EVIDENCE FOR MONOPHYLY AND RELATIONSHIPS OF CHALCIDIOIDEA, MYMARIDAE, AND MYMAROMMATIDAE (HYMENOPTERA: TEREBRANTES)

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Abstract

Twenty-three characters or character systems of adults and larvae of Terebrantes are analyzed for evidence of monophyly and phylectic relationships of Chalcidoidea, Mymaridae, and Mymarommatidae. The taxa are considered to be a monophyletic group based on 3 hypothesized synapomorphies: mesotrochanteral depressor without fu-tr, or mesoscutal portion of t-tr; axillary phragma as site of origin for all or part of t-tr muscle; and independent basal ring absent from male genitalia. The family Mymaridae is considered to be monophyletic based on at least 3 apomorphies: fore wing with hypochaeta; head with frontal, median, and supraorbital sulci; and toruli distinctly closer to inner margin of eye than to each other. Chalcidoidea, including Mymaridae, is considered to be a monophyletic taxon based on 3 apomorphies: prepectus externally visible, at least dorsally adjacent to lateral edge of mesoscutum; mesothoracic spiracle positioned at exposed lateral edge of mesoscutum; and multiporous plate sensilla of antenna with unique structure, as described in text. Mymarommatidae is considered to be the monophyletic sister group of Chalcidoidea based on several apomorphies, including 4 autapomorphies: head composed of frontal and occipital sclerites, which are connected by pleated membrane along hyperoccipital region; hind wing stalk-like, without membrane and terminated in bifurcation that clasps fore wing; fore wing with reticulate pattern formed by raised lineations of membrane; and axillary portion of t-tr muscle absent. Phylectic relationship of Seraphitidae with Mymarommatidae is deemed inconclusive because relevant internal character states of amber fossil seraphitids cannot be determined. It is suggested that mymarommatids be accorded family status, but not be assigned to superfAMILY until phylectic relationships are more accurately determined in Terebrantes. A matrix summarizes character-state distribution of most characters analyzed for Terebrantes, and a cladogram illustrates hypotheses of character-state evolution and proposed relationships.

Résumé

L’ouvrage analyse 23 caractères ou systèmes de caractères d’adultes et de larves de Tébrèbrantes pour l’existence de rapports monophylétiques et phylétiques des Chalcidoidea, Mymaridae et Mymarommatidae. Les taxons sont considérés comme un groupe monophylétique fondé sur 3 synapomorphies hypothétiques, soit le déprimeur métatrochantéral sans fu-tr, ou la portion mésoscutale de t-tr, du phragma axillaire comme point d’origine pour la totalité ou une partie du muscle t-tr, et l’absence d’anneau basal indépendant des génitalia mâles. La famille des Mymaridae est considérée comme monophylétique fondée sur au moins 3 apomorphies, soit l’aile antérieure pourvue d’un hypochète, la tête dotée de sillons frontaux, médians et supraorbitaux et des toruli distinctement plus rapprochés de la bordure interne de l’œil que l’un par rapport à l’autre. Les Chalcidoidea, y compris les Mymaridae, sont considérés comme un taxon monophylétique fondé sur 3 apomorphies, soit un prépectus visible de l’extérieur (au moins dorsalement voisin du bord latéral du mésoscutum), des stigmates métathoraciques situés sur le bord latéral exposé de mésoscutum et des sensilles placoides multipores de l’antenne à structure unique comme le décrit le texte. Les Mymarommatidae sont considérés comme un groupe sœur monophylétique des Chalcidoidea d’après plusieurs apomorphies, y compris 4 autapomorphies, soit la tête composée d’un sclérite frontal et occipital reliés par une membrane plissée le long de la région hyperocippitale, une aile antérieure pédonculée sans membrane et terminée par une bifurcation qui vient s’agréger sur l’aile antérieure, une aile antérieure réticulée formée par des lignes soulévetées de la membrane et l’absence de portion axillaire du muscle t-tr. Le rapport

1This study was conducted in the Department of Entomology, University of Alberta, Edmonton, Alberta, Canada T6G 2E3.
phylétique des Serphitidae avec les Mymarommatidae est jugé peu concluant car il est impossible de déterminer l’état de caractères internes pertinents de Serphitides fossilisés dans l’ambre. Il est proposé d’accorder le statut de famille aux Mymarommatidae, mais de ne pas leur attribuer de superfamille avant d’avoir mieux défini les rapports phylétiques des Térébrantes. Un tableau résume la distribution de la plupart des caractères examinés pour les Térébrantes et un cladogramme illustre certaines hypothèses d’évolution de l’état des caractères et des rapports proposés.

Introduction

Authors disagree about relationships and formal classification of mymarids and mymarommatids in parasitic Hymenoptera (Terebrantes). Mymarids initially were considered as members of the superfamily Proctotrupoidea by Förster (1856) and by Dalla Torre (1898), until Ashmead (1904) proposed the superfamily Chalcidoidea and included Mymaridae as 1 of 14 families. A separate superfamily, Mymaroidae, was proposed for Mymaridae and Signiphoridae by Ghesquière (1942), but most workers since Ashmead have continued to include both taxa in Chalcidoidea. However, Kozlov and Rasnitsyn (1979) hypothesized mymarids originated from the same clade as the extinct family Serphitidae, and thus should be classified in Proctotrupoidea as originally placed by Förster. Rasnitsyn (1980) altered this hypothesis slightly by proposing both serphitids and mymarids were derived from within Scelionidae, but independently at different times. All 3 families were transferred by him by his newly proposed superfamily, Diaprioidae.

Though the first described mymarommatid was misidentified as a species of Proctotrupes Latreille (Proctotrupidae) by Deusburg (1868), placement of mymarommatids in Chalcidoidea was generally accepted until recently. Disagreement centered upon whether mymarommatids are merely aberrant mymarids, and should be accorded some infrafamilial rank in Mymaridae (Annecke and Doutt 1961; Yoshimoto 1975), or whether they are sufficiently distinct to warrant separate familial status2 (Debuche 1948; Königsman 1978a; Yoshimoto 1984). Kozlov and Rasnitsyn (1979) proposed the radically new hypothesis that mymarommatids are not related to chalcids, but to serphitids. They classified mymarommatids as a monobasic subfamily in the otherwise extinct family Serphitidae.

Königsman (1978a) considered monophyly of Chalcidoidea to be highly probable based on wing venation, metallic luster, and antennal, pronotal, and male genital structure. He classified Mymaridae in Chalcidoidea, and stated that though mymarids possess none of the synapomorphic states elaborated for the superfamily, all of their states could either be derived from those of chalcids or else correspond to them. He further considered mymarommatids to share 3 synapomorphies with mymarids: profile of the fore wings; absence of anelli; and overall habitus. He accorded mymarommatids family status, but stated that a more detailed study was required to determine whether they should be included in Mymaridae, or should be considered as the sister group of Mymaridae.

Schauff (1984) also classified mymarids as a family of Chalcidoidea, uniting members on the basis of 3 proposed synapomorphies: presence of an exposed prepectus; elongate sensory ridges (multiporous plate sensilla) on the antennae; and a particular ovipositor structure (though polarity of this latter character was questioned). Mymarommatids were recognized as a separate family, but placement to superfamily was said to be problematic.

I (Gibson 1985) previously described transformation series of states of 13 characters of the pro- and mesothorax in Hymenoptera, and discussed what phylogenetic inferences could be made from the different states. Of 30 hypothesized derived states shared among members of different higher taxa, 2 were considered unique (autapomorphic) for Chalcidoidea in Apocrita: position of mesothoracic spiracle at exposed lateral edge of mesoscutum; and presence of axillar phragma as partial site of origin for mesotergal-mesotro-

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2The family name Mymarommatidae as originated by Debuche (1948) was corrected to Mymarommatidae by Brues et al. (1954).
chanteral (t.2-tr.) muscle. Mymarids were included in the above analysis, but mymaromatids were not.

Shared derived character states can be homologous and the result of inheritance from a common ancestor (synapomorphy), or non-homologous and due to convergence (homoplasly). Because hypotheses of synapomorphy and homoplaspy are made partly on the basis of parsimony and congruence of different character-state transformations, hypotheses of monophyly, and of phylectic relationships, should ideally be made only after a detailed analysis of as many characters as possible. This paper analyzes character states that were used previously to define or to suggest relationships of Chalcidoidea, Mymaridae, and Mymarommatidae, and attempts to determine which shared states are synapomorphic and valid indicators of monophyly or relationships, and which states are symplesiomorphic or homoplasious.

Materials and Methods

Materials. Taxa examined for internal structures include those listed in Appendix III of Gibson (1985) and additional taxa listed below. Character-state distribution in Mymaridae is based on specimens in the Canadian National Collection (CNC), including slide-mounted individuals representing 32 genera or subgenera. Character-state distribution in Mymarommatidae is based on specimens representing the 7 described extant species — *Palaeomyrm mynamalum* (Blood and Kryger 1922), [= *P. succini* Meunier 1901, vide Doutt 1973; *nec P. dauburgi* (Stein 1877)], *P. goethei* (Girault 1920), *P. mirum* (Girault 1931), *P. mirissimum* (Girault 1935), *P. buyckxii* (Mathot 1966), *P. insulare* (Valentine 1971), and *P. cycloppterus* Fidalgo and De Santis (1982); amber inclusions representing 5 of the 7 described extinct species — *Archaeromma minutissimum* (Brues 1910), *A. nearcticum* Yoshimoto (1975), and *P. agapa, P. mandibulatum,* and *P. senonicum* Kozlov and Rasnitsyn (1979); and additional specimens in the CNC, Museum of Comparative Zoology, Harvard University (MCZ), and Zoologisk Museum, Copenhagen, representing undescribed extant and extinct species. Character-state distribution in Seraphitidae is based on study of amber fossil inclusions in the CNC and on the type specimen of *Microserphites parvulus* Kozlov and Rasnitsyn (1979).

Specimen preparation and illustration. Figures 14 and 31 are photographs of slide mounts using a Carl Zeiss Ultraphot II microscope. Other illustrations are SEM photomicrographs, with methods of specimen preparation as described in Gibson (1985). Abbreviations used for figures are explained in the Appendix.

Phylogenetic methods. The philosophical approach used here to determine probable relationships is phylogenetic *sensu* Hennig, i.e. relationship as defined by common ancestry is determined by shared, derived, homologous character states (synapomorphies), but not by shared primitive character states (symphlesiomorphies), nor by independently derived and thus non-homologous character states (homoplasies). Accurate phylogenetic reconstruction requires that similarity due to synapomorphy be distinguished from similarity resulting from the latter 2 causes.

Hypotheses of apomorphy relative to plesiomorphy depend on polarity, or the direction of character-state evolution. Jong (1980) reviewed various methods proposed to distinguish derived (apomorphic) from primitive (plesiomorphic) states. Ideally, a sister group is proposed and out-group comparisons are made. Though the works of Königsmann (1978a, b) and Rasnitsyn (1980) attempted to analyze phylectic relationships of Apocrita, discrepancies in their conclusions illustrate how uncertain is our knowledge of the evolution of Apocrita. Monophyly of Terebrantes is questionable, and most hypotheses of sister-group relationships in Terebrantes are tenuous. Consequently, polarity of character states in this analysis is based partly on the criterion of commonality, i.e. the most widely distributed state in Apocrita is considered to be plesiomorphic. However, when possible,
polarity was hypothesized for character states after comparison of the respective states in Symphyta, hypotheses made of the groundplan (plesiomorphic) state of the character for Apocrita, and transformation series of states hypothesized in Apocrita. Study of character-state distribution is based on extant Hymenoptera, plus fossil serphitids and mymarrommatids.

Hypotheses of synapomorphy relative to homoplasy are based on congruence or non-congruence of character-state transformations and judgments as to which transformation series are most reliable as phylogenetic indicators. In accordance with a system developed by Hechtl (1976), apomorphic states that are the result of loss are considered to be least reliable because it is not possible to determine whether common absence is the result of a single or multiple losses. Apomorphisms that are the result of reductions, those that are part of a functional complex, and those that are both innovative and unique are considered to be increasingly more reliable as indicators of synapomorphy.

**Phylogenetic analysis of structural features**

Twenty-three characters or character systems of adults and larvae are analyzed below. Structural features of adults are discussed first, in morphological sequence beginning with appendages of the head, followed by features of the larvae. Character-state distribution and hypotheses of character-state transformation for 20 of the 23 analyzed character systems are summarized for Terebrantes in Table 1. Characters 12 (fore wing venation) and 23 (structure of larvae) are not included in Table 1 because they detail habits, not specific character states. Character 22 (metallic luster of adults) is not included in the table because of insufficient analysis to be meaningful.

