which in some cases drastically reduced the number of equally parsimonious solutions. Monophyly of Signiphoridae is supported by seven synapomorphies. Four genera, *Chartocerus*, *Thysanus*, *Clytina* and *Signiphora*, are recognized within Signiphoridae based on synapomorphies. *Rozanoviella* **syn.n.** and *Kerrichiella* **syn.n.** are synonymized under *Signiphora*. Species of *Signiphora* are further assigned to four species groups, three of which are demonstrably monophyletic. Nine species or subspecies are transferred to *Chartocerus* from *Signiphora* (*australicus* **comb.n.**, *australiensis* **comb.n.**, *australiensis orbiculatus* **comb.n.**, *beethoveni* **comb.n.**, *corvinus* **comb.n.**, *funeralis* **comb.n.**, *reticulata* **comb.n.**, *ruskini* **comb.n.**, *thusanoides* **comb.n.**), one species to *Thysanus* from *Signiphora* (*melancholicus* **comb.n.**), and one species to *Signiphora* from *Kerrichiella* (*coleoptratus* **comb.n.**). A key to genera of Signiphoridae and species groups of *Signiphora* is presented. A diagnosis, relevant nomenclatural history, and a list of included species are given for each genus and species group, and the biology and distribution of each is summarized.

Introduction

Students beginning to study the parasitic Hymenoptera are often dismayed to discover the instability that has characterized family level classification in the superfamily Chalcidoidae. If one consults the major treatments of the superfamily in the literature, one can find a plethora of family and subfamily classifications. Major nomenclatural changes often have been proposed with little or no justification beyond a statement of the form: 'this group seems to be related to . . .'. I agree with Heraty & Darling (1984), that this unfortunate situation can be resolved only by careful study of definable

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lineages, or monophyletic groups in the sense of Hennig (1966). Once we have learned to recognize and characterize monophyletic lineages, we can begin to construct a natural classification of Chalcidoidea.

This paper summarizes such a study of one distinct group of chalcidoids, the family Signiphoridae. The Signiphoridae are a cosmopolitan group of parasites of Homoptera and Diptera. They are small in size (body length ranges from about 0.5 mm to about 2.0 mm) and many species are not commonly collected. These factors make study of the group difficult, and as a result, signiphorids have been among the least studied chalcidoids. No previous workers approached the study of relationships within the family with an explicitly phylogenetic methodology.

Several authors produced more or less comprehensive treatments of species or reviewed the genera and discussed relationships. Among these, the most useful are the works of Girault (1913a), Kerrich (1953), De Santis (1968), Rozanov (1965), Subba Rao (1974) and Quezada *et al.* (1973). Domenichini (1953, 1954) provided valuable studies of various aspects of signiphorid morphology. As noted by Rozanov (1965), the Neotropical fauna of Signiphoridae is particularly rich and until now has received relatively little attention.

For a small family, the Signiphoridae have endured more than their share of nomenclatural instability. Various workers treated the group as a family, or as a subfamily in the Encyrtidae, Aphelinidae or Eulophidae. The group was divided into from one to seven genera and a variety of generic schemes were proposed. Particularly troublesome has been the use of two different family names. The first family-group name was Signiphorinae, erected by Howard (1894) to contain *Signiphora* Ashmead (1880). Peck (1951) synonymized *Signiphora* Ashmead under the older name *Thysanus* Walker (1840) and changed the family name to Thysanidae. This course was followed by most (but not all) workers until Rozanov (1965) presented a detailed argument for maintaining *Thysanus* and *Signiphora* as distinct. Following Rozanov (1965) most (but not all) used the family name Signiphoridae. A detailed account of this nomenclatural matter is presented in Woolley (1986).

My research involves revisionary study of the Signiphoridae, particularly of the rich Neotropical fauna. Revisions for New World *Signiphora* and of the world species of *Thysanus* and *Clytina* Erdös are nearly complete. In connection with this work, I reviewed the world species. Study of Neotropical *Signiphora*, in particular, presented certain problems for classification. Two groups of Neotropical species did not seem to fit into any of the genera as previously defined. One group seemed to be intermediate between *Rozanoviella* Subba Rao and *Signiphora*. Another group seemed to be similar to, but distinct from, *Rozanoviella* as previously defined. The genus *Kerrichiella* Rozanov apparently was related to, but distinct from, *Rozanoviella* and the two groups of species just mentioned. These and other problems prompted a phylogenetic analysis of the entire family. The objectives of the study were fourfold: (1) to analyse the morphology of signiphorids and determine the relationships of the group to other Chalcidoidea, (2) to evaluate the evidence for monophyly of the Signiphoridae, (3) to evaluate the existing classifications of signiphorids from a phylogenetic perspective, (4) to incorporate into the classification previously unstudied Neotropical species.

In attempting to accomplish these goals, certain methodological problems were encountered. As discussed in detail by Gauld & Mound (1982), students of parasitic Hymenoptera and certain other insect groups often find homoplasy (parallelisms or reversals) in phylogenetic analyses. The studies reported here are no exception. Gauld & Mound (1982), Throckmorton (1965) and others speculated on the evolutionary phenomena that may result in lineages characterized by frequent parallelisms and reversals. These authors provided some recommendations for analysis under various conditions. The analysis that follows was complicated by homoplastic data. Several methods were used in an attempt to sort out the reliable indicators of phylogenetic relationship.

I use the terminology of Gibson (1985, 1986) for thoracic structures. Mesosoma refers to thorax and propodeum. Tergal numbering refers to metasomal terga: T1 is the tergum immediately posterior to the propodeum, T7 bears the spiracles, and so forth. Numbering of sterna refers to metasomal sterna: in females the posterior-most sternum (hypopygium) is S6, in males the posterior-most sternum is S8.

The outgroup

Historically, the Signiphoridae have been considered to be closely related to two families in the Chalcidoidea, the Encyrtidae and the Aphelinidae. Ashmead (1900) first placed the subfamily Signiphorinae in the Encyrtidae and this placement was followed by many authors (Schmiedeknecht, 1909; Girault, 1913a, 1915, 1916a, 1929; Brèthes, 1914; Malenotti, 1918; Crawford, 1913; Richards, 1935; Ferrière, 1953; Yoshimoto, 1965; Riek, 1970; Gordh, 1979). However, none of these authors presented a detailed justification for the union of the two groups, or discussed morphological similarities between the Signiphoridae and Encyrtidae that might set them apart from other Chalcidoidea. On the other hand, Howard (1895) placed *Thysanus* in the subfamily Aphelininae, a scheme that was then followed by several workers (Dalla Torre, 1898; Mercet, 1912; Girault, 1913b; Ashmead, 1904; Schmiedeknecht, 1909) until Mercet (1917) brought *Thysanus* into the 'Signiphorinos'. Kurdjumov (1916) placed his genus *Xana* in the Aphelininae; *Xana* was then transferred to the Signiphoridae by Nikol'skaya (1950). Most recent authors have treated the Signiphoridae at the family level although Gordh (1979) reduced both the Aphelinidae and Signiphoridae to subfamily status and included them in the Encyrtidae.

The Encyrtidae have been regarded as a member of a lineage that includes the Tanaostigmatidae and the Eupelmidae (Trjapitsyn, 1977; LaSalle, 1987). These groups are characterized (with the exception of male Eupelminae) by a convex and enlarged part of the mesopleuron that Gibson (1986) called the acropleuron. LaSalle (1987) provided an explicit hypothesis for the monophyly of a lineage composed of the Encyrtidae, Eupelmidae and Tanaostigmatidae, based on proposed synapomorphies. He also provided evidence that Tanaostigmatidae and Encyrtidae together form a monophyletic lineage, and the relationship of these taxa is further discussed in terms of apomorphic characters by LaSalle & Noyes (1985). Gibson (personal communication) believes that Eupelmidae is probably a grade composed of at least three monophyletic lineages. In any case, Encyrtidae are characterized by a number of synapomorphies including anterior migration of the cerci with concomitant modification of the medial and lateral portions of T4–T7, the separation of the outer plates of the ovipositor from the dorsal portion of the syntergum (T8+T9) (Trjapitsyn, 1968), and a distinctive structure of the thorax in which notauli usually are lacking and in which the broadly triangular axillae meet at the midline and lie posterior to the transverse transscutal sulcus. Of these characteristics, only the lack of notauli is found in Signiphoridae. There would seem to be little basis for the inclusion of signiphorids in either Encyrtidae or the eupelmid–encyrtid lineage.

Several authors (e.g. Gordh, 1979; Riek, 1970; Mercet, 1929; Compere & Annecke, 1961) either classified the Aphelinidae as a subfamily of Encyrtidae or proposed a close relationship between the two groups. For example, Compere & Annecke (1961) mention the expanded mesopleuron found in both *Coccobius* Ratzeburg (Aphelinidae) and encyrtids. Gibson (personal communication) determined that the expanded mesopleuron of *Coccobius* consists of enlarged acropleuron, as found in many eupelmids and all tanaostigmatids and encyrtids. However, this configuration of the acropleuron is only rarely found in aphelinids and probably represents a convergent modification of internal musculature due to selection for jumping ability (Gibson, 1986). A convincing case for a close relationship of Encyrtidae and Aphelinidae has yet to be made.

Domenichini (1954) made a significant contribution to the understanding of the affinities of Signiphoridae by analysing the structure of *Thysanus* and *Chartocerus* in some detail and comparing various aspects of signiphorid anatomy with that of Encyrtidae and Aphelinidae. In particular, Domenichini (1954) directed his attention to the thorax. He found little morphological evidence to support a close relationship between the Encyrtidae and Signiphoridae, except for the lack of notauli as discussed above. He did find certain similarities in structure between the Aphelinidae and Signiphoridae, the most notable of which was an undivided prepectus continuing across the venter between the prosternum and ventral mesepisternum (*sensu* Gibson, 1986). However, the ventral portion of the prepectus is broadly fused with the ventral mesepisternum in all signiphorids. Yashnosh (1976) discusses both a 'divided' and an 'undivided' prepectus in Aphelinidae, but my

studies indicate that in many aphelinids the prepectus is fused with the ventral mesepisternum as in signiphorids. The prepectus/mesepisternal complex of Aphelinidae requires further study, now underway in my laboratory. In addition, the prepectus of signiphorids is connected by an internal apodeme to the pronotum but in the aphelinids the prepectus is connected by a different apodeme to the mesoscutum (Domenichini, 1954). Another similarity between aphelinids and signiphorids mentioned by Domenichini (1954) was the juxtaposition of the posterior margin of the mesotrochantinal plate (*sensu* Gibson, 1986) with the anterior margin of the metasternum in the signiphorids and aphelinids, whereas in encyrtids, eupelmids and tanaostigmatids these two sclerites are separated by a wide, membranous area. Further, he noted that the structure of the mesopleuron is very different in the three families. In encyrtids, the acropleuron is large and convex and both the mesepisternum and mesepimeron are quite reduced (Gibson, 1986). In general, in Aphelinidae the acropleuron is a small anterodorsal region of the mesopleuron and the mesepisternum and mesepimeron are subequal and subrectangular. The mesopleuron has a similar configuration in Signiphoridae. The acropleuron is not greatly enlarged, the mesepimeron is subrectangular, and the upper and lower mesepisterna both have a ventral orientation (ac, eps_2, epm_2: Fig. 3). In summary, Domenichini (1954) recommended that the three groups continue to be recognized as distinct families.

Quezada *et al.* (1973) presented new evidence for their view that the Signiphoridae are more closely related to the Aphelinidae than to any other group of Chalcidoidea. In particular, the genus *Aphytis* Howard was compared to signiphorids. Among the points of similarity noted were a reduced number of funicular segments and an undivided club in the antenna. Several unusual attributes of the mesosoma of Signiphoridae were believed to have counterparts in *Aphytis*. In Signiphoridae the metanotum bears a median sclerite set off by two oblique sutures and a small anteromedial apodeme. The mesosoma is also characterized by a 'relatively long propodeum with a cut-off triangular median salient' (Quezada *et al.*, 1973). The anteromedial apodeme is present in *Aphytis*, but in *Aphytis* and all other Aphelinidae that I have examined, if analogous medial areas are present in the metanotum and propodeum, they are set off from lateral areas by a difference in sculpture or convexity, not by sulci as in Signiphoridae (see also discussion for character 9 below).

At least two additional characteristics indicate a close relationship of the Signiphoridae and Aphelinidae. The first is a broad union of the metasoma and mesosoma and the modification of the first tergum (petiole of most chalcidoids) to a transverse dorsal sclerite at the base of the gaster. As noted below (character 11), the first tergum is further modified in some Signiphoridae. However, the broad union of the mesosoma and metasoma is found in other chalcidoid groups, for example the Trichogrammatidae and some genera of Encyrtidae and Mymaridae. Broad union of the mesosoma and metasoma usually is accompanied by the extension of the endophragma into the metasoma, a condition found in both Signiphoridae and Aphelinidae. A second characteristic common to many Aphelinidae (other than Eriaporinae, some *Coccophagus* spp., etc.) and Signiphoridae is the lack of a postmarginal vein on the forewing.

Some evidence supports a possible sister group relationship between the Signiphoridae and the aphelinid subfamily Azotinae, containing *Azotus* Howard and *Ablerus* Howard. In the Azotinae and Signiphoridae narrow apodemes project forward from the anterolateral angles of sterna 3–6 in females (sta: Fig. 4). Such apodemes have not been noted in other Chalcidoidea. Another possible synapomorphy involves the conformation of the terminal terga. In most Chalcidoidea the eighth and ninth terga have become fused to form a single sclerite, often referred to as the syntergum (Domenichini, 1953, and others), which bears the cerci. Most workers have followed the interpretation of Snodgrass (1941), as has Domenichini (1953): because the ninth tergum normally bears the cerci in the Symphyta and Ichneumonoidea, the apparent eighth tergum of Chalcidoidea must represent the fusion of T8 and T9. The structure of these terga in Signiphoridae is unusual in that a separate sclerite posterior to the tergum bearing the cerci (T8) is found on the metasoma of all females (Fig. 13) and many males. The eighth tergum is continuous with the outer plates of the ovipositor ventrally and its dorsomedial portion is reduced

to a more or less transverse strip which lies under T7 for the most part. The posterior sclerite is subtriangular or elongate in dorsal aspect. It is separated from T8 by a membranous area most easily visible in cleared whole mounts in which the apical portion of the abdomen has become somewhat distended during preparation. Since cerci are borne on T8, or at least are closely associated with the posterolateral margin of T8, the posterior sclerite in the Signiphoridae cannot be homologous with T9 in Symphyta and Ichneumonoidea. I follow Domenichini (1953) and refer to this sclerite as the epiproct, a neutral term which does not imply homology with similar sclerites in other taxa.

While T8 and T9 are generally united to form a syntergum in the Aphelinidae as in other Chalcidoidea, an epiproct is present in females of *Azotus* and *Ablerus* (as noted by Yashnosh, 1976) with a third transverse sclerite lying in the membranous area between the epiproct and T8 (Fig. 14). In females of these genera the epiproct is subtriangular and the cerci are borne at the posterolateral margins of T8, as in Signiphoridae. The syntergum of male *Ablerus* and *Azotus* is very weakly sclerotized and almost membranous, although a pair of lateral, sclerotized regions are apparent in the anterodorsal region. I found no indication of a separate, sclerotized and well-defined epiproct in males of *Ablerus* and *Azotus*.

Yashnosh (1976) and Compere (1955) state that a separate 'tenth tergum' is present in *Aphelinus* Dalman. My examination of *Aphelinus* material, including the slide-mount preparations of Mr. Compere, has shown this interpretation to be incorrect. In fact, T8 and T9 are clearly connected to form a syntergum in both sexes. However, the dorsomedial portions of the syntergum are set off by membranous areas dorsally and to some extent laterally. In dorsal aspect it may appear that an epiproct is present, but in lateral aspect the broad connection between the dorsomedial portion and the lateral portions (which bear the cerci) is clearly visible.

