

# Hymenoptera of the world: An identification guide to families

Edited by Henri Goulet John T. Huber

Centre for Land and Biological Resources Research Ottawa, Ontario

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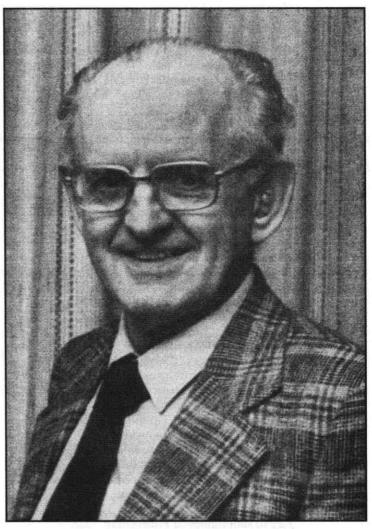
Palaeomymar sp. (male) Line drawing by Henri Goulet

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For Bill Mason (1921-1991), our friend and colleague, for his inspiration and guidance.

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The manual was initially developed for a course on identification of Hymenoptera given on three occasions to a total of 45 students from across Canada and several foreign countries. The students tested early versions of the keys and pointed out inaccuracies or lack of clarity in couplets and illustrations that needed improvement. We thank all of them for their suggestions. In this respect, we want to thank M. Sarazin, who organized the courses.

Several figures were redrawn with permission and are acknowledged below.

Chapters 12 and 16, Cynipoidea and Chalcidoidea Figs. 192–196; from *The Insects of Australia*, Figs. 37.24A,B,D,F,I; 37.25A; 37.26I, respectively, published in 1970 by the Commonwealth Scientific and Industrial Research Organization, Canberra, Australia.

Chapters 9, Apoidea Figs. 95, 100, 101, 102, 104, 106, 113; from R.M. Bohart and A.S. Menke *Specid Wasps of the World: A Generic Revision*, Figs. 8, 42, 56, 65, 136, 151, 190, respectively, published in 1976 by the Regents of the University of California, Berkeley, California.

Chapter 16, Chalcidoidea figures for couplet numbers 1a (right), 30a (top), 4bb (left top), 4bb (left bottom), 31a, 31b, 17d (left), 29a, 27bb (right), 4c (top), 8aa, 8cc, 27bb, 24a (left), 24a (right), 24b, 7aa, 7bb (right); from Z. Bouček, Australasian Chalcidoidea (Hymenoptera), Figs. 67 (in part), 161, 164, 215, 256, 275, 313, 372, 394, 497, 615, 919, 920, 923, 1298, respectively, published in 1988 by the C.A.B. International.

Chapter 12, Cynipoidea figures for couplet numbers 1c, 1d, 1cc, 1dd *left bottom*, 1cc, 1dd *right top*, 1cc, 1dd *right bottom*, 1cc, 1dd *right middle*, 4c top right, 4b, 7ee, 7e; from J. Quinlan, A Revisionary Classification of the Cynipoidea (Hymenoptera) of the Ethiopian Zoogeographical Region. Aspicerinae (Figitidae) and Oberthuerellinae (Liopteridae), Figs. 1, 2, 3, 6, 8, 33, 34, 38, 40, respectively), Bulletin of the British Museum (Natural History) 39(2): 85–133, published in 1979 by the Trustees of the British Museum (Natural History).

# Chapter 1 Introduction (English)

John T. Huber

Since the early 1980s, application of biological control methods against insect pests has had a major resurgence. Parasite Hymenoptera are among the most important agents for biological control and are extremely abundant in most terrestrial habitats. Despite their importance, their biology and taxonomy remain poorly known and their identification is difficult.

This publication is the result of a course on identification of Hymenoptera given three times since 1985 at the Centre for Land and Biological Resources Research (then known as the Biosystematics Research Centre). The initial impetus for the course came from an annual course sponsored since 1980 by the Systematic Entomology Laboratory, United States Department of Agriculture, Washington, D.C. A similar course offered jointly since 1989 by The Natural History Museum, London, and by Sheffield University has also been very successful. The considerable interest in these courses indicated the need for a comprehensive identification guide to all extant families of Hymenoptera.

Keys to families of Hymenoptera in standard textbooks tend to repeat those published earlier, usually using the same characters and format, and often permitting only the more characteristic members of a family to be identified. Rare groups or groups difficult to key out because of unusual attributes often were not included. The keys presented here were written by specialists who tried to include as many exceptional groups as possible to make the keys comprehensive. Therefore, although the guide was written primarily for nontaxonomists and for taxonomy students identifying Hymenoptera for the first time, it should also be useful to more experienced Hymenoptera taxonomists. Ninety-nine families and 20 superfamilies are treated (Table 1), although further research on relationships will almost certainly result in changes to these numbers. At least one new family is known but is not included here, pending its formal description.

Because this guide is intended for a wide group of users, several features were incorporated into the keys to make them easy to use while maintaining accuracy and completeness: each distinct attribute is listed alphabetically in the alternates of the couplets; figures illustrating key attributes are placed with the respective couplets; and terms are standardized. One chapter on structure, including an illustrated glossary of terms, and another on the use of the keys are included to help the first-time user of identification keys to Hymenoptera.

The main emphasis is on family identification using the keys, which are complemented by family sketches. The sketches include a taxonomic diagnosis to supplement the keys, a summary of the biology, the size and distribution, and important (mostly taxonomic) literature references. For several families we have provided sketches and keys for the constituent subfamilies. Also included is at least one habitus drawing of a member of each family and many subfamilies. Literature to specific genera and species is usually excluded. Literature of a more general nature is cited in Chapters 2 and 3.

For convenience, in this text "North America" refers to Canada and the United States only.

Although much effort has gone into key construction, there is always room for improvement. Largely because of differences in size of the various families, the level to which such groups are keyed is variable. Although all extant families are keyed, keys to subfamilies may or may not be included. For example, we have presented keys to the subfamilies of Braconidae and Ichneumonidae because of the large size of each of these two families. When included, not all the subfamily keys give complete world coverage, but North America, at least, is covered.

Using the keys will likely lead to discovering exceptions to them. It is hoped that suggestions for improving the keys will be made to the editors or to the authors of the appropriate section.

Eleven authors contributed to the publication. Because each specialist had his own style of key writing, some editorial changes had to be made to provide a reasonably uniform work. This included compromises and choices in use of morphological terms where several equally meaningful or useful terms could be used. The editors tried to maintain a fairly simple and uniform set of terms, in the keys at least, without losing accuracy or clarity.

If this guide results in greater interest in taxonomy of Hymenoptera and encourages biologists, teachers, students, biological control officers, and other nontaxonomists to identify their own specimens of Hymenoptera to family, then the goal of the authors will have been fulfilled.

# Introduction (français)

Depuis le début de la dernière décennie, l'application des techniques de lutte biologique contre les insectes nuisibles connait un grand essor. Les hyménoptères parasites comptent parmi les agents les plus importants de cette lutte biologique. En dépit de leur importance, leur biologie et leur taxonomie demeurent peu connues et leur identification est difficile.

Suite à une demande accrue de cours d'introduction aux hyménoptères et en l'absence de publications traitant des familles d'hyménoptères au niveau mondial, plusieurs hyménoptéristes conjointement avec le "Systematic Entomology Laboratory" à Washington ont créé un cours portant sur les familles d'hyménoptères parasites. La popularité et le succès de ce cours encouragea une orientation semblable au les Centre de recherches sur les terres et les ressources biologiques au Canada où plusieurs hyménoptéristes ont coopéré à la préparation d'un cours annuel sur toutes les familles d'hyménoptères. Après avoir présenté ce cours à trois reprises, il devint clair qu'un guide détaillé d'identification des familles d'hyménoptères serait un outil indispensable à tout étudiant. Après plusieurs années d'efforts et avec la collaboration de plusieurs scientifiques de ce Centre et d'ailleurs, ce guide voit finalement le jour.

Les quelques guides sur les familles d'hyménoptères se ressemblent dans la construction des clefs d'identification, et ne permettent la reconnaissance que des familles majeures. Certains groupes demeurent difficiles à caractériser à cause d'attributs inhabituels, ou sont simplement ignorés car ils semblent trop peu communs (particulièrement les groupes basés sur de petites espèces qui sont représentées par peu de spécimens dans les collections malgré leur grande abondance en nature). Ce guide-ci se veut l'un des plus complets car les experts qui l'ont rédigé y ont inclus tous les groupes exceptionnels connus. Ainsi, 99 familles et de 20 super-familles y sont traitées (Tableau 1), ces nombres étant appelés à changer à l'avenir avec la poursuite de la recherche sur la classification des hyménoptères. Ce guide s'adresse à tout biologiste ayant un intérêt dans la lutte biologique et à tout débutant désireux de se familiariser avec les hyménoptères. De plus, il sera particulièrement utile à tous les étudiants de la taxonomie, de même qu'aux spécialistes de la systématique des hyménoptères.

Comme ce travail est destiné aussi bien aux débutants qu'aux experts, nous avons simplifié la présentation et les illustrations des clefs d'identification sans pour autant en réduire l'intégralité et la précision. Premièrement, nous avons séparé en paragraphes et dénoté alphabétiquement chaque attribut particulier pour

chacune des deux composantes d'un couplet. Deuxièmement, les abondantes figures illustrant divers attributs apparaissent simultanément avec les couplets correspondants. Troisièmement, seul un vocabulaire uniforme et clair est employé. Enfin, pour aider les personnes peu familières avec les hyménoptères, nous avons préparé des chapitres sur la morphologie et sur l'utilisation des clefs d'identification ainsi qu'un glossaire illustré.

Bien que l'emphase de ce guide soit mise sur les clefs d'identification, les familles qui y sont identifiées sont caractérisées davantage dans de brefs exposés. On y présentent des diagnoses morphologiques qui complètent les clefs, un sommaire sur la biologie, la diversité et la distribution de chaque famille et dans bien des cas, de leurs sous-familles, des références pertinentes et au moins une illustration complète d'une espèce typique à chaque famille. Les références de nature spécifique et générique y sont exclues, cependant sous les chapitres 2 et 3 on mentionne plusieurs travaux d'ordre général.

Par souci de commodité, « Amérique du Nord » dans cet ouvrage correspond au Canada et aux États-Unis seulement.

Malgré tous les efforts apportés à une définition claire de toutes les familles, certaines demeurent néanmoins obscures. De telles différences nous ont contraints de définir les familles à des niveaux différents. Pour certaines grandes familles (e.g., Ichneumonidae et Braconidae), il est beaucoup plus utile et significatif d'examiner également leurs sous-familles. Ainsi, bien que l'on présente des clefs pour toute les familles existantes, seulement quelques clefs aux sous-familles sont inclues, celles-ci couvrant au moins la faune nord-américaine.

Dans un travail de cette envergure, il se glisse inévitablement des erreurs. Il serait donc fort apprécié et souhaitable que tout commentaire apte à améliorer les clefs ou le texte dans une édition ultérieure soit communiqué aux rédacteurs ou aux auteurs respectifs de chaque section.

Avec la contribution de 11 auteurs ayant chacun une approche différente quant à la construction des clefs, il a été nécessaire d'apporter quelques modifications afin que le style et le vocabulaire soient assez uniformes. Certains compromis se sont avérés nécessaires dans le choix de termes morphologiques particuliers afin d'éviter l'ambiguïté et la confusion.

Si ce guide suscite de l'intérêt pour la taxonomie des hyménoptères et encourage les biologistes, les professeurs, les étudiants, et les agents de lutte biologique à identifier leurs propres spécimens d'hyménoptères au niveau familial, alors le but des auteurs aura été atteint.

Table 1. Checklist of superfamilies and families of Hymenoptera arranged alphabetically by superfamily and family within each suborder. The number of subfamilies is given in parentheses only if they are keyed separately within a superfamily.

**SYMPHYTA** 

CEPHOIDEA Cephidae

MEGALOGONTOIDEA

Megalodontidae Pamphiliidae

ORUSSOIDEA Orussidae

SIRICOIDEA Siricidae

**TENTHREDINOIDEA** 

Argidae Blasticotomidae Cimbicidae Diprionidae Pergidae Tenthredinidae

XYELOIDEA Xyelidae

UNPLACED Anaxyelidae Xiphydriidae

# **APOCRITA (ACULEATA)**

APOIDEA (APIFORMES)

Andrenidae
Anthophoridae
Apidae
Colletidae
Ctenoplectidae
Fideliidae
Halictidae
Megachilidae
Melittidae
Oxaeidae
Stenotritidae

APOIDEA (SPHECIFORMES)

Ampulicidae (2) Astatidae (3) Crabronidae (2) Heterogynaidae Mellinidae (2) Nyssonidae (7) Pemphredonidae (2) Philanthidae (6) Sphecidae (3)

CHRYSIDOIDEA
Bethylidae (4)
Chrysididae (4)
Dryinidae (11)
Embolemidae
Plumariidae
Sclerogibbidae
Scolebythidae

VESPOIDEA
Bradynobaenidae (4)
Formicidae (10)
Mutillidae (7)
Pompilidae (3)
Rhopalosomatidae
Sapygidae (2)
Scoliidae (2)
Sierolomorphidae
Tiphiidae (6)
Vespidae (6)

#### APOCRITA (PARASITICA)

CERAPHRONOIDEA

Ceraphronidae Megaspilidae

Agaonidae

**CHALCIDOIDEA** 

Aphelinidae Chalcididae Elasmidae Encyrtidae Eucharitidae Eulophidae Eupelmidae Eurytomidae Leucospidae Mymaridae Ormyridae Perilampidae Pteromalidae Rotoitidae Signiphoridae Tanaostigmatidae Tetracampidae Torymidae Trichogrammatidae

CYNIPOIDEA Charipidae Cynipidae Eucoilidae Figitidae Ibaliidae Liopteridae

EVANIOIDEA Aulacidae Evaniidae Gasteruptiidae

ICHNEUMONOIDEA Braconidae (30) Ichneumonidae (32)

MEGALYROIDEA Megalyridae

MYMAROMMATOIDEA Mymarommatidae

**PLATYGASTROIDEA** 

Platygastridae Scelionidae

**PROCTOTRUPOIDEA** 

Austroniidae Diapriidae Heloridae Monomachidae Pelecinidae Peradeniidae Proctotrupidae Roproniidae Vanhorniidae

STEPHANOIDEA Stephanidae

TRIGONALYOIDEA

Trigonalyidae

# Chapter 2 Order Hymenoptera

William R.M. Mason and John T. Huber

#### General comments

Hymenoptera is one of the four great orders of insects, the other three being Coleoptera, Lepidoptera, and Diptera. Each order includes over 100 000 described species around the world, with Coleoptera having over 300 000. In Canada, Hymenoptera includes about 7000 named species, or about 25% of the total named insects. Experts have estimated less than half of Hymenoptera in Canada have been named, bringing the estimated Canadian fauna to 14 000–16 000 species. At

present, over 18 000 species have been described in North America; a conservative estimate of undescribed species is about 30 000. The size of the world terrestrial fauna in well-known groups is often at least 10 times that of the Nearctic, so that one could estimate 300 000 species of Hymenoptera as a conservative world total. It is difficult to make any general observations about so many species without citing many exceptions, but nevertheless some generalizations are useful.

# **Diagnosis**

For recognition the most useful features are those unique to the group and those that are present in all its members. Only a few morphological attributes fulfill both these conditions in Hymenoptera. In adults the following attributes are the most easily seen.

The mouthparts are mandibulate and the basal sections of the labium and maxilla lie closely attached side by side and have a sharp transverse fold near the basal third. Thus, in side view they have the shape of a figure 7, and the maxillar-labial complex can be folded up behind the head or extended out beyond the mandibles at will by muscular action that swings the basal section (cardo) and simultaneously straightens (for extension) or folds (for contraction) at the transverse joint. The underarm jab punch of a boxer is a similar action by a human arm. Although it is difficult to observe, the labium is only attached by its sides to the maxillae and not, as is usual in other mandibulate insects, directly to the head. The maxillae retain their direct attachment to the head.

The hind wing bears a few to many hamuli in a row, about two-thirds of the way toward its apex along the anterior margin. In a few Hymenoptera some hamuli also occur at the base of the anterior margin. The hamuli engage in a gutter-like sclerotized strip (frenal fold) opposite them on the posterior margin of the fore wing. In flight they cause the fore and hind wings to act as a single airfoil. The hamuli are, of course, absent when wings are reduced or lost. The hamuli are the most reliable and most easily seen diagnostic feature of the Hymenoptera. This feature cannot, of course, be used in the numerous wingless Hynmenoptera.

The ovipositor (valvulae 1 and 2) is articulated to the valvifer at the base and has two pairs of muscles that enable it to be swung downn to drill vertically. When not in use the ovipositor can be

folded up into the sheaths (valvulae 3) by the action of the opposing muscle pair. Most Platygastroidea and the genus *Pelecinus* (Pelecinidae) are exceptional, having lost this flexibility.

One of the most important characters is a genetic one. Sex determination is normally by a haplo-diploid system. In this system unfertilized (haploid) eggs have half the number of chromosomes found in fertilized (diploid) eggs, and both types of eggs develop. Males normally are haploid, whereas females are always diploid and usually result from fertilized eggs. By controlling fertilization of eggs as they are laid, the female can regulate the sex ratio, e.g., fertilized eggs laid in large hosts and unfertilized ones in small hosts. In addition, the haploid sex allows recessive lethal mutations to be rapidly eliminated from the population because they cannot be masked in males and transmitted to the next generation.

Other, usually more practical characters for identifying adult Hymenoptera in the field or laboratory follow, but they are not nearly completely reliable because they may be shared by other insects or may not be present in all Hymenoptera. The following characters should be looked for in combination; no single one is proof that the specimen is a hymenopteran:

- Four membranous wings; the hind wings shorter than the fore wings; the membranes not obscured by scales or dense hair.
- Wings with fewer veins than in many insects, usually four longitudinal veins (rarely five or six), but these are deflected and confused with crossveins in the central part of the wing so that the basal and apical veins do not appear continuous; often there are far fewer veins in species of very small body size.

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- Crossveins rarely more than seven and often difficult to distinguish from longitudinal veins.
- Base of fore wing covered by a small roundish sclerite, the tegula.
- Fore wing usually with a stigma (sclerotized triangular or semicircular area) on the anterior margin at about the midpoint. At its base the stigma is separated from the costal vein by a notch. These features are sometimes (30%) lost in species of very small body size and reduced wing venation.
- Abdominal tergum 1 fused to the metanotum but a movable connection existing between the first and second abdominal segments.
- Usually (90% or more) the apparent abdomen (metasoma) is joined to the apparent thorax (mesosoma) by a very narrow connection (the "wasp waist"); this connection is actually the greatly narrowed articulation of abdominal terga 1 and 2.
- A true, primitive ovipositor with three pairs of valves occurs in the female and is sometimes plainly visible ventrally or apically.

Although many of the above mentioned attributes involve wing structures, it is possible to identify wingless Hymenoptera by other means:

- The mouthparts are mandibulate and have the same folding maxillar-labial complex as winged Hymenoptera (see above).
- Almost all species that are wingless, including those with a relatively wide base to the metasoma, have a narrow connection between the mesosoma and the metasoma. The main exceptions are the minute males of fig wasps (Agaonidae).

- All wingless females have a typical hymenopteran ovipositor, but because many of them are Aculeata, Platygastroidea, or Ceraphronoidea, the ovipositor rarely can be seen without dissection.
- Many have a prognathous or partly prognathous head, the underside of which is readily seen. The sides of the head extend down between the oral fossa and foramen magnum, where they meet to form a median groove, or fuse completely. No true gula (as in Coleoptera) is formed.
- The immature stages of Hymenoptera are usually not as easy to recognize or characterize as adults; but then, apart from the larvae of Symphyta, most people do not see them and have no particular interest in identifying them.

Hymenoptera contains two main larval types: caterpillar-like and grub-like. Symphyta mostly have larvae that are caterpillar-like and crawl about on plants. They are most likely to be confused with Lepidoptera larvae (caterpillars). Most Lepidoptera and Symphyta larvae have three pairs of thoracic legs and an apical pair of abdominal prolegs, but true caterpillars have at most only four pairs of prolegs, on abdominal segments 3-6. Typically, Symphyta larvae have at least five pairs of prolegs, on abdominal segments 2-6. The prolegs of Symphyta do not have crochets, whereas those of Lepidoptera larvae do. Unfortunately, the prolegs usually disappear in burrowing larvae of both orders, making it more difficult to differentiate them. Symphyta larvae have only one simple eye, when present; Lepidoptera larvae have more than one. Apocrita have legless grub-like larvae that are nearly featureless. They are most likely to be confused with certain Coleoptera larvae, e.g., Curculionoidea, or with Cecidomyiidae (Diptera).