1. **Number of antennal articles.** One of 3 character states of the antenna considered by Königsmann (1978a) to indicate probable monophyly of Chalcidoidea was possession of 13 articles by most members. Nikolskaya (1952), Gerdh (1979), and Rasnitsyn (1980) also used this as one state to define Chalcidoidea.

   Number of antennal articles possessed by terebrants is listed in Table 1, character 1. Chalcidoids have from 4 to 26, but the maximum number for most is 13. The only chalcidoids to have more than 13 articles are individuals of *Diglochis Förster* (Pteromalidae), which have 14 (Dzhanokmen 1979), and members of some genera of Eucharitidae. Numerous and diverse chalcidoids have less than 13 articles, including known Aphelinidae, Eulophidae, Signiphoridae, Tetracampidae, and Trichogrammatidae. The most parsimonious explanation for this distribution is that 13 articles is the groundplan number of antennal articles for Chalcidoidea, and that this number was secondarily increased in at least 2 clades, and decreased independently an unknown number of times in other clades.

   Proctotrupidae, Vanchorniidae, and Evaniiidae also have 13 antennal articles (Table 1). Relationships between these 3 families are unknown, as are relationships between them and Chalcidoidea. Consequently, the common number of antennal articles could be due to inheritance from a common ancestor, or the result of convergence, making this state unreliable as an indicator of monophyly for Chalcidoidea.

   Number of antennal articles is also of little value for determining relationships of mymarids and mymarrommatids. The plesiomorphic number of articles for mymarrommatids is most probably 13. Females and males known from the Cretaceous had 13 articles, though the terminal 4 were partly fused and differentiated as a club in females (Yoshimoto 1975). Extant male mymarrommatids also have 13 antennal articles, but females have only 9–11, and the ultimate article is differentiated as a club (Yoshimoto 1984, figs. 89, 90). The club of females apparently is the result of complete fusion of the terminal 4 articles in all species except *P. insulare* (Valentine). The club is subdivided by a suture in females of this latter species. Many male mymarids have 13-articled antennae, but females have
less than 13 articles and a differentiated club. The antennal club and lesser number of articles in females is probably the result of fusion of some of the apical articles, but reduction in number of articles in many females and males is probably also simply the result of loss.

Königsmann (1978a) is correct in stating that the number of antennal articles of mymarids and mymarommatids either corresponds to the number characteristic of chalcidooids, or can be derived from it, but this no more indicates a close relationship with chalcidooids than does the fewer number of articles characteristic of scelionids, serphitids, platygastrids, or ceraphronoids (Table 1).

2. Anellus. The second antennal character state considered by Königsmann (1978a) to indicate probable monophyly of Chalcidoidea was presence of 1 or more ring-like antennal articles, anelli, between the pedicel and flagellum. He assumed secondary loss for those chalcidooids lacking an anellus. Kozlov and Rasnitsyn (1979), and Rasnitsyn (1980), interpreted absence of an anellus from mymarids and mymarommatids as evidence that these are not related to chalcidooids. Schaff (1984) stated that presence of an anellus might be a synapomorphy for Chalcidoidea exclusive of Mymaridae, but absence of an anellus was not evidence that mymarids are unrelated to chalcidooids.

Table 1, character 2, lists distribution of an anellus in Terebrantes. Only chalcidooids and helorids have an anellus. Reference to anelli in Diapriidae (Ambositrinae) and Ichneumonidae by Königsmann (1978a) and Rasnitsyn (1980) is incorrect. Naumann (1982) determined that the basal region of the first flagellomere in ambositrines, which Masner (1961) called the anellus, is only an annular thickening and not an independent antennal article. The same is true for the anellus-like basal region of the first flagellomere of some ichneumonoids (W.R.M. Mason, pers. comm.).

Exact phylectic relationships between Heloridae and Chalcidoidea are unknown, so that presence of an anellus is lessened as a reliable indicator of monophyly for Chalcidoidea. Distribution of an anellus in Chalcidoidea makes this state even more unreliable for phylogenetic inference. Anelli are apparently nothing more than reduced flagellomeres, and designation of 1 or more basal flagellomeres as anelli in many chalcidooids is subjective. Some members of most chalcidooid families lack anelli, as do known Leucospidae and Eucharitidae (Eucharitinae). Königsmann (1978a) may be correct in stating that the wide distribution of an anellus indicates this as a groundplan character of Chalcidoidea, but if so, the anellus is prone to loss.

Mymarommatids and mymarids lack an anellus, though the first flagellomere of some mymarids is quite small (Schaff 1984). As stated by Schaff, absence of anelli in mymarids and mymarommatids does not prove that these are unrelated to chalcidooids, nor that they are related to scelionids and serphitids. If absence of an anellus in mymarids and mymarommatids is plesiomorphic, either taxon could still be the sister group of Chalcidoidea. Furthermore, if absence is plesiomorphic, this state cannot be used as evidence that mymarids and mymarommatids are related to serphitids, or to any other taxon whose members lack an anellus.

3. Geniculate antennae. The third antennal character state considered by Königsmann (1978a) to indicate probable monophyly of Chalcidoidea was geniculate antennae. Terebrantes with geniculate (abruptly bent) antennae have the pedicel markedly narrowed basally, with only a relatively small area of articulation with the scape, and the pedicel and flagellum are held at an abrupt angle to the scape (Fig. 3).

Table 1, character 3, lists distribution of geniculate antennae in Terebrantes. Chalcidooids have geniculate antennae, except for most eucharitines (Eucharitidae, Eucharitinae), which have straight antennae. Eucharitines without geniculate antennae are also unusual in Chalcidoidea because the scape is quite short, which illustrates a general correlation between scape length and geniculate or non-geniculate antennae in Terebrantes.
Relative scape length is admittedly subjective, but terebrants in Table 1 listed with geniculate antennae also have a relatively long and slender scape, whereas those listed with non-geniculate antennae have a relatively short and stubby scape. Monomachids have non-geniculate antennae, with a scape of intermediate length. Most mymarids have geniculate antennae, but a scape of varied shape, from long and slender to short and stubby, even in different sexes of the same species (cf. sc., Figs. 2, 3). However, if the scape is short and stubby, or there is not a distinct bend in the antenna between the scape and pedicel, the pedicel is still markedly narrowed, with only a very small area of articulation with the scape. A short scape in some mymarids is thus indicated to be due to secondary modification.

Rasnitsyn (1980) hypothesized a long scape as one synapomorphy that united members of his new superfamily, Diaprioidea, but Austroniidae, which he included in Diaprioidea, have a relatively short scape. Even if Rasnitsyn’s hypothesis of synapomorphy is correct for the other taxa he included in Diaprioidea, the long scape of members would be convergent with that possessed by chalcidooids and ceraphronoids. Consequently, the typically long scape and associated geniculate antenna of chalcidooids, mymarids, and mymarrommatids could be the result of synapomorphy, symplesiomorphy, or homoplaspy.

4. Multiporous plate sensilla of antenna. Presence of multiporous plate sensilla (= rhinaria, longitudinal ridges or sensilla) on some flagellomeres of mymarids, but not mymarrommatids, was one reason Debauche (1948) separated Mymarrommatidae as a family distinct from Mymaridae. Kozlov and Rasnitsyn (1979) considered absence of antennal sensilla from mymarrommatids to not only differentiate them from mymarids, but to relate them to seraphitids. Furthermore, they and Rasnitsyn (1980), concluded that presence of sensilla on the antennae of mymarids indicated contradictory evidence of relationships, because members of other taxa they assigned to Diaprioidea lack antennal sensilla. They hypothesized the similar sensilla of mymarids and chalcidooids could be the result of independent gain, because ichneumonoids and cynipoids also have elongate antennal sensilla.

Barlin and Vinson (1981) showed that antennal sensilla of chalcidooids differ in at least 4 states from the superficially similar sensilla of ichneumonoids. Chalcidooid sensilla have the distal end free from the antennal surface and they are not surrounded by grooves, as in ichneumonoids. Furthermore, chalcidooid sensilla have pore tubules, unlike the sensilla of other Hymenoptera examined, and in most female chalcidooids studied there were 2 types of antennal sensilla. Unfortunately, mymarids and cynipoids were not included in the study.

I examined external structure of the antennae of males and females of Acmopolynema Ogloglin, Anaphes Haliday, Camptoptera Förster, Chaetomyzar Ogloglin, Gonatocerus Nees, Ooctonus Haliday, and Polynema Haliday (Mymaridae), using SEM. Males examined had at least some sensilla on all flagellomeres, except for the ring-like second flagellomere of Camptoptera. The sensilla were not surrounded by grooves, were ridge-like raised above the antennal surface, and the apex of each sensillum was extended beyond the apex of the article (Fig. 4). Females had few or no sensilla on the flagellomeres, but all had sensilla on the club. The sensilla were projected beyond the apex of flagellomeres, but only rarely so on the club. Debauche (1948) studied distribution of the antennal sensilla in a larger number of mymarid taxa, though he did not examine their structure. He concluded that male mymarids normally have multiporous plate sensilla (= crétes sensorelles sensu Debauche) on all flagellomeres, whereas females have sensilla on the club, but lack these on the first flagellomere and vary in presence or absence of sensilla on other flagellomeres. However, one undescribed species of Gonatocerus does have 2 sensilla on the first flagellomere (J. Huber, in litt.).

I also examined the antennal sensilla of males and females of Ibaiia Latreille (Ibaliidae), Pseudoeucoila Ashmead (Eucoiliidae), Anacharis Dalman (Figitidae), and Andricus
Hartig (Cynipidae) (Cynipoidea), using SEM. The sensilla were flat, or only slightly raised above the plane of the flagellomere (Figs. 5, 6), did not project beyond the apex of the flagellomere (Fig. 6), or only a few did (Fig. 5), and except for the sensilla of *Pseudocoilia* (Fig. 6) were surrounded by very fine grooves (Fig. 5).

Very few taxa were studied to generalize about the structure of mymarid, and particularly cynipoid antennal multiporous plate sensilla. However, external structure of the sensilla of mymarids appears to be similar to that described for various chalcidoids by Barlin and Vinson (1981), and unlike the antennal sensillar structure of cynipoids and ichneumonoids. Consequently, external structure of the antennal sensilla of mymarids and chalcidoids can be tentatively considered as indicative of monophyly of these 2 taxa. Supportive evidence for this hypothesis should be acquired through study of internal structure of the sensilla. Barlin and Vinson (1981) showed that internal structure of the multiporous plate sensilla of chalcidoids differed from that of ichneumonoids. It must also be shown that internal structure of the antennal sensilla of mymarids is like that described for chalcidoids, and that this common structure is dissimilar to the internal structure of the sensilla of cynipoids.

Though I presently interpret lack of antennal multiporous plate sensilla as plesiomorphic for Terebrantes, sensilla of various shapes and presumably diverse structure are possessed by many other terebrants. A comprehensive study is required to determine distribution and structure of the sensilla throughout Terebrantes. It is possible that the antennal sensillar structure of mymarids and chalcidoids is not uniquely derived, but is only part of some transformation series and not necessarily indicative of monophyly.

Mymarommatidae is indicated to be at most the sister group of Mymaridae + Chalcidoidea, if absence of antennal sensilla is plesiomorphic, i.e. not due to secondary loss. Furthermore, if absence is plesiomorphic, it is not evidence of a relationship between mymarommatid and serephitid, as suggested by Kozlov and Rasnitsyn (1979).

5. **Exodont mandibles.** Exodont mandibles do not overlap at the midline and they have outwardly directed teeth (Figs. 7, 8). Table 1, character 5, lists distribution of exodont mandibles in Terebrantes. Mymarommatids and vanhorniids (Vanhornia Crawford) have exodont mandibles, as do individuals of *Exodontomphale* (Chalcidoidea: Eulophidae) (Bouček 1984), and members of 4 tribes of Ichneumonoidea (Ichneumonidae: Tryphoninae–Idiogrammatini; Braconidae: Alysiinae–Alysiini, Dacusini; Opiinae–Exodontiellini) (Wharton 1977). The reconstructed phylogeny for Braconidae by van Achterberg (1984) indicates exodont mandibles are not a groundplan character of Braconidae, but are secondarily derived in the family. Restricted distribution also indicates exodont mandibles are secondarily and independently derived in Eulophidae and Ichneumonidae. However, common occurrence of such mandibles in vanhorniids and mymarommatids could either be the result of inheritance from a common ancestor, or convergence.