In order to evaluate the potential sister group relationship between the Signiphoridae and Azotinae it was necessary to examine the taxonomic structure of the Aphelinidae. Yashnosh (1976) made a major contribution to the classification of the Aphelinidae and provided the framework for a phylogenetic interpretation of aphelinid morphology. She recognized seven subfamilies based on the structure of the mesosoma, features of the female metasoma, and on the structure of the male genitalia. She explicitly defined the plesiomorphic and derived conditions for each of the character systems used. I attempted to integrate this evidence into a single phylogenetic hypothesis. Five binary characters were taken from Yashnosh (1976): (1) antennal club entire or segmented, (2) linae calva on forewing present or absent, (3) pronotum entire or divided, (4) epiproct present or absent, (5) male genitalia with or without digiti. I added a sixth character: (6) anterior apodemes present or absent on female sterna, and two characters which indicate the monophyly of Signiphoridae. The characters were scored for Signiphoridae (male *Chartocerus* were treated separately due to character 4 and the seven subfamilies of Aphelinidae. The data were verified by examination of the following taxa: Aphelininae: *Aphelinus mali* Haldeman, *A.semiflavus* Howard; Aphytinae: *Aphytis chilensis* Howard, *A.melinus* DeBach, *Eretmocerus* spp., *Bestiola mira* Nikol'skaya; Azotinae: *Azotus* spp., *Ablerus clisiocampae* (Ashmead); Coccophaginae: *Coccophagus scutellaris* Dalman; Physcinae: *Coccobius testaceus* (Masi), *C.reticulatus* Compere and Annecke; Prospaltellinae: *Encarsia meritoria* Gahan, *E.haitiensis* Dozier, *Aleurodiphilus americanus* DeBach and Rose (*Aleurodiphilus* was synonymized under *Encarsia* by Hayat, 1983), *Bardylis* sp.; Calesinae: *Cales noacki* Howard; Eriaporinae: *Myiocnema comperei* Ashmead, *Myiocnema* sp.

These data were analysed using a parsimony algorithm. Unfortunately, due to homoplasy, the data are not sufficient to resolve the internal structure of Aphelinidae or the problem of relationship between Signiphoridae and Aphelinidae or some part of Aphelinidae. In particular, the data do not provide definitive evidence for a sister group relationship between Azotinae and Signiphoridae although the presence of apodemes on S3–S6 and an epiproct in females do support such a relationship.

Consideration of taxonomic structure in the outgroup is important in cases in which two or more character states in the group under analysis are also present in a hypothetical outgroup. In such cases, a simple comparison will not suffice to determine character polarities and the

problem becomes one of determining the most parsimonious distribution of character state changes in the context of both groups (Farris, 1982). Further complications arise if the taxonomic structure of the outgroup is poorly known (Maddison *et al.*, 1984; Donoghue & Cantino, 1984). This problem is present in this study due to the inability to precisely resolve the relationship of the Signiphoridae and Aphelinidae as discussed above. In particular, three characters used in the analysis of Signiphoridae are polymorphic in both Signiphoridae and Aphelinidae. The best solution was to include a sufficient number of outgroup taxa such that all possible combinations of these characters known to occur in the outgroup were represented. For this purpose, genera representing all of the aphelinid subfamilies were scored for the characters used in the signiphorid analysis. It was found that an outgroup consisting of two aphelinid taxa, the Coccophaginae and the Azotinae, was sufficient to encompass all observed combinations of character states in the outgroup.

Methods

Selection of taxa

This study was done in the context of extensive revisionary work. Many attributes useful in discriminating between species of Signiphoridae are not used in this analysis because they appear to be too plastic within and between groups of species to have any reliable phylogenetic information. Such characters typically involve coloration patterns, lengths or shapes of structures, etc. Characters that appeared to be relatively stable were retained. All species of Signiphoridae known to me were scored for the final character set. In many cases, two or more species were identical with respect to this character set and these species were combined to form a single OTU. A list of the OTUs used and the species that each OTU represents are included as Appendix B.

The nomenclature used for OTUs reflects genera or species groups that have been used in the literature. In particular, the generic nomenclature of Rozanov (1965) and Subba Rao (1974) served as a starting point for this analysis. The prefix ROZN- denotes species that have been assigned to *Rozanoviella*, the prefix THYS- to species of *Thysanus*, the prefix CLYT- to species of *Clytina*, and the prefix SIGN- to species placed in *Signiphora* by those authors. As noted above, one of the purposes of this analysis was to evaluate other potential suprageneric taxa. Therefore, coding of OTUs also reflects my initial hypotheses about previously unrecognized groups of species. Thus, the prefix MEX- refers to species in a potential *mexicana* species-group in *Signiphora*, and the prefix NGEN- to species in a potential new genus containing several undescribed species. Some of these initial impressions about relationships were supported by the analysis and some were not. The OTUs were coded in this manner for convenience only. Final decisions about generic and species group placement were based on the results of the analyses.

Coding of characters

Characters were coded as binary variates (0, 1) or as integer multistate variates (e.g. 0, 1, 2). The rationale for coding each individual character is explained below. In some cases, multistate characters could be ordered *a priori* into a transformation series (morphocline) without ambiguity. In other cases, *a priori* decisions presented problems of interpretation. For example, can one assume that a mandible with two acute teeth must evolve through a mandible with three teeth to reach a mandible with four teeth? Such assumptions impose constraints on the interpretation of character state evolution, which may not be justified. One solution is offered in the PAUP package (discussed below), in which multistate characters can be treated as unordered series, that is, evolution from any particular state to any other is treated as equally likely and counted as a single step. The consequences of treating multistate characters as ordered or unordered series are explored below. Additive binary coding was also used with multistate characters to determine if different state changes showed more homoplasy than others. Additive binary coding was performed on the data set using the FACTOR algorithm contained in the PHYLIP package (discussed below). FACTOR requires that transformation series (character state trees) be specified *a priori*, thus the additive binary coded data set contains implicit assumptions about the evolution of particular states in multistate characters.

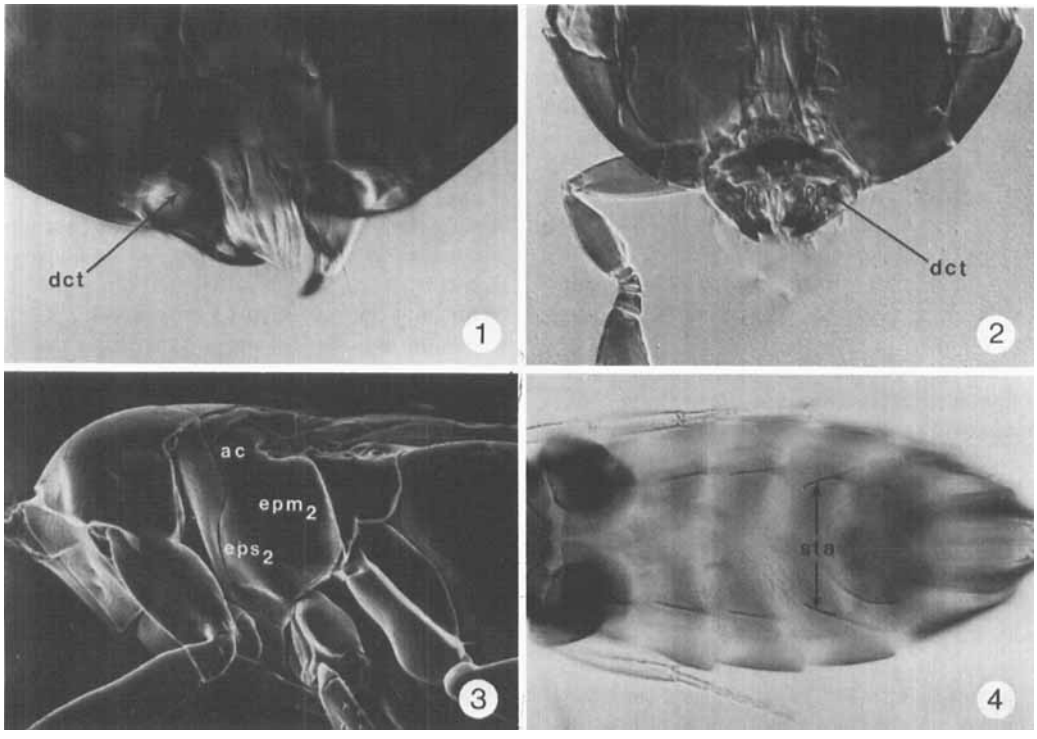
In general, *a priori* decisions concerning the

polarity of morphoclines were unnecessary, as polarization was imposed by outgroup comparisons within each analysis. In some cases, derived states of character are not known to occur in any potential outgroup taxon. Here, *a priori* decisions can be made without difficulty. In cases in which heterogeneity exists for character states both in the outgroup taxa and in the Signiphoridae, I took the approach of searching for the globally most parsimonious solution over both the ingroup and outgroup. If such a solution can be found, it will also be most parsimonious for the ingroup alone (Maddison *et al.*, 1984; Farris, 1982). However, use of outgroup rooting in PAUP allows for results in which ingroup and outgroup relationships are not maintained (i.e. PAUP allows solutions in which a specified ingroup is not monophyletic). This was not a problem with these data because the monophyly of Signiphoridae is well supported, as discussed below. In yet other cases, outgroup comparisons were not possible at all, as character states involved changes in structures found only in the Signiphoridae. That is, assumptions of homology cannot be made for such structures in the outgroup. In these cases, data were scored as missing in outgroup taxa, and the polarity of morphoclines within the Signiphoridae was established on the basis of parsimony. In the description of characters that follows, it may be assumed that (0) represents the assumed plesiomorphic condition (i.e. an *a priori* decision is straightforward) unless it is stated otherwise. In cases in which multistate characters were treated as ordered, the numerical coding reflects the assumed morphoclines.

Characters and character states

In the following description of characters, reference is sometimes made to the presence or condition of particular structures in genera or species groups of Signiphoridae. Some readers may wish to use this section as a reference, therefore the nomenclature used here is consistent with that adopted as a result of these analyses.

1. *Mandibular dentition*. The mandibles of



FIGS 1–4. 1. Mandibles, *Signiphora* sp. nr. *maxima*. 2. Mandibles, *Signiphora merceti*. 3. Mesosoma, lateral aspect, *Chartocerus* sp. 4. Metasoma, *Clytina* sp. (ac: acropleuron, dct: mandibular ducts, eps_2: mesepisternum, epm_2: mesepimeron, sta: sternal apodemes.)

Signiphoridae are well developed and bear from two to four acute teeth. In some species they bear two or three teeth and an oblique dorsal truncation. Dentition was treated as a meristic character. Only the acute teeth were counted, as the presence of oblique truncations is at times ambiguous. Both outgroup taxa have bidentate mandibles.

2. *Mandibular ducts*. The mandibles are hollow and in cleared slide-mounts two or three elongated chitinous processes are visible arising from the distal portion of the inner surface (i.e. from behind the teeth) and projecting into the lumen for half to two-thirds the length of the mandible (dct: Figs 1, 2). The function of these structures is unknown but they appear to be present in all chalcidoids. Khashef (1953) studied the structure of these processes in *Lariophagus distinguendus* Foerster (Pteromalidae). He found that the processes are chitinous and hollow and described a patch of glandular tissue situated in the mandibular lumen between the processes and the ventral inner surface of the mandible. A secretory function for these structures seems likely, but has not been demonstrated. For convenience, I use the term mandibular ducts for these structures. The distal portions of these processes are more or less parallel-sided in most chalcidoids and in most Signiphoridae (dct: Fig. 1), however, in *Thysanus* and in some *Signiphora* spp. the distal portions of the ducts are spherical (dct: Fig. 2). Coding was as follows: ducts parallel-sided (0), ducts with distal portions spherical (1). Due to heterogeneity for this character in the outgroup, it cannot be polarized by a simple outgroup comparison.

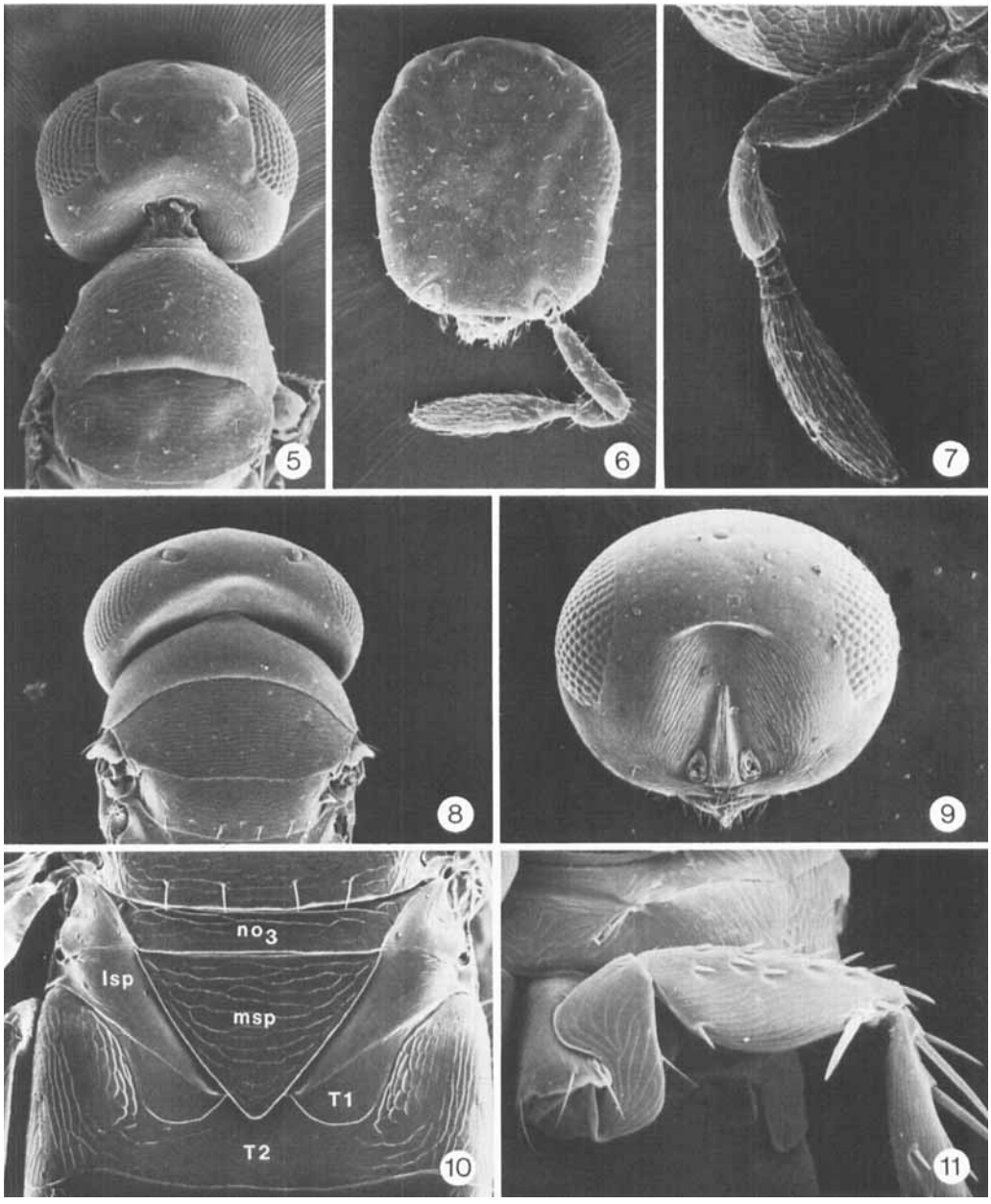
3. *Shape of occipital margin*. The head is more or less spherical in *Thysanus* spp. (except in one undescribed species), and the posterior margin of the vertex in all *Thysanus* and *Clytina* species is broadly rounded (Fig. 5). In other genera of Signiphoridae the head is more or less compressed, appearing hemispherical or lenticular in dorsal aspect (Fig. 8). The posterior margin of the vertex is narrowly rounded in *Chartocerus* species and acute in *Signiphora*. Two character states for the shape of the occipital margin were recognized: broadly rounded (0), narrowly rounded or acute (1). Due to heterogeneity in the outgroup, this character cannot be polarized *a priori*.

4. *Head orientation*. The head is orthognathous and circular in frontal aspect in most Signiphoridae. In *Clytina* the head is subprognathous and elongated dorsoventrally, thus appearing subrectangular in dorsal aspect (Fig. 6). In forms with an orthognathous head the foramen is situated about one half of the distance from the vertex to the ventral margins of the genae and the proboscidial fossa occupies roughly the ventromedial third of the posterior surface of the head. In *Clytina* the foramen is displaced considerably towards the vertex. In addition, in forms with a subprognathous head the hypostomal bridge and anterior tentorial arms are much elongated. Head orientation was treated as a two-state character: orthognathous (0), prognathous (1).