Kukalová-Peck (1991) listed other characters that define the Hymenoptera.

## Order sketch

Hymenoptera is one of the most numerous groups of insects, with many members familiar to everyone. This familiarity is demonstrated by the vernacular names given to Hymenoptera that serve, bother, frighten, or hurt people in their daily lives. Some names are bee, ant, wasp, and sawfly. Farmers, foresters, gardeners, and naturalists usually have a greater interest and a larger vocabulary of names such as nursery pine sawfly, wheatstem sawfly, wood wasp, gall wasp, velvet ant, yellow jacket, alfalfa leaf-cutting bee, bumble bee, honey bee, and so on. This is natural because these people see so many insects and may even have to compete with such insects for a living. Even though a vernacular name like bee or ant may apply to

hundreds of species, the majority of Hymenoptera species go quietly about their business unnoticed and unnamed.

Taxonomists divide Hymenoptera into two main suborders: Symphyta, or sawflies, and Apocrita, or wasp-waisted Hymenoptera.

# **Suborder Symphyta**

The first group, Symphyta, is small (only 7% of Canadian species) and geologically old. Its members first appeared as fossils in the Triassic, about 200 million years ago. The species have preserved most of the ancestral attributes of the order, especially the plant-feeding habits, numerous

wing veins, and the comparatively unmodified abdomen in which the first two segments look very much like the succeeding ones. Most adult sawflies are stubby, soft-bodied Hymenoptera that fly only weakly. The ovipositor of most species is used to pierce plant tissue and is compressed laterally and modified with marginal teeth so that it looks and functions like a saw, hence the name sawfly. The larvae of most species are caterpillar-like, equipped with legs, eyes and antennae, and walk about eating foliage like true caterpillars (Lepidoptera), but a few groups have eyeless, largely legless larvae that bore in various plant tissues, including wood.

# **Suborder Apocrita**

Apocrita are specialized most conspicuously by the greatly narrowed connection between abdominal segments 1 and 2, which gives greater flexibility at that joint. The apparent abdomen, called the metasoma, is thus not the entire abdomen, because tergum 1 is now fused into the thorax, appearing and functioning as part of that body region. The ovipositor is thin and cylindical, and sometimes very long. The fluids that lubricate the ovipositor of sawflies are modified for an additional aggressive function of paralyzing or killing the prey. The larvae are eyeless, legless, with very small antennae or none, and otherwise are nearly featureless; in the most reduced forms the sclerotized head capsule is reduced to a few bands supporting the mouthparts, or it is even reduced to nothing but a pair of mandibles. Apocrita larvae are found in concealed or parasitic situations.

Apocrita include the familiar ants, bees, and wasps, as well as tiny wasp-like parasites seldom noticed by people. Members of the Apocrita are fundamentally carnivorous, feeding on other insects

and spiders. However, several large groups have abandoned the carnivorous life and returned to a plant diet, but in specialized ways. One group, the bees (Apiformes), feed on pollen and nectar, whereas another group, the gall wasps (Cynipidae), make the familiar galls on oak (*Quercus*) and rose (*Rosa*), inside which the larvae feed. Members of some groups of Apocrita feed inside developing seeds or grass stems, and a few species of ants are plant feeders or omnivorous, gathering seeds or leaves or almost any other foodstuffs.

Almost 75% of all species of Apocrita are, during the larval stage, parasitoids of other insects or spiders, although as adults they live as independently as any insect. The female wasp lays her egg or eggs inside (or outside but almost always attached to) the egg, larva, pupa, nymph, or even adult of the particular prey that her larvae need to develop. The parasitic larva, on hatching, proceeds to devour its host in various ways that are usually fatal to the host. When fully grown, the parasitoid larva pupates and finally emerges as another adult parasitoid. Insects that parasitize other animals are called parasitoids to distinguish them from true parasites such as tapeworms (Cestoda).

Most stinging wasps (the females in some groups have lost the ability to sting) and most ants are predators, though some are ectoparasitoids. The predatory social species (that is, all the ants, plus the paper wasps and yellow jackets) hunt and capture insects or spiders and bring them to the nest, where they are shared among the larvae and adults of the colony. The vegetarian social bees similarly distribute nectar and pollen to larvae and adults. The many solitary wasps are almost all specialists, catching just a few kinds of insects or spiders that are placed in small cells, there to nourish the larvae.

# **Higher classification**

A summary of present concepts of the evolution and higher classification of Hymenoptera is given in Gauld and Bolton (1988). The goal of a natural classification is to communicate, in a simplified manner, hypotheses of the evolutionary history of a group. Organisms are classified by recency of common descent. Within a classification, monophyletic groups consist of an ancestor and all its descendants; a paraphyletic group consists of a common ancestor and some, but not all, of its descendants; and a polyphyletic group is an assemblage of descendants from more than one common ancestor. In construction of classifications, monophyly is strived for, though many taxonomists accept paraphyletic taxa. Polyphyly is rejected.

The order Hymenoptera is traditionally divided into Symphyta and Apocrita, as discussed above. Symphyta are generally accepted to be a

paraphyletic assemblage, which in this guide are classified into six superfamilies and two unassigned families. It is treated here in one chapter for convenience.

Apocrita is probably monophyletic and is treated here in several chapters by superfamily. Within Apocrita, two subdivisions are traditionally accepted: Parasitica (sometimes called Terebrantia) and Aculeata. Members of Parasitica have an ovipositor that retains its primitive egg-laying function and is adapted for piercing, and likely are a paraphyletic assemblage. Members of Aculeata, comprising those Hymenoptera whose ovipositor is modified for stinging instead of egg-laying, are demonstrably monophyletic. The biological and morphological distinctions between Parasitica and Aculeata are difficult to draw and are subject to many exceptions, and so it is more useful to deal

with a series of superfamilies; in this guide 14 superfamilies are recognized. Although some of them are clearly monophyletic, the monophyly of most groups has yet to be demonstrated.

The correct phylogenetic relationships of superfamilies within the order and suborders have not yet been fully determined. Certain groups of superfamilies clearly belong together and can be arranged from most primitive to most advanced, for example, Chrysidoidea (primitive); Vespoidea, Apoidea (advanced). Other superfamilies are grouped together for practicality because their members are few and their relationships to other superfamilies are ambiguous, for example, Evanioidea, Megalyroidea, Stephanoidea, and Trigonalyoidea. Within each superfamily the included families may be arranged by each author either alphabetically or according to their hypothesized relationships in light of current

knowledge. Their relationships will almost certainly be changed as more information becomes available.

The terms microhymenoptera and macrohymenoptera are used in this guide for convenience, not as formal taxonomic units. Members of microhymenoptera are mostly small (usually under 3 mm long) species with reduced venation. They have only one pair of spiracles on the metasoma or none at all. Included are Chalcidoidea, Cynipoidea, Proctotrupoidea, Ceraphronoidea, Platygastroidea, and a few rare groups.

Members of macrohymenoptera are usually much larger, including the familiar bees, wasps, and ants. They almost always have numerous veins and cells, at least in the fore wing, and have four to seven pairs of spiracles on the metasoma. Included are stinging Hymenoptera (Apoidea, Vespoidea, Chrysidoidea) and Ichneumonoidea.

# Literature on Hymenoptera

Relatively few general works specifically devoted to the Hymenoptera exist. Those published since 1950 and a few older references still of great use or interest are listed here. They include any paper or book dealing with various aspects of the entire order for either a country or a major geographical region. Works treating only a part of the order are listed in the appropriate superfamily chapter. In addition, several general textbooks of entomology that include chapters on Hymenoptera are listed. Works on Hymenoptera, including keys, intended for amateurs are by Cooper (1945), Berland (1958a, 1958b), Zahradnik (1985), and Betts (1986). These works vary considerably in quality, and the keys should be used with care. Cooper (1945) contains useful information on collecting, rearing, and studying Hymenoptera.

Keys The only world keys to Hymenoptera are by Handlirsch (1925) and Brues et al. (1954). Keys to all the families for a particular country or region are given by van Achterberg (1982) for northwestern Europe, Borror et al. (1989) for North America, Bouček (1957) for Czechoslovakia, Ceballos (1941–43) for Spain, Costa Lima (1960) for Brazil, Delvare and Aberlenc (1989) for Africa and South America, Landin (1971) for Sweden, Oehlke (1989) for Germany, Oehlke (1969) for eastern Germany, Prinsloo and Eardley (1985) for South Africa, Richards (1977) and Gauld and Bolton (1988) for Great Britain, and Riek (1970) and Naumann (1992) for Australia.

**Biology** Summaries of biology are given by Arnett (1985), Berland and Bernard (1951a, 1951b), Bischoff (1929), Borror et al. (1989), Bouček (1957), Brown (1982), Clausen (1940), Costa Lima (1960, 1962), Daly et al. (1978), Gauld and Bolton

(1988), Grandi (1966), Kryzhanovskii and Malyshev (1963), Malyshev (1959, 1968), Naumann (1992), Prinsloo and Eardley (1985), Richards and Davies (1977), Riek (1970), Riek and Cardale (1974), Ross et al. (1982), and Schmiedeknecht (1930).

**Phylogeny** Königsmann (1976, 1977, 1978a, 1978b) and Rasnitsyn (1980, 1988) analyzed infraordinal relationships of the order from a phylogenetic perspective. Rasnitsyn (1980, 1988, 1990) and Rasnitsyn and Kulicha (1990) also discussed the fossil Hymenoptera and the general classification of the order.

**Biological significance, Conservation** Gauld et al. (1990) provided an overview of the importance of the order and conservation of Hymenoptera in Europe.

Catalogs, checklists and regional surveys Few checklists or catalogs for the entire order have been published for any country or region since Dalla Torre (1892–1902) published his world catalog. The only such catalogs are by Wu (1941) for China, Ceballos (1956) for Spain, and Krombein et al. (1979) for North America. Fitton et al. (1978) and Hirashima (1989) published checklists for Britain and Japan, respectively. Pagliano and Scaramozzino (1990) published a checklist of generic and subgeneric names of Hymenoptera of the world. Masner et al. (1978) surveyed the Canadian fauna.

**Newsletters** Several newsletters for special-interest groups are available that are useful for those who wish to make contact with specialists around the world. The newsletters cover the entire order except for Cynipoidea and a few small, rare superfamilies. Their purpose is to provide a forum for communication and informal discussion among

researchers working on the biology or taxonomy of specific groups of Hymenoptera. A list of the newsletters and their editors is given below. The

specialized, formal journals devoted to social insects, such as the honey bee, *Apis mellifera* Linnaeus, are not included.

# **Newsletters for Hymenopterists**

Newsletter and date started	Groups covered	Editors
Proctos 1975	Proctotrupoidea Scelionoidea Ceraphronoidea	L. Masner Agriculture Canada Centre for Land and Biological Resources Research K.W. Neatby Building Central Experimental Farm Ottawa, ON K1A 0C6 Canada
		N.F. Johnson Department of Entomology 1735 Neil Avenue Ohio State University Columbus, OH 43210 USA
Ichnews 1976	Ichneumonoidea	P. Marsh Systematic Entomology Laboratory United States Department of Agriculture % United States National Museum NHB 168 Washington, DC 20560 USA
		M. J. Sharkey Agriculture Canada Centre for Land and Biological Resources Research K.W. Neatby Building Central Experimental Farm Ottawa, ON K1A 0C6 Canada
		D. Wahl American Entomological Institute 3005 S.W. 56th Avenue Gainesville, FL 32608 USA
Sphecos 1979	Aculeata (except bees and ants)	A. Menke Systematic Entomology Laboratory United States Department of Agriculture c/o United States National Museum NHB 168 Washington, DC 20560 USA
Chalcid Forum 1983	Chalcidoidea	E.E. Grissell and M.E. Schauff Systematic Entomology Laboratory United States Department of Agriculture c/o United States National Museum NHB 168 Washington, DC 20560 USA

G.A.P. Gibson and J.T. Huber

Centre for Land and Biological Resources Research

K.W. Neatby Building Central Experimental Farm Ottawa, ON K1A 0C6

Canada

Trichogramma

News 1983

Trichogramma and other egg parasitoids

S.A. Hassan

BBA

Institut für biologische Schädlingsbekämpfung Heinrichstrasse 243 D-6100, Darmstadt

Germany

**Symphytos** 

1984

Symphyta

H. Goulet

Centre for Land and Biological Resources Research

K.W. Neatby Building Central Experimental Farm Ottawa, ON K1A 0C6

Canada

D.R. Smith

Systematic Entomology Laboratory United States Department of Agriculture c/o United States National Museum NHB 168

Washington, DC 20560

**USA** 

Melissa 1986

Apoidea (bees only) R.J. McGinley and B.B. Norden Department of Entomology Smithsonian Institution NHB 105

Washington, DC 20560

**USA** 

C.D.Michener

Entomological Museum, Snow Hall

University of Kansas Lawrence, KS 66045

USA

Notes from Underground 1989

Formicidae

(ants)

M. Moffet and S. Cover MCZ Laboratories Harvard University

Cambridge, MA 02138

**USA** 

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  976–1276, in Grassé, P.-P. Traité de zoologie,
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# **Chapter 3 Structure**

John T. Huber and Michael J. Sharkey

## **General comments**

This guide is intended to familiarize the reader with the families of Hymenoptera, not hymenopteran morphology. We therefore attempt to use the simplest acceptable terms for structures. Terms used in the keys are defined and illustrated in the glossary. A brief overview of hymenopteran morphology, accompanied by labeled drawings of bodies and wings representing some major groups of Hymenoptera, is given to orient the reader and put into perspective many of the terms used.

When the reader goes beyond this guide to identify specimens to the level of genus or species, a plethora of other, often synonymous, morphological terms will be encountered. In part, this occurs because over many years various terms have been replaced by more exact or more generalized terms and different terms have been applied to homologous structures in various groups. Consequently, any given structure may have several names applied to it, and one term may apply to several distinct structures. This confusion is nowhere more apparent than in names applied to the wing veins, where several major systems are used.

It is beyond the scope of this guide to define all terms as they have been applied to structures within Hymenoptera. The following annotated list of references will help the interested reader.

Bohart, R.M., and A.S. Menke. 1976. Sphecid wasps of the world: a generic revision. University of California Press, Berkeley, California, USA. ix + 695 pp.

The morphology chapter, especially the sections on wing venation and the lists of synonyms for various terms, is useful to all who work on aculeate Hymenoptera.

Brothers, D.J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. University of Kansas Science Bulletin 50:483-648.

Includes the first cladistic analysis of Aculeata, with a detailed discussion of characters.

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## Body orientation and relationship of parts

Hymenoptera should be mounted in a uniform manner for study. Small specimens are mounted on triangular or rectangular cards, glued to the right side of the thorax so that the dorsal, ventral, and left sides of the body are clearly visible. Larger specimens are pinned through the mesoscutum slightly to the right of the midline or are glued by the right side of the thorax to the side of a pin. Whether pointed or pinned, the head of the specimen should face to the left when it is examined in lateral view. When examined in dorsal view, positional terms used in the keys are based on the assumption that the head of the specimen faces away from the observer, and the wings are stretched out either horizontally away from the body or vertically above the body.

Accurate descriptions of structures and their positions relative to one another are essential for clear understanding and must be consistent in keys and descriptions. The terms of relative positions used in this publication are illustrated (Fig. 1) and defined below. Because leg positions vary, depending on which leg is discussed and how it is bent, it is convenient to describe features of each part of any leg as though it were extended

horizontally and at right angles to the long axis of the body, regardless of its natural orientation in the living insect or its position in a mounted specimen.

There are only eight descriptors of position used in the keys, though these are combined in various ways when necessary, e.g., anterodorsal, posterolateral.

**anterior** Toward or at the head end of the body or structure (front, frontal).

**posterior** Toward or at the hind end of the body or structure (rear, back).

**dorsal** Toward or at the top or upper surface of the body or structure (above).

**ventral** Toward or at the bottom or lower surface of the body or structure (below).

medial/median Toward or at the centre, or central area or line, of the body or structure (middle, mid).

**lateral** Toward or at the side of the body, or the margin or edge of a structure.

For the appendages (mouthparts, antennae, wings, legs, genitalia) additional descriptors are:

apical The end farthest away from the body (apex); at or toward the tip (distal).

basal The end closest to the body (base); at or toward the base (proximal).

The terms basal and apical as applied to the thorax—mesosoma have been used in the literature with the thorax—abdomen (mesosoma—metasoma) junction as the central reference point. However, to avoid confusion in this publication and to eliminate the need for a reference point, these two terms are not used for the body; instead, anterior and posterior are used.

The prefix sub- may be added to describe an attribute near the extremes, e.g., subapical, sublaterally.

Length, width, and height (not depth) and their corresponding adjectives (long, wide, high) are used when giving measurements or proportions of a structure. Depth is used only when describing how deep a pit is or when describing certain types of sculpture. Further information on orientation is given in Mackerras (1970) and Scholtz and Holm (1985).

# Morphology

## Head, antennae, and mouthparts

(Figs. 6-10, 13, 14)

The **head** is the anterior division of the insect body. It is shaped like a rectangular six-sided box with its longitudinal axis usually oriented vertically and the mouthparts directed ventrally (hypognathous). The position of various parts is described for a head oriented in this manner. The

head is divided into six areas, which are sometimes further subdivided (Figs. 6-9). The relative size of these areas varies greatly and is often defined and demarcated somewhat differently among the various groups of Hymenoptera. Useful reference points are the toruli anteriorly, compound eyes laterally, three ocelli dorsally, foramen magnum posteriorly, and oral cavity ventrally. The rim of the foramen magnum is articulated with the propleura, connecting the head to the rest of the body.

The anterior surface of the head from the oral cavity to the anterior ocellus and between the compound eyes is the face (Fig. 6). The face is usually subdivided into at least three areas: clypeus, face (in the narrow sense) and frons. The clypeus (not to be confused with the labrum) is the ventral area, immediately above the margin of the oral cavity. The dorsolateral corners, or lateral margins, of the clypeus include the anterior tentorial pits, which are small, often inconspicuous pits located on either side. A clearly visible to inconspicuous line (epistomal groove) between and below the pits indicates the dorsal and lateral margins of the clypeus. The face (in the narrow sense) is the medial area, above and sometimes beside the clypeus. The dorsal margin of the face is defined by an imaginary transverse line at the level of the ventral margins of the toruli (antennal sockets). The frons is the dorsal area, above the face. The dorsal margin of the frons is defined by an imaginary transverse line between the compound eyes at the level of the anterior margin of the median ocellus.

The dorsal surface of the head, between the dorsal margins of the compound eyes and including the ocelli, is the **vertex** (Figs. 7, 8). The vertex is defined anteriorly by the dorsal margin of the frons and posteriorly by the occipital carina or groove. If there is no ridge or groove, the vertex is defined posteriorly either by an imaginary line between the compound eyes at the level of the posterior margins of the lateral ocelli, or by the highest point of the head behind the lateral ocelli if the ocelli are lower than the area of the head posterior to them.

The posterior surface of the head is divided into five areas which may not all be present or well defined in a particular species: occiput, postocciput, postgena, gena, and hypostoma (Figs. 8, 9). The occiput is the dorsal part between the occipital groove or carina, when present, and the postoccipital groove. The ventral part between these two grooves is the postgena. The narrow ring-like postocciput is between the postoccipital groove and the foramen magnum. The gena is the ventral or lateral area below and behind the eye and in front of the occipital groove, when present. The gena is delimited anteriorly by an imaginary line between the ventral apex of the compound eve and the anterior articulation of the mandible. If the occipital groove or carina is absent, the occiput merges with the vertex and can be considered as the entire area (excluding the postocciput) above the foramen, and the gena as the entire area lateral to and below the foramen. The **hypostoma** is a narrow sclerite bordering the oral cavity posteriorly and separated from the gena and postgena by the hypostomal carina.

The antennae (Fig. 14) are a paired structure composed, from the base, of three segments: scape, pedicel, and flagellum (Fig. 13). The flagellum is usually secondarily divided into two or more flagellomeres. The scape is attached to the front of the head by a socket (torulus). Between the socket and base of the scape there is often a short, narrow radicle that sometimes is distinctly differentiated from the scape. The radicle is a part of the scape and is not counted as a separate segment.

The mouthparts (Figs. 6, 9, 10) surround the oral cavity anpd are composed of four externally visible components. From anterior to posterior these components include the following: labrum (usually hidden behind the clypeus), paired mandibles, paired maxillae, and labium. Each maxilla may be subdivided into cardo, stipes, lacinia, and galea. The labium may be subdivided into submentum, mentum, prementum, glossa, and paraglossa. Both the maxillae and the labium bear segmented palpi.