Nothing is known about the life history of mymarommatids, but the very small body size of individuals (0.75 mm or less, excluding antennae) may indicate that they parasitize eggs of other insects, or possibly arachnids. If so, their mandibles may be used to break the chorion of the host egg so that the adult can escape. Exodont mandibles of Alysiinae (Braconidae) are similarly used to break away the cap of the puparium of their host cyclorrhaphous Diptera (Griffiths 1964).

6. **Structure of the head.** Mymarommatids differ from other hymenopterans in structure of the head. The head is composed of a convex frontal sclerite (fsc, Figs. 8, 9), and a separate, flat, occipital sclerite (osc, Fig. 9). The 2 sclerites articulate near each mandibular base, and are connected by pleated membrane along the hyperoccipital region (pmb, Fig. 9). The membranous region is extensible because it is pleated, hence the head can expand or contract in an accordion-like manner! Numerous specimens of an undescribed species near *Palaeomyrmex anomalum* (Blood and Kryger) showed this. Some of the specimens
have the dorsal edge of the occipital sclerite deeply angled in the head, hood-like covered by the vertex, whereas others have the dorsal edge of the occipital sclerite angled away from the frontal sclerite, with the connecting membrane stretched between the 2 as a convexly expanded region. Apparently sclerotized, arch-like “ribs” are visible in the membrane, and these presumably function in pleating the membrane.

A pleated, membranous, hyperoccipital region was not visible in all mymarrommatids examined because of the manner in which some specimens were mounted. However, a convex frontal region and a flat occipital region were evident in all individuals, indicating a membranous region was probably also present. Consequently, I interpret a pleated, membranous, hyperoccipital region as a probable autapomorphy that indicates monophyly of Mymarrommatidae.

The head of mymarids is also unusual for hymenopterans. Three sets of sulci, the median (ms), frontal (fs), and supraorbital sulci (ss, Fig. 3), subdivide the head into a frontal, dorsal, and 2 lateral regions. [The sulci are often called carinae or suturets, but I use the terms suture and sulcus as defined by Daly (1964)]. All mymarids have the 3 sets of sulci (Debauche 1948; Schauf 1984), which Ogloblin (1959) discovered represent lines of inrolled and flexible cuticle (= trabeculas sensu Ogloblin).

Other hymenopterans are not known to have this particular head structure, though Trjapitzin (1977) lists 4 genera of Encyrtidae (Chalcidoidea) with a similar pattern of light-colored membranous lines. Numerous Eulophidae (Chalcidoidea) also have a transverse or V-shape sulcus on the frons [see figures in Yoshimoto (1977, 1978) and Schauf (1985)], as do some Aphelinidae. Furthermore, some Trichogrammatidae (Chalcidoidea) have both a transverse sulcus on the frons and a vertical sulcus along the inner margin of each eye (see Viggiani 1978, fig. 1). Unfortunately, internal development of the lines or sulci is unknown.

Ogloblin (1959) suggested the lines of inrolled and flexible cuticle on the head of mymarids allow expansion of the head, though function of this was unknown. Bäkkendorf (1934) found adults of several different mymarid species he studied used their mandibles to chew through the host egg chorion, as was noted for Caraphractus cinctus Walker by Jackson (1961). Neither author mentioned seeing the head expand during adult emergence from the host egg. Consequently, if the lines of inrolled cuticle are correlated with head expansion, function of this is likely something other than rupturing the egg chorion. Trjapitzin (1977) suggested the lines of weakness on the head of encyrtids give the head a greater elasticity, and the same may be true for the lines of inrolled cuticle of mymarids.

Because only mymarids have the pattern of median, frontal, and supraorbital sulci, this head structure can be tentatively considered as an apomorphic state that indicates monophyly of Mymaridae. However, distribution of similar lines or sulci in Encyrtidae, Eulophidae, Aphelinidae, and Trichogrammatidae must be studied to determine if they are a groundplan character for each family, or were independently derived in each family. The lines must also be studied to determine if they are internally developed as regions of inrolled cuticle. If so, presence may indicate a relationship with Mymaridae. Functional significance of the sulci and lines should also be determined prior to hypotheses of homology or independent gain.

7. Position of antennal toruli. Most Mymaridae have a more or less rectangular to triangular head in lateral view, with the toruli and inner eye margins subcontiguous, or separate by only about 1 diameter of the torulus. Thus, each torulus (to, Fig. 3) is much closer to the eye margin than are the toruli to each other. Members of the subfamily Eubroncinae [Eubroncus and Stomarotontrum Yoshimoto, Kozlov, and Trjapitzin (1972)] are exceptional in having the head projected wedge-like in lateral view. Vertex and frons are in a continuous plane that is acutely angled to the face, and because the toruli are near the angle of the head they are closer to each other than to the eyes.
Relative distance between the antennal toruli compared with distance between each
torulus and eye margin is highly varied in Terebrantes. Most terebrants other than mymar-
ids have the toruli closer to each other than to the eye margin (to, Fig. 8), or distance
between the toruli is similar to that between each torulus and eye margin. Some Pterom-
alidae (Chalcidoidea) have widely spaced toruli similar to most mymarids (Schaff 1984),
as do some Eulophidae (Chalcidoidea) (see for example Miller 1962) and some Ichneu-
monoideae. Restricted distribution indicates that this is the result of secondary modification
in each taxon. Furthermore, toruli position in Eubronciniae (Mymaridae) is correlated with
the unusual head structure, which undoubtedly is secondarily derived in the family. Con-
sequently, widely spaced toruli that are positioned very close to the inner eye margins can
be considered as an apomorphy that indicates monophyly of Mymaridae.

8. Pronotal shape. Nikolskaya (1960) considered that chalcidoids were distinguished from
other terebrants by their ‘‘saddle-like’’ pronotum (Figs. 18, 19). Koonsmann (1978a)
considered this pronotal shape to indicate probable monophyly of Chalcidoidea, whereas
Rasnitsyn (1980) considered the similarly shaped pronota of austroniids and monomachids
to indicate a relationship between Chalcidoidea and members of Diaprioidea. Gibson (1985)
concluded pronotal shape to be correlated with presence or absence of an independent
prepectus.

Individuals of Stephanidae, Monomachidae, and most Chalcidoidea have an inde-
dependent and relatively large prepectus (cf. pre, Figs. 15, 18, 19). They also have the
pronotum relatively long in dorsal view, hence more or less ‘‘saddle-like’’ in lateral view
(Figs. 18, 19), and loosely connected to the mesopleuron. Consequently, the pronotum is
variedly mobile relative to the mesothorax. Terebrants without an independent prepectus
have the dorsal surface of the pronotum markedly reduced, hence the pronotum is more
or less triangular in lateral view (Fig. 16). The pronotum is also rigidly connected to the
mesopleuron. Roproniids and austroniids have a relatively small but independent prepectus,
and the pronotum is intermediate in both shape, and degree of mobility, between the
2 extremes described above.

The correlation among an independent prepectus, pronotal shape, and pronotal–meso-
pleural attachment, is clearly illustrated by different chalcidoids and mymarids. Most chal-
cidoids have an independent prepectus that is varied in size and shape, and a pronotum
that is more or less mobile relative to the mesothorax. Individuals of Eucharitinae (Euchar-
itidae) and Perilampidae are exceptional in having the prepectus secondarily fused to the
pronotum (Bouček 1978), and the latter rigidly attached to the mesopleuron. Eucharitines
also have a pronotum that is triangular in lateral view (Fig. 21), like the pronota of other
terebrants without a prepectus, though the pronotum of perilampids is more or less saddle-
like. Most mymarids also have an independent prepectus (pre, Figs. 24–27, 29). Pronotal
shape is quite varied, from saddle-like (Figs. 24, 26) to markedly reduced dorsally (Figs.
22, 29), but only individuals of Pitloymar Annecke and Doult have a pronotum that is
triangular in profile and rigidly connected to the mesopleuron (Fig. 23). Individuals of
Pitloymar also lack an evident prepectus, indicating the latter is secondarily fused to the
pronotum as in perilampids, eucharitines, and numerous other terebrants.

Pronotal shape is not significant for determining phylogenetic relationships of Chal-
cidoidea, including Mymaridae, because an independent prepectus is plesiomorphic for
Terebrantes (Gibson 1985). Hence, a saddle-like and mobile pronotum is undoubtedly also
plesiomorphic, and not evidence of monophyly or relationship with other terebrants.

Mymarommatids have a pronotum that is markedly reduced dorsally, hence triangular
in lateral view (Fig. 10). This is apomorphic, but is correlated with reduction or loss of
the prepectus (see character 9), which is hypothesized to have occurred a probable 4 times
during the evolution of Terebrantes (Gibson 1985), in addition to independent loss in
Perilampidae, Eucharitinae, and Mymaridae (Chalcidoidea). Because of differences in
structure and attachment of the pronotum to the mesopleuron, I suspect that similarity of shape between the pronota of mymaromatids and other terebrants without an independent prepectus is the result of convergence.

9. Prepectus. Presence of an independent sclerite, the prepectus, between the pronotum and mesopleuron has been used by various authors as a defining state of Chalcidoidea. Chalcidoids were the only terebrants thought to have a prepectus, until Rasnitsyn (1980) discovered the sclerite concealed beneath the posterolateral edge of the pronotum in Stephanidae (pre, Fig. 15) and Monomachidae. I studied the various sclerites positioned between the pro- and mesothoracic segments in hymenopterans to determine homologies, and concluded that a prepectus was a groundplan character of the order and plesiomorphic for Terebrantes (Gibson 1985).

Table 1, character 9, lists distribution of a prepectus in Terebrantes. Because an independent prepectus is plesiomorphic for Terebrantes, presence cannot be used as evidence for monophyly of Chalcidoidea, or of relationships with other terebrants with a prepectus. However, the prepectus is exposed in most chalcidoids, at least dorsally adjacent to the lateral edge of the mesoscutum (pre, Figs. 18–20), and this is apomorphic in Apocrita. Graham (1969) stated that the prepectus was absent from some Macromesus Walker (Pteromalidae: Macromesinae), but individuals have a very small prepectus that is visible only near the lateral edge of the mesoscutum (Z. Bouček, pers. comm.). The prepectus is also very small and inconspicuous in numerous Chalcididae, but at least a tiny prepectus is exposed between the mesopleuron, pronotum, and mesoscutum (pre, Fig. 20). Eucharitines and perilampids lack an evident prepectus, but only because the latter is secondarily fused to the pronotum (Bouček 1978). A carina (Darling 1983, figs. 35–37, 60, 61) or furrow (Fig. 21) indicates the probable line of fusion in many eucharitines and perilampids, as does position of the mesothoracic spiracle at the dorsal edge of the carina or furrow (msp, Fig. 21) (see character 11 for correlation between position of spiracle and prepectus).

Rasnitsyn (1980) stated that a prepectus is present in some mymarids, but not in others, and in some individuals appears to be a part of the mesopleuron that is incompletely separated by a suture. He suggested the sclerite could be a secondary formation in mymarids, and not homologous with the true prepectus. The prepectus certainly is highly varied in Mymaridae, probably as much so as for other Chalcidoidea, but there is no evidence supporting an hypothesis of secondary formation. The prepectus is closely associated with the mesopleuron in numerous mymarids, and it is variably fused to the mesopleuron in some, but the same is true for the prepectus of other chalcidoids. The prepectus (pre) is moderately sized, and subrectangular (Fig. 25) to triangular (Fig. 29) in numerous mymarids, but it is very large (Fig. 24) or extremely reduced (Figs. 22, 27) in others, as also in other chalcidoids. Size and shape of the prepectus are even extremely varied in some mymarids presently classified in the same genus. Some individuals of Gonatocerus Nees have a large and conspicuous prepectus (Fig. 26), whereas others have a linearly reduced prepectus (Fig. 27). Furthermore, individuals of one species of Gonatocerus seen did not have an evident prepectus, but had a membranous region between the pronotum and mesopleuron (mb, Fig. 28). This membranous region is probably secondary and is not the prepectus because the mesothoracic spiracle is near the posterodorsal angle of the membranous region rather than near the anterodorsal angle (msp, Fig. 28) (see character 11 for correlation between position of spiracle and prepectus).