5. *Segmentation of male funicle*. The antennae of Signiphoridae are composed of from four to seven segments: an elongate scape, which is rarely dilated ventrally, an elongate and subconical pedicel, a reduced funicle of from one to four short annelli or ring segments, and a more or less elongate, unsegmented club (Fig. 7). Sexual dimorphism for the number of funicle segments occurs in some species; therefore, funicle segmentation for males and females was treated as two separate characters. The number of funicle segments in the antennae of male Signiphoridae varies from one to four. The number of male funicle segments was treated as an unordered meristic character, or as an ordered character using the following transformation series: 1⟨=⟩2⟨=⟩3⟨=⟩4. In coding antennal segmentation for outgroup species, homology of funicle segments between Signiphoridae and Aphelinidae could not be assumed. For example, *Coccophagus* spp. have a single annellus, a three-segmented funicle, and a three-segmented club. Azotinae have two annelli, a four-segmented funicle, and an unsegmented club. Both taxa have seven flagellomeres, suggesting that the distinction between annelli, funicle and club is artificial within Aphelinidae. Therefore, male and female funicle segmentation for outgroup taxa were scored as missing.

6. *Female funicle*. Coded as male funicle segments with the following exception, no female Signiphoridae are known with a two-segmented funicle, thus the ordered coding was as follows: 1⟨=⟩3⟨=⟩4.

7. *Club segmentation*. The club is elongate and unsegmented in all Signiphoridae (Fig. 7). Coccophaginae have a three-segmented club and



FIGS 5–11. 5. Head, pro- and mesothorax, dorsal aspect, *Thysanus ater*. 6. Head, frontal aspect, *Clytina* sp. 7. Antenna, *Signiphora townsendi*. 8. Head and thorax, dorsal aspect, *Chartocerus* sp. 9. Head, frontal aspect, *Signiphora flavella*. 10. Metanotum, propodeum, and anterior part of metasoma, dorsal aspect, *Signiphora coquilletti*. 11. Middle femur, ventral aspect, *Signiphora flavella*. (lsp: lateral sclerite propodeum, msp: medial sclerite propodeum, no_3: metanotum, T1: first tergum, T2: second tergum.)

Azotinae have an unsegmented club. However, as discussed above, homology of the unsegmented signiphorid and azotine clubs is questionable. Club segmentation was coded as a two-state character: club segmented (0), club unsegmented (1).

8. *Notauli.* Signiphoridae bear no trace of notauli on the mesoscutum (Fig. 8). Most Aphelinidae (and most other Chalcidoidea) bear complete notauli. This character was coded as follows: notauli present (0), absent (1).

9. *Propodeum.* The structure of the propodeum of signiphorids is characteristic and unique in the Chalcidoidea. It is elongate and triangular with a triangular medial portion delimited by sulci from the lateral portions (msp, lsp: Fig. 10). These sulci converge posteriorly and are joined at the posterior midpoint of the propodeum; the point of juncture is either rounded or acutely pointed. In some species these sulci lie underneath of and anterior to the posterior margins of the medial triangular sclerite, thus the posterior portion of the medial sclerite forms a salient and lamelliform process that projects over the first and second terga to some degree. Three character states for the propodeum form a straightforward morphocline: propodeum without a medial sclerite (0), a propodeum with a medial sclerite that lacks a posterior process (1), propodeum with a medial sclerite that bears a posterior process (2).

10. *Axillae.* In cleared slide-mounts of Signiphoridae two oblique internal carinae are visible which set off triangular areas that are apparently homologous with the axillae of other chalcidoids. However, these areas are not delimited by external sulci, as seen, for example, in scanning electron micrographs. In the outgroup taxa, the axillae are prominent and set off by external sulci. The presence of external sulci delimiting axillae was coded as a binary character: present (0), absent (1).

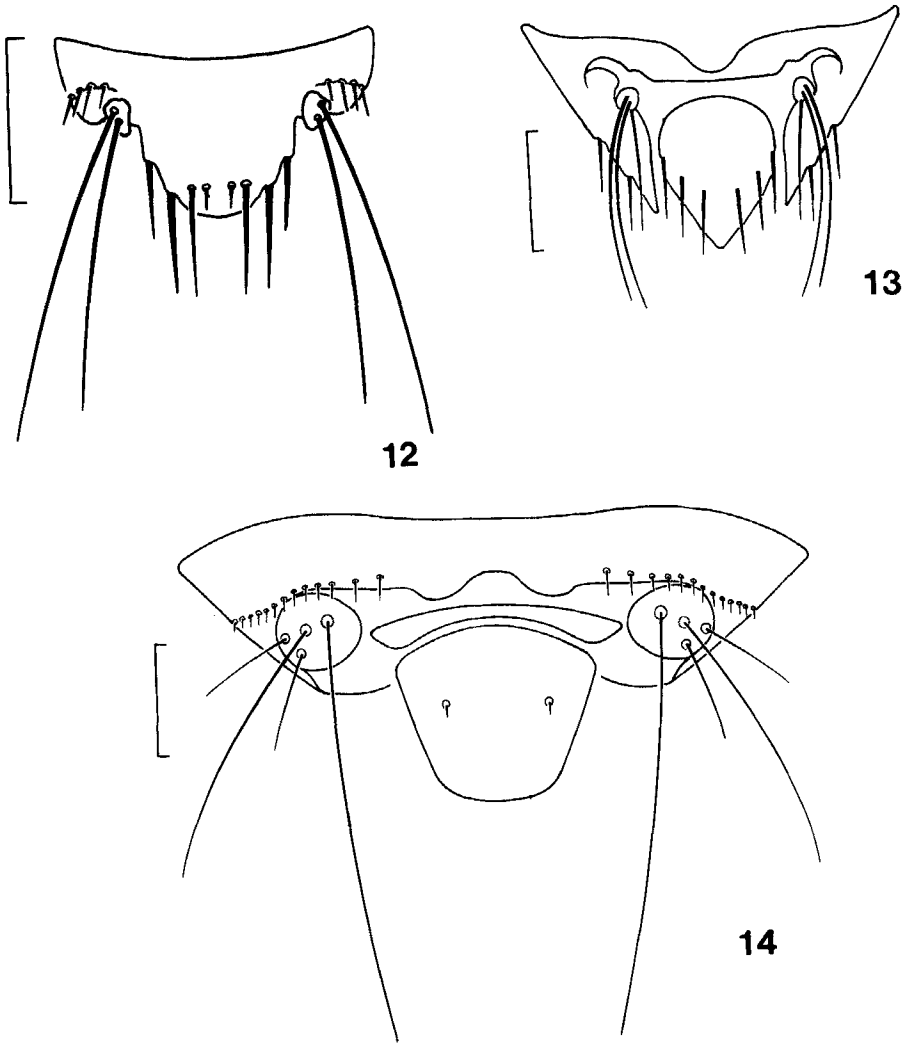
11. *Posterior margin of T1.* The posterior margin of the first tergum of signiphorids is either transverse or bilobed (T1: Fig. 10). The first tergum in Aphelinidae is transverse. A transverse posterior margin for T1 was coded as (0), a bilobed margin as (1).

12. *Anterior projections on S3 to S6 in females.* In all female Signiphoridae that I have examined, the third to sixth sterna bear a pair of more or less elongate apodemes on their anterolateral margins (sta: Fig. 4). These apodemes project under the preceding sternum for a distance which varies between species. Similar apodemes have not been observed in any male Signiphoridae or in other Chalcidoidea of either sex, except in female *Azotus* and *Ablerus*, as discussed above. This character was coded as binary: apodemes absent (0), apodemes present (1). The two outgroup taxa display both character states, therefore this character cannot be polarized *a priori*.

13. *Epiproct in females.* The structure of the apical terga in Signiphoridae, Azotinae and other chalcidoids is discussed above. Briefly, an epiproct is present in all female Signiphoridae (Fig. 13) and in female Azotinae (Fig. 14). Since some signiphorids display a sexual dimorphism for this attribute, it was coded as a separate binary character for females: epiproct absent (0), epiproct present (1). Due to heterogeneity in the outgroup, this character can only be polarized on the basis of parsimony within the context of particular analyses.

14. *Epiproct in males.* A separate, sclerotized, well-defined epiproct is present on most male signiphorids but is not found on male *Chartocerus* (Fig. 12). This character was coded for males as for females: epiproct absent (0), present (1). A syntergum is present on male Coccophaginae. As discussed above, the apical region of the syntergum of male Azotinae is very weakly sclerotized, but a separate, sclerotized and well-defined epiproct is not apparent. Two lateral, sclerotized areas are present on the anterodorsal region of the syntergum, separated by a membranous area. This configuration differs from that found in Coccophaginae (and other Aphelinidae) or in male *Chartocerus*. I coded this character as a missing data point for male Azotinae. An alternative was to code this character as '2' for male Azotinae and treat the series as unordered. However, because this character state (2) would simply appear as an autopomophy for Azotinae, either coding would have exactly the same effect in the analysis.

15. *Ventrolateral processes on the syntergum in males.* Certain species of *Signiphora* display a further modification of the syntergum in the male. In these species, the syntergum is produced laterally and folded ventrally to form two lateral lobes lying beneath the posterolateral margins of the medially emarginate S7 or partly projecting mesad of such (Fig. 16). In one group of species these ventrolateral lobes are more



FIGS 12–14. Terminal segments of metasoma, dorsal aspect, scale bars represent 30 μm. 12. Syntergum, *Chartocerus* sp. (male). 13. Syntergum and epiproct, *Signiphora coquilletti* (female). 14. Syntergum and epiproct, *Ablerus* sp. (female).

strongly developed and they bear a number of stout spines projecting medially and posteriorly (Fig. 18). These attributes were coded as an unordered, three-state character or as the following morphocline: processes absent (0), processes present but inconspicuous (1), processes present, conspicuous and bearing large spines (2). Inconspicuous and conspicuous processes are obviously derived characters for Signiphoridae and it would seem reasonable (but not certain) that the conspicuous process with long spines evolved from inconspicuous processes.

16. *Male S7 with posteromedial emargination.* In some species of *Signiphora* the posterior margin of S7 in males bears a deep, medial emargination. In these species S8 has a curved shape (more or less matching the shape of the emargination in S7) with the medial portion of S8 anterior to the lateral portions (S7, S8: Figs 16, 18). In other Signiphoridae and in the outgroup taxa, S7 in males is not emarginate (Figs 15, 17). This character was coded as follows: emargination absent (0), present (1).

17. *Medial denticles on male genitalia.* In most signiphorids, the phallobase is more heavily

sclerotized at its posterior end between the points of articulation of the digital sclerites. In many signiphorids this region bears a pair of more or less elongate denticles (md: Fig. 15), the presence of which is apparently unique in the Chalcidoidea. These medial denticles are lacking in *Thysanus* (Fig. 17) and in some *Signiphora* species. In certain other *Signiphora* spp. they are large and falcate. The phallobase of genitalia bearing these medial denticles often displays a sclerotic medial ridge on the dorsal surface, visible in cleared slide-mounts as a longitudinal darkened streak terminating at the anterior margin of the phallobase. I have not observed these medial denticles in the outgroup taxa (or in other chalcidoids). These attributes were coded as an unordered multistate character or the following transformation series was assumed: medial denticles absent (0), present but not falcate (1), present, robust and falcate (2).

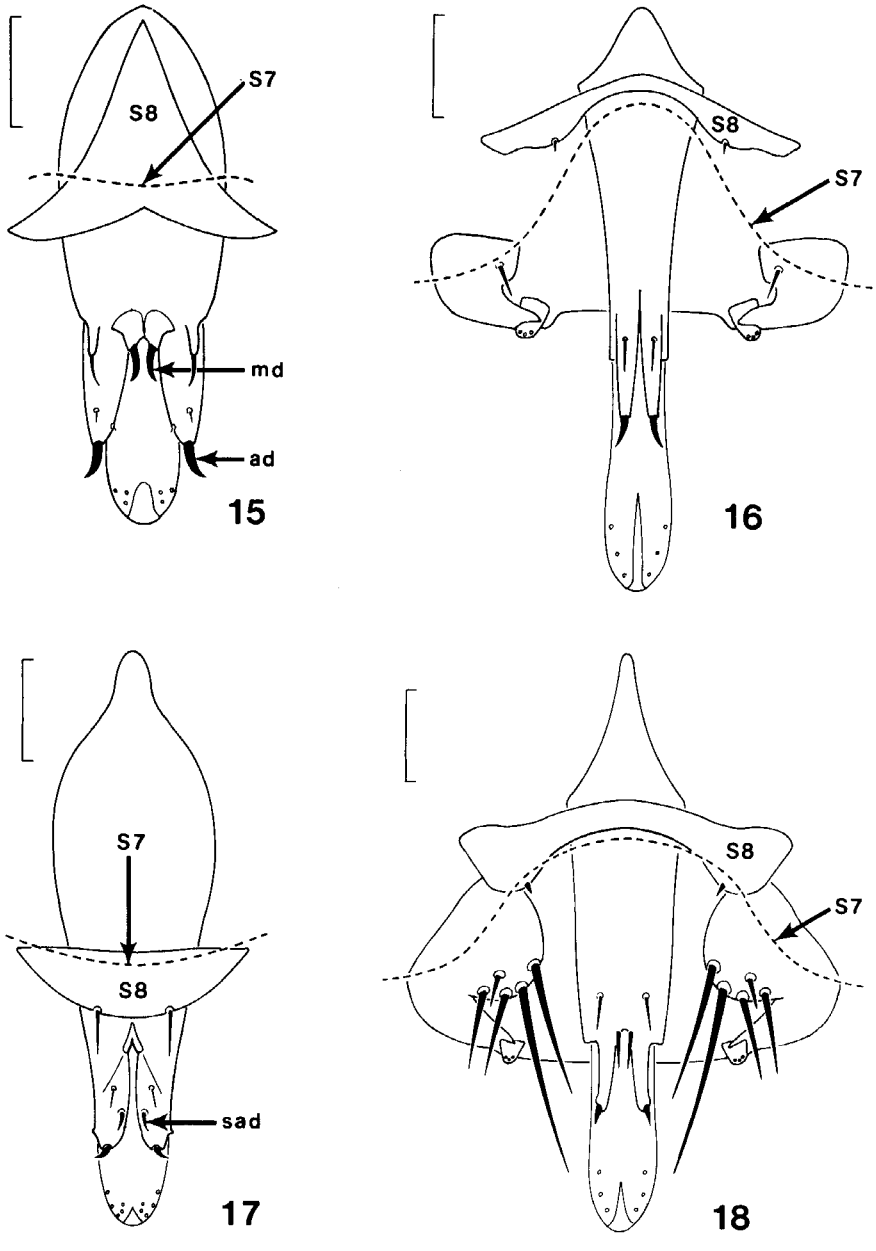
18. *Denticles on digiti of male genitalia.* The digiti of most signiphorid males bear a single denticle at the apex (ad: Fig. 15), generally short and curved laterally but occasionally elongate. The digiti of male *Thysanus* bear a second subapical denticle on each digitus (sad: Fig. 17). This character was coded as follows: one apical denticle (0), one apical and one subapical denticle (1).

19. *Microtrichiae on forewing.* The fore- and hindwings of all Signiphoridae lack microtrichiae except for very few setae or bristles that occur in characteristic locations. The absence of vestiture of fully developed wings is unusual in the Chalcidoidea and is a synapomorphy for Signiphoridae as well as a convenient recognition characteristic. The presence or absence of microtrichiae was coded as a binary character: present (0), absent (1).

20. *Discal seta on forewing.* The forewings of many Signiphoridae bear a single, long, dorsal seta in the middle of the discal area posterior to the marginal vein (discal seta: Fig. 19). The point of insertion of this seta lies in or close to an oblique crease, generally found running in a posteromedial direction back across the wing from a point just posterior to the stigmal vein. Presence or absence of a discal seta on the forewing was coded as a binary character: absent (0), present (1).

21. *Setae on forewing submarginal vein.* The submarginal vein of signiphorids bears one or two long setae on the dorsal surface. The number of setae on the submarginal vein was treated as a meristic character. The Azotinae bear a single seta on the submarginal vein. *Coccophagus* species bear several to many. The homology of the setae in *Coccophagus* with those in Signiphoridae is questionable; therefore, this character was scored as missing for the outgroup taxon Coccophaginae.