## Thorax/mesosoma and legs

(Figs. 2-5, 11, 12)

The thorax is the middle division of the insect body. It can be imagined as a six-sided rectangular box with its long axis oriented horizontally. It is composed of three segments: prothorax, mesothorax and metathorax. When wings are present, the first pair (fore wings) is on the mesothorax, and the second pair (hind wings) is on the metathorax. In members of the suborder Symphyta the first segment of the abdomen is similar to the remaining segments; there is no distinct constriction between the first and second segments (Figs. 2, 3). In members of the suborder Apocrita the first segment of the abdomen is widely and immovably connected to the metathorax and usually narrowly and flexibly connected to the rest of the abdomen (Figs. 4, 5). This first abdominal segment is the **propodeum**, and the apparent thorax (true thorax plus propodeum) is the mesosoma (middle body).

Each segment of the thorax is divided into a dorsal area (notum), lateral area (pleuron), and ventral area (sternum). The notum and pleuron are usually large and may be further subdivided, but the sternum is undivided, reduced, and, on the mesothorax and metathorax, considered to be invaginated internally and represented only by a median longitudinal line. From anterior to posterior the notum may consist of up to three

separate areas: scutum, scutellum, and postnotum. The pronotum is undivided (Figs. 2–5). The mesonotum is usually divided into mesoscutum and mesoscutellum (Fig. 4), and, in the suborder Symphyta, mesopostnotum (Fig. 2). The metanotum is not clearly divided or is undivided in Apocrita (Fig. 4), but in Symphyta it is usually divided into the metascutum and the metascutellum (Fig. 2). A metapostnotum is distinguishable in most families of Hymenoptera though it is not clearly visible without dissection (Whitfield et al. 1989).

The paired **propleuron** is undivided and occupies the lateroventral area behind the head (Figs. 3, 5). The propleuron is usually loosely and flexibly connected to the pronotum and to the rest of the thorax. The fore leg is connected to the posteroventral apex of the propleuron. The **mesopleuron** is the largest of the pleura and is usually subdivided into an anterior **mesepisternum** and posterior **mesepimeron** (Figs. 3, 5), though the division may be very inconspicuous in some Apocrita. The **metapleuron** is small and may be divided in the same way as the mesopleuron (Figs. 3, 5).

Any given sclerite of the thorax/mesosoma may be subdivided into named areas by grooves or ridges, which also have specific names applied to them, but which may vary depending on the taxon. Terms applied to parts of the thorax/mesosoma are therefore numerous and often confusing.

A leg consists of six primary segments from base to apex: coxa, trochanter, femur, tibia, tarsus, and pretarsus (Fig. 11). The femur sometimes has a partial secondary division basally, the trochantellus, making it appear as though the trochanter is two-segmented. Each tibia usually has one or two spurs apically. In many Hymenoptera one of the protibial spurs is modified into a cleaning apparatus for the antenna.

The **tarsus** is secondarily subdivided into three to five **tarsomeres**, each of which may bear a ventral pad, the **plantar lobe**. The **pretarsus** (Fig. 12) consists of two claws and associated structures.

## Abdomen/metasoma and genitalia

(Figs. 2-5)

The **abdomen** is the posterior division of the insect body. It can be imagined as a horizontal cylinder. Primitively, the abdomen consists of 11 segments, but because of fusion and loss usually no more than 10 segments are visible. As discussed above, in Apocrita the first abdominal segment is fused to the thorax as the **propodeum** and the remaining (usually nine) segments are collectively called the **metasoma** (Figs. 4, 5). Each segment

consists of a dorsal plate or **tergum** and a ventral plate or **sternum** (Figs. 3, 5). There are no special pleural sclerites, and a **spiracle** opens at the side of one or more terga, which often extend ventrally to cover the lateral surfaces of the abdomen. If the terga and sterna are subdivided into smaller sclerites, they are called **tergites** and **sternites**, respectively.

Female Hymenoptera have an egg-laying apparatus or **ovipositor**, which may be concealed or exposed, depending on the species. The ovipositor is protected by a pair of **ovipositor sheaths** (Figs. 2, 3). In aculeate Hymenoptera the ovipositor has become modified exclusively for stinging and no longer functions for egg laying (Figs. 4, 5). The genitalia of male Hymenoptera are concealed and vary from simple, tubular structures with the parts greatly reduced, to relatively complex and elaborate structures.

#### Wings1

(Figs. 13-19)

The system used here for naming wing veins and cells is the Comstock and Needham (1898-1899) system updated by Comstock (1918), Ross (1936) and others (see Mason 1990 for additional references). Unfortunately, there are other systems employed by hymenopterists such as the Rohwer-Gahan (1916) system widely used for the Ichneumonoidea. The authors of the chapters on Apoidea, Chrysidoidea, and Vespoidea prefer a different system of naming wing cells. One reason for this, given by Michener (p. 310 in this publication), is that it is sometimes impossible to determine the true origins of some wing cells. For example, the three submarginal cells of most aculeate Hymenoptera are 1R1, 1Rs, and 2Rs. When the number is reduced to two, one cannot determine whether the missing vein is the second abscissa of Rs or 1r-m. Therefore, when naming these cells, the use of the generic term submarginal is more practical than the more specific terms 1R1, 1Rs and 2Rs. For comparison, the equivalent (when the complete complement of three cells is present) names of veins and cells used in the Comstock-Needham system are tabulated in Chapter 7 (p. 130). For a comparison of the updated Comstock-Needham system and other systems see Day (1988).

In many small parasitic Hymenoptera (e.g., Chalcidoidea, Proctotrupoidea, Ceraphronoidea, Platygastroidea, and some Chrysidoidea) the wing venation is very reduced, and a simplified nomenclature is used (Fig. 14). From the base of the wing the veins are submarginal, marginal, and postmarginal; a stigmal vein branches posteriorly

<sup>1</sup> The reader may find this section rather difficult, but do not despair; all veins and cells are well illustrated in the keys, and so it is not necessary to understand the system of naming veins to key out a specimen.

from the junction of the marginal and postmarginalveins. The stigmal vein may be knobbed apically as the stigma (see glossary), which sometimes sends off a little stub, the uncus, toward the postmarginal vein. The names of these veins do not connote any homology with similarly named veins in other Hymenoptera but are simply a convenient system of naming veins that has developed for these groups. The probable equivalents in the Comstock-Needham system are given in parentheses in Fig. 14.

Another factor that complicates hymenopteran wing nomenclature is that the homologies of the wing veins with those of other insect orders have not been finalized, so that some change in names will undoubtedly occur. For example, Kukalová-Peck (1991) presented a somewhat different interpretation from the rather conservative approach adopted here. Eady (1974) and Day (1988) compared the various systems that have been used by hymenopterists.

The Comstock-Needham system recognizes eight major longitudinal veins, abbreviated by capital letters. Starting from the anterior margin of the wing they are as follows: costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu) and three anal (1A, 2A, 3A) veins. In addition, there may be a short jugal (J) vein in some Symphyta and Apoidea.

Primitively, a longitudinal vein consists of two main, basal branches, an anterior convex and a posterior concave branch. These in turn may be further branched. In Hymenoptera the posterior main branch of all veins except the radius has been lost. For the radius the anterior branch is designated R1 (radius) and the posterior branch is designated Rs (radial sector). (A better terminology would be "radius anterior" and "radius posterior" but the terms radius and radial sector are already widely used in Hymenoptera so we continue to use them.) Otherwise, if a vein branches, the most anterior branch is given the subscript 1 and the more posterior branches the subscripts 2, 3....

A vein may have several segments or abscissae. They are delimited by the intersection of other veins, usually crossveins. Thus a vein that is intersected by two other veins has three abscissae, numbered consecutively from the base to the apex of the wing, e.g., when Cu has three abscissae, they are 1/Cu (the basal portion of Cu), 2/Cu, and 3/Cu (the apical portion of Cu). In this publication the numerical value of the abscissae and the vein name are separated by a slash; this convention facilitates naming of the anal vein abscissae. For example, the first abscissa of the first anal vein is 1/1A. Vein abscissae vary with the species so that 3/Cu of one species is not necessarily homologous with 3/Cu of another species. In contrast, we have attempted to homologize vein branches and crossveins.

Crossveins, indicated by lowercase letters, take the name of the veins they connect, with the anterior vein given first. Thus, a crossvein that connects R with M is r-m. If there are several r-m crossveins, they take numerical values as well, e.g., 1r-m, 2r-m, and so on. If a crossvein joins two branches of the same vein, the crossvein takes the name of the major longitudinal vein, e.g., a crossvein between R and Rs is called r-rs.

Two veins may fuse for part or all of their length, appearing as one. The resulting vein takes the name of both component veins joined by a plus (+) sign. For example, Rs and M are often fused for portions of their lengths; the fused portion is called Rs+M. Veins may fuse end to end, so that it is impossible to know exactly where the first one ends and the second begins. In this case the composite veins are joined with an ampersand (&). For example, in all Ichneumonidae and many Braconidae the first abscissa of vein Rs+M is lost and the junction Rs and M cannot be ascertained; the vein is therefore termed Rs&M.

Wing cells, abbreviated by capital letters, take the name of the vein lying anterior to them. If several fused veins form the anterior boundary of a cell, the cell takes the name of the vein that would be most posterior. Thus, the cell posterior to C+Sc+R is the radial cell (R). If more than one cell is directly behind a vein, the cells are numbered consecutively from the base, e.g., three medial cells would be 1M, 2M, and 3M.

New wing veins may arise in certain lineages. Such veins are either given a new name or are named (misleadingly) after the vein to which they are most similar in position. We follow the latter approach for convenience but distinguish the new vein from its namesake by an ('), as in the braconid subfamily key, couplet no. 3.

Wing veins vary from heavily sclerotized and tubular to barely visible and distinguishable only as a slight concave line when light is reflected from the wing surface. These vein types have been named by Mason (1986) as tubular, nebulous, and spectral veins and are defined in the glossary.

The surfaces of both the fore and hind wings are subdivided into areas that are delimited by folds, flexion lines, or furrows. Though each of these terms has a specific functional connotation, all are called folds in this publication, for simplicity. A notch often indicates the point where a fold meets the wing margin. The wing margin may bulge between notches or between the wing base and a notch; these bulges are called lobes.

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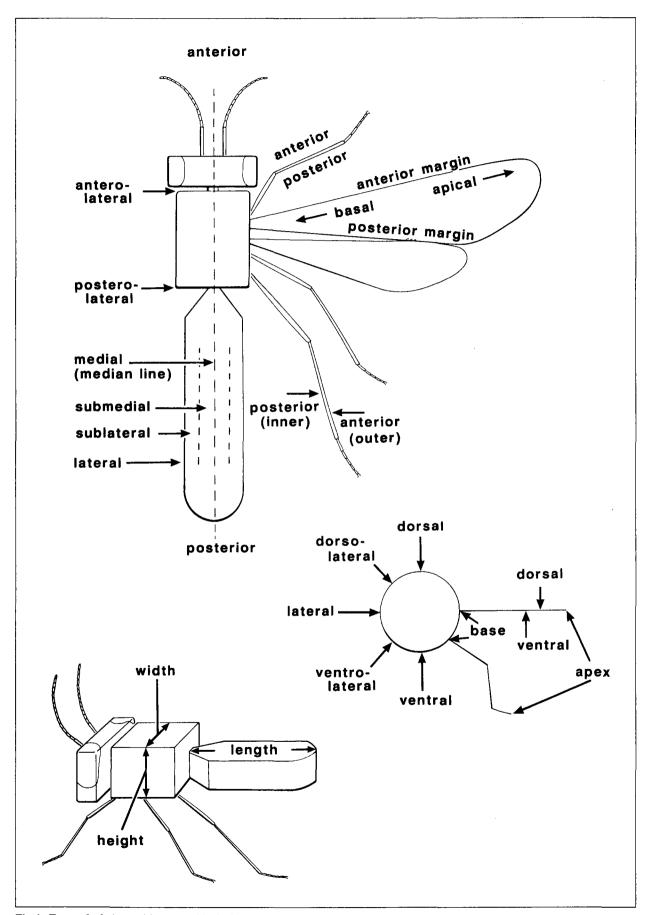


Fig. 1. Terms of relative position as used in the keys.

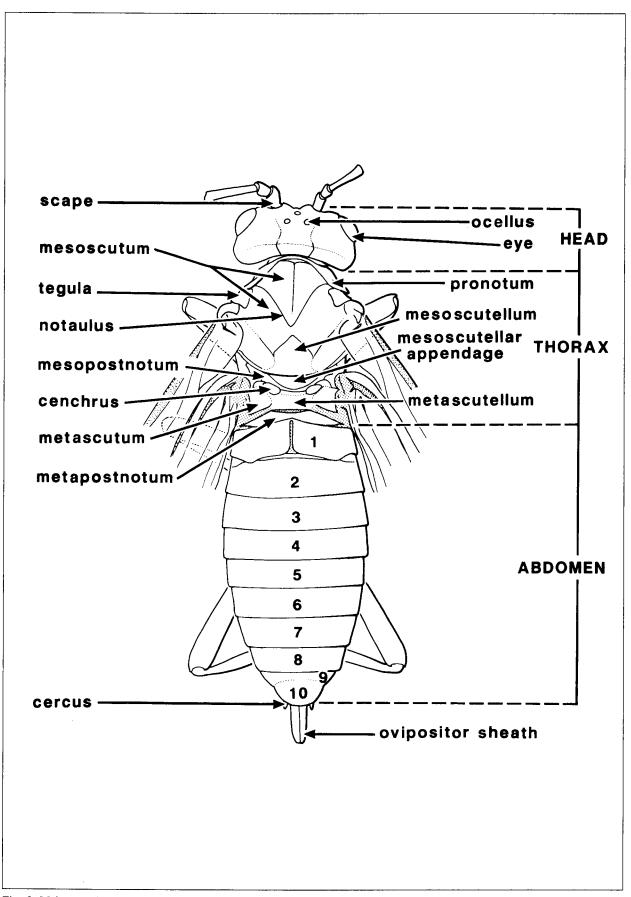


Fig. 2. Main morphological divisions and structures of a species of Symphyta, Aglaostigma quattuordecimpunctatum (Norton) (Tenthredinidae): dorsal view.

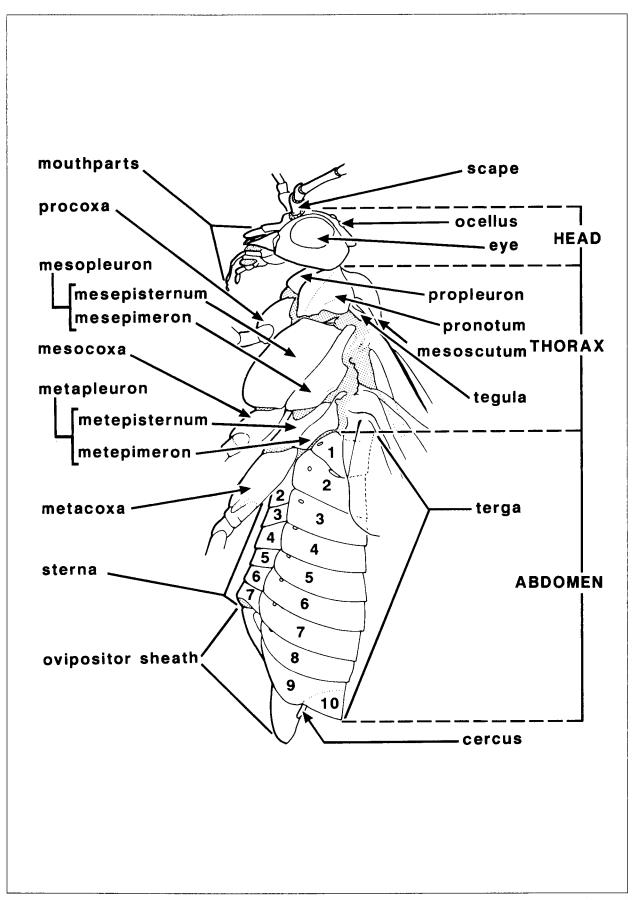


Fig. 3. Main morphological divisions and structures of a species of Symphyta, Aglaostigma quattuordecimpunctatum (Norton) (Tenthredinidae): lateral view.

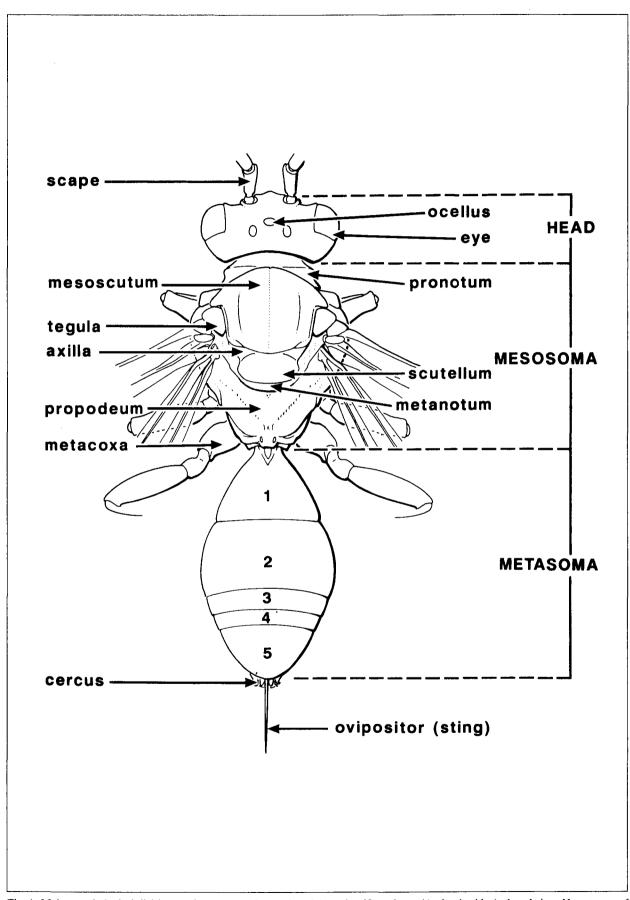


Fig. 4. Main morphological divisions and structures of a species of Apocrita, *Nomada* sp. (Anthophoridae): dorsal view. *Note*: tergum 6 retracted into 5 and not visible.

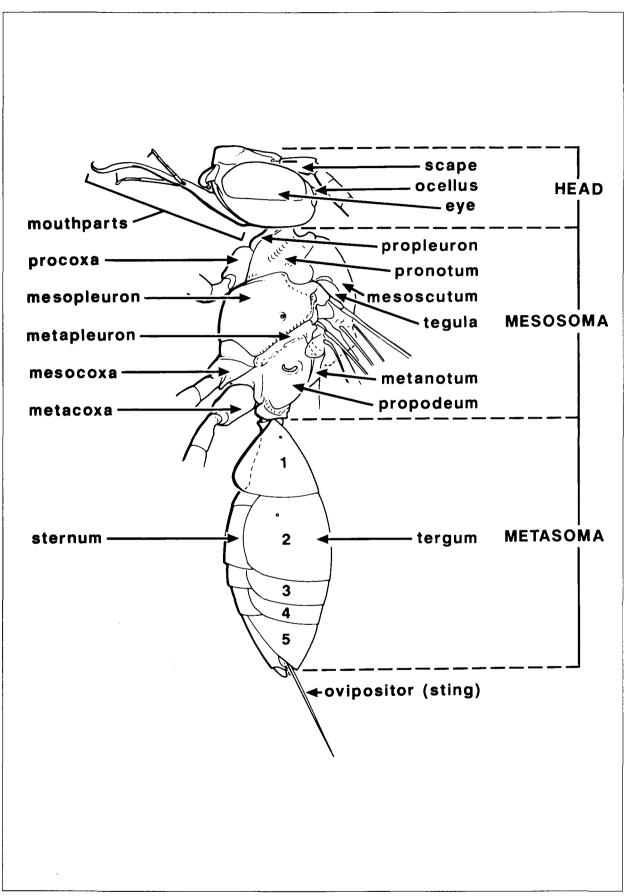
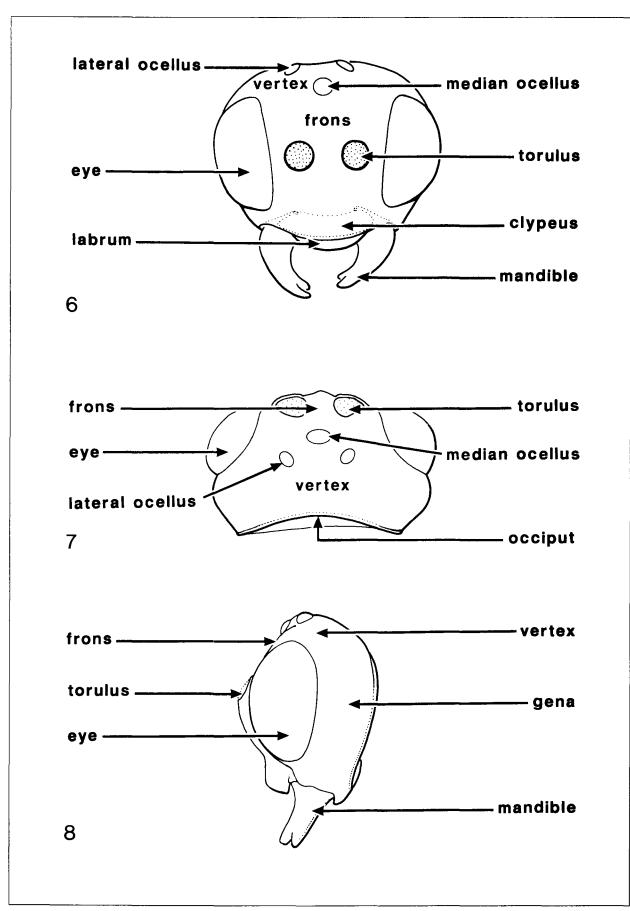


Fig. 5. Main morphological divisions and structures of a species of Apocrita, *Nomada* sp. (Anthophoridae): lateral view. *Note*: tergum 6 retracted into 5 and not visible.