Rasnitsyn (1980) was correct in stating that the prepectus is absent from some mymarids, but absence is apparently uncommon and there appears to be a correlation between very small body size and a reduced prepectus. Most instances in which the prepectus is superficially absent are because of the very small size of individuals, a reduced prepectus, or both. When the prepectus is markedly reduced, it may appear to be absent without high magnification of scanning electron microscopy (pre, Figs. 22, 27). Furthermore, because
most mymarids have the pro- and mesothoracic segments flexibly united, a narrow prepectus can be concealed between the 2 in air-dried, shrivelled specimens. Schauf (1984) incorrectly concluded that the prepectus was fused to the pronotum in *Stephanodes* Enoch because the mesothoracic spiracle is advanced anterior of the more typical position. Individuals of *Stephanodes* have a prepectus though (pre, Fig. 25), and the advanced spiracular position is simply a secondary modification, as discussed under character 11. Individuals of *Pitomymar* Annecke and Doutt do lack an externally exposed prepectus (Fig. 23), but this apparent absence is most likely the result of secondary fusion of the prepectus with the pronotum (as discussed under character 8).

Scelionidae lack an independent prepectus, but many have a sulcus or row of crenulate delineating a region on the pronotum (net, Fig. 16) below the mesothoracic spiracle. Rasnitsyn (1980) considered this region to be the prepectus fused to the pronotum, but Masner (1979) considered it to be a secondarily delineated part of the pronotum, which he termed the netron. I agree with Masner (1979) that the netron is a secondarily delineated part of the pronotum, for reasons given in Gibson (1985).

Seraphitids lack an externally visible prepectus, but because only amber inclusions are available for study I could not determine whether an independent prepectus exists beneath the posterolateral edge of the pronotum, as in stephanids, monomachids, and rupronids. I suspect that the prepectus is absent because the posterolateral edge of the pronotum appears to be rigidly attached to the mesopleuron, and the pronotum is of a similar shape to the pronota of terebrants without an independent prepectus.

Mymarommatids also lack an externally visible prepectus, and the pronotum is similarly shaped to the pronota of most terebrants that lack an independent prepectus (cf. Figs. 10, 16). Though this indicates an independent prepectus was absent, presence or absence remains uncertain even after internal study of the pronotum. A structure was revealed on the inner surface of pronota dissected from specimens of an undescribed species near *Palaeomyrmex anomalum* (Blood and Kryger). The structure (pre?, Fig. 12) and posterolateral edge of the pronotum form a wide groove (gr, Fig. 12), hence the posterolateral edge of the pronotum is clearly visible from an inner view (Fig. 12). The structure is apparently connected to the anterolateral margin of the mesopleuron by membrane from its posterior margin (cf. mb, Figs. 12, 13), but because of the minute size of the pronota I was unable to determine if the structure was sclerotized, or whether it was an independent or fused prepectus.

For most terebrants without an independent prepectus I hypothesized (Gibson 1985) that the prepectus was reduced and fused to the inner edge of the pronotum as the "posterior pronotal inflection" (ppi, Fig. 17). A relatively deep groove is formed between the inner posterior pronotal inflection and outer posterolateral pronotal edge in such individuals (gr, Fig. 17), and the pronotum and mesopleuron are rigidly united because the anterior edge of the mesopleuron fits into the groove in a tongue-and-groove interlocking mechanism. The posterior pronotal inflection is at the same level as the posterolateral pronotal edge, hence the outer edge of the pronotum is not visible from an inner view (Fig. 17). Internal structure of the pronotum of these individuals is thus similar, but differs in details, from the internal structure of the pronotum of mymarommatids (cf. Figs. 12, 17). Consequently, if the internal structure on the mymarommatid pronotum is the fused prepectus, I suspect that fusion occurred independently to other terebrants.

I previously hypothesized an exposed prepectus as a groundplan character for Hymenoptera, and a concealed prepectus as a synapomorphy for Siricidae + Xiphydriidae + Orussidae + Apocrita (Gibson 1985). Mymarids, chalcidoids, and austronids are the only terebrants known to have an independent and at least partly exposed prepectus, although ceraphronoids and megalryids have what is hypothesized to be an exposed prepectus that is fused to the pronotum. Exposure of the prepectus in the above terebrants is hypothesized as secondary and apomorphic in Terebrantes. Furthermore, differences in position of the
mesothoracic spiracle relative to the prepectus (character 11) indicate that exposure of the
prepectus in mymarids and chalcidooids was independent to that of other taxa (Gibson
1985). Consequently, an exposed prepectus can be considered as a synapomorphy that
indicates monophyly of Mymaridae + Chalcidoidea.

Though state of the prepectus is uncertain in serphitids and mymarrommatids, the
prepectus is at least concealed beneath the posterolateral edge of the pronotum, if present.
This is the hypothesized plesiomorphic state for Apocrita, hence either taxon is indicated
to be at most the sister group of Mymaridae + Chalcidoidea.

10. Pronotal relationship to tegula. One of the most commonly used characters to define
Chalcidoidea is that the posterolateral edge of the pronotum does not touch the tegula
(Figs. 18–20). This pronotal state was used by Nikolskaya (1952, 1960), Riek (1970),
Königsmann (1978a), Gordo (1979), and Rasnitsyn (1980), though Rasnitsyn indicated
the state varied in mymarids and Yoshimoto (1984) indicated it varied in mymarids and
other chalcidooids.

Most chalcidooids and mymarids are the only terebrants with the posterodorsal edge
of the pronotum distinctly separate from the tegula (Table 1, character 10). This is apomorphic,
but the state results from another apomorphy shared by mymarids and chalcidooids,
an exposed prepectus that is interposed between the pronotum and tegula. The dorsal
surface of the pronotum does extend over the mesoscutum and prepectus to the tegula
in members of Leucospidae and Signiphoridae, but this is undoubtedly secondarily and inde-
pendently derived. The posterodorsal angle of the pronotum also appears to extend to the
tegula in Eucharitinae (Fig. 21), Perlampidae (Chalcidoidea), and in Pitomyrma (Mymar-
idae) (Fig. 23), but this is because the prepectus is secondarily fused to the pronotum to
form a composite structure. In other chalcidooids, how far removed the pronotum is from
the tegula depends on size of the prepectus (cf. pre, Figs. 24, 25).

Kozlov and Rasnitsyn (1979) considered that there was a tendency toward widening
of the upper part of the mesopleuron in mymarrommatids and in Microserphites Kozlov
and Rasnitsyn (Serphitidae), resulting in a more or less conspicuous dorsal mesopleural
region between the pronotum and fore wing base. They interpreted this as evidence that
mymarrommatids and serphitids were related, and further concluded that Microserphites
was an intermediate taxon between Mymarommatidae and Serphitidae s.s. Though the
pronotum is separated from the fore wing base by a narrow dorsal region of the meso-
pleuron in mymarrommatids, widening of the mesopleuron is illusory. All terebrants have
the pronotum and fore wing base separated by a narrow mesopleural region, but this is
not obvious in most individuals because the intervening mesopleural region is covered
by the tegula. The pronotum superficially appears to extend to the base of the fore wing, but
actually only extends to the base of the tegula (tg, Figs. 23–25). Some mymarids appar-
ently have the tegula fused to the dorsal edge of the intervening mesopleural region (tg,
Fig. 26), and the region consequently is more conspicuous. However, comparing these
specimens with mymarids having an independent tegula shows that the only difference is
whether the tegula is apparent or not; there is no fundamental difference in structure of
the mesopleuron (cf. Figs. 23 and 25 with 26). Mymarrommatids also lack an evident tegula
(Figs. 10, 11), most likely because of fusion with the mesopleuron, correlated with small
body size. Consequently, the dorsal mesopleural region between the pronotum and wing
base is more or less conspicuous (Fig. 10). The only known specimen of Microserphites parvulus
also lacks an evident tegula, but absence is probably an artifact because the
dorsum of the mesosoma is not preserved in the amber inclusion. The mesopleural region
illustrated between the pronotum and fore wing base by Kozlov and Rasnitsyn (1979) is
typical of the mesosoma of any terebrant without an evident tegula (cf. Fig. 26 and fig.
7 of Kozlov and Rasnitsyn (1979)). I therefore consider Kozlov and Rasnitsyn’s (1979)
description of a widened dorsal mesopleural region in mymarrommatids and Microserphites
to be inaccurate. I do not accept such a region as evidence of a relationship between mymarommatids and seraphitids, nor as evidence that Microserphites is an intermediate taxon between Mymarommatidae and Serphitidae s.s.

11. Relative position of mesothoracic spiracle. Riek (1970, p. 913) initially alluded to the unique placement of the mesothoracic spiracle in chalcidooids, stating that “Chalcidoidea are the only Hymenoptera in which the ‘prothoracic’ [sic] spiracle is situated at or above the level of the tegula”. A somewhat more accurate description is that chalcidooids have the mesothoracic spiracle situated at the exposed lateral edge of the mesoscutum (msp, Figs. 18–21). The mesothoracic spiracle is situated below, and is separated from the exposed lateral edge of the mesoscutum in other hymenopterans. The spiracle is either concealed by a prominent pronotal lobe (prl, Fig. 15), is exposed between the pronotum and mesopleuron, as in scelionids (msp, Fig. 16) and seraphitids, or is situated on the pronotum. However, in all instances there is at least a small region of the pronotum between the spiracle and exposed lateral edge of the mesoscutum (Figs. 15–17).

I previously proposed that Stephanidae have the plesiomorphic structure of the inter-segmentalia (sclerites in the membrane between the pro- and mesothoracic segments) for Terebrantes, and hypothesized that there were at least 3 independent transformation series from this structure during evolution of the infraorder (Gibson 1985). Stephanidae have the mesothoracic spiracle above the dorsal edge of the prepectus, with both spiracle (msp) and dorsal edge of the prepectus (pre) below the lateral edge of the mesoscutum (Fig. 15). In one proposed transformation series (represented by ichneumonoids), the prepectus was hypothesized to be reduced and fused to the posterolateral edge of the pronotum, without changes in the relative positions of the prepectus, mesothoracic spiracle, or lateral edge of the mesoscutum. In the second proposed transformation series (represented by terebrants that have either an independent prepectus (Table 1, character 9, state 3) or a posterior pronotal inflection (state 3a), which I consider to be the fused prepectus (ppi, Fig. 17)), the prepectus was hypothesized to be dorsally extended to the lateral edge of the mesoscutum behind the mesothoracic spiracle. Consequently, the spiracle is in a plesiomorphic position relative to the lateral edge of the mesoscutum (below and separate from edge), but in an apomorph position relative to the prepectus (below dorsal edge). Inclusion of gasteruptionids (state 4) and megalyrids and ceraphronoids (state 3b) in this transformation series is uncertain because of structural differences in the pronotum (see Gibson 1985). However, the mesothoracic spiracle is below and is separate from the lateral edge of the mesoscutum in members of these 3 taxa, hence the hypothesis of autapomorphy made below for Chalcidoidea is not affected. Chalcidooids have both the dorsal edge of the prepectus and the mesothoracic spiracle at the exposed lateral edge of the mesoscutum. This structure is hypothesized to represent a third transformation series from the plesiomorphic stephanid-like condition, in which both prepectus and mesothoracic spiracle were dorsally extended to the lateral edge of the mesoscutum. Consequently, the mesothoracic spiracle retains a plesiomorphic position relative to the prepectus (at anterodorsal angle), but is in an apomorphic position at the lateral edge of the mesoscutum (msp, Figs. 18–21). Some chalcidooids have the spiracle advanced anterior to, or above, the anterodorsal angle of the prepectus (Fig. 19), rather than adjacent to the prepectus (Fig. 18), but I consider these to be secondary modifications.

Mymarids have the mesothoracic spiracle (msp) positioned between the pronotum, mesoscutum, and prepectus (Figs. 22, 29), or formed into a tubercle with the pronotal edge (Figs. 24, 25), or positioned on the pronotum itself (Figs. 26–28). However, in all instances the spiracle is at, or is somewhat above the lateral edge of the mesoscutum (msp, Figs. 22–29). I consider the former state to be plesiomorphic for mymarids because it is shared with chalcidooids, and I consider the latter 2 states to be secondarily derived in Mymaridae. As for some chalcidooids, some mymarids have the mesothoracic spiracle
advanced anterior to the anterodorsal angle of the prepectus (cf. **msp**, Figs. 19, 25). I interpret this similarity between some members of both taxa to be the result of convergence.