22. *Seta M6 on forewing marginal vein.* The marginal vein of signiphorids bears a number of long, dorsal setae on its anterior (leading) and posterior (trailing) margins. The number of dorsal setae present varies somewhat but the location of particular setae, when present, does not vary (with few exceptions), so that it is possible to treat individual dorsal setae on the marginal vein as homologous. I have assigned a notation to the individual dorsal setae on the marginal vein. Fig. 19 shows a marginal vein in which six dorsal setae are present. Four setae are present on the anterior margin and are numbered M1 to M4. Seta M5 lies on the posterior margin apical to M1 but proximal to M2. Seta M6 also lies on the posterior margin between the points of insertion of M2 and M3. Two rules allow this notation to be applied without ambiguity (with a few exceptions). Seta M1, if present, is always proximal to M5 (always present), and seta M3 is always distal to M6. The presence of absence of particular setae is characteristic of particular genera or species. *Chartocerus* spp. (Fig. 20) have a characteristic venation in which seta M1 is present or absent, two anterior setae are proximal to M6 (M2 and M2B) and two anterior setae are distal to M6 (M3 and M4). Seta M6 is lacking in both *Thysanus* and *Clytina*, but is present on most other signiphorids. The presence or absence of setae M6 in Signiphoridae was coded as a simple binary character: absent (0), present (1). Species of Azotinae have a similar setation on the fore-wing ventation but it is difficult to determine homologies between setae. On *Alberus clisiocampae* (Ashmead), four or five dorsal setae are present on the anterior edge of the marginal vein (corresponding to M1–M4, Fig. 19). Two dorsal, posterior setae are present in the distal quarter of the marginal vein (cf. Figs 2, 3, Darling & Johnson, 1984), the proximal of which may be homologous with seta M6 of Signiphoridae. However, *A.clisiocampae* has no seta corresponding to M5, and the distal-most posterior seta has no counterpart in Signiphoridae. Other Azotinae do have a seta cor-



FIGS 15–18. Male genitalia, ventral aspect, scale bars represent 30 μm. 15. *Chartocerus* (*Chartocerus*) sp. 16. *Signiphora* n.sp. 1. 17. *Thysanus ater*. 18. *Signiphora frequentior*. (ad: apical denticle, md: medial denticle, sad: subapical denticle, S7: posterior margin of seventh sternum, S8: eighth sternum.)

responding to M5. Although setation like that of *A.clisiocampae* occurs in some *Azotus* spp., other *Azotus* have a somewhat different pattern (cf. Figs 363–380, Nikol'skaya & Yashnosh, 1966). The venation of *Coccophagus* is quite setose and no homologies with Signiphoridae are apparent. This character was scored as a missing data point for Coccophaginae and as present for Azotinae.

23. *Shape of hindwing*. The hindwing of Signiphoridae varies considerably in width but generally (except in brachypterous species) it is

subequal in length to the forewing. The shape of the hindwing ranges from broadly rounded (e.g. the *dipterophaga* species group of *Signiphora*) (Fig. 24), to slightly rounded (e.g. *Chartocerus*) (Fig. 23), to almost parallel-sided (actually slightly spatulate, e.g. the *flavopalliata* species group of *Signiphora*) (Fig. 22). The distinction between broadly rounded and slightly rounded hindwings is subjective, but the distinction between either and parallel-sided wings is less so. Therefore the shape of the hindwing was coded a a binary character: broadly or slightly rounded (0), parallel-sided (1). The hindwing is broadly or slightly rounded in the outgroup taxa.

24. *Discal seta on hindwing*. Many signiphorid hindwings bear a single discal seta just under the apical portion of the marginal vein (Fig. 23), the presence or absence of which is constant within genera, except in *Signiphora*, where it varies between species groups. This attribute was coded as a binary character: discal seta absent (0), discal seta present (1).

25. *Spines on middle femur*. The middle femur of most signiphorids is robust and bears several rows of short, stout setae along the anterior margin (Fig. 11). Most signiphorids have from one to four long spines (i.e. longer than the width of the middle femur) in the posteroapical area of the femur and one or two short spines just apical to the long spine(s) (Fig. 11). The number and relative length of these spines is useful in discriminating between species, but their position varies little throughout the family. The number of long spines in the posteroapical area was coded either as an unordered meristic character, or as the following transformation series: 0 ⟨=⟩1⟨=⟩2⟨=⟩3 or 4.

26. *Shape of middle femur*. The middle femur on males of some species of *Signiphora* is strongly dilated in a posterior direction and flattened dorsoventrally (cf. Figs 10–13; Subba Rao, 1974). This attribute has a clear polarity and was coded as follows: male middle femur not dilated (0), dilated (1).

27. *Shape of middle tibia*. The shape of the middle tibia in Signiphoridae is either subcylindrical (widest part near the midpoint) (Fig. 25) or obconic (widest part in apical third to almost at apex) (Fig. 26). An obconic middle tibia also bears a number of long, dorsal spines arranged in a distinctive pattern, while subcylindrical middle tibia bear only scattered setae. Also characteristic of most Signiphoridae is a more or less well developed and pectinate midtibial spur (Fig. 26). In the two known *Clytina* spp. and in the outgroup taxa, the middle tibia is subcylindrial, bears scattered setae, and lacks a pectinate midtibial spur (Fig. 25). This complex of apparently correlated attributes was coded as: cylindrical middle tibia bearing scattered setae and a simple midtibial spur (0), obconic middle tibia bearing long, dorsal spines and a pectinate midtibial spur (1).

28. *Calcar on fore leg*. The fore tibia on many chalcidoids bears a long spur at the apex, the calcar, which together with one or more rows of short, stout setae on the basitarsus (the strigil) form an antennal-cleaning apparatus. The calcar of *Thysanus, Clytina* and *Chartocerus* is curved and bifid at the apex (Fig. 27), the form common in all families of Chalcidoidea except the Eulophidae (including Elasminae), Trichogrammatidae and some Tetracampidae. In *Signiphora* the calcar is pectinate (Fig. 28). The condition of the calcar was coded as a binary character: not pectinate (0), pectinate (1).

The algorithms

Several computer packages were used in the analyses and all were run on a Digital Equipment Corporation VAX 11/750 minicomputer in the Department of Entomology, Texas A&M University. The PAUP package (Swofford, 1985) contains a complete set of tools for parsimony analysis, including several refinements of the well-known Wagner method (Kluge & Farris, 1969; Farris, 1970). The program is able to handle missing data and unordered multistate characters and global branch-swapping is available for the estimation of shortest tree topologies. In cases in which a number of equally parsimonious solutions result, the program will hold all shortest trees in memory and perform branch-swapping on all of them, if the MULPARS option is used. This was always done during global branch-swapping.

It is important to note that PAUP outputs a multifurcation in a tree topology as a set of bifurcations. For example, a trifurcation is output (or saved in memory) as two bifurcations connected by an interval with zero branch length. For any trifurcation, three such topologies are possible. In assembling sets of equally parsimonious solutions, PAUP treats all such totally bifurcating

trees as distinct. In the discussions herein, reference is sometimes made to a number of equally parsimonious tree structures found by PAUP given a set of input parameters. Unless otherwise stated, the actual number of unique tree structures is less, perhaps far less, than the number presented. One can find the actual number of different topologies by exhaustive examination and this was done in some cases.

In the PAUP analyses reported here, the following parameters were always used (see Swofford, 1985, for full explanations). Rooting of tree structures found was by the outgroup method unless otherwise stated (in one case the method of Lundberg (1972) was used). The BLRANGE and CSPOSS options were used to determine the set of optimized character-state-change distributions possible for each tree topology. During the construction of trees, the CLOSEST addition sequence was specified. In one case a strict consensus tree (Rohlf, 1982) was calculated for a set of equally parsimonious trees using Swofford's CONTREE algorithm.

Joe Felsenstein, University of Washington, provided another very useful set of algorithms in his PHYLIP package (Felsenstein, 1984). In particular, the CLIQUE algorithm in PHYLIP was used to perform character compatibility analyses (Le Quesne, 1972; Estabrook, 1979; Estabrook *et al.*, 1976a, b) and the FACTOR algorithm was used to recode data sets containing multistate characters to data sets in the additive binary coded form (Sokal & Sneath, 1963; Kluge & Farris, 1969).

Analytical methodology

The OTU by character matrix is included as Appendix A and the list of species that each OTU represents is included as Appendix B. The two OTUs AZOTINAE and COCCOPHA were used as the outgroup to the Signiphoridae. In five cases the modifications coded as character states for signiphorid taxa involved modifications of structures unique to Signiphoridae, or in which ingroup/outgroup homology was questionable. This situation is comparable to NC (no comparison) missing data in phenetic analyses. These characters were coded as missing in the outgroup taxa.

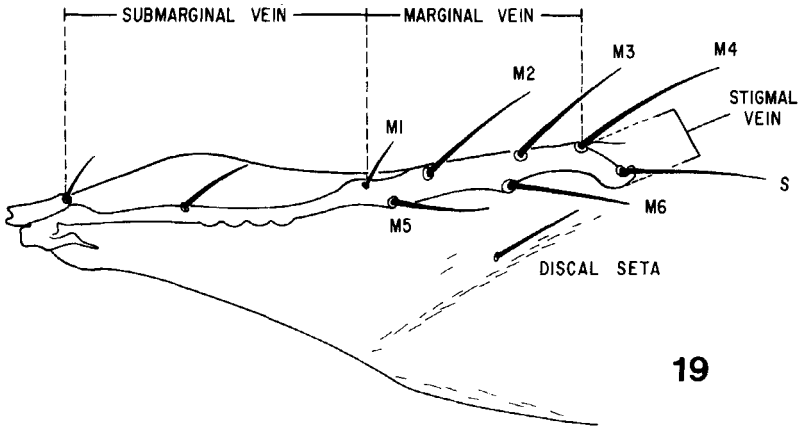
Full character set. Initially, the full character set was submitted to the PAUP algorithm. All multistate characters were treated as unordered characters, that is character state changes from any state to any other state were treated as equally likely. Global branching-swapping with the MULPARS option was used. In practice, constraints on memory available to the program dictated that a maximum of 1000 trees could be stored in memory at any one time, a number which seemed more than sufficient. However, results from this analysis indicated that over 1000 equally parsimonious solutions were possible. Clearly, some means was needed to reduce the noise in the data to find the meaningful information. Several techniques were tried.

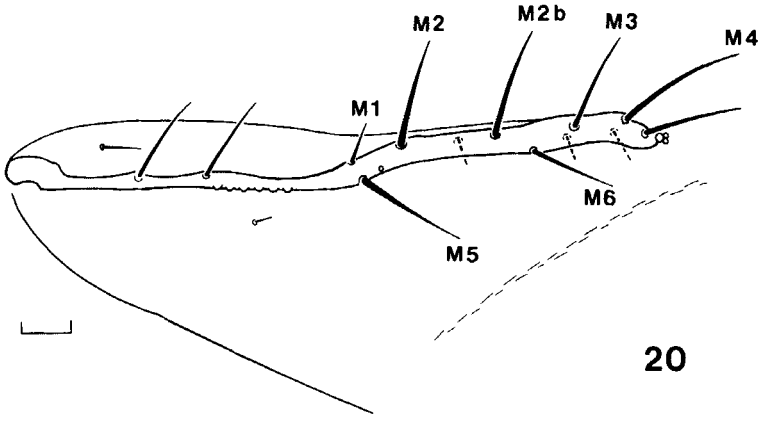
Compatibility analysis. A character compatibility analysis was run using the CLIQUE option of PHYLIP. This algorithm will not accept missing data points in the data matrix. This limitation required several modifications to the data. The outgroup taxa contained several missing data points, which arose from two sources as discussed above. Therefore, they could not be used in the compatability analysis. Construction of an artificial 'ancestral' taxon would have met with the same problem.

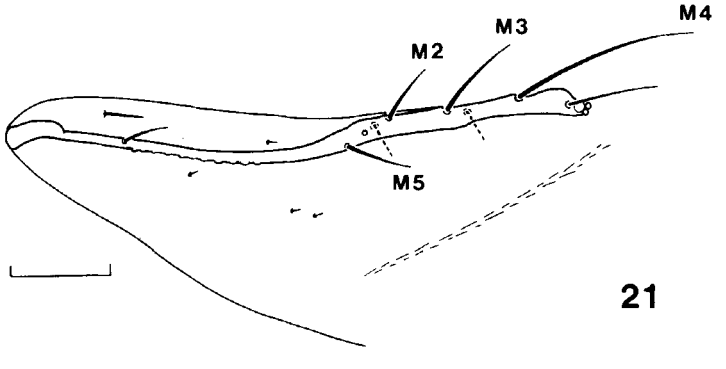
Four missing data points were present in the ingroup taxa, involving four terminal taxa. These represented species that are known only from one sex, so a character, such as the number of female funicle segments, was unknown. In order to perform the compatibility analysis I had two choices, either omit the taxa, or guess at what the character would be if the opposite sex were known. Neither choice is very palatable, but I choose the latter because it is at least testable by discovery of the opposite sex in the future. This dilemma will be familiar to users of the WAGNER 78 algorithm.

The CLIQUE algorithm also requires binary character data. Therefore the original character set was additive-binary-coded using the FACTOR algorithm of PHYLIP. This procedure requires the specification of character state trees (hypothetical morphoclines) for each multistate character. FACTOR does not, however, require the polarization of morphoclines. For example, with a three-state morphocline: A⟨=⟩B⟨=⟩C, either A or C could be plesiomorphic and B is intermediate in either case. The character state trees used are described above for each multistate character.

While the results of the compatibility analysis are discussed below, one pertinent result can be considered now. For one multistate character,







FIGS 19–21. Forewing venation, scale bars represent 30 μm. 19. *Signiphora flavopalliata*. 20. *Chartocerus* (*Chartocerus*) sp. 21. *Thysanus ater*. (M1–M6: individual setae on marginal vein.)

number of spines on the middle femur (25), considerable homoplasy occurs with transformations between two character states (one spine or two spines). The changes from spines absent to one spine, and from two spines to either three or four spines are not homoplastic, and were included in the largest clique of compatible characters. Thus, by recoding this character to the following sequence: 0=spines absent, 1=one or two spines, 2=three or four spines, the effects of homoplasy for the intermediate states could be eliminated. This was done for subsequent analyses.

Strauch (1984) suggested another method to deal with homoplastic characters using compatibility methods. The largest clique of compatible characters is used to define the major lineages. Then, homoplastic characters within each major lineage are re-examined to see if any may be compatible in the context of a particular lineage (branch of a tree). This can be done by running a second compatibility analysis for taxa that constitute such a monophyletic subset of the original taxa. If a larger clique of characters result for the subset, the additional characters are added to the tree structure, subject to the constraint that any new characters must be consistent with the largest original clique of characters. Strauch's (1984) method was used following compatibility analysis for the lineage defined by a pectinate calcar (28) and propodeum with a medial sclerite bearing lamelliform process (9).

Reduced character set. One straightforward method to remove the effects of homoplasy from a parsimony analysis is to remove homoplastic characters. One criterion was employed. Characters were arbitrarily eliminated from further analyses if they consistently showed an initial unit character consistency of less than 0.50 in the initial parsimony analyses. A distance matrix was recalculated to find taxa that had thus become redundant. Redundant taxa were eliminated to form a set of taxa that were uniquely defined by the reduced character set. This reduced data matrix was submitted to PAUP for calculation of minimum length trees using global branch-swapping. All remaining multistate characters were treated as unordered.

Ordered versus unordered characters. It was apparent from parsimony analyses done on the additive-binary coded data that specification of morphoclines for multistate characters drastically reduced the number of equally parsimonious tree topologies. However, this reduction in equally parsimonious solutions is gained at the cost of additional *a priori* hypotheses. In order to assess the effects of hypothetical character state trees on the number of resulting solutions, the reduced character set data was analysed using various combinations of ordered and unordered morphoclines for multistate characters. Five multistate characters were involved (Table 2). Each character was treated as ordered in turn, and then each possible combination of characters, and finally all five characters were treated as ordered.

Results

Full character set. Using the full set of twenty-eight characters with all multistate characters unordered and global branch swapping, over 1000 equally parsimonious solutions were obtained. The overall consistency index (CI) for these solutions was 0.529. Recoding character 25, the number of spines on the middle femur, as discussed above, and repeating the analysis again yielded over 1000 trees, now with a CI of 0.543. Strict consensus trees could have been derived for each set of 1000 solutions. However, since it was not known how large the set of equally parsimonious solutions actually was, it was not known if equally parsimonious solutions existed that might have differed in topology from any consensus solutions.