Figs. 6-8. Head of Zele sp. (Apocrita: Braconidae): Fig. 6, anterior view; Fig. 7, dorsal view; Fig. 8, lateral view.

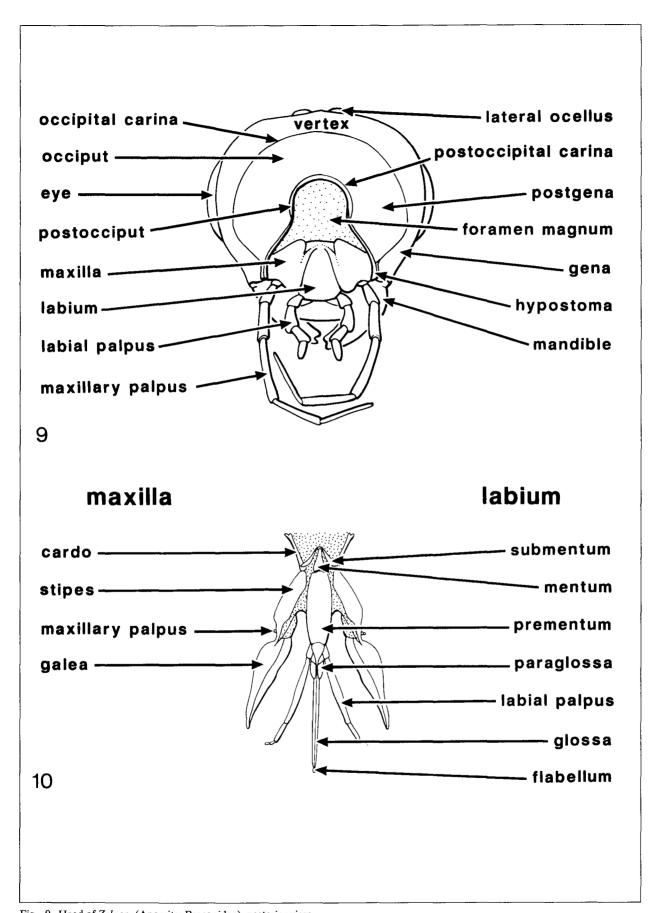


Fig. 9. Head of *Zele* sp. (Apocrita: Braconidae), posterior view. Fig. 10. Mouthparts of *Apis* sp. (Apocrita: Apidae), dorsal view.

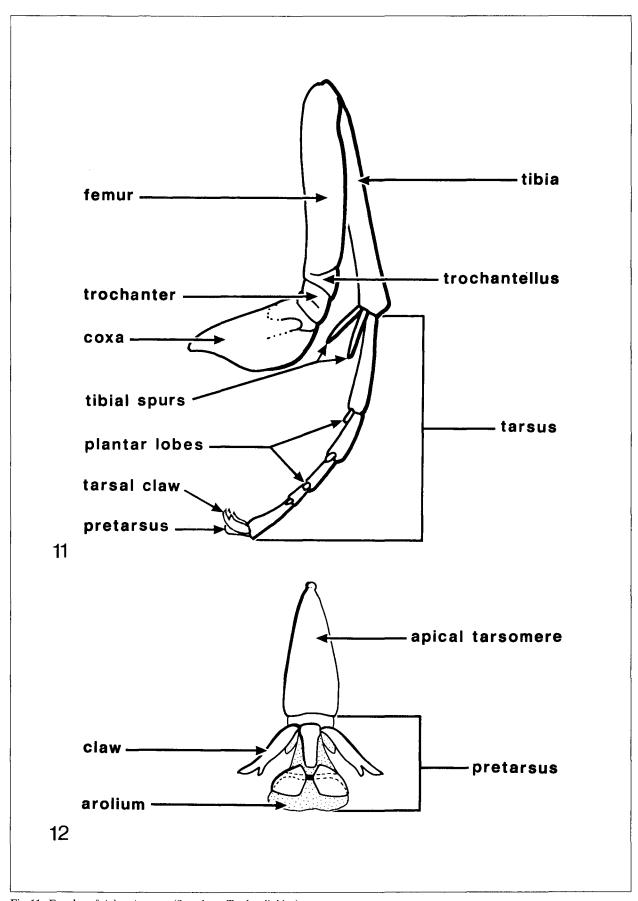


Fig. 11. Fore leg of Aglaostigma sp. (Symphyta: Tenthredinidae). Fig. 12. Pretarsus of Pamphilius sp. (Symphyta: Pamphiliidae).

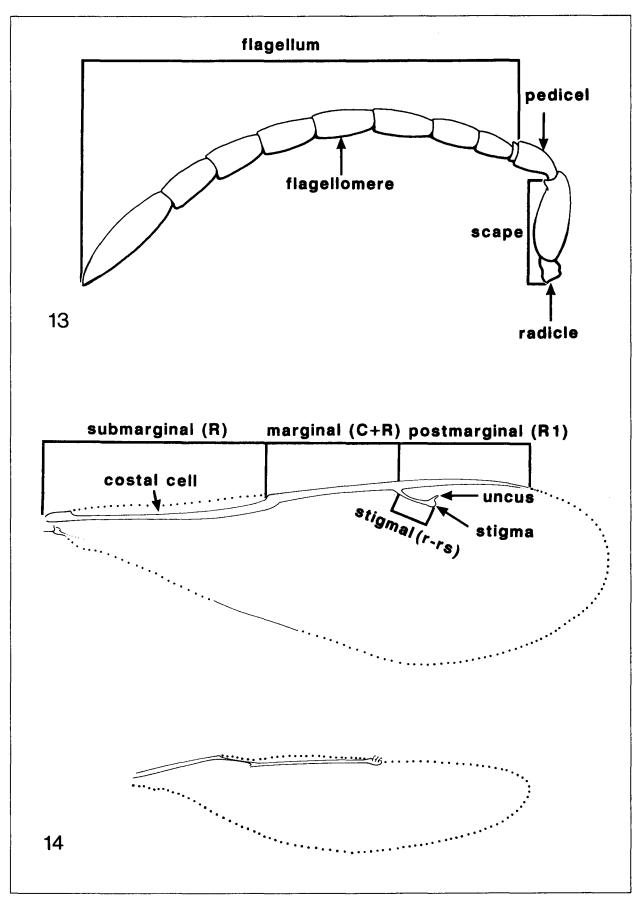


Fig. 13. Antenna of *Macroneura* sp. (Apocrita: Eupelmidae). Fig. 14. Fore and hind wings of a pteromalid (Apocrita: Chalcidoidea).

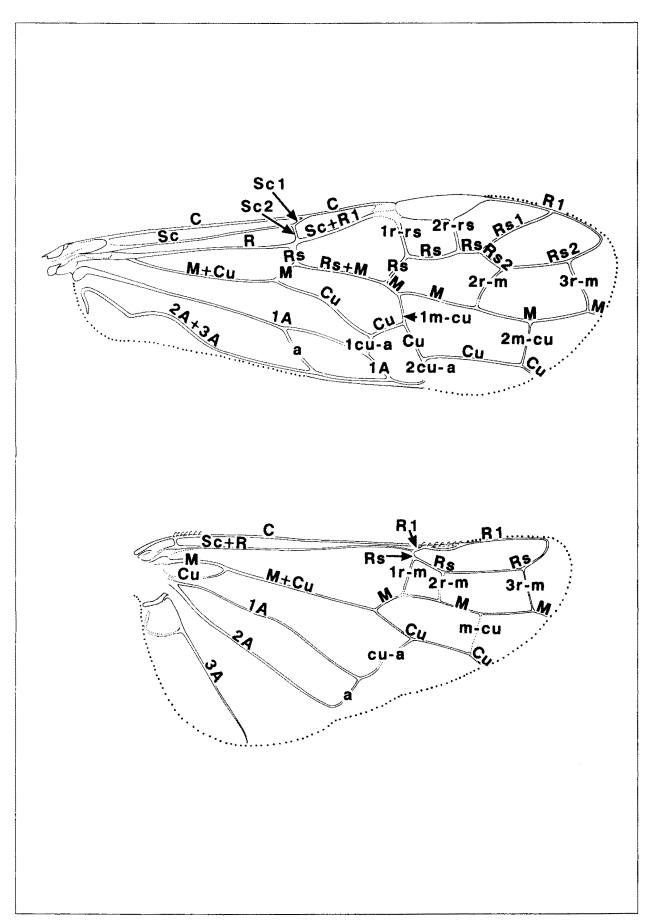


Fig. 15. Wing veins of Macroxyela sp. (Symphyta: Xyelidae).

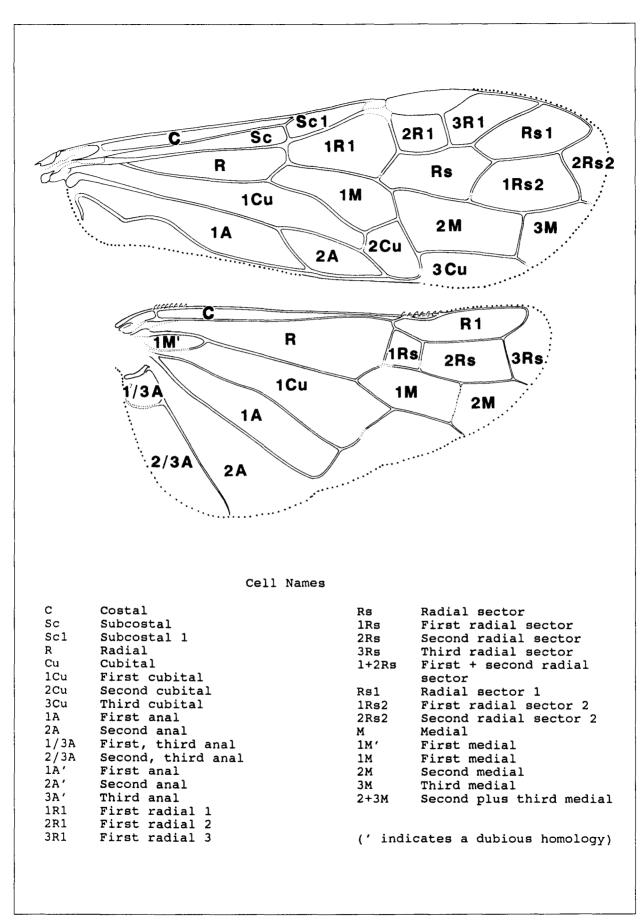


Fig. 16. Wing cells of Macroxyela sp. (Symphyta: Xyelidae).

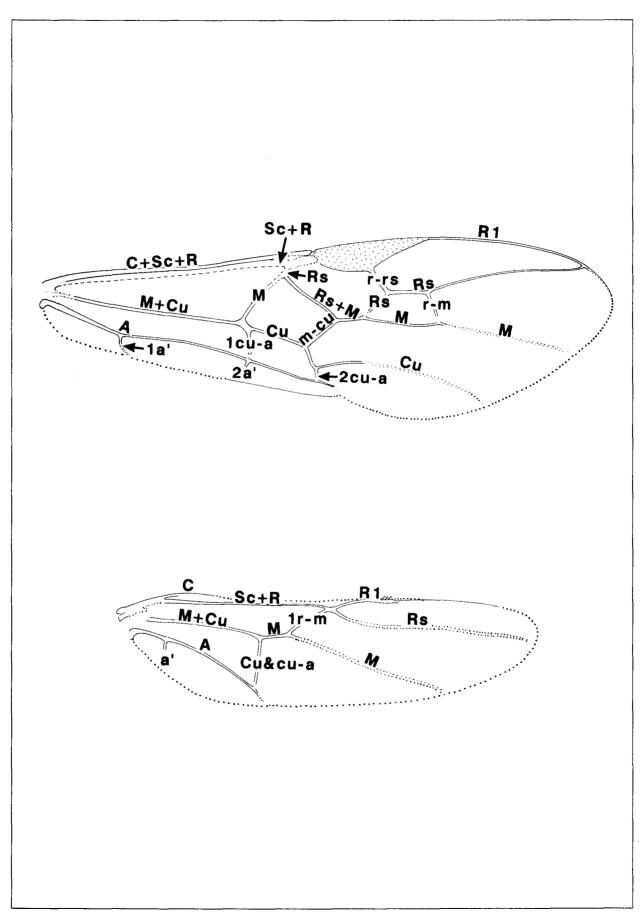


Fig. 17. Wing veins of Helcon sp. (Apocrita: Braconidae).

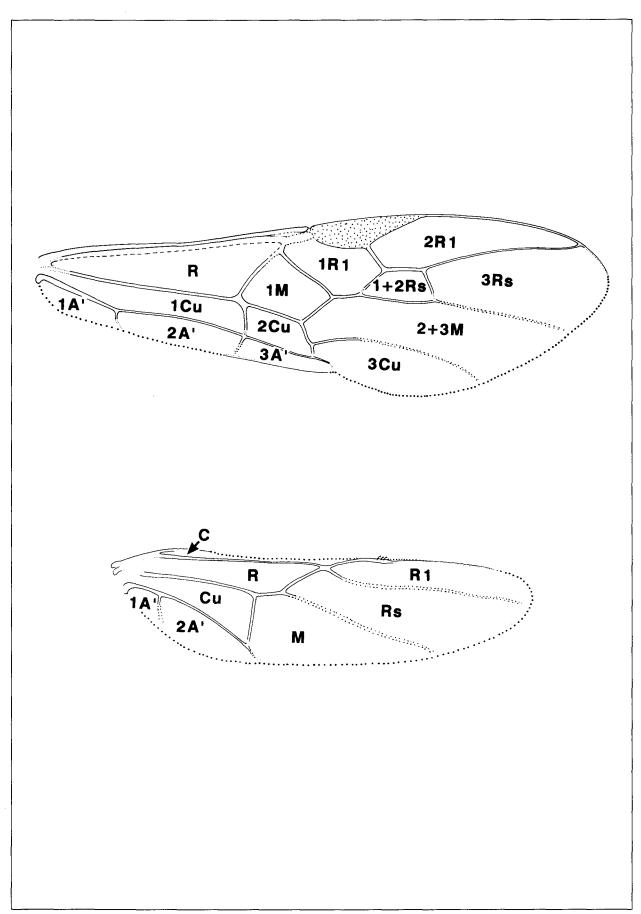


Fig. 18. Wing cells of *Helcon* sp. (Apocrita: Braconidae). Cell names given with Fig. 16.

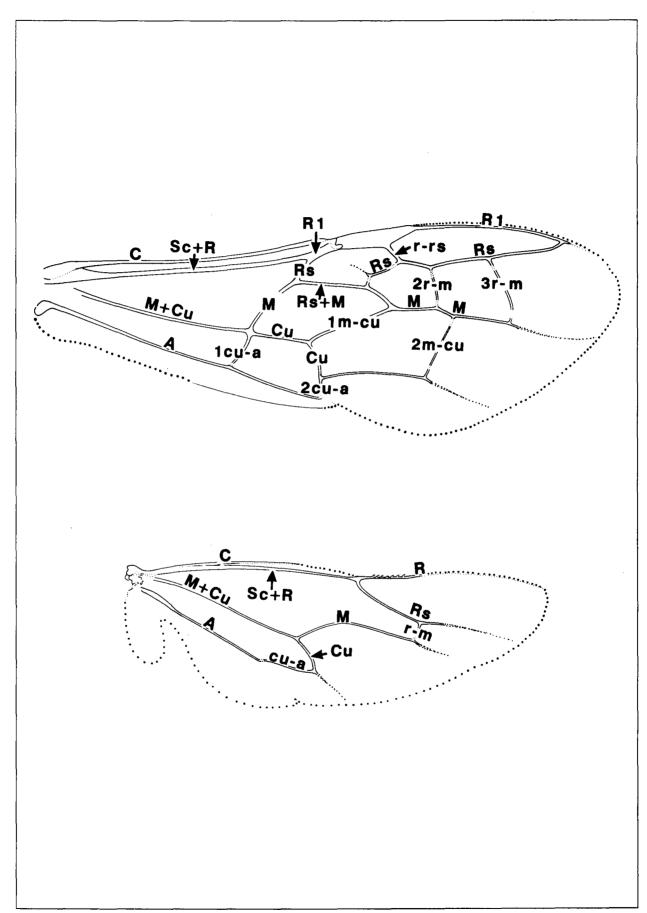


Fig. 19. Wing veins of Dolichurus sp. (Apocrita: Ampulicidae).

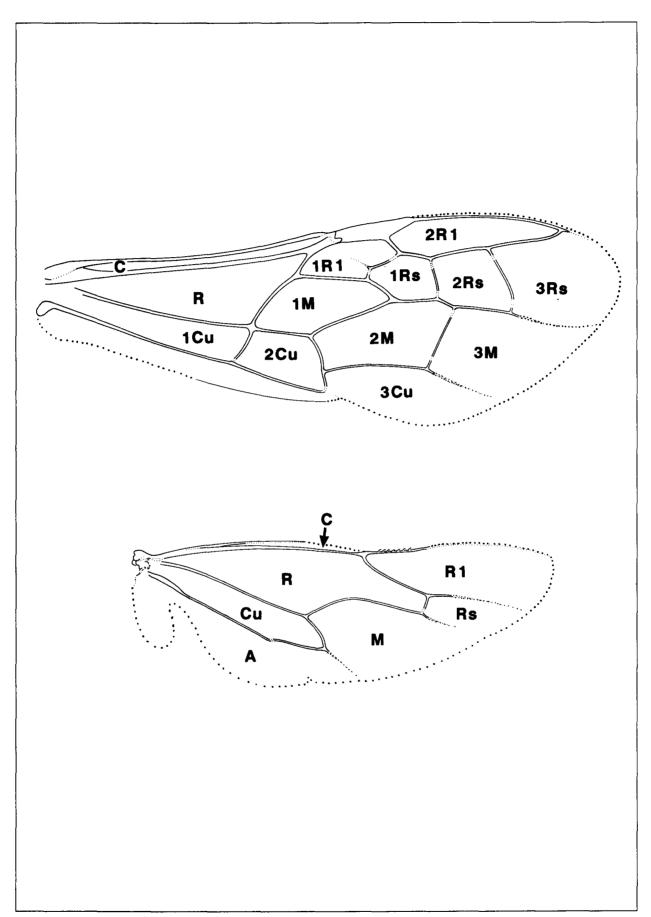
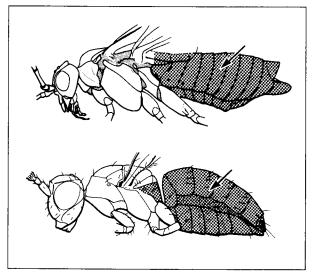


Fig. 20. Wing cells of *Dolichurus* sp. (Apocrita: Ampulicidae). Cell names given with Fig. 16.