A mesothoracic spiracle is not externally evident in mymaromatids (Fig. 10), but what appears to be the spiracle is visible near the posterolateral edge of the pronotum at about mid-height in specimens mounted laterally on slides (**msp**, Fig. 14). Though visible in slide-mounted specimens, the spiracle is not evident if the pronotum is removed and examined internally by SEM (Fig. 12), and must therefore lie between the presumed prepectus and wall of the pronotum.

Mymarids and chalcidooids are the only terebrants with the mesothoracic spiracle at or above the lateral edge of the mesoscutum (Table 1, character 11, Figs. 18–29). Consequently, this position can be considered as apomorphic and indicative of monophyly of Mymaridae + Chalcidoidea, whether or not the 3 previously hypothesized transformation series are accurate. Furthermore, position of the mesothoracic spiracle relative to the mesoscutum is apparently plesiomorphic in mymaromatids, as it is in scelionids and seraphitids. Any of these taxa are thus indicated to be at most the sister group of Chalcidoidea.

Concealment of the mesothoracic spiracle beneath the posterolateral edge of the pronotum is also an apomorphic state that indicates monophyly of Mymaromatidae. Almost all terebrants have the mesothoracic spiracle exposed in lateral aspect (**msp**, Figs. 16, 18–29), or covered by a prominent pronotal lobe (**prl**, Fig. 15). Only mymaromatids and some evaniids have the posterolateral edge of the pronotum straight, with the spiracle concealed below (Gibson 1985). This state is apparently secondarily derived in Eranidae because numerous evaniids have a distinct pronotal lobe concealing the spiracle. Similarity of structure between evaniids and mymaromatids is thus indicated to be due to convergence.

**12. Fore wing venation.** Fore wing venation of chalcidooids is reduced to a single vein complex near the costal margin of the wing (Fig. 31). Most taxonomists term the veins of this complex as the submarginal (**smv**), marginal (**mv**), stigmal (**stv**), and postmarginal veins (**pmv**, Fig. 31). One or more of these veins are punctiform, or are absent from the fore wings of numerous chalcidooids, but in others there are partially pigmented or otherwise indicated remnants of additional veins (Fig. 31). Most scelionids have a fore wing venation similar to that of most chalcidooids, i.e. with only a **smv**, **mv**, **stv**, and **pmv**. However, some scelionids also have 1 or more of the veins punctiform or absent. Mymarids likewise have a fore wing venation similar to that of most chalcidooids and scelionids, except that the venation is even more reduced in most mymarids. Individuals of mymarid genera from the Holarctic lack a postmarginal vein, and except for *Arescon* Walker, venation is limited to the basal third of the fore wing (**fwv**, Fig. 32) (Schauff 1984). However, individuals of at least 2 genera from Australia have a postmarginal vein, and individuals of several genera from Australia and New Zealand have the venation extended half the distance of the wing, or beyond (J. Noyes, *in litt.*). Fore wing venation of mymaromatids is reduced to a single, short, thick vein within the pedunculate wing base.

Königsmann (1978a) considered the "characteristic venation" of chalcidooids to indicate probable monophyly of the superfamily, and Rasnitsyn (1980) used reduced fore wing venation as one state to characterize Chalcidoidea, as have most workers before him. Both concluded that reduced fore wing venation was important for recognition of, and phylogenetic analysis of Chalcidoidea, and each considered the similarly reduced venation of chalcidooids and scelionids as the result of convergence, because of small body size, rather than phylectic relationship. Convergence is certainly possible, if not probable, as is indicated by the highly reduced fore wing venation of Ceraphronoidea, Platygastriidae, Diapriidae, and most Proctotrupidae and Cynipoidea. However, an hypothesis of homoplasy
rather than synapomorphy for the similar venation of chalcidoïds and scelionids is based on ideas of relationships formed from an analysis of other characters, not on an analysis of the venation itself.

Fore wing venation of mymarids and mymarommatids could be derived through reduction from the venation of chalcidoïds or scelionids. Consequently, venation cannot be used as evidence for relationships between these taxa, but it does indicate that Serphitidae is at most the sister group of Scelionidae, and was not derived from Scelionidae, as proposed by Rasnitsyn (1980). Serphitids are unlike mymarids, mymarommatids, chalcidoïds, and scelionids, having a more complete fore wing venation, including a large pterostigma (Rasnitsyn 1980, fig. 132). The more complete venation would have to be the result of reversal if serphitids were derived from scelionids.

13. Fore wing hypochaeta. One of 2 states that Schaff (1984) considered as autapomorphic for Mymaridae was presence of a hypochaeta, i.e. a distally hooked seta on the ventral surface of the fore wing that is inserted near the costal margin and is directed towards the anal margin (hyc, Fig. 32). All mymarids apparently have a hypochaeta (Debauche 1948), and members of some genera have more than one, though Schaff (1984) found the hypochaeta to be small and often difficult to see in members of 5 genera he studied. These genera apparently comprise a monophyletic group in Mymaridae, and a single reduction was hypothesized to explain character-state distribution of the reduced hypochaeta. Consequently, a fore wing hypochaeta can be interpreted as an autapomorphy that indicates monophyly of Mymaridae.

14. Reticulate fore wing. The membrane of mymarommatid fore wings is not smooth as in other hymenopterans; rather, it has a reticulate or alveolate appearance when viewed with a dissecting or compound microscope.

Fore wings of individuals of the extinct mymarommatid genus, Archaeoromma, were described as reticulate in the original description, but non-reticulate in the discussion (Yoshimoto 1975). Study of type-material of Archaeoromma nearcticum Yoshimoto shows the fore wings to be reticulate, though the pattern is often obscure in fossil specimens because of the optical properties of amber. Study of the fore wings of one mymarommatid species by scanning electron microscopy also shows that the reticulate pattern is formed by a mesh-like network of raised lineations (Fig. 30). I assume the reticulate pattern is likewise formed in other mymarommatid species, and consequently interpret a mesh-like pattern of raised lineations as an autapomorphy that indicates monophyly of Mymarommatidae.

15. Hind wing structure. The hind wings of most Hymenoptera are broadest beyond the articulation with the metathorax, with the wing membrane narrowed toward and extended to the articulation. Most mymarids are exceptional in having petiolate hind wings, i.e. origin of the wing membrane is distal to the metathorax on a long stalk-like vein (Fig. 32). The wing membrane is also more or less parallel-sided (Fig. 32), though the membrane is so reduced in individuals of Mymar Curtis that the hind wing resembles a bristle. Schaff (1984) noted that a petiolate hind wing is often used as a character to distinguish mymarids from other chalcidoïds, and that it could be a synapomorphy for members of the family. However, he also noted that the hind wings of individuals of Paranaphoidea Girault are broader and more typically “chalcidoïd”. Furthermore, the wing membrane extends to the base of the hind wing, albeit very narrowly, in individuals of Anagroidea Girault, and in Eubroncinae. Consequently, the hind wings are similar to those of some other chalcidoïds, including many trichogrammatids (see Doutt and Viggiani 1968). If the hind wing structure of Eubroncinae and Anagroidea is plesiomorphic for Mymaridae, stalked hind wings cannot be used as an apomorphy supporting monophyly of Mymaridae.
Mymarommatids differ from other hymenopterans in having each hind wing reduced to a stalk-like structure that is bulbously expanded at the base and terminated in a bifurcation (hw, Figs. 11, 33). The distal bifurcation is presumably formed by a single hamulus and the reflexed end of the reduced wing (Fig. 33). The anal margin of the fore wing is clasped by the bifurcation in natural repose so that fore wing and hind wing act as one. This unique hind wing structure can be interpreted as a further autapomorphy that indicates monophyly of Mymarommatidae.

16. Mesotrochanteral depressor. The mesotrochanteral depressor is a mesothoracic muscle that inserts into the basomedial edge of the mesotrochanter. Mesocoxa and trochanter are so articulated that contraction of the muscle rotates the apex of the trochanter ventrally and medially. I previously described states of the mesotrochanteral depressor from representatives of most families of Hymenoptera, and hypothesized the plesiomorphic state for Apocrita to be a muscle with 3 sites of origin: a small fan-shaped muscle from the mesofurca (mesofurcal-trochanteral depressor: fu₁-tr₂), and a larger tubular muscle (meso-tergal-trochanteral depressor: t₁-tr₂) from the axilla and from the posterior of the mesoscutum (Gibson 1985).

Table 1, character 16, lists states of the mesotrochanteral depressor in Terebrantes. Megalyridae have the hypothesized plesiomorphic state for Apocrita, except for a slightly different site of origin for fu₁-tr₂ (Gibson 1985, fig. 44). Other terebrants for which states of the mesotrochanteral depressor are known lack 1 or more of the 3 original parts. Only Stephanidae, Ceraphronoidea, Chalcidoidea, and Diapriidae (other than Ismarinae) retain a tergal (t₁-tr₁) part of the depressor. Stephanids and non-ismarine diapriids have fu₁-tr₂ and the axillar portion of t₁-tr₂ (Gibson 1985, figs. 41, 42), whereas ceraphronoids lack fu₁-tr₂, but have both the mesoscutal and axillar portions of t₁-tr₂ (Gibson 1985, fig. 43). Fu₁-tr₂ is also absent from chalcidooids and t₁-tr₂ appears to consist of 2 parts in many taxa. If an anterior part (t₁-tr₂a) is distinguished, it seemingly originates from the mesoscutum, whereas the posterior part originates from the axilla (t₁-tr₂a) (Fig. 34). However, this similarity to the mesotrochanteral depressor of ceraphronoids is superficial. Chalcidooids differ from other hymenopterans with t₁-tr₂ in that the anterior portions of these muscles do not arise from the mesoscutum, but from axillar phragmata that project beneath the mesoscutum from the axilla (axp, Fig. 35). [The axillar phragmata of chalcidooids have also been termed the “anterior connecting processes of the postmesoscutum” by Grandi (1929), “apodemes of the posterior plate of the mesonotum” by James (1926), and “pseudophragma of the postscutellum” by Bucher (1948).]

I previously hypothesized that chalcidooids evolved from an ancestor having only the axillar portion of the mesotrochanteral depressor, and that this muscle was secondarily increased in size through origin of an axillar phragma in the common ancestor of Chalcidoidea (Gibson 1985). All chalcidooids I dissected had at least tiny axillar phragmata, except for some members of Eupelmidiae. These exceptions will be described in a subsequent paper, but result from the mesosoma being secondarily modified for increased jumping ability.

The mesotrochanteral depressor of mymarids (Fig. 34) is as described for non-eupelmid chalcidooids. Examination of slide-mounted mymarommatid specimens shows a similar state of the muscle, except that origin of t₁-tr₂ is only from the axillar phragma (t₁-tr₂a), the axilla itself being without muscle.

State of the mesotrochanteral depressor in scelionids is very different from that described for most chalcidooids. The muscle originates from the mesopleuron adjacent to the mesofurcal lateral arm (Gibson 1985, fig. 51). I consider this structure to represent the terminal state in a transformation series composed of 3 events. The first event was loss of t₁-tr₂ from the hypothesized plesiomorphic state of the mesotrochanteral depressor for
Apocrita, leaving only fu₂-tr₂ (Table 1, character 16, state 3). The second event was expansion of fu₂-tr₂ from the mesofurcal lateral arm onto the mesopleuron as pl₂-tr₂ (state 3a), and the third event was loss of the furcal portion of the muscle to leave only pl₂-tr₂ (state 3b). Individuals of Proctotrupidae, Peleciniidae, Evaniiidae, and Vanhorniidae have what I consider to be the intermediate state in this transformation series (Table 1). Consequently, one or some combination of these 4 families (excluding Platygastridae and other families for which state of the mesotrochanteral depressor is unknown) is indicated as the sister group of Scelionidae.

Relationships of serpithids with extant terebrants cannot be inferred using state of the mesotrochanteral depressor because it is not possible to examine internal structure in fossil inclusions. However, state of this muscle does not support Kozlov and Rasnitsyn’s (1979) and Rasnitsyn’s (1980) hypothesis that Mymaridae and Serpithidae s.l. (inclusive of mymarommatids) were derived from Scelionidae. It is not possible to derive the mesotrochanteral depressor of mymarids and mymarommatids directly from the depressor of scelionids. The muscles of mymarids and mymarommatids appear to represent terminal states in one transformation series, and the muscle of scelionids the terminal state in an independent transformation series, from the hypothesized plesiomorphic state of the mesotrochanteral depressor of Apocrita. Thus, not only is a sister-group relationship not supported, but mymarids and mymarommatids are indicated to be only distantly related to scelionids.