Reduced character set. Seven characters (2, 11, 17, 20, 21, 23 and 24) consistently had a unit consistency index of less than 0.50 in the initial parsimony analyses. Removal of these characters followed by global branch swapping produced a set of 735 equally parsimonious trees.

Ordered versus unordered characters. The *a priori* ordering of multistate characters into morphoclines produced a dramatic decrease in the number of equally parsimonious solutions (Table 2). Imposing an ordering on all five remaining multistate characters resulted in a single solution (Fig. 29) with a length of thirty-five steps and a CI of 0.829. Treating character 6, the number of segments in the female funicle, as unordered alone or in combination with any other character(s) produced a thirty-four step tree. The reason for this is simple: a state change for character 6 from 3 to 1 (in *Kerrichiella*) is

TABLE 1. Terminal taxa of *Signiphora* on Figs 29 and 30, the OTUs which each represents, and proposed species-group classification.

Terminal taxon	OTUs which terminal taxon represents		Species group
	Fig. 29	Fig. 30	
S.flavopalliata	SIGNFLAV	SIGNFLAV	*flavopalliata*
	SIGNALEY	SIGNALEY	*flavopalliata*
	MEXIMEXI		*flavopalliata*
	MEXBIFSC		*bifasciata*
	MEXINSP7		*bifasciata*
	MEXUNINO		*bifasciata*
Signiphora n.sp. 6	MEXINSP6	MEXINSP6	*flavopalliata*
S.mexicana	n.a.*	MEXIMEXI	*flavopalliata*
Signiphora n.sp. 2	MEXINSP2	MEXINSP2	*bifasciata*
S.bifasciata	n.a.	MEXBIFSC	*bifasciata*
		MEXINSP7	*bifasciata*
		MEXUNINO	*bifasciata*
S.hyalinipennis	MEXHYALI	MEXHYALI	*bifasciata*
	MEXISP11	MEXISP11	*bifasciata*
'Kerrichiella'	KERRICHI	KERRICHI	*coleoptratus*
S.pulchra	MEXPULCH	MEXPULCH	*dipterophaga*
'New Genus'	All NGEN-OTUs	All NGEN-OTUs	*dipterophaga*
S.maxima	ROZMAXIM	ROZMAXIM	*dipterophaga*
	ROZNRMAX	ROZNRMAX	*dipterophaga*
	ROZNNSP4	ROZNNSP4	*dipterophaga*
'Rozanoviella'	ROZNCOMP	ROZNCOMP	*dipterophaga*

* n.a. The terminal taxon does not appear in Fig. 29.

TABLE 2. Results of treating various combinations of characters as ordered or unordered. Combinations of characters in cells are numbered as they are in the text. All trees in which character 6 was unordered, alone or in any combination, had a length of thirty-four steps. All other trees had length of thirty-five steps. Note that in the case in which all characters were ordered, the forty-five different, bifurcating solutions were determined to be topologically identical (Fig. 29). In the other cases, the number of unique topologies was not determined, but is less than the number shown.

No. of characters unordered	No. of equally parsimonious, bifurcating solutions			
	45	105	315	735
None	All characters ordered			
One character	1	15	5	
	6			
	25			
Two characters	1, 6	1, 15	1, 5	5, 15
	1, 25	6, 15	5, 25	
	6, 25	15, 25	20, 21	
Three characters	1, 6, 25	1, 15, 25	1, 5, 6	1, 5, 15
		6, 15, 25	1, 5, 25	1, 6, 15
			5, 6, 25	5, 6, 15
				5, 15, 25
Four characters		1, 6, 15, 25	1, 5, 6, 25	1, 5, 6, 15
				1, 5, 15, 25
				5, 6, 15, 25
Five characters				1, 5, 6, 15, 25

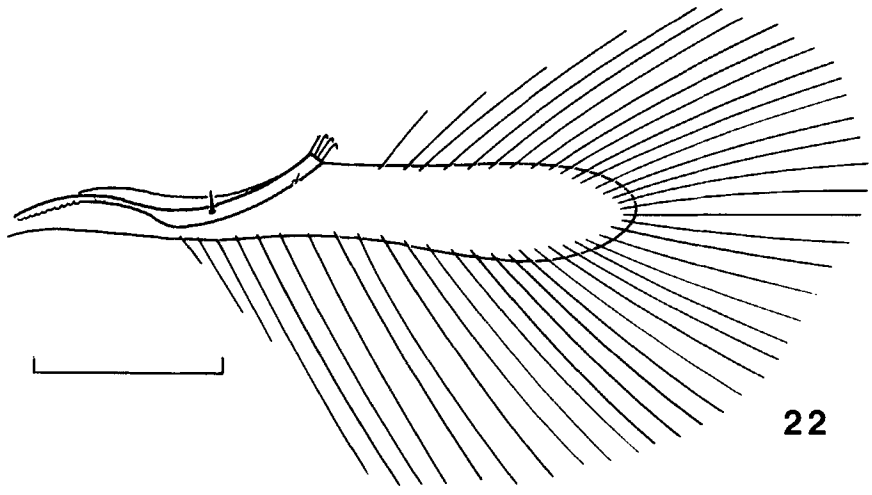
counted as one step if the character is unordered and as two steps if it is ordered. Treating characters 1, 6 or 25 as unordered, alone or in any combination, had no effect on the number of trees produced. If character 15, projections on the syntergum, was unordered, 105 trees resulted, and 315 trees resulted if character 5, segments in male funicle, was unordered. If both characters 5 and 15 were unordered together, 735 equally parsimonious solutions resulted. Again, the actual number of topologically different solutions is much less than 105, 315 or 735 (due to multifurcations) but the actual number of distinct topologies was not determined. A strict consensus solution for the set of 735 trees resulting if all characters are unordered was examined. The primary effect of unordering characters is to lose some resolution of relationships between the taxa above the node defined by characters 9 and 28 in Fig. 29. The structure of the remainder of the cladogram is not affected. For example, one of the effects of unordering character 15, the ventrolateral projections on the syntergum in males, is to allow an equally parsimonious solution in which this character changes from state 0→1 (no projections to small projections) in 'New Genus' taxa and from state 0→2 (no projections to large projections) in *S.maxima* and *Rozanoviella* spp. If character 5, funicle segments in males, is treated as unordered, the sister group relationship between *Kerrichiella* and *Signiphora* n.sp. 2 is lost in the consensus tree. That is, *Kerrichiella* arises from a pentafurcation at the base of this lineage.

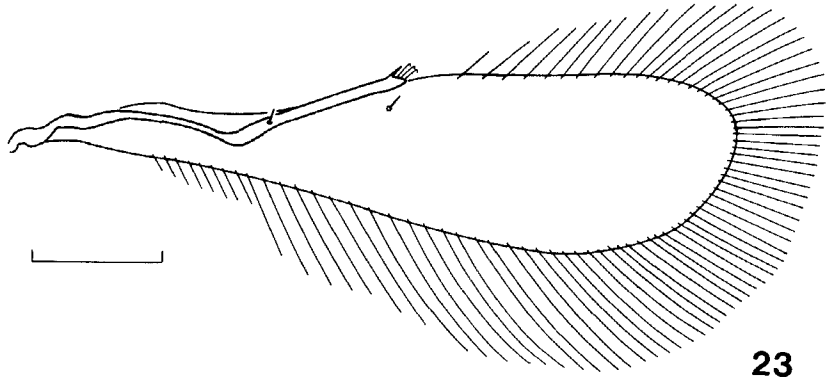
Compatibility analysis. A single largest clique of twenty-seven additive binary coded characters (of thirty-seven total characters) was obtained. Because both the outgroup taxa and the hypothetical ancestor were deleted due to missing data, the tree structure for this analysis was initially unrooted. A rooted tree for this subset of characters was obtained by submitting the data to PAUP using the following procedure. A matrix of between-taxa distances was computed for this character set. Taxa that were redundant (0 distance to other taxa) were deleted. Global branch-swapping was used to find the most parsimonious solution, which was then rooted using the Lundberg method (Lundberg, 1972). Lundberg rooting in PAUP finds the shortest ingroup topology and then finds the location to add the outgroup that results in the least additional length. One most parsimonious solution was found, with an overall CI of 0.897. One character (3) was homoplastic with the outgroup taxon AZOTINAE, while two characters (25 and 27) showed reversals. The structure of this cladogram did not differ substantially from Fig. 29. However, with this drastically reduced character set, only seven terminal taxa with character states 6^3, 9^2, 28^1 could be resolved, versus nine such taxa in Fig. 29. In the discussions that follow, a superscripted notation is used to indicate character numbers followed by character states, e.g. 6^3 represents state 3 of character 6.

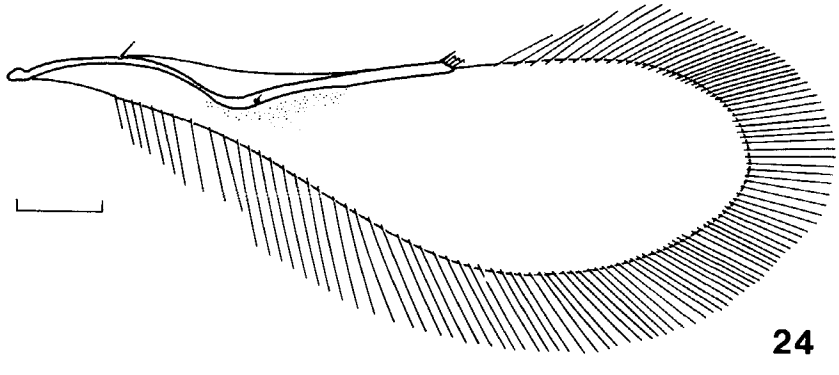
As discussed above, Strauch's (1984) method was employed following compatibility analysis to determine if any homoplastic characters could be retrieved for the lineage defined by the presence of a lamelliform process on the median sclerite of the propodeum (9^2) and a pectinate calcar (28^1). A single largest clique of thirty-two additive-binary characters was found for this subset of taxa. The following additional characters were compatible within this lineage only: 1 (states 3⟨=⟩2 only), 2, 6 (3 annelli ⟨=⟩4 annelli only), 21 and 23. As a result, more taxa within this lineage could be discriminated. Table 1 lists the relevant terminal taxa in Figs 29 and 30 and the OTUs which each terminal taxon represents. A cladogram showing the revised topology for this lineage is shown as Fig. 30.

Discussion

Imposition of *a priori* transformation series for characters 5 and 15 in particular produced cladograms with somewhat better resolution of relationships in one lineage. Treating character 15 as unordered allows for the equally parsimonious independent derivation of inconspicuous and conspicuous projections on the male syntergum. However, treating this character as ordered is actually the more conservative hypothesis. It may later be shown, for example, that conspicuous and inconspicuous projections are not distinct character states, but that they represent two points in a continuum of configurations for this structure. If that were true, then a reasonable coding might reflect only the presence or absence of such processes on the syntergum. Such a hypothesis would be consistent with the result obtained by treating this character as ordered (0 ⟨=⟩ 1 ⟨=⟩ 2) (Figs 29, 30).







FIGS 22–24. Hindwings, scale bars represent 100 μm. 22. *Signiphora perpauca*. 23. *Signiphora hyalinipennis*. 24. *Signiphora frequentior*.

The effect of ordering character 5 is to tie *Kerrichiella* and *Signiphora* n.sp. 2 together based only on the presence of two funicle segments in male antennae (Figs 29, 30). However, the number of male funicle segments is further reduced to one in *Kerrichiella*. The two taxa share only one 'synapomorphy' (reduced funicle segmentation) and they share no uniquely derived character state. Thus, there is no strong indication of relationship and this grouping appears to be an artefact of an *a priori* specification of a transformation series. Even worse, the derived character states are reductions, notoriously unreliable indicators of relationship (Hecht & Edwards, 1977).

Ground-plan for the Signiphoridae

Fig. 29 makes several statements about the relationships of Signiphoridae and Aphelinidae and about the evolution of character states in Signiphoridae. Signiphoridae and Azotinae are linked by three synapomorphies: (1) an unsegmented club, (2) anterior projections present on S3–S6 of females, (3) an epiproct present. As discussed above (character 7), assuming a one to one homology between flagellomeres of Signiphoridae and Aphelinidae is questionable, therefore, the unsegmented club of Azotinae and Signiphoridae may not be a reliable indication of relationship. An epiproct occurs so sporadically in Chalcidoidea that the absence of a sclerotized epiproct must be presumed to be plesiomorphic. A parallel gain of an epiproct in female Azotinae and Signiphoridae is certainly possible, especially since the conformation of these terga is somewhat different in each group. However, a sister group relationship is still indicated by the presence of anterior apodemes on S3–S6 in both taxa. No such apodemes are found on any other chalcidoids, to my knowledge. No synapomorphies here unite Coccophaginae with Azotinae+Signiphoridae. The usefulness of Coccophaginae in these analyses has been to polarize character state changes below Azotinae in Fig. 29.

These results suggest that Aphelinidae are paraphyletic with respect to Signiphoridae. However, the taxonomic structure of the Aphelinidae is poorly resolved from a phylogenetic standpoint. It would be premature to propose nomenclatural changes in the status of Azotinae or Signiphoridae to reflect the possibility that they are sister groups, or to reflect the possibility that Aphelinidae are paraphyletic. Students of aphelinid phylogeny should allow for these possibilities in future analyses.

The Signiphoridae themselves are characterized by five hypothesized synapomorphies which are present in all taxa: (1) absence of microtrichiae from the forewing, (2) structure of the antenna, which includes an unsegmented club and one to four annelli, (3) triangular median region of the propodeum delimited by two lateral sulci, (4) notauli absent from the mesoscutum, (5) axillae not externally visible and indicated only by oblique, internal carinae. Two additional synapomorphies are homoplastic and subsequently lost in one or a few signiphorid taxa: (6) at least one long spine present on the anteroventral area of the middle femur (lost in one species of *Clytina*), and (7) obconic middle tibia with long dorsal spines (lost in both known species of *Clytina*). These results also suggest that presence of seta M6 on the marginal vein of the forewing is a ground-plan state for Signiphoridae, subsequently lost in *Thysanus* and *Clytina*. The presence of seta M6 appears to be a symplesiomorphy for Signiphoridae. As discussed above, many Azotinae possess a seta which may be homologous.

These results (Fig. 29) also require a bidentate mandible (character 1) as a ground-plan state for Signiphoridae. Tridentate mandibles then occur as a parallelism in the common ancestor to *Thysanus* and *Clytina* and in a single species of *Signiphora*. A narrow or acute occipital margin is a ground-plan state, with parallel evolution of a rounded occipital margin in Azotinae and the common ancestor to *Thysanus* and *Clytina*. Three annelli in male signiphorids and four annelli in females are ground-plan character states, followed by the addition of one annellus in male *Thysanus* and the loss of one annellus in female *Signiphora*. However, homoplasy is present here (a reversal to four annelli in females of the 'New Genus' group). Some readers may prefer a scheme in which the larger number of annelli is pleisiomorphic in both sexes. Although the consensus among chalcidoid workers is that eleven flagellar segments (with eight funicle segments including annelli) are plesiomorphic for Chalcidoidea, considerable reduction in antennal segmentation has taken place in Aphelinidae, in which from three to seven

flagellar segments are found (including annelli). I prefer to allow the polarity of these characters within Signiphoridae to be set on the basis of parsimony.

As noted above (Results), seven characters (2, 11, 17, 20, 21, 23, 24) were found to be highly homoplastic in the context of the other data. It is perhaps surprising that three of these characters were of so little use in inferring relationships within Signiphoridae. I have not observed medial denticles (character 17) on the male genitalia of other Chalcidoidea. Although these denticles occur only in some Signiphoridae (see Appendix A), these results suggest that the expression of this character is very unstable. Similarly, the discal setae on both the fore- and hindwings (characters 20 and 24) are unique features as setae in analogous locations are not found in other chalcidoids. Again, these results suggest that these setae have an unstable pattern of expression in Signiphoridae.