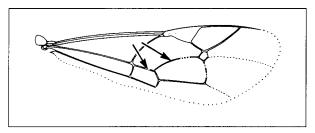
### Glossary

Terms are defined as they apply to Hymenoptera and include only those used in the keys of this publication. Additional terms may be used in the family sketches or in other publications but are not included in the glossary; their definitions can be found in the works cited in the previous section. Names of wing veins and cells are also defined and illustrated in the previous section. Because some of the terms we use have been applied in a different sense in other works, care must be taken when comparing terms used in our keys with those used in other keys. The illustrations following each definition in the glossary should be used as guides only because they are sometimes schematic and show the structure as represented in only one or two species. Depending on the species being examined, the size, shape, and relative position of a structure varies. This must be considered when comparing the glossary illustrations with the specimen being keyed. Abbreviations: adj. adjective; pl. plural; cf. compare.

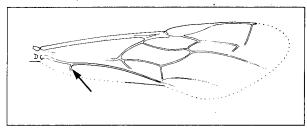
abdomen (adj., abdominal) The principal posterior division of the body, posterior to the leg-bearing segments and composed of 10 or fewer apparent segments; in most Symphyta abdominal segment 1 is easily recognized by its median split (cf. metasoma, propodeum).



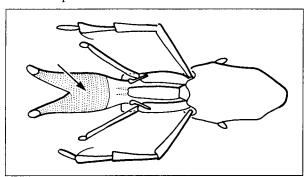
**abscissa** (pl., **abscissae**) A segment of a wing vein that is delimited by the intersection of other veins.



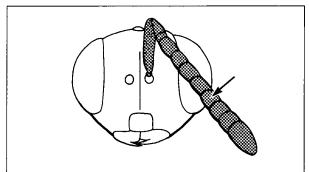
acute Sharply angled, less than 90°.adventitious vein A wing vein that is not homologized with a standard wing vein.



**annulate** Ringed; formed in ring-like segments or color patterns.

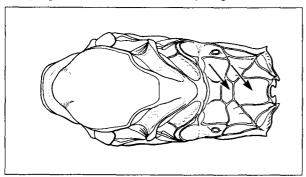


antenna (pl., antennae; adj., antennal) A paired, segmented sensory appendage of the head between the compound eyes, which consists of three segments having intrinsic muscles (see also scape, pedicel, and flagellum).

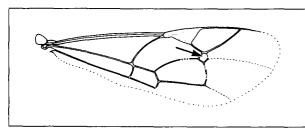


**apex** (pl., apices; adj., apical, apico-) Part of a structure farthest from its point of attachment to the body.

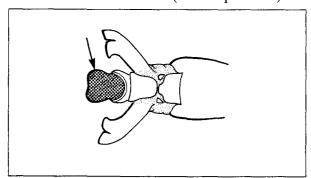
areola (pl., areolae; adj., areolate) In Ichneumonidae, the median area of the propodeum that is enclosed by ridges.



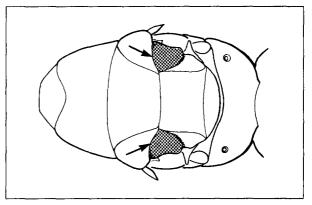
**areolet** In Ichneumonidae, the small cell in the centre of the fore wing; the first radial sector cell.



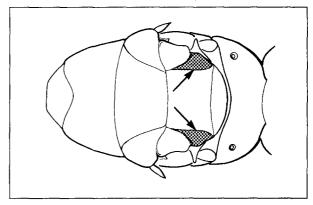
**arolium** (pl., **arolia**) A pad-like median lobe between the tarsal claws (see also pretarsus).



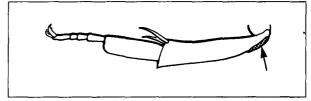
axilla (pl., axillae; adj., axillar) In groups with a transscutal articulation, posterolateral portion of the mesoscutum separated from the mesoscutum lateral to the scutellum; usually triangular (see also scutum).



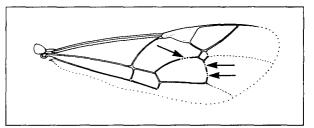
axillula (pl., axillulae; adj., axillular) In Chalcidoidea, the lateral subdivision of the scutellum delimited by a longitudinal line.



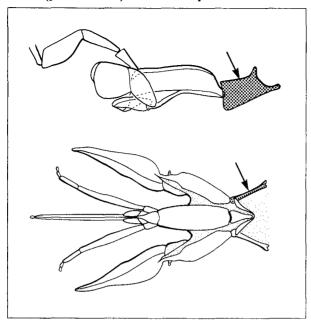
base (adj., basal, basi-) Part of a structure nearest to its point of attachment to the body.
basitibial plate In Apoidea, a small, flat, hairless, raised region of the dorsal surface of the metatibia at its base.



bulla (pl., bullae) In Ichneumonidae, unpigmented area of a vein where it is crossed by a wing fold or line of flexion.

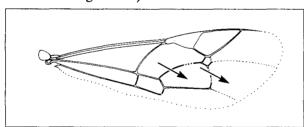


cardo (pl., cardines) The basal part of the maxilla.

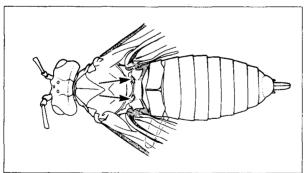


carina (pl., carinae; adj., carinate) A ridge or raised line.

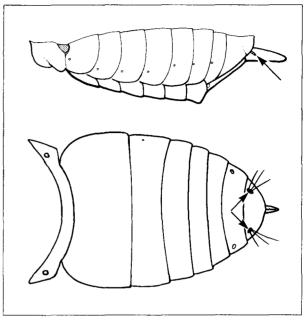
cell The area between the veins of a wing; it is closed when completely surrounded by veins, otherwise it is open (see morphology section for naming of cells).



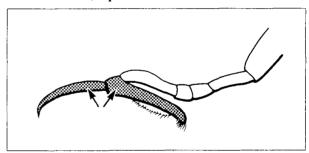
cenchrus (pl., cenchri) In Symphyta, a paired, circular, or oval structure on the sublateral portion of the metascutum.



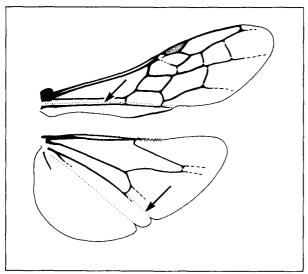
cercus (pl., cerci; adj., cercal) A paired, posterior, sensory appendage of the last (morphological tenth) abdominal tergum, which usually bears several setae. With a reduction of the apical segments of the metasoma, the cerci often appear to be on a more anterior segment.



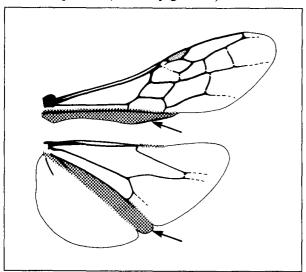
chela (pl., chelae; adj., chelate) In Dryinidae, the modified tarsus in which the apical tarsomere forms a clasping structure with its opposable tarsal claw; a pincer.



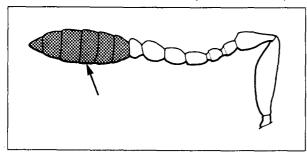
claval fold The furrow on the fore wing just anterior to, and parallel with, vein 1A, and extending to the claval notch on the wing margin.



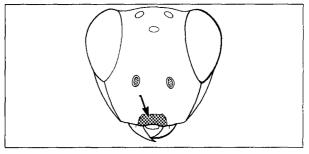
claval lobe The posterior portion of a wing behind the claval fold and in front of the jugal fold, when present (see also jugal lobe).



**club** The enlarged apical flagellomere or flagellomeres of an antenna (see also funicle).

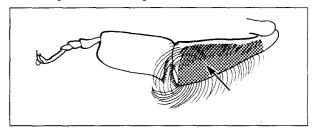


**clypeus** (adj., **clypeal**) The medial sclerite of the head immediately above the labrum; often defined dorsally and laterally by the epistomal groove.

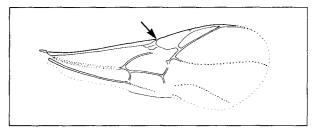


**compressed** Flattened from side to side (higher than wide).

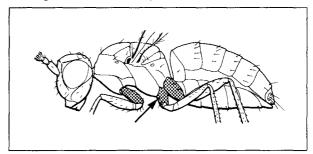
concave Pertaining to a linear structure, margin, or surface that is curved inward (cf. convex).
convex Pertaining to a linear structure, margin, or surface that is curved outward (cf. concave).
corbicula (pl., corbiculae) In Apiformes, the concave, smooth region of the metatibia that is margined by a fringe of setae arising from the margins; it forms a pollen basket.



costal notch The excision of the wing margin between the apex of the costal vein and the base of the stigma.



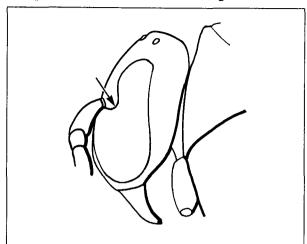
coxa (pl., coxae; adj., coxal) The first segment of a leg, between the body and the trochanter.



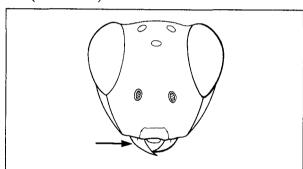
**depressed** Flattened from top to bottom (wider than high).

disc (adj., discal) The central surface of any structure.

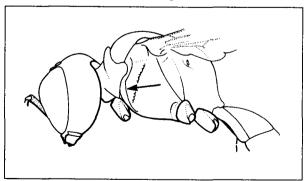
**emarginate** Notched; with an obtuse, rounded, or quadrate section cut out of a margin.



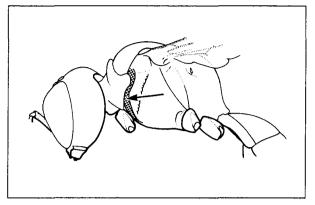
endodont mandible A mandible with the teeth facing inward so that when the mandibles are closed their tips point toward each other's base (cf. exodont).



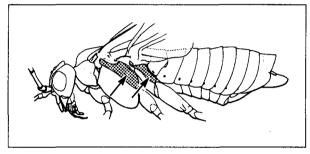
epicnemial carina The ridge on the mesopleuron that more or less parallels the anterior margin of the mesepisternum and that delineates the posterior margin of the epicnemium.



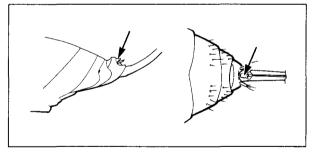
epicnemium (adj., epicnemial) The anterior portion of the mesopleuron delimited posteriorly by the epicnemial carina (see also prepectus).



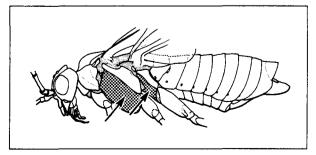
epimeron (pl., epimera; adj., epimeral) The portion of a pleuron posterior to the pleural groove (cf. episternum).



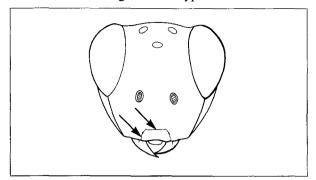
**epipygium** In Chalcidoidea, a small, more or less sclerotized, fingernail-like flap attached to the last metasomal tergum between the cerci.



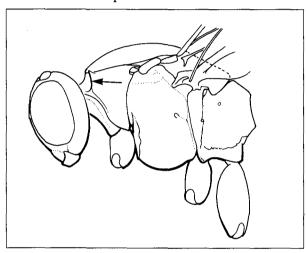
episternal groove See mesepisternal groove. episternum (pl., episterna; adj., episternal) The portion of a pleuron anterior to the pleural groove (cf. epimeron).



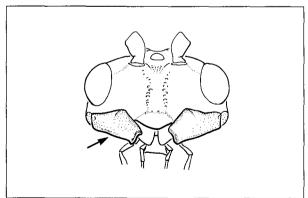
**epistomal groove** A groove defining the lateral and dorsal margin of the clypeus.



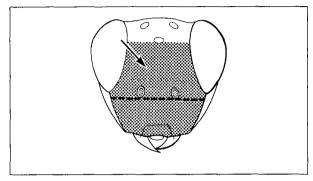
**epomia** (pl., **epomiae**) In Ichneumonoidea, an oblique ridge crossing the transverse furrow on the side of the pronotum.



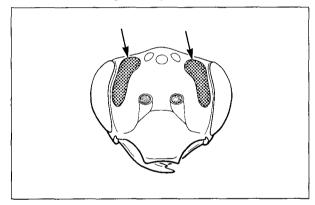
**exodont mandible** A mandible with the teeth facing outward so that when the mandibles are closed their tips point anteriorly or away from each other (cf. endodont).



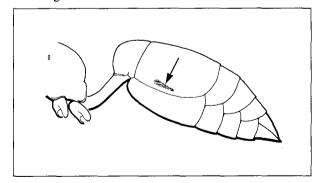
face (adj., facial) In Parasitica, the anterior surface of the head between the eyes from the ventral margin of the toruli to the oral cavity, excluding the clypeus; in Symphyta and Aculeata, anterior surface of the head between the eyes from the ocelli to the oral cavity, including the clypeus.



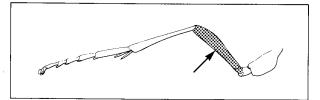
facial fovea In Apoidea, a depressed, often finely and densely pubescent area along the inner orbit of a compound eye.



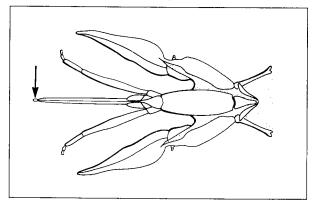
**felt line** In Mutillidae and Bradynobaenidae, a longitudinal line of flattened setae and secretory pores laterally on metasomal tergum 2.



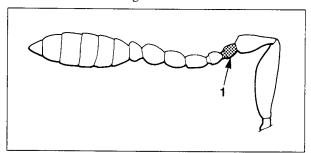
**femur** (pl., **femora**; adj., **femoral**) The third segment of a leg, between the trochanter and tibia.



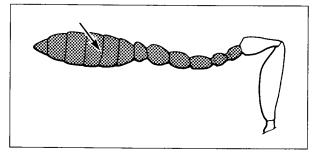
**flabellum** (pl., **flabella**) In Apiformes, a small thin plate at the apex of the glossa.



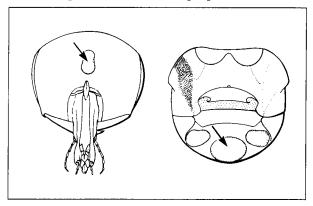
**flagellomere** A segment-like subdivision of the flagellum; it is numbered consecutively from the base of the flagellum.



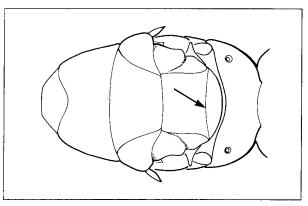
**flagellum** (pl., **flagella**; adj., **flagellar**) The third primary division or segment of the antenna; it articulates with the pedicel basally and almost always is subdivided into flagellomeres.



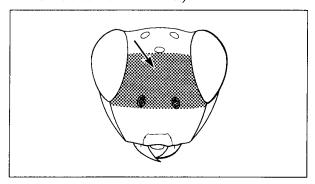
foramen (pl., foramina) A hole in the body wall through which vessels or nerves pass. The foramen magnum is the central hole in the back of the head; the propodeal foramen is the hole in the posterior area of the propodeum.



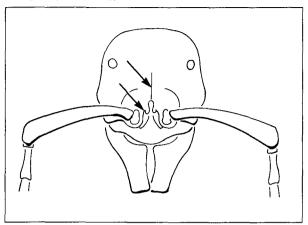
frenum (pl., frena; adj., frenal) In Chalcidoidea, the transverse line on the scutellum that delineates a posterior portion of the scutellum, the frenal area.



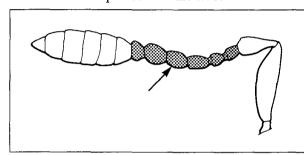
frons The area of the head between the ventral margin of the toruli and the anterior margin of the median ocellus. (Note: this is not equivalent to the true frons of larvae.)



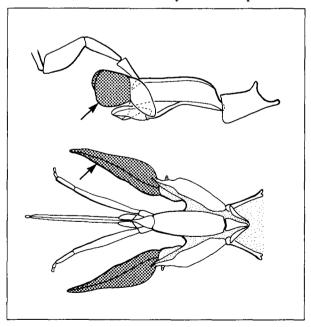
frontal carina A longitudinal ridge or pair of ridges on the frons between (and sometimes partly covering) the toruli.



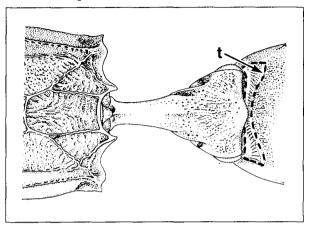
**funicle** (adj., **funicular**) A group of flagellomeres between the pedicel and the club.



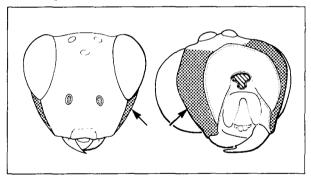
galea (pl., galeae) The outer apical lobe of the maxilla, articulated basally with the stipes.



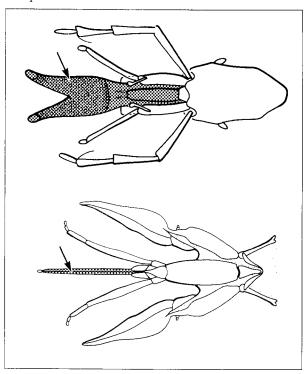
gastrocoelus—thyridium (pl., gastrocoeli) In Ichneumonidae, the usually transverse impression anterolaterally on metasomal tergum 2. The gastrocoelus includes the thyridium (t), which is the surface area with specialized sculpture, whereas the gastrocoelus is the impression itself.



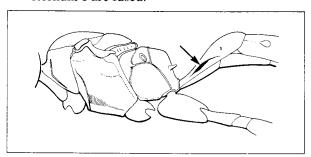
gena (pl., genae; adj., genal) The cheek; the lateral part of the head between the compound eye and, when present, the occipital carina; otherwise, the lower (in hypognathous head) or anterior (in prognathous head) part of the back of the head between the compound eye and the occiput.



**glossa** (pl., **glossae**) The paired, fused, median lobe of the labium articulated basally with the prementum.

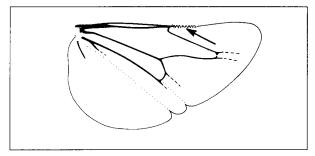


glymma (pl., glymmae) In Ichneumonidae, the paired groove or pit on the side of metasomal segment 1 between its base and the spiracle; it is nearly always present when sternum 1 is free from tergum 1 but absent when tergum 1 and sternum 1 are fused.

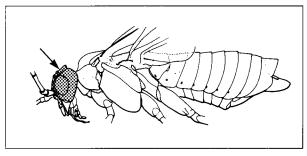


**groove** A linear impression on a sclerite (see also suture).

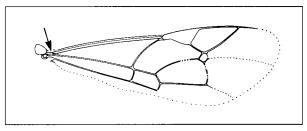
hamulus (pl., hamuli) One of a series of small bristle-like hooks on the anterior margin of the hind wing; in some groups there may be a basal and an apical series of hamuli.



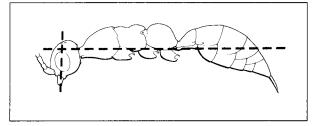
**head** The principal anterior division of the body; it bears the mouthparts and antennae.



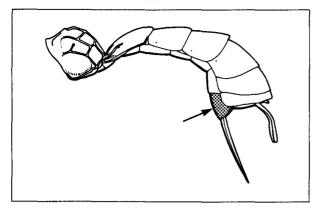
**humeral plate** The anterior sclerite of the wing at the base of vein C.



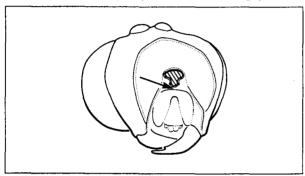
hypognathous With the head more or less at a right angle to the plane of the body (vertical), so the mouthparts are directed ventrally (cf. prognathous).



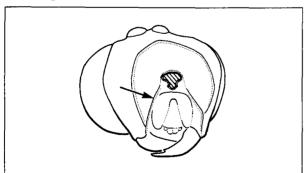
**hypopygium** (adj., **hypopygial**) The last visible sternum of the abdomen.



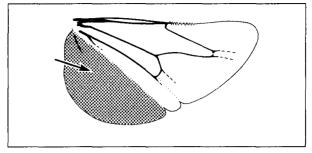
hypostomal bridge The sclerotized posterior part of the head that sometimes separates the foramen magnum from the oral cavity (the bridge may sometimes be formed by the median fusion of the postgena or gena and is then called the postgenal or genal bridge).