Only ceraphronoids, mymarommatids, mymarids, and chalcidoids are known to have a mesotrochanteral depressor composed of only t₂-tr₂. I consider similarity of the mesotrochanteral depressor in ceraphronoids and the latter taxa to be the result of convergence because I consider the anterior portion of t₂-tr₂ in mymarommatids, mymarids, and chalcidoids to be secondarily derived and non-homologous with the anterior portion of the muscle in ceraphronoids. Whether this is accurate or not, only mymarommatids, mymarids, and chalcidoids have axillary phragmata for attachment of t₂-tr₂. Consequently, axillary phragmata can be interpreted as a synapomorphy that indicates monophyly of the taxa. I further consider absence of the axillary portion of t₂-tr₂ in mymarommatids to be the result of secondary loss, and hence a further autapomorphy that indicates monophyly.

17. Two-segmented petiole. A petiole composed of 2 segments (Mt₁ and Mt₂, Fig. 36) was the primary evidence used by Kozlov and Rasnitsyn (1979) and Rasnitsyn (1980) to support their hypothesis that mymarommatids are more closely related to serpithids than to mymarids. Mymarommatids and serpithids are the only terebrants to have a petiole that is definitely 2-segmented. Yoshimoto (1975) described the chalcidoid genus Distylopus (Tetracampidae: Distylopinae) from Canadian Cretaceous amber, and described a 2-segmented petiole for the single male for which the genus was established. However, study of the holotype of D. bisegmentus Yoshimoto indicates the petiole is probably only 1-segmented. The basal region that Yoshimoto interpreted as the first petiolar segment appears to be a constricted portion of the petiole for insertion into the propodeal orifice. A false impression of segmentation is enhanced by color differences between the basal, yellowish translucent region, and the apical, brownish opaque region. This color difference apparently is because the basal region does not contain remnants of body material, whereas the apical region does. Whether the petiole of D. bisegmentus is 2-segmented or not, the 2-segmented petiole of mymarommatids and serpithids could either be the result of convergence, or inheritance from a common ancestor.

18. Metasomal spiracles and cerci. Table 1, characters 18a and 18b, lists distribution of metasomal spiracles and cerci, respectively, in Terebrantes. Most chalcidoids can be distinguished from most other terebrants by the combination of these 2 character states.

Chalcidoids either have digitiform or button-like cerci on the 8th metasomal segment (or 9th segment if this is separate) and spiracles on only the 7th metasomal segment. Domenichini (1953) stated that individuals of Encyrtus fuliginosus Compere (Encyrtidae)
and Monopleurothrix kiefferi Mayr (Eupelmidae: Tanaostigmatinae) also have spiracles on the petiole (1st metasomal segment), but this is untrue for the first species (J. Noyes, in litt.) and likely is untrue for the latter species. Ichneumonoids are the only terebrants to have functional spiracles on more than the 7th metasomal segment. Mymarommatids and most mymarids are similar to chalcidoïds in having cerci on the 8th metasomal segment (eer, Figs. 37, 39), and metasomal spiracles on only the 7th segment (sp, Figs. 37, 39). Individuals of 4 mymarid genera studied by Schauff (1984) lack metasomal spiracles, and 3 independent losses were hypothesized for absence in these taxa.

Most other terebrants differ from typical chalcidoïds in state of the metasomal spiracles, cerci, or both. Most ichneumonoids have spiracles on the first 5–7 metasomal segments; scelionids, platygastrids, proctotrupids, vanhorniids, trigonalids, and ceraphronoids lack metasomal spiracles; and though female pleciniids have spiracles on the 7th metasomal segment, the spiracles are not externally visible (Mason 1984). Furthermore, evaniids, platygastrids, pleciniids, roproiniids, proctotrupids, vanhorniids, scelionids, and most cynipoids have the cerci either concealed, reduced to setiferous sensory plates, or absent. Presence or absence of metasomal spiracles and cerci was not determined for most fossil serpithidoid because of their poor state of preservation. However, one well-preserved female (MCZ #5330) had digitiform cerci on the 8th metasomal segment and metasomal spiracles on the 7th segment only. I assume these states are the same for other serpithidoids.

W.R.M. Mason (pers. comm.) considers functional spiracles on metasomal segments 1 through 7 as the groundplan state for Apocrita because aculeates and most ichneumonoids have this pattern. He further proposes that reduction of metasomal spiracles to only the 7th segment may be a synapomorphy for Apocrita exclusive of aculeates and ichneumonoids. If so, functional spiracles on the 7th metasomal segment in chalcidoïds is plesiomorphic. Retention of distinct cerci is undoubtedly a plesiomorphic state, so that chalcidoïds differ from most other terebrants only in retention of both plesiomorphic states. This is useful to identify chalcidoïds, but not as evidence of monophyly of Chalcidoidea, nor as evidence of relationships with other terebrants.

Presence of spiracles on the 7th metasomal segment in Mymaridae, Mymarommatidae, and Serphitidae does not support Kozlov and Rasnitsyn’s (1979) and Rasnitsyn’s (1980) hypothesis that these taxa were derived from within Scelionidae. Scelionids lack these spiracles and presence in members of the former taxa indicates that their ancestor(s) had metasomal spiracles.

19. Metasomal structure of females. Female chalcidoïds and mymarids have all metasomal sternae displaced anterior to the base of the ovipositor, or have some of the sternae extended beneath the ovipositor sheaths toward the apex of the metasoma. The ovipositor sheaths are visible along the ventral midline of the metasoma in the former instance, but in the latter instance the sheaths are partly or entirely concealed by one or more of the sternae. During oviposition the ovipositor rotates about its base so that the apex is lowered from the metasoma anterior to the apex of the metasoma. Rotation of the ovipositor is possible because the sternae are only loosely connected to the terga, and the apex of any sternum that extends over the sheaths is widely displaced downward away from the metasomal apex.

Similarity in metasomal structure and mode of ovipositor extension led Schauff (1984) to mention this as one possible synapomorphy for Mymaridae + Chalcidoidea, though he cautioned the similarity could be symplesiomorphic. Rasnitsyn (1980) stated that the similarity indicated contradictory conclusions regarding relationships of Mymaridae. Females of most other taxa he included in Diapriidea, including those of Scelionidae, have the sternae and terga relatively rigidly united so that they cannot be widely displaced from each other. The ovipositor is concealed within the metasoma in normal repose, and
is protruded posteriorly from the metasomal apex during oviposition, rather than rotated ventrally away from the metasoma.

Serpithids and mymarommatids have the ovipositor concealed by the apical sternum, or hypopygium (hyp, Figs. 37, 39). However, the hypopygium can be widely displaced in mymarommatids, and apparently could be displaced to a lesser extent in serpithids (Rasnitsyn 1980). Metasomal structure and mode of ovipositor extension is thus similar to that of chalcidooids and mymarids. Because Rasnitsyn (1980) considered mymarids, m yardommatids, and serpithids to be derived from scelionids, he suggested the metasomal structure and mode of ovipositor protrusion characteristic of scelionids was secondarily lost in the former 3 taxa.

Table 1, character 19, lists type of metasomal structure and mode of ovipositor extension in Terebrantes. Numerous other terebrants have a similar metasomal structure and mode of ovipositor extension to that of chalcidooids, mymarids, mymarommatids, and serpithids. The structure is undoubtedly plesiomorphic for Apocrita and Terebrantes because a similar structure is also characteristic of Symphyta. Unlike Rasnitsyn (1980), I consider the similar metasomal structures of mymarids, mymarommatids, and serpithids to be due to symplesiomorphy, and not the result of secondary loss of the apomorphic scelionid structure.

Metasomal structure different from the plesiomorphic condition is simply listed as “apomorphic” in Table 1, character 19. This is because recent studies of Proctotrupidae (= Serphidae sensu Townes and Townes 1981), Scelionidae (Austin 1983), Vanhorniidae (Mason 1983), and Pelcinidae (Mason 1984) have shown structure of the metasomal–ovipositor complex to be conspicuously varied. Austin (1983) suggested that differences in structure indicate that the ovipositor was concealed in the metasoma several independent times during the evolution of Terebrantes, most likely for greater protection of the fragile ovipositor.

20. Basal ring in male genitalia. Rasnitsyn (1980) stated that mymarids are like chalcidooids, but unlike scelionids, in lacking a basal ring from the male genitalia. Snodgrass (1941) first discovered that a basal ring was absent from the phallobase [sensu Snodgrass, = genital sheath sensu Vasey (1974)] of the male genitalia of most chalcidooids. However, there was a groove across the ventral surface near the base of the phallobase in males of 2 species he studied, Tarymyx fagopyrum (Provancher) [= Callimome sakeni (Ashmead)] (Torymidae) and Leucopsis affinis (Say) (Leucospidae). Snodgrass interpreted the basally delineated region of the phallobase (br, Fig. 38b) as remnants of a basal ring that was fused to the parameres. This structure of the phallobase was found for other leucospids by Bouček (1974), for males of Trichogramma Westwood (Trichogrammatidae) by Nagarkatti and Nagaraja (1968), and for males of some Pteromalidae by Vasey (1974). However, these studies, and the comprehensive survey of chalcidoid male genitalia by Domenichini (1953), indicate that a complete annular or independent basal ring is lacking.

Male genitalia of mymarids remain inadequately studied, but the comparative study of Viggiani (1973) indicates a basal ring is lacking from the phallobase. A basal ring was also lacking from the genitalia of males of 2 extant mymarommatid species that I examined, Palaeomymar anomalum and a closely related, undescribed species from Japan. Whether or not male serpithids had a basal ring could not be determined from the fossils available for study.

Snodgrass (1941, figs. R, S, plate 10) illustrated male genitalia for only 2 species of Scelionidae, representing the genera Scelio Latreille and Sparasion Latreille (Scelioninae). The genitalia were similar and had a distinctively elongate, tubular, or at least ventrally sclerotized basal ring at the base of the aedeago-volsellar shaft [sensu Snodgrass]. Such an elongate basal ring was previously illustrated by Nixon (1936) for males of 2 species of Telenomus Haliday and 1 species of Trissolcus Ashmead [= Microphanurus Kieffer]
Nixon did not illustrate a basal ring in the male genitalia of different species of *Telenomus*, *Trissolcus*, and *Eumicrosoma* Gahan (= *Nardo* Nixon) in other papers, but he stated in one (Nixon 1937) that the drawings were incomplete and did not show details that seemed to be of no specific value or that were difficult to see. Basic structure of the basal ring does not appear to vary in Telenominae except for relative size (N. Johnson, in litt.). Consequently, it is likely that a basal ring was present, but that the latter was left out of the illustrations because Nixon did not consider it to be of taxonomic value. Ritchie and Masner (1983) likewise did not illustrate the basal ring in the genitalia of *Baricus* Förster (Scelioninae) males, because they considered the basal ring of no value in distinguishing species (A. Ritchie, in litt.). An elongate basal ring in the male genitalia is thus indicated as a groundplan character of Scelionidae.

Table 1, character 20, lists known distribution of a basal ring in Terebrantes. Vasey (1974) described male genitalia for representatives of most families of Terebrantes, but did not include Austroniidae, Megalyridae, Vanhorniidae, Roproniidae, Monomachidae, and Trigonalidae. Presence or absence of a basal ring is unknown for Austroniidae and Megalyridae because male genitalia have not been described for these taxa, but Mason (1983) recently found a basal ring present in the male genitalia of *Vanhornia eucnemidarum* Crawford (Vanhorniidae). I dissected 1 male each of *Ropronia garmani* Ashmead (Roproniidae), *Monomachus* sp. (Monomachidae), and *Poecilogonatus costalis* (Cresson) (Trigonidae), and all had a basal ring. Presence of a basal ring listed in Table 1 for the latter 3 families is based only on my dissections.