The structure of the cladogram (Fig. 29) for *Chartocerus*, *Thysanus* and *Clytina* is sensitive to the polarity of character 14, epiproct in males. The most parsimonious solution (Fig. 29) requires an epiproct in females and not in males as ground-plan character states for Signiphoridae. The epiproct in male signiphorids other than *Chartocerus* is acquired independently. This hypothesis is reasonable given that a separate, sclerotized and well-defined epiproct is not apparent in male Azotinae. However, recall that much of the syntergum on male Azotinae is very membranous and difficult to observe. If it is later shown that male Azotinae do, in fact, possess a sclerotized epiproct, the polarity of character 14 in Signiphoridae will reverse. In the context of the other data presented here, reversing the polarity of character 14 alone results in 315 thirty-six step trees (one step less parsimonious than Fig. 29). The consensus tree for these solutions lacks resolution of relationships above the basal node for Signiphoridae and the node in Fig. 29 defined by character states 9^2 and 28^1. In these solutions, to the synapomorphies for Signiphoridae+Azotinae (Fig. 29) is added 14^1, epiproct present in males. Reversing polarity of character 14 allows for tree topologies in which possession of four annelli in males becomes a ground-plan state for Signiphoridae, and *Thysanus* spp. become the sister group of remaining Signiphoridae, which lose one annellus in males. *Clytina* spp. are sister group to *Chartocerus*+*Signiphora*. A margined occiput becomes a synapomorphy for *Chartocerus*+*Signiphora* rather than a ground-plan state of Signiphoridae which is independently lost in Azotinae and *Thysanus*+*Clytina*.

Chartocerus

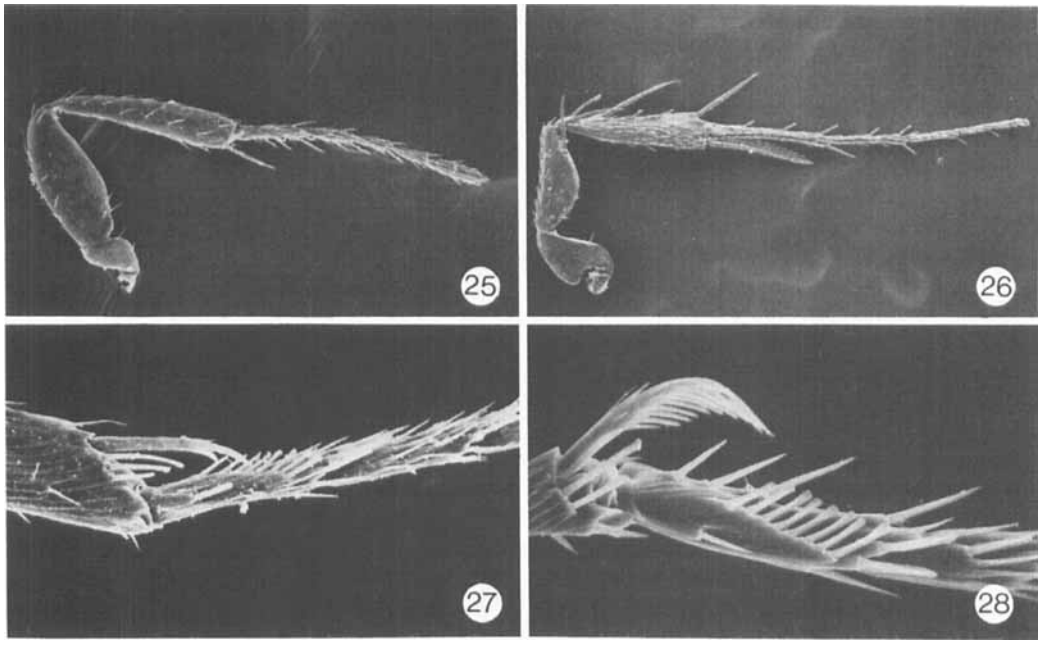
The lack of an epiproct in male *Chartocerus* (14°) suggests a sister group relationship to the remainder of Signiphoridae. All other male Signiphoridae have an epiproct present in males (14^1). Monophyly of *Chartocerus* is indicated by the presence of three or four spines on the middle femur (25^2) and a characteristic setation on the marginal vein of the forewing (Fig. 20) in which seta M1 is usually absent and seta M2B is always present. Because this wing venation is an autapomorphy for *Chartocerus*, it is not informative in inferring relationships and it was not included in the data set.

Signiphora and (Thysanus+Clytina)

These taxa share a single synapomorphy, an epiproct on the male metasoma (14^1). *Thysanus* and *Clytina* species both share a rounded occipital margin (3°). This condition is not known to occur in other Signiphoridae but does occur in at least some Azotinae and thus is homoplastic with respect to one member of the outgroup used. The shape of the occipital margin is quite variable in Aphelinidae in general. Another synapomorpy shared by *Thysanus*+*Clytina* is the loss of seta M6 from the marginal vein of the forewing (22^0) (Fig. 21). Synapomorphies for *Thysanus* and *Clytina* themselves are shown in Fig. 29 and are discussed under the diagnoses for the genera below.

Signiphora

Another lineage was defined in all solutions, regardless of method. This group contained species originally placed in *Signiphora* (OTUs with the prefix SIG-), *Rozanoviella* (prefix ROZN-), *Kerrichiella* (KERRICHI), those which I had recognized as a tentative 'New Genus', and the *bifasciata* species group (prefix MEX- in some cases). All of these species share two synapomorphies: (1) a pectinate calcar on



FIGS 25–28. 25–26. Middle legs. 25. *Clytina* sp. 26. *Signiphora frequentior* (female). 27–28. Apex of fore tibia and basal tarsomeres. 27. *Thysanus ater*. 28. *Signiphora flavella*.

the fore tibia (28^1), and (2) a lamelliform process extending posteriorly from the median sclerite of the propodeum over some portion of T1 (9^2). These characters exhibit no homoplasy in the taxa studied here. As noted above, a median sclerite on the propodeum is not known to occur in other Chalcidoidea and a lamelliform process on the median sclerite is clearly apomorphic for these taxa. A pectinate calcar is found in the mymarid genus *Erythmelus* Enock (Schauff, 1984), but this is clearly a convergence with no bearing on these analyses. There can be little doubt as to the monophyly of this lineage. In addition, most females in this lineage have three annelli in the antenna (6^3) (Fig. 29), a synapomorphy which is reversed in the 'New Genus' spp., in which females have four annelli.

Further resolution of relationships within this lineage was difficult due in part to homoplasy in certain characters. A more serious problem is the lack of sufficient reliable characters. Certain lineages are definable as discussed below, but these tend to occur as multifurcations with other species or lineages. Many of the complications encountered in these analyses (many equally parsimonious solutions, etc.) were due to problems within this lineage.

These species fall into three groups in Fig. 29: (1) species in which an emargination is present on S7 in males (16^1), (2) species in which the male funicle is reduced (5^2), and (3) the remaining species which are not defined or further resolved. Fig. 30 was obtained by finding the largest clique of characters compatible in these species alone. This seems justified as the monophyly of this group is well supported. In any case, better resolution for these taxa can be obtained with the additional characters and four lineages are now apparent within the group: (1) species in which the distal ends of the ducts in the mandibles are enlarged (2^1), (2) species with an emarginate S7 in males (16^1) and usually with some sort of projection on the lateroventral angles of the syntergum in males (15^1 or 15^2), (3) species in which at least the male funicle is reduced, and (4) all other species, not further defined.

Further structure is also apparent in the first group of species. Most have one seta on the submarginal vein of the forewing (21^1) and a parallel-sided hindwing (23^1), but these attributes are lacking in one or two species.

In the second group, males of *S. hyalinipennis* lack ventrolateral projections on T8 (15^0) while

males of *S.pulchra* have them but individuals of this species are not further modified (15^1). Another lineage (the 'New Genus') is characterized by a four-segmented female funicle (6^4), and a third lineage is characterized by more extensive modification of the male syntergum (15^2). The three subgroups are shown as a trifurcation in Fig. 30.

One of the objectives of this study was to evaluate the validity of *Signiphora*, *Rozanoviella* and *Kerrichiella*. In addition, two other groups of species (a potential new genus and a *mexicana* group) were subjected to scrutiny. Results presented here do not support a totally unambiguous resolution to these questions. In fact, some instability in the results occurs with respect to these taxa depending on which characters are used for analysis. It is certainly apparent that additional reliable characters would be useful in evaluating the relationships of these taxa. However, Fig. 30 contains the most information and is the best set of working hypotheses at present.

By including in *Signiphora* all species that share the two synapomorphies discussed above (pectinate calcar and lamelliform process on median propodeal sclerite) the genus is demonstrably monophyletic. This course has been adopted. Further structure within *Signiphora*, as so defined, is accommodated with a species group classification as discussed below. In particular, the tentative 'New Genus' is shown to represent only a subgroup within a *dipterophaga* species group and some members of the tentative '*mexicana* species group' (not including *S.mexicana*) form a *bifasciata* species group.

The flavopalliata species group. This group is monophyletic based on the presence of mandibular ducts which are expanded distally (Fig. 2). With two known exceptions (*S.mexicana* and *S.tumida*), these species have one seta on the submarginal vein of the forewing, and with three exceptions (the above and a new species), these species have hindwings with parallel margins (Fig. 22). Thus, the bulk of this group can be characterized by three synapomorphies. Some further structure is apparent within this group. In some fifteen species the discal seta (Fig. 19) is lacking from the forewing. This may indicate another lineage, however, the remaining species are not demonstrably monophyletic and this

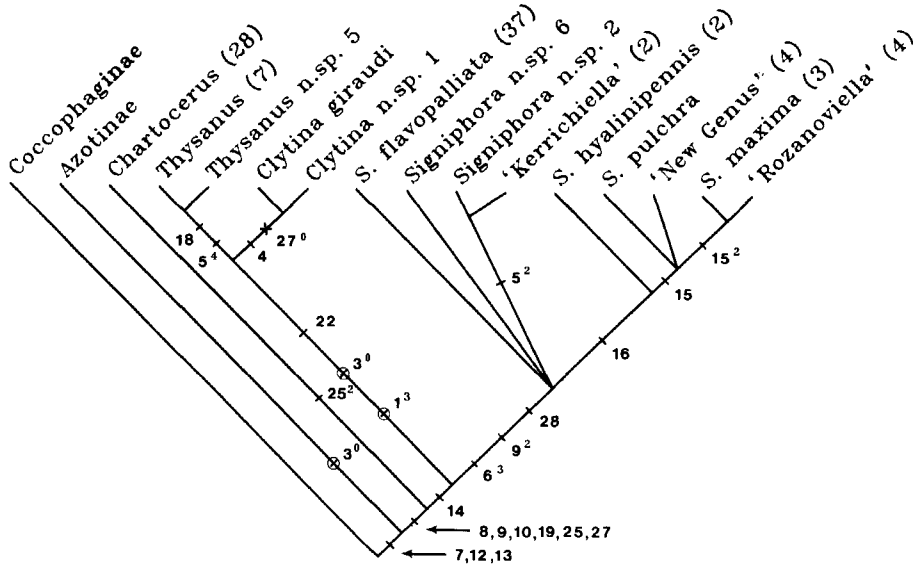


FIG. 29. The single most parsimonious solution obtained with the reduced character set when all multi-state characters were ordered into transformation series. Length=35, consistency index=0.829. Parallelisms are indicated by a circled tic mark, reversals by an '×' mark, autapomorphies are not shown. The number of species represented by each terminal taxon is indicated in parentheses and the OTUs which each terminal taxon represents are shown in Table 2. Character-state changes are from 0 to 1, unless the character number bears a superscript indicating the derived character state.

character appears to be highly homoplastic in signiphorids as a whole (it had very low unit CI values in the initial analyses).

The dipterophaga species group. This lineage (Fig. 30: *S.pulchra*+'New Genus'+*S.maxima*+*Rozanoviella*) can be characterized by a single reliable synapomorphy: the presence of either large or small ventrolateral projections on the syntergum of males (Figs 16, 18). The relationship of *S.hyalinipennis* and a closely related new species (included with *hyalinipennis*, Figs 29, 30) to this group are problematic. An emarginate S7 in males would suggest that both species should be placed in this group (Fig. 30). However, this character is weakly expressed in these species and it is, in fact, polymorphic in both of them. In addition, the conformation of S8 in both species is like that of other *Signiphora* (cf. Fig. 15) and quite unlike the 'dumb-bell' shaped S8 characteristic of the *dipterophaga* group species (Figs 16, 18). The projections on T8, the distinctive shape of S8, and the strongly emarginate S7 form a complex of modifications to the male genital opening which provide strong evidence for the monophyly of the *dipterophaga* group. Therefore, I include *S.hyalinipennis* (and the new species) in the *bifasciata* group. Two lineages may be present in the *dipterophaga* group. In the species included in *Rozanoviella* by previous authors and in *S.maxima* the ventrolateral projections on T8 in males are particularly well developed (Fig. 18). Males of several of these species also have dilated middle femora (cf. Figs 10–13): Subba Rao, 1974). The species represented by 'New Genus' in Figs 29 and 30 represent another lineage which is characterized by four annelli in the female antenna.

The coleoptratus species group. Several synapomorphies unite the two known species in this group (indicated in Figs 29–32 as '*Kerrichiella*'): (1) a robust, almost spherical habitus, (2) a reduced setation of the marginal vein in the forewing, (3) extremely short marginal fringe of the forewing (cf. Fig. 32: Rozanov, 1965). One of these species displays a reduction in the funicle in both sexes. There can be little question that these species represent a monophyletic lineage. However, no characters were found that are informative as to the relationship of these species to other Signiphoridae. As noted above in the Discussion (second paragraph), Fig. 30 would suggest that *Signiphora* n.sp. 2 should be included in this group. However, this species shares no synapomorphies with the *coleoptratus*

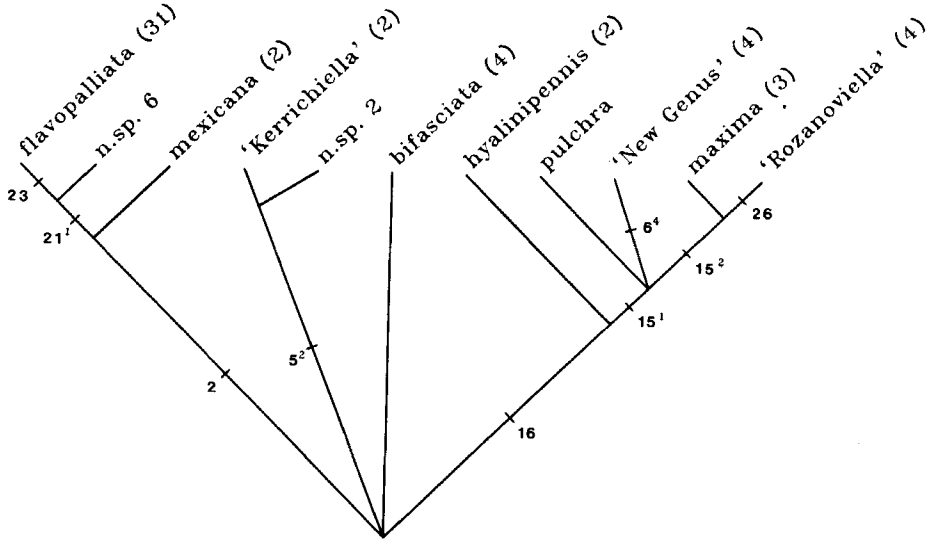


FIG. 30. Solution obtained for *Signiphora* spp. using the single largest clique of thirty-two additive-binary characters that are compatible within this lineage only. Consistency index=1.00. Autapomorphies are shown if they are discussed in the text. Species groups of *Signiphora* proposed here include the following terminal taxa, *flavopalliata* group: *flavopalliata*, n.sp. 6, and *mexicana*; *bifasciata* group: n.sp. 2, *bifasciata*, and *hyalinipennis*; *coleoptratus* group: '*Kerrichiella*'; *dipterophaga* group: *pulchra*, 'New Genus', *maxima* and '*Rozanoviella*'. The number of species represented by each terminal taxon is indicated in parentheses and the OTUs which each terminal taxon represents are shown in Table 2.

species and its placement in this lineage in Fig. 30 is an artefact of an *a priori* specification of a transformation series for character 5. Therefore, I place this species in the *bifasciata* group.

The bifasciata species group. This group includes the following taxa from Fig. 30: *Signiphora* n.sp. 2, *hyalinipennis* and *bifasciata*. The group is paraphyletic, and these species display a preponderance of plesiomorphic traits for *Signiphora*.