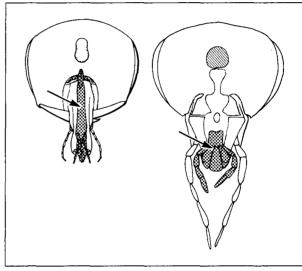
hypostomal carina The ridge on the back of the head along the oral cavity that normally delimits the hypostoma from the postgena and occiput.



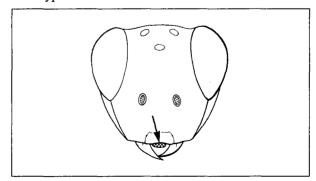
jugal lobe The posterior area of the wing behind vein 1A and set off from more anterior areas by a slight fold (jugal fold) on the wing and by a notch on the wing margin (see also claval lobe).



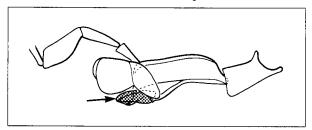
labium (adj., labial) The posterior, medial appendage of the mouthparts between and behind the maxillae, composed of the submentum, mentum, prementum, glossa, paraglossa, and labial palpi.



labrum (adj., labral) The anterior, medial appendage of the mouthparts attached to the underside of, and often concealed by, the clypeus.

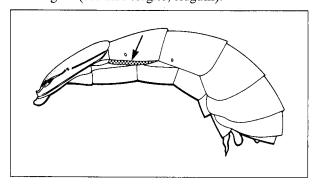


**lacinia** (pl., **laciniae**) The inner apical lobe of the maxilla, articulated to the stipes.

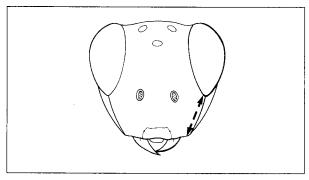


lamina (pl., laminae; adj., laminate) A thin plate or leaf-like process.

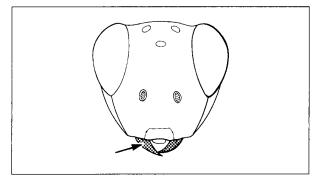
laterotergite The lateral part of an abdominal/metasomal tergum that is marked by a crease or groove, or is even completely detached from the main dorsal part of the tergum (see also tergite, tergum).



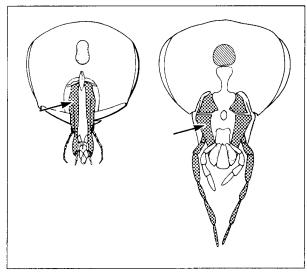
malar space The shortest distance between the base of the mandible and the margin of the compound eye.



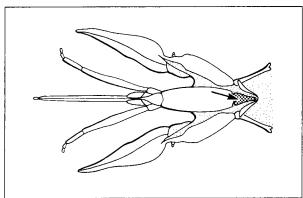
mandible (adj., mandibular) The paired, heavily sclerotized biting and chewing lateral appendage of the mouthparts between the labrum and maxilla.



maxilla (pl., maxillae; adj., maxillary) The paired appendage of the mouthparts between the mandible and labium, consisting of the cardo, stipes, lacinia, galea, and maxillary palpus.

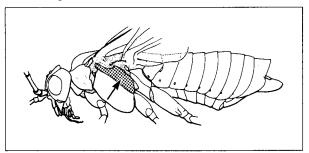


mentum A labial sclerite articulating basally with the submentum and apically with the prementum; often fused with the latter and indistinguishable as a separate sclerite.

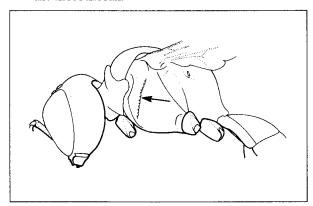


mes-, meso- A Greek prefix meaning middle or mid; used with Latin, latinized, or Greek words to indicate the middle (often second) part of a structure.

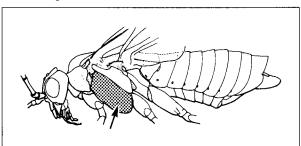
**mesepimeron** The posterior subdivision of the mesopleuron, usually small relative to the mesepisternum or almost absent.



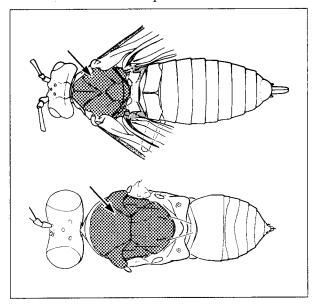
mesepisternal groove A groove on the mesopleuron, extending ventrally from a pit under the base of the fore wing and, when complete, reaching the anteroventral margin of the mesothorax.



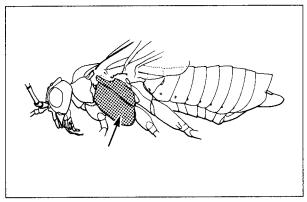
**mesepisternum** The anterior subdivision of the mesopleuron, usually comprising most of the mesopleuron.



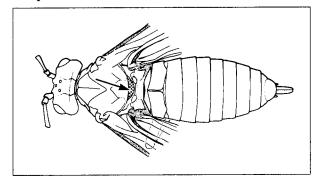
**mesonotum** The dorsal part of the mesothorax.



**mesopleuron** The lateral and ventral part of the mesothorax (see also mesosternum).

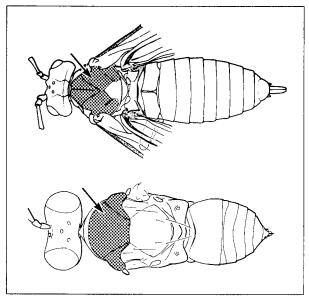


mesoscutal lobe See mesoscutum.
mesoscutellar appendage In Symphyta, the
posterior subdivision of the mesoscutellum,
usually crescent-shaped and overhanging the
postnotum of the mesothorax.

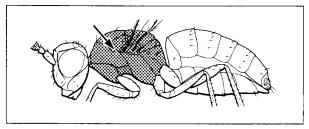


mesoscutellum See scutellum.

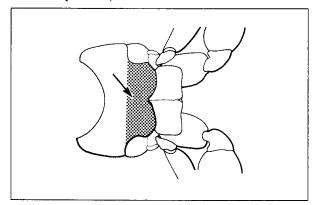
mesoscutum The mesonotum excluding the scutellum; in groups with a transscutal articulation, the portion of the mesonotum anterior to the articulation; the mesoscutum is usually divided by the notauli into a medial part and two lateral lobes (see also scutum).



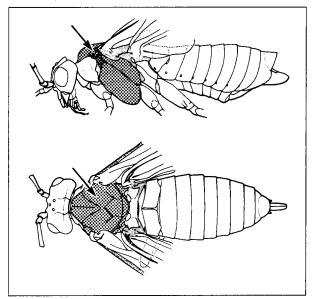
mesosoma (pl., mesosomata; adj., mesosomal) In Apocrita, the thorax plus the propodeum (cf. thorax).



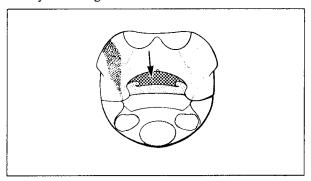
mesosternum The sternum of the mesothorax, usually invaginated and not visible, but sometimes inappropriately used as a general term for the ventral surface of the mesothorax, such as when it is modified into a flattened plate with posteriorly projecting lobes (see also mesopleuron).



mesothorax The second and largest of the three primary subdivisions of the thorax, bearing the middle pair of legs and, when present, the fore wings.

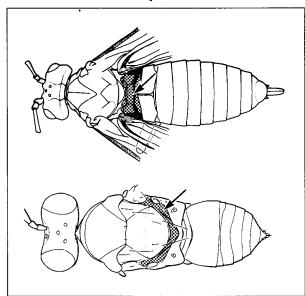


mesotrochantinal plate The ventral part of the mesothorax inflected towards the metasternum beneath the base of the mesocoxae; visible only by removing the mesocoxae.

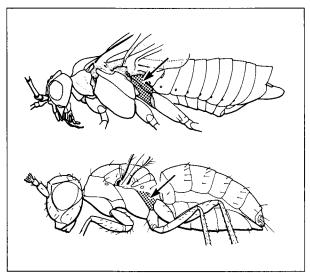


met-, meta- A Greek prefix meaning hind or posterior; used with Latin, latinized, or Greek words to indicate the posterior (usually third) part of a structure.

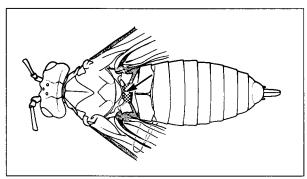
metanotum The dorsal part of the metathorax.



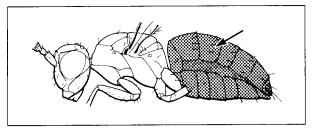
**metapleuron** The lateral and ventral part of the metathorax.



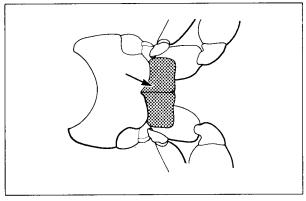
**metascutellum** In Symphyta, the middle region of the metanotum.



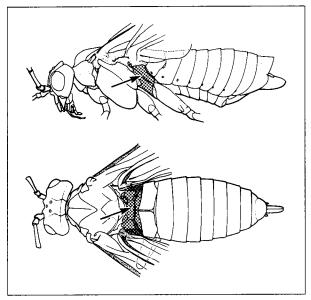
metasoma (pl., metasomata; adj., metasomal) In Apocrita, the apparent abdomen, consisting of the abdomen excluding the first segment or propodeum. In this publication the first metasomal segment which is often shortened, and narrowed, and not clearly visible, is numbered 1 (cf. abdomen).



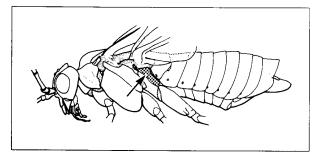
metasternum The sternum of the metathorax, usually invaginated and not visible but sometimes used as a general term for the ventral surface of the metathorax.



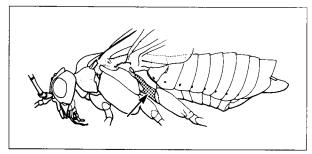
metathorax The third of the three primary subdivisions of the thorax, bearing the hind pair of legs and, when present, the hind wings.



**metepimeron** The posterior subdivision of the metapleuron.



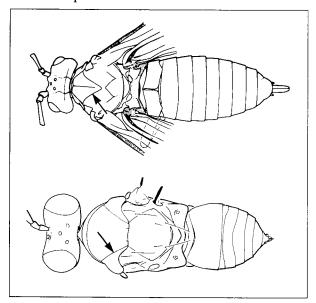
**metepisternum** The anterior subdivision of the metapleuron.



**mouthparts** The appendages of the head used for feeding, including the labrum, hypopharynx, mandibles, maxillae, and labium.

nebulous vein A wing vein that is uniformly pigmented (not darker on its margins), without a tubular structure; it can be seen with both reflected and transmitted light (cf. spectral, tubular veins).

**notaulus** (pl., **notauli**) The usually oblique, longitudinal groove on the mesoscutum, often dividing the mesoscutum into medial and lateral parts.

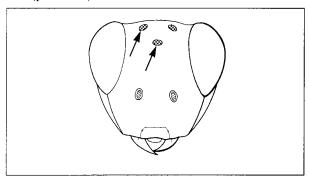


**notopleural suture** A groove separating the mesonotum from the mesopleuron.

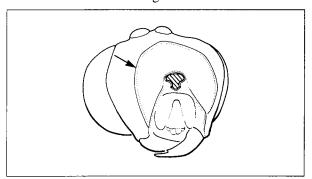
**notum** (pl., **nota**; adj., **notal**) A thoracic tergum, usually subdivided into a scutum and a scutellum.

oblique scutal carina In Spheciformes, the ridge on the mesoscutum extending obliquely posteriorly and medially from the lateral margin near the posterior of the tegula.

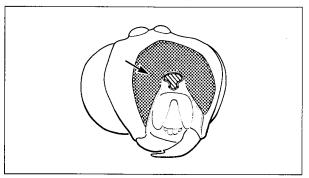
ocellus (pl., ocelli; adj., ocellar) A simple eye, consisting of a single, usually round or oval facet. Hymenoptera usually have three ocelli: one median (anterior) and two lateral (posterior).



occipital carina A ridge on the posterior surface of the head that separates the occiput from the vertex and gena; the ventral part of the ridge is sometimes called the genal carina.



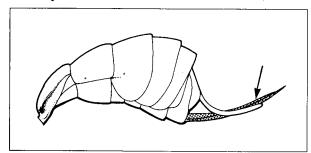
occiput (adj., occipital) The posterior part of the head behind the vertex dorsally and the genae laterally. If an occipital carina is present, the occiput is the area between it and the very narrow postocciput surrounding the foramen magnum (see also postgena).



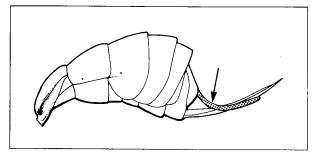
**oral cavity** The opening of the head from which the mouthparts are suspended.

orbit The narrow border around the eye. The inner and outer orbits are those parts of the face plus the frons and the gena, respectively, immediately next to the eye.

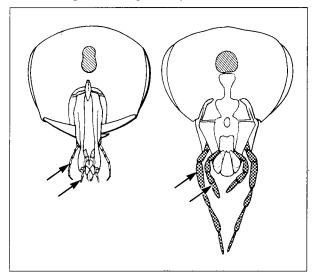
ovipositor In females, a slender, paired and interlocking, saw-like or tubular structure used for laying the eggs or, in Aculeata, for stinging or, in some Ichneumonoidea, for both; it may be concealed or may extend beyond the apex of the body and is protected by a pair of ovipositor sheaths.



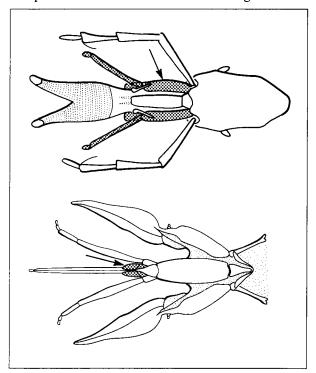
**ovipositor sheath** A paired, sclerotized structure enclosing the external part of the ovipositor.



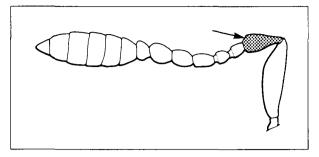
palpus (pl., palpi; adj., palpal) Paired sensory appendages of the maxilla and labium, consisting of one to six segments and one to four segments, respectively.



paraglossa (pl., paraglossae) A paired, lateral lobe of the labium articulated basally with the prementum lateral to the base of the glossa.



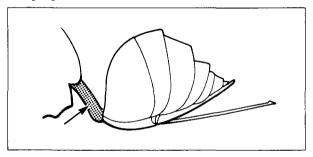
**pedicel** The second primary division or segment of the antenna; it articulates apically with the flagellum and basally with the scape.



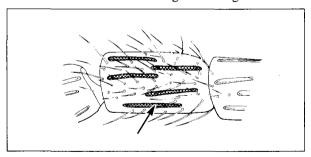
**pedunculate** An intermediate, club-like condition between sessile and petiolate (see also petiolate).

petiolate Stalked.

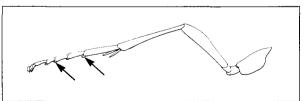
petiole Part of the metasoma, usually metasomal segment 1; the usually narrow, parallel-sided stalk joining the rest of the metasoma to the propodeum.



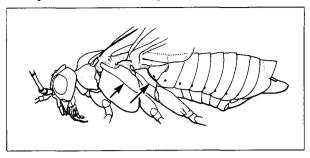
placoid sensillum (pl., sensilla) An elongate, appressed, plate-like or rounded roof-like or groove-like sensory structure; it is usually mentioned when referring to the flagellomeres.



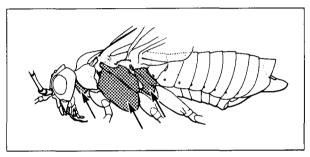
**plantar lobe** A small membranous pad projecting from the ventral apex of tarsomeres 1-4.



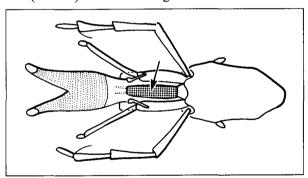
pleural groove A groove on the mesopleuron and metapleuron extending between the wing base and the coxal articulation; it separates the episternum from the epimeron.



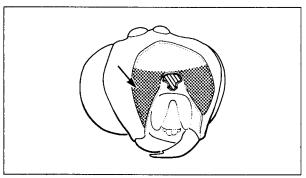
pleuron (pl., pleura; adj., pleural) The lateral part of a body segment, commonly of a thoracic segment where the pleuron occupies the lateral as well as the ventral areas of the mesothorax and metathorax.



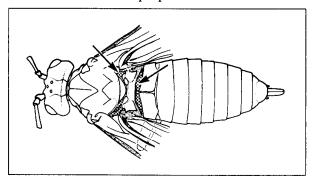
posterior lingual plate A sclerite on the posterior (ventral) surface of the glossa.



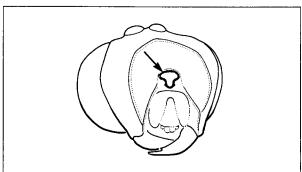
postgena (adj., postgenal) The lower part of the occiput; when the occipital carina is absent, the gena and postgena are continuous, and the entire lower area constitutes the gena (see also occiput).



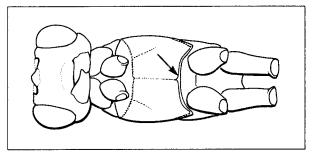
postnotum A posterior sclerite of the mesonotum and metanotum behind the scutellum. The postnotum of the metathorax is fused dorsally with abdominal tergum 1 and laterally with the metepimeron; in Apocrita the postnotum is rarely visible, and then only as an impressed line in front of the propodeum.



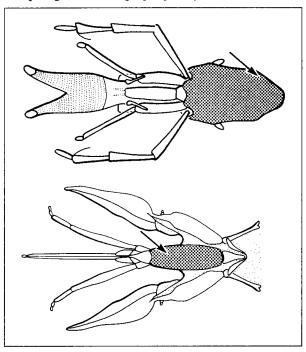
**postocciput** (adj., **postoccipital**) A narrow area surrounding the foramen magnum; it is separated from the occiput by the postoccipital groove.



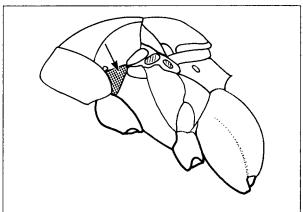
postpectal carina In Ichneumonoidea, the posterior transverse carina ventrally on the mesopleuron, just in front of the mesocoxa.



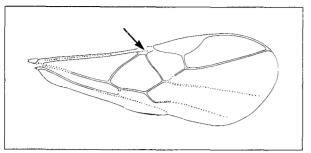
**prementum** A labial sclerite articulating basally with the mentum and bearing the glossae, paraglossae, and palpi apically.



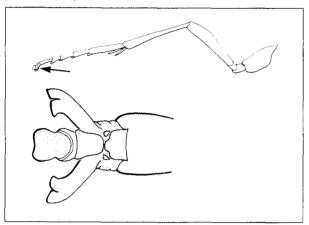
**prepectus** A sclerite of the thorax between the pronotum and the mesepisternum (see also epicnemium).



**prestigma** The enlarged and sclerotized apex of one or more veins on the anterior margin of the wing basal to the costal notch and almost continuous with the stigma.

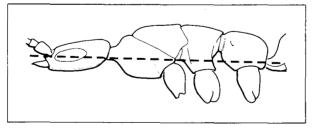


**pretarsus** The apical segment of a leg, bearing the claws and associated structures (see also arolium).

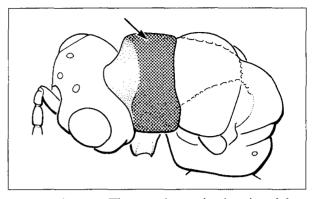


**pro-** A Latin prefix meaning before or anterior; used with Latin, latinized, or Greek words to indicate the anterior (usually first) part of a structure.

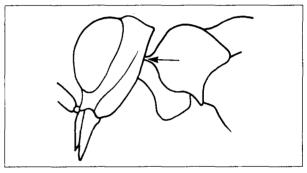
**prognathous** With the head more or less in the same plane as the body (horizontal) so the mouthparts are directed anteriorly (cf. hypognathous).