Presence of an independent basal ring in the genitalia of male Symphyta and most male Apocrita indicates this as a groundplan character of Hymenoptera and as synapomorphic for Terebrantes. Absence of an independent basal ring from the male genitalia of Mymarommatidae, Mymaridae, and Chalcidoidea may thus be a synapomorphy that indicates monophyly of these taxa. However, the basal ring is lacking from the male genitalia of *Atanycolus* Förster (Ichneumonoidea: Bracconidae) and *Aphanogmus* Thomson (Ceraphronoidea: Ceraphronidae) (Vasey 1974), and is indicated to be absent from the male genitalia of *Psilus* Panzer (= *Galesus* Haliday) (Diapriidae) (Snodgrass 1941). Furthermore, the basal ring is reduced to a linear strip at the base of the phallobase in many terebrants, and may be present as an incomplete ring (Vasey 1974). Absence of the basal ring from the male genitalia of the above-listed taxa is undoubtedly the result of secondary loss because other ichneumonoids, ceraphronoids, and at least some diapriids have a basal ring (Snodgrass 1941; Vasey 1974). However, the above examples illustrate that independent reduction or loss of the basal ring is possible. Consequently, I do not consider absence of a basal ring from the male genitalia of mymarommatids, mymarids, and chalcidoids as reliable evidence of monophyly.

### 21. Cuspid in male genitalia

Königsmann (1978a) proposed absence of cuspides from the male genitalia as a synapomorphy for Cynipoidea + Chalcidoidea. Males of both taxa have the volsella composed of only a digitus, if volsellae are present. A "chelate structure" in the genitalia of male *Trichogramma* Westwood (Chalcidoidea: Trichogrammatidae) was tentatively proposed as the fused cuspis and digitus by Nagarkatti and Nagaraja (1968). However, other known chalcidoid males lack cuspides, and it is likely that the chelate structures are only secondarily modified digiti. Cuspis-like processes are also known from the genitalia of male *Synergus* Hartig (Cynipoidea: Cynipidae) (Vasey 1974), but again these processes are likely the result of secondary modification because they are lacking from other cynipoids.

Table 1, character 21, lists known distribution of cuspides in the genitalia of male terebrants. The list was compiled primarily from Snodgrass (1941), Vasey (1974), and my own dissections (discussed under character 20). Listed distribution is based on very few taxa, but indicates absence of cuspides from the male genitalia of cynipoids and chalcidoids...
is not likely synapomorphic, but more likely reflects loss at a more inclusive phylogenetic level, or is the result of independent loss.

22. Metallic luster of adults. Königsmann (1978a) considered metallic luster, characteristic of numerous chalcidoids, to be a groundplan character of Chalcidoidea that indicated probable monophyly of the superfamily. He considered a single derivation of metallic luster in the common ancestor of Chalcidoidea, and subsequent loss of the luster several independent times, as more probable than multiple origins of the luster in the superfamily. However, known Signiphoridae, Aphelinidae, and Trichogrammatidae, and almost all known Leucospidae, Chalcididae, and Eurytomidae lack metallic luster. Because phyletic relationships are unresolved in Chalcidoidea, it is not possible to postulate whether the common ancestor of chalcidoids had metallic luster, or whether metallic luster evolved once or more in one or more clades.

Mymarommatids lack metallic luster, as do almost all mymarids. Some species of *Erythmelus* Enoch have a slight, but distinct metallic luster (*J. Huber, in litt.*), though this is most likely secondarily derived. Consequently, absence of metallic luster from mymarommatids and mymarids is indicated as symplesiomorphic, and not valuable for determining phyletic relationships of these taxa.

23. Structure of larvae. Rasnitsyn (1980) concluded that the most reliable indicator of mymarid relationships was the structure of their larvae. He considered their larvae to share a rather distinctive structure with scelionid larvae.

Two general types of 1st-instar mymarid larvae ("saciform" and "mymariform") were described by Clausen (1940). It is the typical mymariform larvae that are most similar to the "teleform" 1st-instar larvae of Scelionidae. Mymariform and teleform larvae have a long caudal appendage and most representatives have long body setae. Both types of larvae also have prominent cephalic processes and are unsegmented, or have only indistinct segmentation.

Though mymariform and teleform larvae are superficially similar, character states either differ in detail or are shared with larvae of some other terebrants. Clausen (1940), for example, also termed one type of 1st-instar larva of Trichogrammatidae (Chalcidoidea) as mymariform, most likely because it too has a caudal appendage and long body setae. Jackson (1961) also discovered that larvae of some mymarid species, which are otherwise typically "mymariform", lack body setae. Furthermore, mymarid 1st-instar larvae have several transverse rows or rings of setae, if present, whereas scelionid 1st-instar larvae have only a single row or ring of setae near the anterior edge of the abdomen. Because both caudal appendage and setae function in movement of the larvae in the host egg (Clausen 1940), independent gain of these states is probable. Differences in details also occur in the cephalic processes and segmentation of mymariform and teleform larvae. Mymariform larvae have the head extended as a median curved process above the minute mandibles, whereas teleform larvae have large mandibles, often a fleshy lateral process above each mandible, a median process below the mandibles, or both. Most scelionid 1st-instar larvae also have the body subdivided into more or less equal parts by a distinct constriction, but otherwise are without segmentation. Segmentation is apparent or inapparent in mymarid 1st-instar larvae, but the body is not differentiated by a distinct constriction.

Königsmann (1978a) hypothesized similarity of mymarid and scelionid 1st-instar larvae to be the result of convergence because individuals of both taxa are parasitoids of eggs of other insects (scelionids also of spider eggs), and consequently the larvae have a similar habitat. Though the larvae are superficially similar, differences in details of structure tend to support Königsmann’s hypothesis. Trichogrammatidae are also egg parasitoids, and since some of their larvae are similar to mymariform larvae this further supports Königsmann’s hypothesis. As Schaff (1984) stated, our knowledge of scelionid and mymarid
Table 1. Matrix of character states analyzed in the text (excluding 12, 22, and 23), with an explanation of the symbols used for the matrix and hypotheses of transformation of the states in Terebrantes (* = exception discussed in text)

<table>
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<th>18b</th>
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7–11 9, 10–13 5, 99–112 9, 13 5, 5, and 13 13 in Cretaceous representatives.
14 14 hypothecated as groundplan number by Masner (1970).
10–10 in one undescribed genus (L. Masner, pers. comm.).
11 13 14 most common, and characteristic of most families and subfamilies (see Weid 1952 and Quinan 1979).
15 14 in Ismaianidae, Ambositrae, and most Belytinae; 12:14 most common in Diapriinae (L. Masner, pers. comm.).
1b 15 14 in Ichneumonoidea: Tryphorinae (Idiogrammatinae); Braconidae: Alysiidae (Alysiini, Dacusini), Opiinae (Exodontiellini).
1c At least concealed, but unknown if free, fused, or absent.
1d In females; males with metasomal spiracles absent (W.R.M. Mason, pers. comm.).
1e Digirtiform in Megaspilidae, sensory plates in Braconidae.
1f Digitiform in Belytinae, Ambositrae, and Ismaianidae; sensory plates in Diapriinae (L. Masner, pers. comm.).
1g Absent or reduced to small lateral extensions of the vescicular plates in Braconidae; state unknown for Paxyrommatidae (Vasey 1974).
Definition of symbols used in matrix and hypotheses of transformation series

(ts = hypothesized transformation series)

1. Number of antennal articles. Number of antennal articles possessed by males; known range of articles given if number not constant for each sex. A larger number of articles is considered as pleisiomorphic and a smaller number is considered apomorphic, but exact transformation series are unknown.

2. Anellus. – = absent; + = present. (ts: – → +)


4. Multiporous plate sensilla of antennae. 1 = clavate, ridge-like convex with distal end free from article, not surrounded by groove; 2 = absent, or otherwise structured. Transformation series uncertain because internal and external structure is insufficiently known for antennal sensilla of other terenats.

5. Exodent mandibles. – = absent; + = present. (ts: – → +)

6. Head structure. 0 = single sclerotized capsule; 1 = frontal and occipital sclerites connected by pleated, membranous, hypocercipital region; 2 = single sclerite with median, frontal, and supraorbital sulci. (ts: 0 → 1 → 0 → 2)

7. Position of antennal toruli. 0 = distance between toruli of similar distance or less than distance between torulus and inner eye margin; 1 = distance between toruli much greater than distance between torulus and inner eye margin. (ts: 0 → 1)

8. Pronotal structure. 0 = long dorsally, hence saddle-like in lateral view, loosely attached to mesopleuron and highly mobile relative to mesothorax; 1 = intermediate in shape and degree of mobility between 0 and 2; 2 = reduced dorsally, hence triangular in lateral view, and rigidly united with mesopleuron. (ts: 0 → 1 → 2)

9. Prepectus. 0 = dorsal edge below spiracle and lateral edge of mesoscutum, concealed, independent; 1 = dorsal edge below spiracle and lateral edge of mesoscutum, concealed, fused to postero lateral edge of pronotum; 2 = dorsal edge extended with spiracle to lateral edge of mesoscutum, exposed, independent; 3 = dorsal edge extended above spiracle to lateral edge of mesoscutum, concealed, independent; 4 = lost. (ts: 0 → 1 → 2 → 3 → 4)

10. Relationship of pronotum to tegula. 0 = extended postero-dorsally to tegula; 1 = separated from tegula by interposed prepectus. (ts: 0 → 1)

11. Placement of mesothoracic spiracle. 0 = below and separate from exposed lateral edge of mesoscutum; 1 = at exposed lateral edge of mesoscutum. (ts: 0 → 1)

12. Fore wing hypochaeta. – = absent; + = present. (ts: – → +)

13. Fore wing membrane. 0 = smooth; 1 = reticulate. (ts: 0 → 1)

14. Hindwing structure. 0 = wing membrane extended to base of wing; 1 = wing membrane origin distally from stalk-like vein; 2 = with only stalk-like vein, no membrane. (ts: 0 → 1; 0 → 2)

16. Mesosternothorax depressor. 0 = with fu–tr3, and origin of t1–tr3 from mesoscutum and axilla; 1 = with fu–tr2, and origin of t1–tr3 from axilla only; 2 = with t1–tr3 only, origin from mesoscutum and axilla; 3 = with fu–tr3 only; 4 = with p1–tr2; 5 = with p2–tr3; 6 = with p3–tr4 only. (ts: 0 → 2; 0 → 1 → 3 → 4 → 5 → 6)

17. Petiole. 1 = 1 segment; 2 = 2 segments. (ts: 1 → 2)

18a. Metasomal spiracles. 1–7 = segments 1–7; M7 = segment 7 only; 0 = none. (ts: 1–7 → M7 → 0)

18b. Cercus. 0 = digitiform; 1 = reduced (flattened button-like structures or as setiferous, sensory plates); 2 = absent. (ts: 0 → 1 → 2)

19. Relative structure of metasoma and ovipositor. 0 = ovipositor rotates about basal line of axis, protruded ventrally from metasoma anterior to metasomal apex during oviposition, and if covered by sterna then latter widely displaced from terga during oviposition; 1 = modified from above, "apomorphic". (ts: 0 → 1)

20. Basal ring of male genitalia. + = present; – = absent. (ts: + → –)

21. Cupulis of male genitalia. + = present; – = absent. (ts: + → –)
larvae remains limited. Until more comprehensive surveys are made, and homology and function of similar larval structures are determined in an effort to distinguish homoplasy from synapomorphy, hypotheses of relationships based on larval structure must be considered tenuous at best.

**Discussion**

Figure 1 illustrates proposed phyletic relationships of Chalcidoidea, Mymaridae, and Mymarommatidae based on hypotheses of character-state evolution proposed in the text and summarized in Table 1. Numbers in parentheses correspond to numbering of the characters in the text.

**Relationships of Mymaridae and Chalcidoidea.** A relationship of Mymaridae with Chalcidoidea is much more strongly supported by this analysis than is the relationship of Mymaridae and Scelionidae proposed by Rasnitsyn (1980). Monophyly of Chalcidoidea, including Mymaridae, is supported by 3 hypothesized synapomorphies for members: an unique external structure of the antennal multiporous plate sensilla, position of the mesothoracic spiracle at the lateral edge of the mesoscutum, and an exposed prepectus. Adult mymarids are additionally like other chalcidooids, and dissimilar to scelionids, in having a mesotrochanteral depressor consisting of only the axillar part of t1-tr2 (lacking mesoscutal part), in having an axillary phragma as a partial site of origin for tr1-tr2, and in lacking an independent basal ring from the male genitalia. These latter 3 character states are hypothesized as synapomorphies for Mymarommatidae + Chalcidoidea. Whereas adult mymarids are hypothesized to share 6 apomorphic states with other chalcidooids, I found no states shared by mymarid and scelionid adults that I interpret as apomorphic. Furthermore, state of the mesotrochanteral depressor in scelionids indicates members of this taxon are only distantly related to mymarids and chalcidooids. I therefore consider the similar 1st-instar larval structure of mymarids and scelionids to be the result of convergence, most likely because of a similar larval habitat.
It is tempting to hypothesize a sister-group relationship of Mymaridae with other Chalcidoidea because of the distinctive structure of adult mymarids. However, presence of an anellus is the only known apomorphic state that indicates possible monophyly of Chalcidoidea exclusive of Mymaridae. Because at least some members of most chalcidoid families lack an anellus, and because the first flagellomere of some mymarids is quite small, I do not consider an anellus as reliable evidence of monophyly of Chalcidoidea excluding Mymaridae. Consequently, relationship of mymarids to other chalcidoids remains unresolved.  