Conclusions

A classification with four genera is supported by these results: *Chartocerus*, *Thysanus*, *Clytina* and *Signiphora*. De Santis (1968) defined two subfamilies in the Signiphoridae: the Thysaninae in which he included *Thysanus*, *Neosigniphora* (represented by the OTU THYSRUST herein), *Clytina* and *Chartocerus*, and the Signiphorinae in which he included *Signiphora* and *Kerrichiella*. Later, De Santis (1981) added *Rozanoviella* to the Signiphorinae. This subfamily classification has not been widely followed, although it was used by Gordh (1979). The Thysaninae as delimited by De Santis (1968) is paraphyletic. Results presented here indicate that *Chartocerus* is the sister group to all other signiphorids, and that *Signiphora* is a sister group to the lineage composed of *Thysanus*+*Clytina*.

To salvage the subfamily classification would require the description of a new subfamily to hold *Chartocerus*. The subfamilies of De Santis (1968) could then be treated as tribes, corresponding to *Signiphora* and *Thysanus*+*Clytina*. However, the evidence for a sister group relationship between *Chartocerus* and the remainder of the family is not strong and *Chartocerus* itself is characterized primarily by plesiomorphic traits. Given the evidence presently available, the erection of a new subfamily to hold a single genus is not justified.

In the remainder of this section I present a key to the genera of Signiphoridae and species groups of *Signiphora*, and give brief discussions of each taxon. Diagnoses of genera and species groups are brief and limited to synapomorphies and other outstanding attributes. All of these taxa are under revision and will be redescribed more completely later. New synonymy and several new combinations are proposed. In all cases these decisions were based on study of the type specimens for the taxa involved. Unless an author is cited, comments on distribution and biology are based on my own study of signiphorid material.

Key to Genera of Signiphoridae and Species Groups of *Signiphora*

1 Calcar of fore leg without comb of fine setae (Fig. 27); propodeum without lamelliform process posteriorly; female antenna with 4 annelli 2

– Calcar of fore leg with comb of fine setae (Fig. 28); propodeum with lamelliform process posteriorly (Fig. 10); female antenna usually with 3 or fewer annelli (one group of species with 4 annelli) (*Signiphora*).....4

2(1) Forewing with seta M6 absent from marginal vein (Fig. 21); head with occipital margin rounded; hindwing with parallel margins; males with epiproct present; middle femur usually with 1 long spine (rarely more).....3

– Forewing with seta M6 present on marginal vein and with additional dorsal seta on marginal vein between M2 and M3 and (M2b: Fig. 20); head with occipital margin narrowly rounded; hindwing with posterior margin weakly rounded; males without epiproct; middle femur with 3 or 4 long spines ..... *Chartocerus*

3(2) Head prognathous and subrectangular in dorsal aspect; female antenna with 4 annelli, male with 3 annelli; middle tibia subcylindrical and without long spines on dorsal surface; mandibular ducts parallel-sided (not enlarged distally); digitus with single apical denticle, medial denticles present on genitalia (as in Fig. 15) ..... *Clytina*

– Head hypognathous and generally circular in dorsal or frontal aspect; antenna of both sexes with 4 annelli; middle tibia obconic and bearing long spines on dorsal surface; mandibular ducts enlarged distally (as in Fig. 2); digitus with two denticles, one at apex and one at midpoint, medial denticles absent from genitalia (Fig. 17) *Thysanus*

4(1) Forewing with 1 seta on submarginal vein; hindwing with 2 setae on marginal vein, with parallel margins, and without discal seta; male genitalia lacking medial denticles *S.flavopalliata* group (most species)

– Forewing submarginal vein with 2 setae (one species with 1 seta but lacking other characters above); hindwing with 1 seta on marginal vein, with posterior margin weakly or broadly rounded, and discal seta present or absent; male genitalia with or without medial denticles 5

5(4) Mesoscutum with 2 setae; mandibular ducts enlarged distally; middle femur with 1 long spine *S.flavopalliata* group (two known species)

- Mesoscutum with more than 4 setae; mandibular ducts parallel-sided; middle femur with 1 or 2 long spines 6

6(5) Forewing without seta M6 on marginal vein, and with very short marginal cilia (longest cilia: width forewing about 0.05) ..... *S.coleoptratus* group

- Forewing with seta M6 present on marginal vein, and with marginal cilia variable, often long (longest cilia: width forewing at least 0.20) ... 7

7(6) Hindwing without discal seta, and with posterior margin broadly rounded (Fig. 24); syntergum of male with ventrolateral projections (Figs 16 and 18); female antenna with 3 or 4 annelli *S.dipterophaga* group

- Hindwing usually with discal seta (lacking in *S.unifasciata* which lacks other characters of *dipterophaga* group), and with posterior margin weakly rounded (Fig. 23); syntergum of male without ventrolateral projections; female antenna always with 3 annelli .... *S.bifasciata* group

Chartocerus Motschulsky, 1859

Chartocerus Motschulsky, 1859: 171; type-species *Chartocerus musciformis* Motschulsky, 1859, by monotypy.

Matritia Mercet, 1916: 5; type-species *Signiphora (Matritia) conjugalis* Mercet, 1916, by original designation.

Xana Kurdjumov, 1916: 80; type-species *Xana nigra* Kurdjumov, 1916, by monotypy; preoccupied by *Signiphora nigra* Ashmead, 1900; replacement name *Xana kurdjumovi* Nikol'skaya, 1950.

Signiphorina Nikol'skaya, 1950: 321; type-species *Signiphora mala* Nikol'skaya, 1950, by original designation.

Diagnosis. Two synapomorphies characterize this genus: (1) Three or four long spines on mid femur, (2) an additional seta is present on the dorsal surface of the forewing marginal vein, between setae M2 and M3 on the anterior margin (M2: Fig. 20). As discussed above, *Chartocerus* displays a preponderance of plesiomorphic characters.

Discussion. Mercet (1916) described *Matritia* as a subgenus of *Signiphora*. Girault (1929, 1932, 1933) described three additional species of *Matritia*, treating the taxon at the genus rank. Nikol'skaya (1950) brought *Xana* Kurdjumov into the Signiphoridae, treated *Matritia* as a junior synonym of *Xana* and described *Signiphorina*. Rozanov (1965) brought *Chartocerus* into the Signiphoridae for the first time. He delimited three subgenera: *Chartocerus*, *Xana* (treating *Matritia* as a junior synonym) and *Signiphorina*. Most authors have treated *Xana* and *Matritia* as synonyms. However, the priority of one name or the other is in doubt. The matter was discussed in detail elsewhere (Woolley, 1986).

Rozanov (1965) and others (e.g. Hayat, 1970, 1976; Hayat & Verma, 1980) used several characters to separate subgenera of *Chartocerus*. Most of these characters involve relative lengths and widths of the hindwing and antennal club, and length of the marginal cilia relative to the width of the fore- and hindwings. The attributes used to separate *Xana* (or *Matritia*) from *Signiphorina* do not present any character states that are readily ordered into transformation series, thus none were included in the analyses reported here. Study of *Chartocerus* species has not yet revealed any new characters that would justify retaining *Xana* (or *Matritia*) and *Signiphorina* as subgenera.

The subgenus *Chartocerus*, on the other hand, may represent a distinct lineage. A potential synapomorphy for this subgenus was described by Rozanov (1965) and discussed by Hayat & Verma (1980). *Chartocerus musciformis* and *C.walkeri* have distal papilliform processes on the phallobase of the male genitalia (Fig. 15), lateral to the digiti. The position of these structures corresponds with that of the parameres of other Chalcidoidea, although homology with parameres is questionable. In addition to paratypes of *C.walkeri*, I have seen two other male specimens with such genitalia. Both of these species are known only from the Oriental region.

Chartocerus is currently under revision on a world basis by the author. It would be premature to address the subgeneric classification until the species level taxonomy is better understood.

Limits. I include the following species: *australicus* (Girault) (1913a: 226), **comb.n.** (from *Signiphora*); *australiensis* (Ashmead) (1900: 410), **comb.n.** (from *Signiphora*); *australiensis orbiculatus* (Girault) (1915: 68), **comb.n.** (from *Signiphora*); *axillaris* De Santis (1973: 152); *beethoveni* (Girault) (1915: 71), **comb.n.** (from *Signiphora*); *conjugalis* (Mercet) (1916: 523); *corvinus* (Girault) (1913a: 225), **comb.n.** (from *Signiphora*); *dactylopii* (Ashmead) (1900: 410); *delicata* (Girault) (1932: 2); *elongatus* (Girault) (1916a: 41); *fimbriae*

Hayat (1970: 396); *funeralis* (Girault) (1913a: 224), **comb.n.** (from *Signiphora*); *gratia* (Girault) (1932: 4); *hebes* (Girault) (1929: 311); *hyalipennis* Hayat (1970: 391); *intermedius* Hayat (1976: 162); *kerrichi* (Agarwal) (1963: 390); *kurdjumovi* (Nikol'skaya) (1950: 321); *musciformis* Motschulsky (1859: 171); *nigra* (Ashmead) (1900: 410) (=*argentinus* Brèthes, 1913: 97); *novitskyi* (Domenichini) (1955: 18); *ranae* (Subba Rao) (1957: 388); *reticulata* (Girault) (1913c: 166), **comb.n.** (from *Signiphora*); *rozanovi* Sugonyaev (1968: 369); *ruskini* (Girault) (1921: 188), **comb.n.** (from *Signiphora*); *simillimus* (Mercet) (1917: 11); *subaeneus* (Foerster) (1878: 69) (=*mala* Nikol'skaya, 1950: 320); *thusanoides* (Girault) (1915: 71), **comb.n.** (from *Signiphora*); *walkeri* Hayat (1970: 393). Rozanov (1965) listed *beethoveni*, *corvinus*, *funeralis*, *reticulata* and *thusanoides* as possibly belonging to *Chartocerus* (*Xana*).

Biology. Commonly reared as hyperparasites of Encyrtidae and Aphelinidae (and perhaps other families) from Pseudococcidae, Coccidae, Psyllidae and Aphididae. Records also exist for rearings from Dactylopiidae and Asterolecaniidae. Some species are known to parasitize larvae or pupae of Chamaemyiidae (Diptera) that are predators of mealybugs. Clausen (1924) found *C.elongatus* to be an external, obligate hyperparasite of various encyrtids on *Pseudococcus maritimus* in California. I know of no evidence for any *Chartocerus* acting as a primary parasite.

Distribution. The two species included in the subgenus *Chartocerus* (*Chartocerus*) (Hayat & Verma, 1980) are known only from India and Sri Lanka, but otherwise the genus is cosmopolitan.

Thysanus Walker, 1840

Thysanus Walker, 1840: 234, type-species *Thysanus ater* Haliday, by monotypy.

Triphasius Foerster, 1856: 83, 84; type-species *Thysanus ater* Haliday; unnecessary replacement name for *Thysanus* Walker.

Plastocharis Foerster, 1856: 145; type-species *Thysanus ater* Haliday; replacement name for *Triphasius* Foerster.

Thusanus Walker, 1872: 114, unjustified emendation of *Thysanus* Walker, 1840.

Neosigniphora Rust, 1913: 164; type-species *Neosigniphora nigra* Rust, 1913, by original designation; preoccupied by *Signiphora nigra* Ashmead, 1900; replacement name *Thysanus rusti* Timberlake, 1924: 246.

Diagnosis. Two synapomorphies characterize *Thysanus*: (1) male antenna with four annelli, (2) digitus of male genitalia with two denticles, one at the apex and one at the midpoint on the medial surface. In addition, *Thysanus* spp. (along with *Clytina* spp.) lack seta M6 from the forewing marginal vein, and have a rounded occipital margin. *Thysanus* species have tridentate mandibles (except for one new species, which has four teeth) and the mandibular ducts are expanded distally (an apparent parallelism with some *Signiphora* spp.). Rozanov (1965) and others (e.g. Quezada *et al.*, 1973) noted an anterior projection of the phallobase of the male genitalia in *Thysanus*. Males of *T.ater* generally have such a projection but it is lacking from males of some other *Thysanus* spp., and present in certain other signiphorids (cf. Fig. 18). In most species of *Thysanus*, the midtibial spur is relatively short, on the order of half the length of the middle basitarsus, as opposed to other signiphorids in which the spur and basitarsus are subequal in length.

Discussion. As noted above, *Thysanus rusti* Timberlake (the OTU THYSRUST in this study) displays all of the synapomorphies of *Thysanus* spp. Rozanov (1965) and Gordh (1979) treated *Neosigniphora* as a junior synonym of *Thysanus*. However, De Santis (1968, 1979) and Hayat & Verma (1980) treated *Neosigniphora* as a valid genus, based on the supposedly acute occipital margin in *T.rusti*. The occipital margin of other *Thysanus* (and *Clytina* spp.) is rounded. The type specimens of *T.rusti* are in balsam and in poor condition. The shape of the occipital margin cannot be discerned. I have examined the few other available specimens of *T.rusti*, all of which are slide-mounted, and in these the occipital margin appears to be rounded. One would prefer to examine live material or well-preserved dry material to observe this character. However, even if the occipital margin of *T.rusti* is acute, as De Santis (1968) suggests, this would constitute an autapomorphy for this species only, and would not justify retaining *Neosigniphora* as a valid genus.

Limits. I include the following species: *ater*

Haliday, 1840 (in Walker, 1840: 234); *melancholicus* (Girault) (1913a: 218) **comb.n.** (from *Signiphora*); *nigrellus* (Girault) (1913a: 233); *rusti* Timberlake (1924: 246). This genus is currently under revision by the author and several new species have been identified. Based on the brief original description, *S.longiclava* Girault (1917: 20) may also belong in *Thysanus*. *Thysanus nigrellus* (Girault) has never been included in *Thysanus* (*sensu stricto*), although Peck (1951) and others placed the species in *Thysanus* (*sensu lato*).

Biology. *Thysanus ater* and *T.rusti* have been reared from Diaspididae. Gordh (1979) and Rozanov (1965) refer to *T.ater* as a hyperparasite, but I know of no detailed studies of its biology.

Distribution. *Thysanus ater* is apparently cosmopolitan, as it is known from North America, Europe, the Soviet Union, Israel and India. Apart from a new species from South Africa, the other species are known only from the Nearctic and Neotropical regions.

Clytina Erdös, 1957

Clytina Erdös, 1957: 62; type-species *Clytina giraudi* Erdös, by original designation.

Diagnosis. One synapomorphy characterizes this genus: the head is prognathous and subrectangular in dorsal aspect (Fig. 6). However, this character involves a complex of modifications to the head, as discussed above (character 4). The midtibiae of *Clytina* lack the modifications found in other Signiphoridae, being more or less cylindrical (not obconic) and lacking the long spines on the dorsal surface (Fig. 25). This is an apparent reversal for a set of derived characters found in all other Signiphoridae. *Clytina* spp. share a rounded occipital margin and the loss of seta M6 from the forewing marginal vein with *Thysanus* spp. Another trait makes recognition of *Clytina* species relatively easy: the pronotum is unusually long for a signiphorid and is quite setose.

Limits. One species has been described, *C.giraudi* Erdös, and I have seen an undescribed species.

Biology. *Clytina giraudi* is recorded as a pupal parasite of Chloropidae (Erdös, 1957).

Distribution. *Clytina giraudi* is known from Hungary, France and Soviet Central Asia, and the undescribed species is known from Costa Rica.

Signiphora Ashmead, 1880

Signiphora Ashmead, 1880: 30; type-species *Signiphora flavopalliata* Ashmead 1880, by monotypy.

Signiphorella Mercet, 1916: 5; type-species *Signiphora (Signiphorella) merceti* Malenotti, 1916, by original designation.

Kerrichiella Rozanov, 1965: 513 **syn.n.**; type-species *Thysanus coleoptratus* Kerrich, 1953, by action of International Commission of Zoological Nomenclature, Opinion 1143, 1979.

Rozanoviella Subba Rao, 1974: 526 **syn.n.**; type-species *Signiphora polistomyiella* Richards, 1935, by original designation.

Diagnosis. Two synapomorphies characterize this genus: (1) calcar of fore tibia with a medial comb of fine projections (Fig. 28) and (2) medial sclerite of propodeum with a posterior lamelliform process. In addition, most *Signiphora* have three annelli in both sexes.