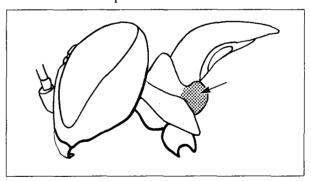
pronotal collar The horizontal surface of the pronotum posterior to the sloping, and often narrowing, region immediately behind the head.



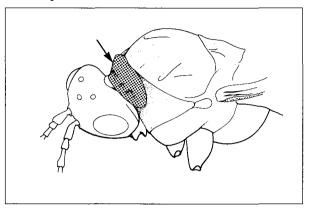
**pronotal flange** The anterior projecting rim of the pronotum; it is often hidden by the head.



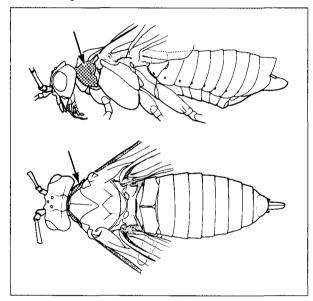
**pronotal lobe** The rounded posterolateral extension of the pronotum covering the mesothoracic spiracle.



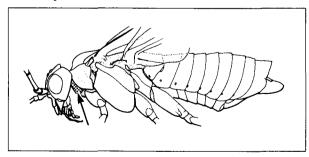
**pronotal plate** In Cynipoidea, the dorsal disc of the pronotum.



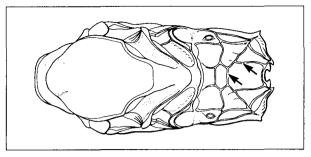
**pronotum** (adj., **pronotal**) The dorsal sclerite of the prothorax; in most Hymenoptera, occupying also the dorsolateral or lateral part of the prothorax.



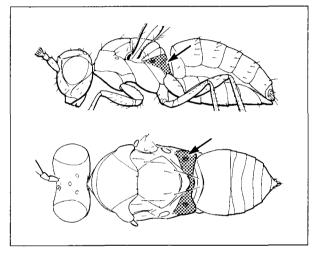
**propleuron** (pl., **propleura**) The lateral part of the prothorax. In Hymenoptera, it is displaced somewhat by the pronotum so as to occupy an oblique position ventrolateral and anterior to the pronotum.



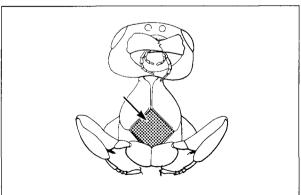
**propodeal carina** In Ichneumonoidea, one or more named, usually distinct, transverse or longitudinal ridges on the propodeum.



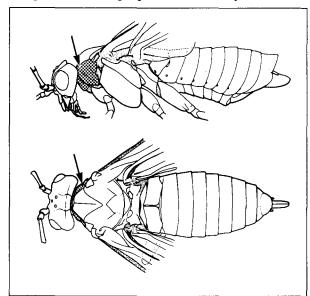
propodeum (adj., propodeal) In Apocrita, the first tergum of the abdomen, widely and immovably fused with the metanotum and with each metapleuron of the thorax, and usually narrowly and flexibly joined to the rest of the abdomen (see also abdomen, metasoma, thorax).



**prosternum** A ventral sclerite of the prothorax, between the propleura.

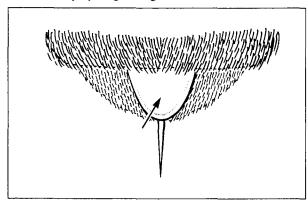


**prothorax** The first of the three primary subdivisions of the thorax, composed of the pronotum, the propleuron, and the prosternum.

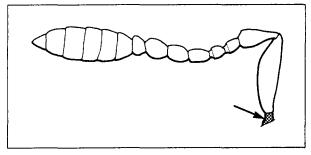


**pubescence** The short, fine, often closely set setae on the body.

punctate Bearing fine, impressed points or pits.
 pygidial plate A specialized area of the tergum of the last externally visible segment of the metasoma; it is usually flattened and defined laterally by ridges or grooves.



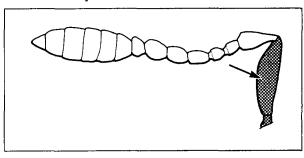
radicle The basal part of the scape often strongly defined by a constriction; it articulates with the torulus.



**recumbent** Referring to a seta lying parallel to the body surface.

reticulate Covered with a network of lines; meshed.

scape The first primary division or segment of the antenna; it articulates apically with the pedicel and basally with the torulus.

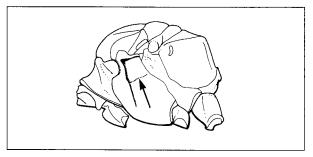


sclerite A hardened plate of the integument; it is separated from other such plates by sutures or membrane.

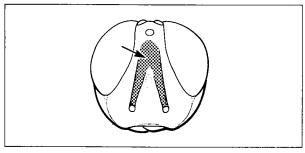
sclerotized Referring to the body integument; relatively stiff and usually darkly pigmented areas compared with usually colorless and flexible membranous areas.

scopa (pl., scopae) In Apiformes, a brush-like structure of short stiff hairs of equal length used for collecting pollen.

**scrobal groove** A horizontal groove on the mesopleuron that may be continuous with the episternal groove anteriorly and ends at the pleural groove posteriorly.

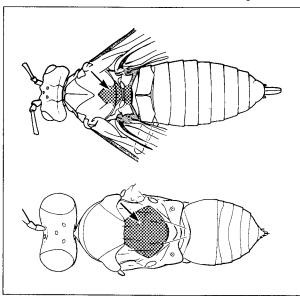


scrobe (adj., scrobal) A groove in the body integument for the reception or concealment of an appendage, e.g., a longitudinal depression of the head above each torulus for reception of the scape or a groove on the mesopleuron for reception of the mesofemur; the scrobe of the mesepisternum is a small pit.

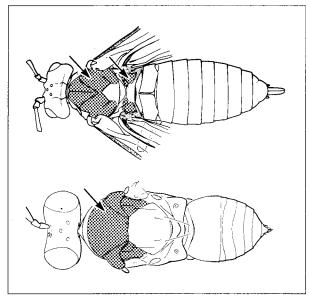


**sculpture** Markings or a pattern of impressions or elevations on the surface of a structure.

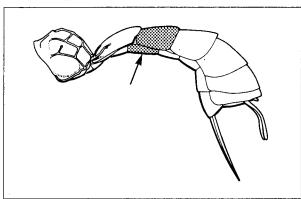
scutellum (pl., scutella; adj., scutellar) The middle region of the mesonotum or metanotum, behind the scutum. In Apocrita, only the mesoscutellum is evident and is simply called the scutellum, whereas in Symphyta both the mesoscutellum and metascutellum are present.



scutum (pl., scuta; adj., scutal) The anterior sclerite of a notum, in front of the scutellum. In Apocrita, the mesoscutum is functionally only the area in front of the transscutal articulation; the axilla, although morphologically part of the mesoscutum, is treated as separate (see also axilla).



**segment** A ring or subdivision of the body or of an appendage between areas of flexibility, and bearing intrinsic muscles.



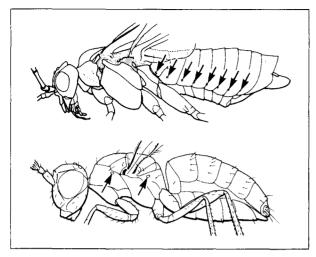
sensillum (pl., sensilla) A simple sense organ, such as a seta, or one of the structural units of a compound sense organ.

sessile One structure attached to another, without a distinct constriction (cf. pedunculate, petiolate).

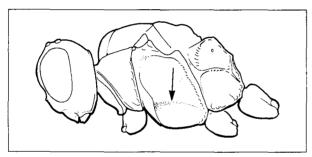
seta (pl., setae; adj., setal) A slender, hair-like, usually sensory extension of the cuticle, connected to the body wall by a socket.

spectral vein A wing vein that is indicated only by a ridge or furrow on the wing surface; it has no trace of pigment and can only be seen with reflected light (cf. tubular, nebulous veins).

spiracle (adj., spiracular) A small, round or oval lateral opening on a body segment through which air enters the tracheae.

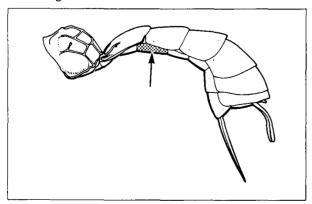


sternaulus (pl., sternauli) The horizontal lateroventral carina or groove near the lower margin of the mesopleuron, extending from the lower end of the epicnemial carina toward the mesocoxa.

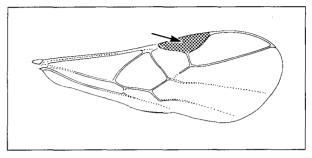


sternite The sclerotized subdivision of a sternum bounded by grooves or by membranous lines or areas (see also sternum).

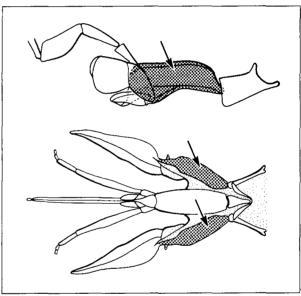
sternum (pl., sterna; adj., sternal) The ventral division of a body segment, which may be subdivided into sternites; usually only refers to the segments of the abdomen/metasoma and to the prothorax. The sterna of the mesothorax and metathorax are considered to be invaginated within the thorax.



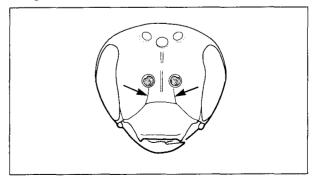
stigma A thickly sclerotized and usually darkly pigmented area on the fore wing margin at the apex of the costal vein. In Chalcidoidea, a knob-like enlargement of the apex of the stigmal vein.



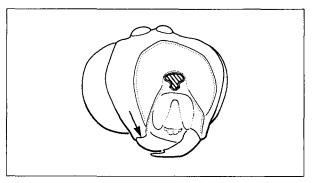
stipes (pl., stipites; adj., stipital) A major sclerite of the maxilla, articulating basally with the cardo, apically with the galea and lacinia, and laterally with the maxillary palpus.



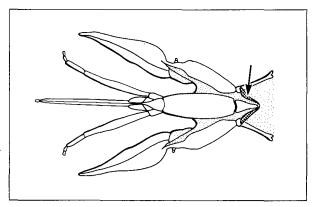
sub- Latin prefix meaning under; also used commonly to mean somewhat or almost (e.g., subequal is synonymous with almost equal).
subantennal groove In Apiformes, one or two fine grooves between the torulus and the clypeus.



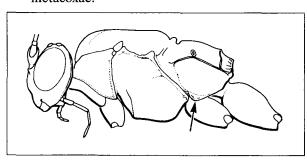
subgenal carina A ridge bordering the gena ventrally; it extends from the hypostomal carina to the anterior or facial articulation of the mandible.



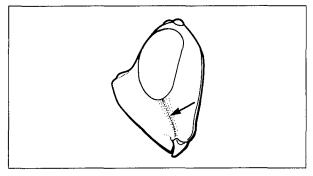
submentum The basal sclerite of the labium articulating apically with the mentum; in Apoidea, an often V-shaped sclerite (often called the lorum) with an arm articulating with each cardo and medially articulating with the mentum.



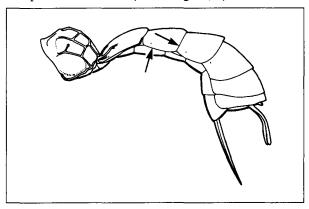
submetapleural carina A ridge on the ventral margin of the lower part of the metapleuron, between the bases of the mesocoxae and metacoxae.



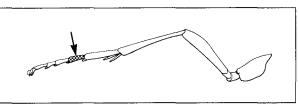
**subocular groove** A groove extending from the ventral margin of the eye to the anterior or facial articulation of the mandible.



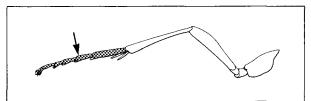
suture A line or membranous area on the cuticle indicating the junction of two formerly separate plates or sclerites (see also groove).



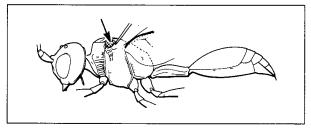
tarsomere A subdivision of the tarsus; each tarsus has 3-5 tarsomeres.



tarsus (pl., tarsi; adj., tarsal) The fifth segment of a leg, attached basally to the tibia and subdivided into tarsomeres.

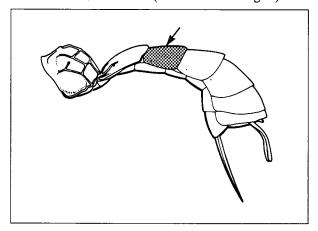


**tegula** (pl., **tegulae**) A small, scale-like sclerite covering the base of the fore wing, basal to the humeral plate.

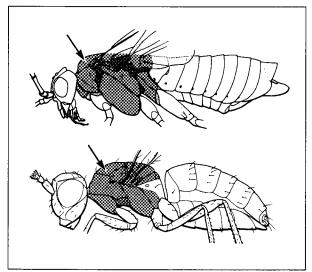


**tergite** A sclerotized subdivision of a tergum bounded by grooves, or membranous lines or areas (see also laterotergite, tergum).

tergum (pl., terga; adj., tergal) A dorsal sclerite of a body segment, which may be subdivided into tergites; specifically used for the abdomen/metasoma (see also laterotergite).

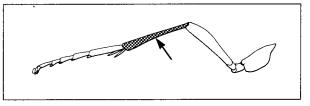


thorax (pl., thoraces; adj., thoracic) The principal middle division of the body to which the legs are attached, between the head and abdomen (cf. mesosoma).

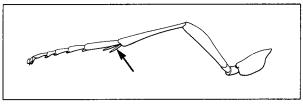


thyridium See gastrocoelus.

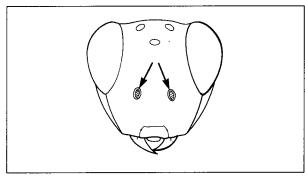
tibia (pl., tibiae; adj., tibial) The fourth segment of a leg, between the femur and the tarsus.



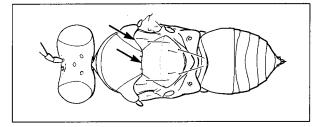
tibial spur A spine-like, multicellular extension of the cuticle connected to an appendage by a socket; usually found apically on the tibiae.



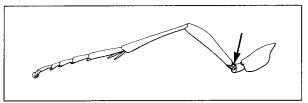
torulus (pl., toruli) A paired socket on the front of the head upon which the scape is articulated.



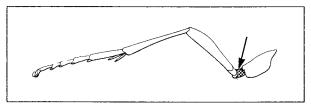
transscutal articulation A line of weakness across the mesonotum between the fore wing bases, which secondarily separates the posterolateral angles of the mesoscutum beside the scutellum (see also axilla, scutum).



**trochantellus** The basal end of the femur; it looks like a second segment of the trochanter.

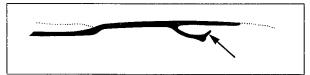


**trochanter** The second segment of a leg, between the coxa and femur.

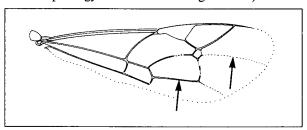


truncate Cut off squarely at the tip.
tubular vein A pigmented wing vein that is hollow
and therefore appears darker laterally and
lighter medially; it can be seen with both
reflected and transmitted light (cf. nebulous,
spectral veins).

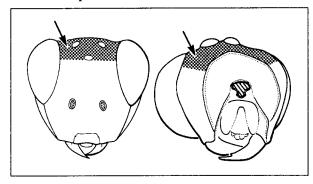
uncus In Chalcidoidea, a short, narrow stub near the apex of the stigmal vein directed towards the postmarginal vein.



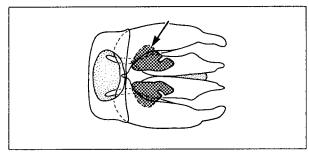
vein (adj., veinal) Narrow, usually dark thickenings of a wing arising at the wing base and branching towards the apex (see also nebulous, spectral, tubular veins, and morphology section for naming of veins).



vertex The top of the head between the eyes, from the anterior margin of the median ocellus to the occiput.



volsella (pl., volsellae) . A paired, median inner appendage of the male genitalia.



# Chapter 4 Use of keys

Henri Goulet and William R.M. Mason

#### **General comments**

The specimen to be keyed It is important to have a life-like specimen that is properly pinned or pointed. The ideal specimen should be clean and complete with the wings, legs, and antennae outstretched and spread away from the body and from each other. If the specimen is soft-bodied it should not be shriveled or collapsed; if possible it should be critical-point-dried or freeze-dried. With experience, specimens that are less than perfectly preserved or mounted can be identified correctly, but first-time users of keys will find it easier to work with intact, well-preserved, and well-mounted specimens.

**Magnification requirements** Specimens should be examined with a stereomicroscope using a magnification range of  $40-60\times$ . Although most characters can easily be studied at lower magnifications, higher magnifications  $(100-150\times)$  are usually needed to study the characters of very small Hymenoptera, e.g., Chalcidoidea.

**Lighting** Good light is essential for proper examination of specimens. Most microscope lamps provide sufficient light for studying Hymenoptera at the lower magnification range given above. However, the quality of lighting is often poor because glare from smooth surfaces obscures the clarity of surface structures. If you use a simple and inexpensive diffuser it greatly increases clarity of the structures seen. The light beam is diffused by placing a  $2 \times 2$  cm  $- 3 \times 5$  cm piece of thick (0.02) mm) tracing acetate (of the type used by draftspersons) between the light source and specimen. Sharply defined glareless views of surface structures are obtained when the acetate is less than 20 mm from the specimen, and the greatest clarity is obtained when the acetate is as close as 1–3 mm from the specimen. When the acetate sheet is very close to the specimen, be careful to avoid breaking off appendages.

Key construction Each couplet is arranged in contrasting pairs of statements. Within the first statement of each couplet, separate characters or groups of related characters are labeled by single letters (a, b, and so on); within the second statement of the couplet double letters (aa, bb, and so on) are used to designate the contrasting characters or groups of related characters. You should compare, for example, 8a with 8aa, 8b with 8bb, and for clarification you can refer to the illustrations. We have sometimes added statements in parentheses for clarification or as additional attributes to reinforce characterization of the group

(taxon), but they are usually not contrasted with the alternative half of the couplet. A page number in parentheses is given when you reach a group name; it leads either to another key or to a discussion of the group.

**Illustrations** Each illustration associated with a couplet is not necessarily one of the taxon included by the couplet but is a similar expression of the character to be observed; other parts of the figure should be ignored. For instance, when the character to be observed concerns the stigma you should ignore other venation in the figure. All illustrations required for each couplet are printed on the page facing the couplet or directly above the couplet for easy comparison. Each illustration or group of illustrations has the same letter(s) as the corresponding statement letter within the couplet. For example, if you are at couplet 16 the illustration associated with statement bb is coded as bb. If a range of possibilities exists, then there may be more than one figure that has the same code; for example, several figures may be coded b but only one coded bb. Arrows, sometimes with abbreviations or key words, are added to an illustration to draw attention to the location of the attribute in question. Easily interpreted characters (such as number of flagellomeres or tarsomeres) or attributes widely understood as being typical or normal (a normal tarsus versus a chelate tarsus) are not illustrated.

We have taken great care to make the keys as complete as possible. Although we tried to illustrate each couplet sufficiently, many couplets do not include the complete range of variation because of space limitations. Thus, a figure may only illustrate part of the range of variation for that section of the couplet. You should be careful not to use the habitus drawings accompanying the family discussions to identify specimens until you have considerable familiarity with a group, because great diversity in habitus can occur in a single family. A list of habitus drawings with generic names for each illustration is given in Appendix 1.

Terms used in the keys The main purpose of a key is to be functional. Therefore we use common English adjectives instead of technical terms wherever feasible without a loss of accuracy. You should consult Chapter 3, particularly the part treating relative position, so as to become familiar with the technical terms used in the keys. Several keys contain couplets with conjunctions such as and, but, if, or and so on. They are given in boldface to

draw attention to them. Note these terms carefully to avoid mistakes when keying out a specimen.

We make a fairly rigorous attempt at uniformity among the keys, but, we hope, without reducing clarity and accuracy. In the keys and descriptions only the left half of an insect is described. Thus, paired (bilaterally symmetrical) structures (such as appendages) are described or discussed in the singular unless reference is to all of a serially homologous set, e.g., "legs black" (all three pairs are black), but "fore leg black" (only one pair is black). Using the singular improves clarity, e.g., "head in anterior view with torulus touching clypeus." This approach may cause some confusion initially when you observe a bilaterally symmetrical or paired structure in dorsal view: two

parts of the structure are evident yet the structure is described in the singular. In certain situations, however, use of the plural is necessary, e.g., "toruli closer to eyes than to each other."