**Relationships and classification of Mymarommatidae.** I include Mymaridae in Chalcidoidea because I consider that there are no reliable apomorphies supporting monophyly of Chalcidoidea excluding Mymaridae. Whether Mymarommatidae should also be classified in Chalcidoidea depends on what character states are used to delimit the superfamily. Mymarommatidae would be included in Chalcidoidea if the superfamily is defined on presence of axillar phragmata, presence of only an axillary portion of the meso- and metathoracic depressor muscle, and absence of a basal ring from the male genitalia (Fig. 1). Alternatively, if Chalcidoidea is diagnosed on structure of the multiporous plate sensilla, presence of an exposed prepectus, and position of the mesothoracic spiracle (Fig. 1), Mymarommatidae would be excluded. I prefer to delimit Chalcidoidea on the latter 3 external character states, rather than on internal characters, and I thus exclude Mymarommatidae from Chalcidoidea.  

As the hypothesized sister group of Chalcidoidea (Fig. 1), mymarommatids should be accorded the same superfamily status. However, there is considerable disagreement concerning membership and validity of established terebrant superfamilies. I see little present advantage in recognizing one more monotypic superfamily, particularly when relationships of mymarommatids and serphitids remain uncertain. Monophyly of Mymarommatidae + Chalcidoidea is only supported by internal character states that cannot be examined in fossil serphitids. It is therefore possible that Mymarommatidae + Serphitidae are a monophyletic clade, based on a 2-segmented petiole, and that they together are the sister group of Chalcidoidea. Though I presently consider this to be unlikely, for reasons given below, I propose that mymarommatids be treated as a family and not be assigned to any superfamily until relationships proposed in this paper are more fully investigated and tested with additional characters.  

Though mymarommatids and serphitids share a 2-segmented petiole, external structure of individuals is otherwise very different. Kozlov and Rasnitsyn (1979) considered serphitids to be more similar to scelionids in structure, particularly in structure of the head and mesosoma. Furthermore, most female serphitids have a secondary bend in the flagellum of the antenna, similar to the antenna of many female scelionids and platygastrids. The lateral regions of the metasomal terga also appear to be slightly flexed in some individuals with a fully expanded metastoma, and there is a distinct submarginal groove (sensu Masner 1980) in some specimens with a compressed metastoma. This metasomal structure is not evident in all specimens and could be an artifact of preservation, but it might also represent an incipient stage in the evolution of laterotergites, characteristic of most Scelionidae. Scelionids have several apomorphic states (highly reduced fore wing venation, modified metasomal structure, absence of metasomal spiracles) that indicate serphitids were not actually derived from Scelionidae as suggested by Kozlov and Rasnitsyn (1979), but they could be closely related to scelionids based on similarities of external structure. Though synapomorphies are not yet documented for Serphitidae + Scelionidae, this relationship requires much less secondary modification in external structure of individuals than does a sister-group relationship between Serphitidae and Mymarommatidae. Consequently, I consider the only apomorphic state shared by serphitids and mymarommatids, a 2-segmented petiole, to be the result of convergence.
Relationships of the clade Mymarommatidae + Chalcidoidea. If Mymarommatidae is the sister group of Chalcidoidea, it remains to be answered what is the sister group of Mymarommatidae + Chalcidoidea. Königsmann (1978a) proposed Cynipoidea as the sister group of Chalcidoidea, and Eunapioidae (Evaniidae, Aulacidae, and Gasteruptiidae sensu Königsmann) as the sister group of Cynipoidea + Chalcidoidea. Eunapioids were proposed as the sister group of cynipoids and chalcidooids based on restriction of metasomal spiracles to only the 7th metasomal segment, and on common possession of 13 antennal articles by males and females (13:14 in most cynipoids was hypothesized to be a modified groundplan character). Distribution of metasomal spiracles (character 18) and number of antennal articles (character 1) given in Table 1 shows that the character states are not tenable synapomorphies for Eunapioidae + Cynipoidea + Chalcidoidea.

Königsmann (1978a) proposed Cynipoidea as the sister group of Chalcidoidea based on absence of cupules from the volsellae of male genitalia, and because in females the 3rd valvulae (sheaths) extend into the 2nd valvifers in a continuous transition. I was unable to determine if Königsmann originally proposed this latter state as a synapomorphy for Cynipoidea + Chalcidoidea, but Domenichini (1953) stated that many chalcoid females have the 3rd valvulae differentiated from the 2nd valvifers as articulated appendages. Distribution of cupules in the male genitalia of terebrants also indicates that their absence is not a tenable synapomorphy for Cynipoidea + Chalcidoidea (Table 1, character 21).

Though actual distribution of the character states does not appear to support any of Königsmann’s purported synapomorphies for Eunapioidae + Cynipoidea + Chalcidoidea, a relationship between Cynipoidea and Chalcidoidea has long been suggested. Ashmead (1896) considered chalcidooids to be derived from cynipoids, uniting the taxa on the basis of one symplesiomorphy (structure of the female metasoma and ovipositor) and one apomorphy (fore wing without stigma). Bradley (1958) also hypothesized a close relationship between cynipoids and chalcidooids, stating that fore wing venation of chalcidooids could only be derived and interpreted from the fore wing venation of cynipoids. He interpreted fore wing venation of chalcidooids based on similarities between the venation of Leucospis Fabricius (Chalcidoidea: Leucospidae) and Ibalia Latreille (Cynipoidea: Ibalidae) (Bradley 1955). However, this does not establish phylogenetic affinity. Furthermore, Rasnitsyn (1980) considered fore wing venation and some variants of hind wing venation of chalcidooids to resemble venation of Proctotrupoidea (sensu Rasnitsyn), though the predominance of hind wing venation was said to be more typical of Diaprioidea (sensu Rasnitsyn) or Mesoserphidae (an extinct family assigned by Rasnitsyn to Proctotrupoidea). The similarities were attributed to a “common tendency” by Rasnitsyn, rather than to inheritance. Finally, Farish (1972) noted a similarity in cleaning behavior between cynipoids and chalcidooids. They were the only apocritans studied not to have one type of wing-cleaning movement, in which the wings are held at the side and the hind legs clean only the dorsal surface of the wings. Cynipoids, chalcidooids, and some ichneumonoids studied used both hind legs to clean the dorsal and ventral surface of a wing simultaneously. However, generalizations were based on study of only 1 cynipoid, 11 chalcidooids, several ichneumonoids, 2 diapriids, 1 helorid, and 1 ebanid.

Convincing evidence for a sister-group relationship between Cynipoidea and Chalcidoidea thus appears to be lacking. If cynipoids are the sister group of chalcidooids this necessitates the common ancestor had both t₁-tr₂ and f₂-tr₂, and that chalcidooids lost f₂-tr₂ whereas cynipoids lost t₁-tr₂, convergent towards most other terebrants (Table 1, character 16). It also requires the common ancestor had the plesiomorphic position and structure of the mesothoracic spiracle and prepectus, and that this was modified in cynipoids so the prepectus was projected above the spiracle and fused to the pronotum to form a tongue-and-groove interlocking mechanism with the mesopleuron, also as in most other terebrants (Table 1, character 9, state 3a).
Rasnitsyn (1980) suggested chalcidooids probably were most closely related to either Diaprioidia sensu Rasnitsyn or to the extinct family Mesoserphidae, which he included in Proctotrupoidea. These relationships were proposed on the basis of similarities in fore wing and hind wing venation, an independent prepectus in chalcidooids and some diaprioids (which Rasnitsyn thought might have been inherited from mesoserphids), and on similarities in pronotal shape and structure of the antennae in chalcidooids, austroniids, and monomachids. However, at least the independent prepectus and correlated pronotal shape are symplesiomorphic.

No apomorphic states were found in the present study to indicate the probable sister group of Mymarommatidae + Chalcidoidea, but I suspect that it is some combination of several higher taxa of Terebrantes and not just one family, or one superfamily such as Cynipoidea. I consider this likely because I believe Mymarommatidae + Chalcidoidea represent a very early clade in the evolution of Terebrantes, based on the number of plesiomorphic features members retain (an independent prepectus, mesothoracic spiracle at the anterodorsal angle of the prepectus, mesothrochanteral depressor with a tergal portion, cerci and metasomal spiracles present, and structure of the female metasoma). If an early divergence of mymarommatids and chalcidooids in the evolution of terebrants is correct, then such apomorphic states as geniculate antennae, reduced number of antennal articles, and reduced fore wing venation are most probably convergent with most or all other terebrants with these same states. Of unknown significance is the interesting pattern exhibited by chalcidooids of retained plesiomorphic features that are conspicuously modified. These include, for example, an independent prepectus that is exposed, a mesothoracic spiracle that is at the anterodorsal angle of the prepectus, but also at the lateral edge of the mesoscutum, and a tergal portion of the mesothrochanteral depressor that arises all or in part from an axillary phragma.

Although I have not resolved relationships of Mymarommatidae + Chalcidoidea with other Terebrantes, I have indicated the problems involved for doing so. My primary interest in discussing these problems, to paraphrase Gordh (1979, p. 744), is to stimulate research on Chalcidoidea and other Terebrantes because they are a fertile area for investigations in biology, behavior, ecology, and systematics. A more accurate understanding of the true phyletic relationships of Chalcidoidea will not only require more detailed investigations of this superfamily, but also of other Terebrantes, both extant and extinct.

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References


(Date received: 1985 05 13; date accepted: 1985 08 15)
Appendix: List of abbreviations used for figures

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>aed</td>
<td>aedeagus</td>
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<tr>
<td>ax</td>
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<td>axp</td>
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<td>br</td>
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FIGS. 2–9 (scale bar = μm). 2 and 3, Gonatocerus sp., head and basal antennal articles: 2, male; 3, female. 4–6, antennal articles: 4, Gonatocerus sp., male; 5, Anacharis sp., female; 6, Pseudeucoila sp., male. 7–9, Polytoma-nar sp., nr. anomalum (Bl. and Kr.), head: 7, anterior view; 8, frontal view; 9, posterolateral view.
Figs. 18–25 (scale bar = μm). Lateral pronotum-mesothorax: 18, Tarynus sp.; 19, P. pallipes (Prov.); 20, Brachymera obscurata (Walk.); 21, Pseudometagea sp.; 22, Comptoptera (Macrometoptera) sp.; 23, Philomynar sp.; 24, Brachymynar sp.; 25, Sephanodes sp.
Figs. 26–33 (scale bar = μm). 26–28, Gonatocerus spp., lateral pronotum-mesothorax. 29, Polynema sp., lateral pronotum-mesothorax. 30 and 31, fore wing: 30, Palaecomynar sp., nr. anomalum (Bl. and Kr.); 31, Leucospis a. affinis Say. 32, Gonatocerus sp., fore and hind wing. 33, Palaecomynar sp., nr. anomalum (Bl. and Kr.), hind wing.
Figs. 34–39 (scale bar = μm). 34 and 35, Gonatocerus sp.; 34, sagittal section of mesosoma, mesofurca and various muscles removed; 35, isolated scutellar-axillar complex. 36 and 37, Palaeomyrmex sp., nr. anomalum (Bl. and Kr.). 36, petiolar segments; 37, metasoma exclusive of petiolar segments. 38, Leucopis a. affinis Say, male genitalia: 38a, dorsal view; 38b, ventral view. 39, Palaeomyrmex sp., nr. anomalum (Bl. and Kr.), apex of metasoma.

ERRATUM

p. 226, Table 1, column 7: for "-" read "0"
for "+" read "1"

p. 228, Fig. 1, Mymarommatidae clade:
for $t_2$-tra read $t_2$-$tr_2$. 