Discussion. Mercet (1916) erected *Signiphorella* for the single species *S.merceti* Malenotti. Most authors have treated this genus as a junior synonym of *Signiphora*. *Signiphora merceti* is a rather highly derived member of the *flavopalliata* species group of Signiphora. *Rozanoviella* and *Kerrichiella* may represent distinct lineages, however their relationships to the remainder of *Signiphora* are not clear. In particular, there is no evidence that either (or both) of these lineages form a sister group to the remainder of *Signiphora*. The best solution is to treat these apparent lineages as species groups in *Signiphora*, without nomenclatural standing. *Signiphora*, as so defined, is readily definable on the basis of synapomorphies.

The flavopalliata species group

Diagnosis. Three synapomorphies indicate the monophyly of this group. All species have mandibular ducts which are expanded distally (Fig. 2). With two known exceptions (*S.mexicana* and *S.tumida*), these species have one seta on the submarginal vein of the forewing, and with three exceptions (the above and a new species), these species have hindwings with

parallel margins (Fig. 22). The following will further aid in recognizing these species. Body coloration highly variable, ranging from predominantly black or brown with some white, yellow or tan colour on the mesosoma, through predominantly yellow or pale with some brown or dusky colour on the mesosoma and/or metasoma, to entirely yellow or pale; mesoscutum with two submedial setae; hindwing with two setae on marginal vein (Fig. 22); male genitalia usually lacking medial denticles (but present and falcate in *S.mexicana* and *S.tumida*); male S8 ranging from a transverse strip to broadly triangular.

Limits. The following species are included: *aleyrodis* Ashmead (1900: 412); *aspidioti* Ashmead (1900: 412); *borinquensis* Quezada, DeBach & Rosen (1973: 549); *caridei* Brèthes (1914: 8); *coquilletti* Ashmead (1900: 412); *euclidi* Girault (1935: 4); *fax* Girault (1913a: 223); *flava* Girault (1913a: 214); *flavella* Girault (1913a: 214) (=*basilica* Girault, 1913a: 215); *flavopalliata flavopalliata* Ashmead (1880: 29); *flavopalliata desantisi* De Santis (1973: 148); *flavopalliata occidentalis* Howard (1894: 223); *insularis* (Dozier) (1933: 98); *louisianae* (Dozier) (1933: 100); *lutea* Rust (1913: 163); *maculata* Girault (1913a: 221); *magniclava* (Dozier) (1933: 99); *merceti* Malenotti (1916: 181); *mexicana* Ashmead (1900: 411); *perpauca* Girault (1915: 71); *rectrix* Girault (1915: 71); *thoreauini* Girault (1916a: 4); *townsendi* Ashmead (1900: 412); *tumida* De Santis (1973: 150) and *xanthographa* Blanchard (1936: 18). A revision of these species is nearing completion. Several of the species listed above will be synonymized under other members of the group and several new species will be described.

Biology. Three described species, *borinquensis*, *flavella* and *merceti*, are known to be uniparental, primary parasites of Diaspididae. *Signiphora borinquensis* and *S.merceti* display an unusual mode of development (Quezada *et al.*, 1973; Agekyan, 1968). Eggs of these species are deposited internally in female scales, the first and second instars feed as internal parasites. The larvae then emerge through the host integument and complete development as external parasites. *Signiphora flavella* is known to be a primary parasite (DeBach *et al.*, 1958) and it apparently is an ectoparasite (Matta V., 1979, cited as *S.aspidioti*). Notes and records for *S.perpauca* that I have examined indicate that this species is a primary external parasite of Diaspididae. *Signiphora coquilletti, aleyrodis* and *townsendi* are known to be obligate hyperparasites of Aphelinidae and Platygasteridae in Aleyrodidae (e.g. Woolley & Vet, 1981). *Signiphora flavopalliata occidentalis* is known to be an obligate hyperparasite of Diaspididae (DeBach, 1953). *Signiphora fax* is apparently also a hyperparasite of Diaspididae. The other species listed have been reared from Diaspididae or Aleyrodidae, but no further information is available.

Distribution. *Signiphora flavella* and *merceti* appear to be more or less cosmopolitan. *Signiphora euclidi, perpauca* and *rectrix* were described from Australia, but *S.perpauca* is also a common parasite of armoured scale in the New World. The other species are known only from the Nearctic or Neotropical regions, or both.

The bifasciata species group

Diagnosis. A phenetic characterization of this group is as follows. Relatively large and robust species, with body colour predominantly black with metallic reflections and a variable amount of white, yellow or tan colour on the posterior sclerites of the mesosoma; mesoscutum with 9 to more than 20 setae (in comparison to the *flavopalliata* group in which the mesoscutum usually bears 2 setae); submarginal vein of forewing with 2 setae (usually 1 seta in *flavopalliata* group), marginal vein of hindwing with 1 seta in proximal quarter (an additional apical seta is present on hindwing of *flavopalliata*-group species); medial denticles present on male genitalia (variously lost in other species groups), robust and falcate in some species; male S8 triangular (cf. Fig. 17) (not 'dumb-bell' shaped as in *dipterophaga* group (Figs 16, 18)).

Limits. The following species are included: *bifasciata* Ashmead (1900: 411) (=*platensis* Bréthes, 1913: 96), *fasciata* Girault (1913a: 219); *hyalinipennis* Girault (1913a: 220); *noacki* Ashmead (1900: 410); *rhizococci* Ashmead (1900: 411); *unifasciata* Ashmead (1900: 410); and several undescribed species.

Biology. Little is known of the biology of these species beyond rearing records. Records indicate that individuals of the following families are parasitized: Coccidae, Pseudococcidae, Psyllidae, Diaspididae and Asterolecaniidae,

with the majority of records from the first three families.

Distribution. Most species have a Neotropical distribution, with the ranges of some extending through parts of Mexico into south Texas and/or Arizona.

The dipterophaga species group

Diagnosis. A complex of modifications to the male genital opening provides evidence for the monophyly of these species : (1) small or large ventrolateral projections on the syntergum (Figs 16, 18), (2) a 'dumb-bell' shaped S8, and (3) S7 broadly emarginate (Figs 16, 18). In addition, the group can be characterized as follows. Generally large and robust species with predominantly black or brown body coloration with weak metallic reflections, although some species ('New Genus' in Figs 29, 30) are predominantly yellow with varying amounts of brown or dusky colour on the mesosoma and metasoma; female antenna with 3 or 4 annelli ('New Genus' species), male with 3 annelli; mesoscutum with 6 to more than 30 setae; forewing with 2 setae on submarginal vein, and with or without discal seta; hindwing with 1 seta in the proximal quarter of marginal vein; male genitalia with or without medial denticles.

Limits. The following species are included: *dipterophaga* Girault (1916b: 401); *frequentior* (Kerrich) (1953: 803); *maxima* Girault (1913a: 217); *polistomyiella* Richards (1935: 132); *pulchra* Girault (1913a: 215); *zosterica* (Kerrich) (1953: 805). The group is currently under revision. Several new species have been identified, including all of the species represented by 'New Genus' in Figs 29 and 30.

Biology. Most of the species in this group, so far as is known, are pupal parasites of Diptera. Recorded hosts include species of Tachinidae and Drosophilidae. The biology of one species in the 'New Genus' subgroup, discussed above, is known: it is pupal parasite of Drosophilidae that are predators of Pseudococcidae. In contrast, *S.pulchra* has been reared from several genera of Diaspididae. All other *Signiphora* parasitize Homoptera, and parasitization of dipteran pupae is clearly a derived trait in this species group. It is interesting that both characters 15 and 16 are rather weakly expressed in *S.pulchra* so that this species has retained both the plesiomorphic host asssociation and a relatively plesiomorphic morphology.

Distribution. *Signiphora pulchra* stands out again as the only member of this species group with a Nearctic distribution. Otherwise, these species are Neotropical, with distributions extending in some cases as far north as San Luis Potosí or Veracruz, Mexico.

The coleoptratus species group

Diagnosis. Several synapomorphies indicate the monophyly of this group: (1) robust and almost spherical habitus, (2) forewing with reduced setation on marginal vein, and (3) forewing with extremely short marginal cilia (cf. Fig. 32: Rozanov, 1965). In addition, the following characterize these species. Body coloration black or brown with weak metallic reflections, lacking any yellow, white or tan areas: mesoscutum with approximately 80–100 small setae; forewing with 2 setae on submarginal vein, with 4 dorsal setae on marginal vein (setae M1 and M6 absent), and without discal seta; hindwing broadly rounded, with 1 seta in proximal quarter of marginal vein, and without discal seta; male genitalia with medial denticles.

Limits. Two species are included: *coleoptratus* (Kerrich) (1953: 802) **comb.n.** (from *Kerrichiella*) and *giraulti* Crawford (1913: 348).

Biology. Kerrich (1953) suspected that *Signiphora coleoptratus* was a tertiary hyperparasite through *Gahaniella tertia* Kerrich (Encyrtidae) in *Planococcus citri* (Risso) (Pseudococcidae). The holotype of *Signiphora giraulti* was reared from the same host. Other records on material I examined indicate rearings from mealybugs.

Distribution. These species are not commonly collected, to say the least. Both species were described from material collected in Trinidad. I have also seen material from Antigua, West Indies; Caqueta Commissary, Colombia; and Yahuarmayo, Peru.

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APPENDIX A. Data matrix for Signiphoridae and outgroup taxa. A question mark (?) indicates a missing data point. The values shown for character 25 are those obtained after recoding, as discussed in the text. The original coding for character 25 is shown in parentheses.

Taxon	Character																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
COCCOPHA	2	0	1	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0
AZOTINAE	2	1	0	0	?	?	1	0	0	0	0	1	1	?	0	0	0	0	0	0	1	1	0	0	0	0	0	0
CHARTOCS	2	0	1	0	3	4	1	1	1	1	0	1	1	0	0	0	1	0	1	0	2	1	0	1	2 (3)	0	1	0
THYSATER	3	1	0	0	4	4	1	1	1	1	1	1	1	1	0	0	0	1	1	0	1	0	1	1	1	0	1	0
THYSNSP5	4	1	0	0	4	4	1	1	1	1	1	1	1	1	0	0	0	1	1	0	2	0	1	1	1 (2)	0	1	0
THYSNSP6	3	1	0	0	4	4	1	1	1	1	1	1	1	1	0	0	0	1	1	0	2	0	1	1	1 (2)	0	1	0
THYSRUST	3	1	0	0	4	4	1	1	1	1	0	1	1	1	0	0	0	1	1	0	2	0	1	1	1	0	1	0
CLYTGIRD	2	0	0	1	3	4	1	1	1	1	0	1	1	1	0	0	1	0	1	0	1	0	1	1	0	0	0	0
CLYTNSP1	3	0	0	1	3	4	1	1	1	1	0	1	1	1	0	0	1	0	1	0	2	0	1	1	1	0	0	0
SIGNALEY	2	1	1	0	3	3	1	1	2	1	1	1	1	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1
SIGNFLAV	2	1	1	0	3	3	1	1	2	1	1	1	1	1	0	0	0	0	1	1	1	1	1	0	1	0	1	1
MEXBIFSC	2	0	1	0	3	3	1	1	2	1	0	1	1	1	0	0	2	0	1	1	2	1	0	1	1	0	1	1
MEXHYALI	2	0	1	0	3	3	1	1	2	1	0	1	1	1	0	1	2	0	1	1	2	1	0	1	1 (2)	0	1	1
MEXIMEXI	2	1	1	0	3	3	1	1	2	1	0	1	1	1	0	0	2	0	1	1	2	1	0	1	1	0	1	1
MEXINS11	2	0	1	0	3	3	1	1	2	1	0	1	1	1	0	1	1	0	1	1	2	1	0	1	1 (2)	0	1	1
MEXINSP2	2	0	1	0	2	?	1	1	2	1	0	1	1	1	0	0	2	0	1	1	2	1	0	1	1	0	1	1
MEXINSP6	3	1	1	0	3	?	1	1	2	1	0	1	1	1	0	0	1	0	1	1	1	1	0	1	1	0	1	1
MEXINSP7	2	0	1	0	3	3	1	1	2	1	1	1	1	1	0	0	2	0	1	1	2	1	0	0	1 (2)	0	1	1
MEXPULCH	2	0	1	0	3	3	1	1	2	1	1	1	1	1	1	1	1	0	1	1	2	1	0	0	1 (2)	0	1	1
MEXUNINO	2	0	1	0	3	3	1	1	2	1	0	1	1	1	0	0	1	0	1	0	2	1	0	0	1 (2)	0	1	1
ROZMAXIM	2	0	1	0	3	3	1	1	2	1	0	1	1	1	2	1	1	0	1	0	2	1	0	0	1	0	1	1
ROZNCOMP	2	0	1	0	3	3	1	1	2	1	0	1	1	1	2	1	1	0	1	0	2	1	0	0	1	1	1	1
ROZNNSP4	2	0	1	0	3	?	1	1	2	1	0	1	1	1	2	1	1	0	1	1	2	1	0	0	1 (2)	0	1	1
ROZNRMAX	2	0	1	0	3	3	1	1	2	1	0	1	1	1	2	1	1	0	1	1	2	1	0	0	1	0	1	1
KERRICHI	2	0	1	0	1	1	1	1	2	1	0	1	1	1	0	0	1	0	1	0	2	1	0	0	1 (2)	0	1	1
NGENNSP1	2	0	1	0	3	4	1	1	2	1	1	1	1	1	1	1	0	0	1	1	2	1	0	0	1 (2)	0	1	1
NGENS19A	2	0	1	0	3	4	1	1	2	1	0	1	1	1	1	1	0	0	1	0	2	1	0	0	1 (2)	0	1	1
NGENS19B	2	0	1	0	3	4	1	1	2	1	0	1	1	1	1	1	1	0	1	0	2	1	0	0	1 (2)	0	1	1
NGENNSP3	2	0	1	0	3	4	1	1	2	1	0	1	1	1	?	1	0	0	1	1	2	1	0	0	1 (2)	0	1	1
NGENNSP5	2	0	1	0	3	4	1	1	2	1	0	1	1	1	1	1	1	0	1	0	2	1	0	1	1 (2)	0	1	1

APPENDIX B. List of OTU's and taxa which each represents.

OTU	Taxa which OTU represents
COCCOPHA	Coccophaginae (Aphelinidae)
AZOTINAE	Azotinae (Aphelinidae)
CHARTOCS	*Chartocerus* spp.
THYSATER	*Thysanus ater, T.nigrellus*
THYSNSP5	*Thysanus* n.sp. 5
THYSNSP6	*Thysanus* n.sp. 6
THYSRUST	*Thysanus rusti, T.melancholicus, Thysanus* n.spp. 2 and 3
CLYTGIRD	*Clytina giraudi*
CLYTNSP1	*Clytina* n.sp. 1
SIGNALEY	*Signiphora aleyrodis, S.aspidioti, S.borinquensis, S.caridei, S.coquilletti, S.flava, S.flavella, S.louisianae, S.lutea, S.maculata, S.merceti, S.thoreauini, S.townsendi, S.xanthographa* and *Signiphora* n.spp. 3, 8 and 10
SIGNFLAV	*Signiphora fax, S.flavopalliata flavopalliata, S.flavopalliata occidentalis, S.flavopalliata desantisi, S.insularis, S.perpauca* and *Signiphora* n.spp. 4, 13, 14, 15, 16
MEXBIFSC	*Signiphora bifasciata, S.rhizococci, S.fasciata, S.platensis*
MEXHYALI	*Signiphora hyalinipennis*
MEXIMEXI	*Signiphora tumida, S.mexicana, S.magniclava*
MEXINSP2	*Signiphora* n.sp. 2
MEXINSP6	*Signiphora* n.sp. 6
MEXINSP7	*Signiphora* n.sp. 7
MEXISP11	*Signiphora* n.sp. 11
MEXPULCH	*Signiphora pulchra*
MEXUNINO	*Signiphora unifasciata, S.noacki*
ROZMAXIM	*Signiphora maxima* (previously placed in *Rozanoviella*)
ROZNCOMP	*Signiphora polistomyiella, S.frequentior, S.zosterica, S.dipterophaga* (previously placed in *Rozanoviella*)
ROZNNSP4	*Signiphora* n.sp. 4
ROZNRMAX	*Signiphora* n.sp. near *maxima*
KERRICHI	*Signiphora giraulti, S.coleoptratus* (previously placed in *Kerrichiella*)
NGENNSP1	*Signiphora* n.sp. 1
NGENSP2A	*Signiphora* n.sp. 19 (in part)
NGENSP2B	*Signiphora* n.sp. 19 (in part)
NGENNSP3	*Signiphora* n.sp. 3
NGENNSP5	*Signiphora* n.sp. 5