A word of encouragement for the student At first the keys may look esoteric and difficult to use. Indeed, initially they will be, but with careful reading of each couplet and with practice, the characters will become much more understandable and the keys more comprehensible. Familiarize yourself with basic insect morphology by studying Chapter 3. Be patient and persevere, and you will discover that most specimens you have can be keyed out correctly.

## Preamble to superfamily key

The key contains 71 couplets (72 keyed units), but only 20 superfamilies are recognized in the conservative classification used here. Obviously, some groups key out more than once. The most diverse is Chrysidoidea, parts of which fall into 15 couplets, eight for winged and seven for wingless or short-winged species. Members of this superfamily are united chiefly by an internal feature of the female genitalia, quite impractical for use as a key character; in addition, almost every family of Chrysidoidea includes both winged and flightless members, which run to separate parts of the key. Another diverse superfamily is Vespoidea, which keys to nine couplets, six of which are for the numerous flightless species. On the other hand, 10 smaller superfamilies key out at only one couplet each and five others at only two couplets.

Among groups that key out in several couplets, it is convenient for the user to know the couplets most commonly reached. Chrysidoidea (except Dryinidae and very small species) mostly key to 27, but very small Bethylidae go to 36 and 46; most Dryinidae key to 21, whereas the numerous wingless dryinids run to 59. Most Vespoidea arrive at 32 if winged, but the majority of wingless females key to 65. Most Apoidea will run to 29, but very hairy bees can optionally be keyed to 24. The most numerous Hymenoptera, worker ants (Formicidae), run very rapidly to couplets 49 and 50, but typical winged ants key to 32 with other Vespoidea. Ichneumonoidea usually run to 19 and most Chalcidoidea to 43 and 44. Proctotrupoidea mostly key to 40, with large species going to 22, but Diapriidae key to 38 and 48. Almost all Evanioidea key to 26. Most other groups key out at one couplet.

Do not be daunted by the length of the key: the median number of steps to arrive at any group is between 9 and 10. Only three superfamilies have some individuals that need more than 14 steps, and

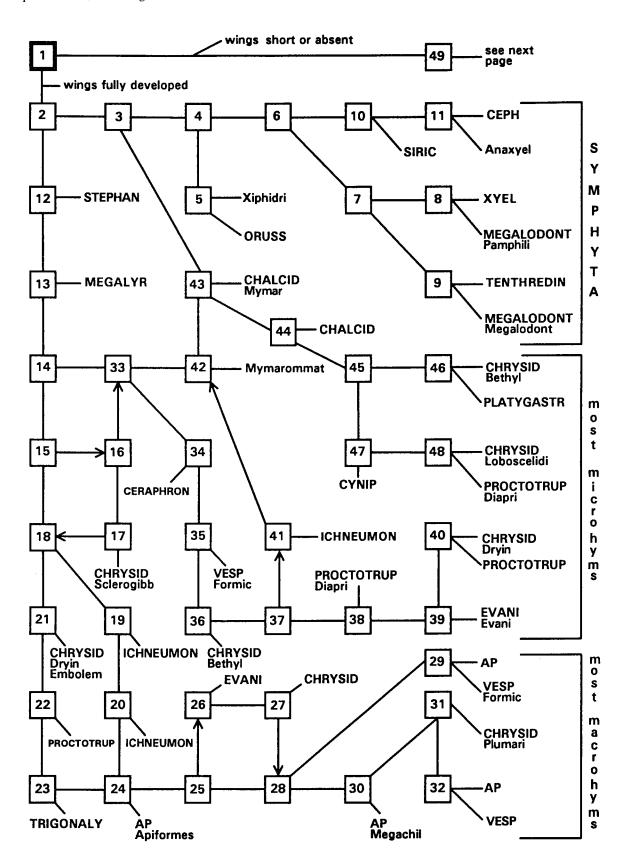
a maximum of 18 steps are needed for a few Vespoidea.

The key has been made as user-friendly as possible by several devices in addition to features outlined in the previous section. First, the confusion caused by conditional clauses (introduced by words such as if, both-and, either-or, and but) has been eliminated as much as possible. This effort usually required extra couplets or extra subheadings, but it avoids misinterpretations and speeds the user's passage though the key. Second, in cases of continuous variation (e.g., presence or absence of a stigma, or length of the shortened fore wing in some Ichneumonidae and Bethylidae) The user's decision has been made noncritical, either by constructing the key to allow specimens in an intermediate range to run correctly on either side of the couplet (e.g., 1, 14, 15, 16, 24) or by using a loop. Third, loops are also used to try to prevent misinterpretation of difficult characters leading the user onto false paths. For instance, most chalcidoids key easily from 33 to 42, but some of the smallest, such as Mymaridae, have the membrane in front of R (submarginal vein) in the fore wing so reduced as to be almost invisible, so that a beginner may easily interpret them as having a vein on the anterior margin. But, nevertheless, they will run through 34, 37, and 41 to 42, where they are reunited with other chalcidoids. The same route may be followed in keying some minute Bethylidae and Platygastroidea.

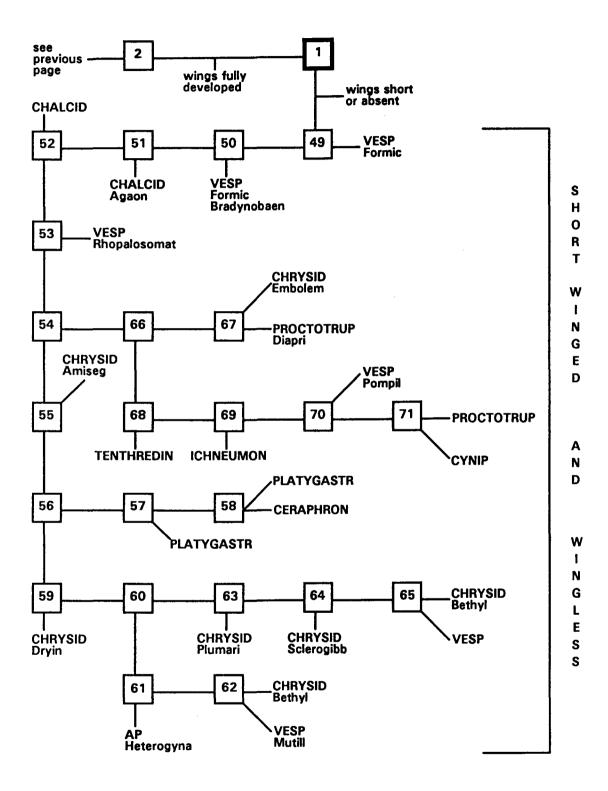
A flowchart (pp. 62 and 63) is added to help serious users understand the location and function of the feedback loops. Loop 3–43 accommodates the rather numerous chalcidoids with broadly attached metasoma; loop 16–33 redirects Diapriidae that have, or may appear to have, three cells in the fore wing, back to the microhymenoptera part of the key (33–48); it also sends a few very large Chalcidoidea and Cynipoidea

## Flowchart for superfamily key

(Direction of flow is always from the lower to the higher number. Names are abbreviated; superfamilies are set in capital letters, to distinguish them from families and subfamilies.)



## Flowchart for superfamily key (concluded)



to the microhymenoptera section if their strong nebulous veins are interpreted as tubular; loop 15–18 returns Aculeata and Braconidae without a stigma to the mainstream of macrohymenoptera (18–32) and renders uncritical the decision on whether a stigma is present or not; loop 20–24 redirects a few Aculeata (Rhopalosomatidae and some small Spheciformes) back to the Aculeata after separating Ichneumonoidea; and loop 25–28 redirects a few male Mutillidae and Spheciformes after separating most Evanioidea and Chrysidoidea.

The traditional separation for winged Vespoidea and Apoidea (separation of tegula from pronotum) is used but couplets 29–32 and 24 have been added to take care of exceptions among Megachilidae, winged Formicidae, and a few small Pemphredonidae. The tegula character is unworkable for Chrysidoidea, and they are keyed elsewhere.

Venational characters are used in this key more precisely than many entomologists are used to. It is important to distinguish between tubular and nebulous veins (see Glossary) when counting closed cells. A cell that reaches the margin of the wing is considered open if no tubular vein occurs along the complete margin of that cell, and a cell that has one or more of its enclosing veins nebulous is also considered open for use of this key. Bullae (see Glossary) are interpreted as not spoiling the closure of a cell.

Some vaguely quantitative terms can be defined to some degree. Rarely means less than 1%, often much less; seldom, up to 10%; occasionally, up to 25%; sometimes, 25-50%; often, 50-75%; frequently, 75-90%; usually, up to 95% or more; and almost always, 99% or more. Parenthetical remarks in key couplets contain information often useful in identification, such as notes on minimum magnification needed, geographical restrictions of some groups, and useful features that may not be

found in all specimens. The reciprocal condition is not necessarily excluded from specimens in the other half of the couplet.

Writers of keys to higher groups are standing, so to speak, on the shoulders of previous generations who discovered the characters we still use to define units. All we can do is define the old characters more accurately, make accommodation for exceptions, and juggle the order in which they are used. Really new characters are scarce. They must be invented when recently discovered groups are added (couplets 61 and 63 for female Plumariidae and Heterogynaidae) or as a practical matter for additions of non-Holarctic groups rarely considered in most keys (couplets 13, 31, 35, 48, 62, and 68). A few characters seem to be newly used as key characters, though several have been mentioned in phylogenetic studies (Gibson 1985, Brothers 1975, Mason 1983, Rasnitsyn 1980). They are found in couplets 4, 12c, 22, 41c, 52b, 56c, 62c, 65a, 65c, 65d, 69a, and 70.

Some colleagues and contributors to this publication offered useful suggestions during the long process of key construction. Our thanks go especially to Lubomir Masner, who gave his time and knowledge generously in suggesting characters and their arrangements, particularly for microhymenoptera. Without his help, the treatment of these minute and little-known parasites would have been much less efficient. Gary Gibson also gave advice, particularly concerning that almost endlessly diverse group, Chalcidoidea: couplets 44, 51, and 52 are largely written by him. Henri Goulet pointed out several characters useful for separating groups of Symphyta. Finally, Denis Brothers provided an extensive critique of the aculeate part of the key and made many improvements. His knowledge of rare Old World tropical species resulted in numerous changes, especially for the flightless forms in couplets 60-65.

## References

Brothers, D.J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. University of Kansas Science Bulletin 50:483–648.

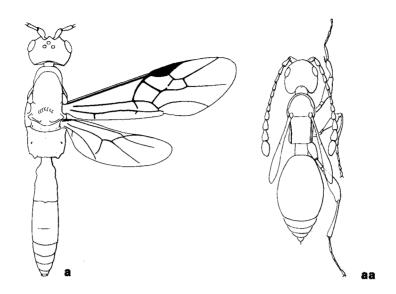
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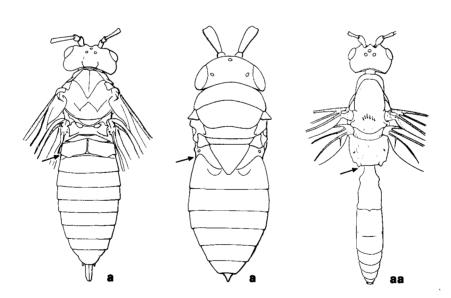
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Rasnitsyn, A.P. 1980. Origin and evolution of hymenopterous insects. Trudy Paleontologicheskogo instituta. Akademiya nauk SSSR 174:1-192. [In Russian.]

## Chapter 5 Key to superfamilies of HYMENOPTERA

William R.M. Mason

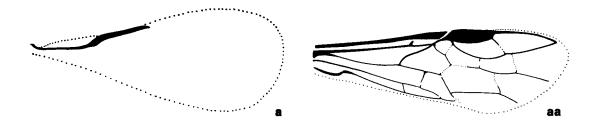


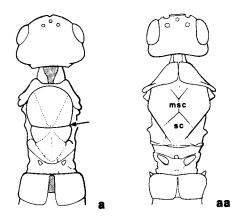


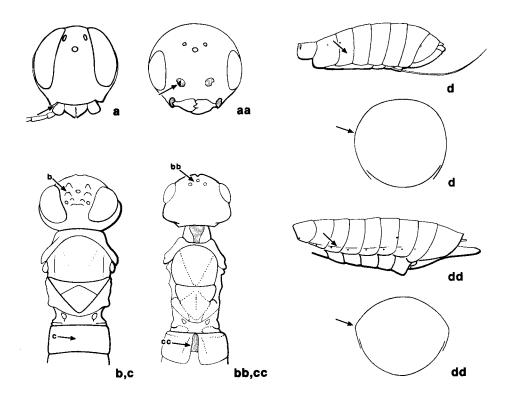
- - aa. Body with strong and usually conspicuous dorsal and lateral constriction between abdominal segments 1 and 2, thus delimiting the mesosoma and metasoma ........................(APOCRITA) 12

All recognized superfamilies and some families of disputed superfamily status.

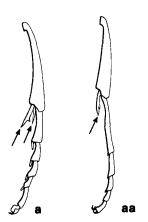
Because a few species are variable, showing every stage of wing reduction, this division is arbitrary: doubtful cases key through either side of the couplet.



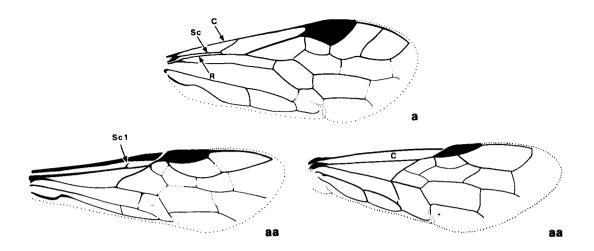




- 5(4) a. Torulus below level of ventral margin of eye.
  - b. Head with crown of backward-pointing teeth around median ocellus.
  - c. Abdominal tergum 1 not divided medially.
  - d. Abdominal terga evenly rounded at sides ...... ORUSSOIDEA (p. 103)
  - aa. Torulus above level of ventral margin of eye.
  - bb. Head without such crown of teeth.
  - cc. Abdominal tergum 1 divided medially.
  - dd. Abdominal terga angular at sides ..... XIPHYDRIIDAE (p. 111)

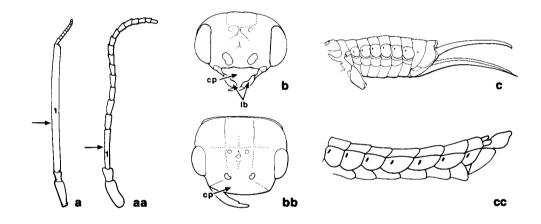


- - aa. Protibia with 1 apical spur (female often with long, thin ovipositor) ...... 10



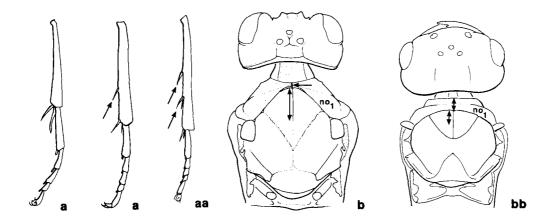
a. Fore wing with longitudinal vein Sc between veins C and R (sometimes veins R and Sc touching)

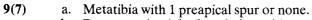
aa. Fore wing without longitudinal vein Sc; at most a short vein (Sc1) dividing costal cell (C)



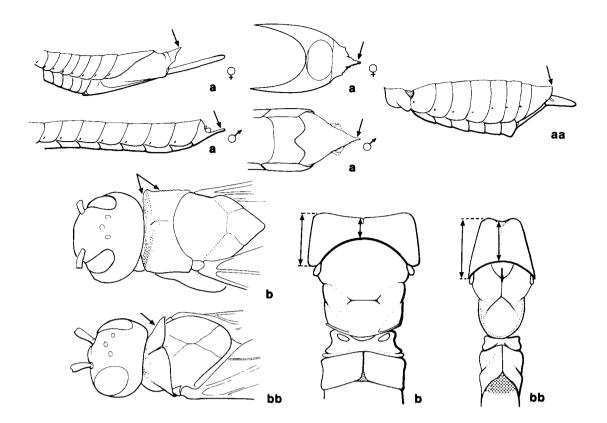
- a. Flagellomere 1 much wider than, and 1-4 times as long as, combined length of following small flagellomeres.
  - b. Clypeus (cp) about two-thirds as wide as face between eyes; labrum (lb) conspicuous below clypeus.

  - aa. Flagellomere 1 about as wide as, and no longer than, combined length of following 3 flagellomeres.
  - bb. Clypeus (cp) about as wide as face between eyes; labrum hidden behind clypeus.
  - cc. Abdomen strongly flattened dorsoventrally, all but last 2 or 3 segments sharply folded at side ...... (PAMPHILIIDAE) MEGALODONTOIDEA (p. 102)

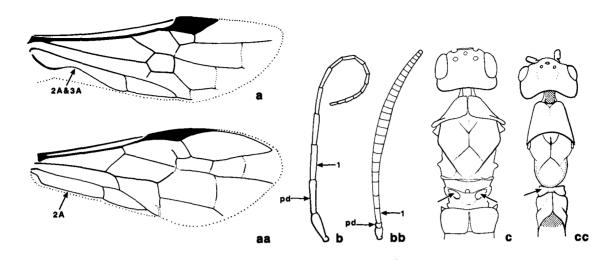




- b. Pronotum (no<sub>1</sub>) in dorsal view with posterior margin strongly concave; excavation (measured medially) much longer than median length of pronotum . . . . . . TENTHREDINOIDEA (p. 105)
- aa. Metatibia with 2 or 3 preapical spurs.

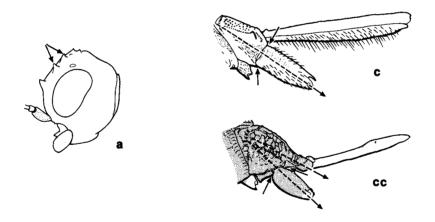


- 10(6) a. Last tergum of female and last sternum of male each with apical, median, cylindrical projection with concave tip.
  - b. Pronotum in lateral view with a horizontal dorsal surface and with a vertical, concave anterior surface; pronotum in dorsal view with posterior margin strongly concave, with medial length about one-third lateral length ............................... (SIRICIDAE) SIRICOIDEA (p. 104)
  - aa. Last tergum and last sternum of both sexes apically thin and without cylindrical projection.



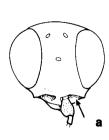
- 11(10) a. Fore wing with posterior-most vein (2A&3A) sinuate and in part far from posterior margin of wing.
  - b. Pedicel (pd) as long as flagellomere 1.

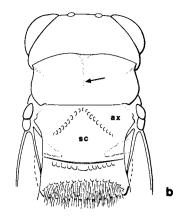
  - aa. Fore wing with posterior-most vein (2A) straight, parallel to, and mostly close to posterior margin of wing.
  - bb. Pedicel (pd) much shorter than flagellomere 1.

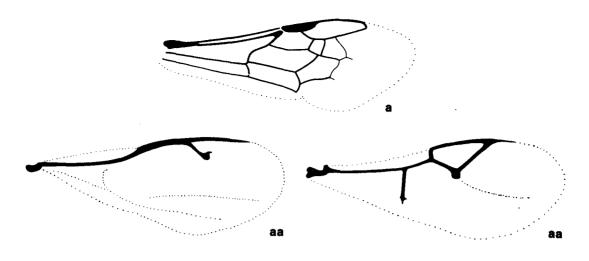


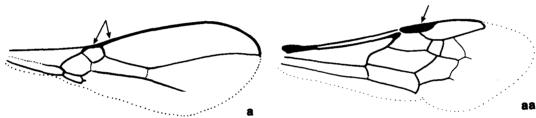
- 12(2) a. Head globular, with crown of teeth around median ocellus.
  - b. Body slender, usually 5-35 mm long; female with ovipositor as long as, or longer than, body (see habitus, Fig. 189).

  - aa. Head usually not globular and rarely with circle of teeth around median ocellus.
  - bb. Body shape and size various, often stout or small; ovipositor often short or concealed.



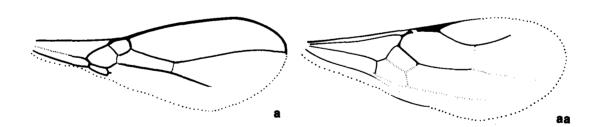






 15(14)
 a. Fore wing without stigma<sup>4</sup>
 16

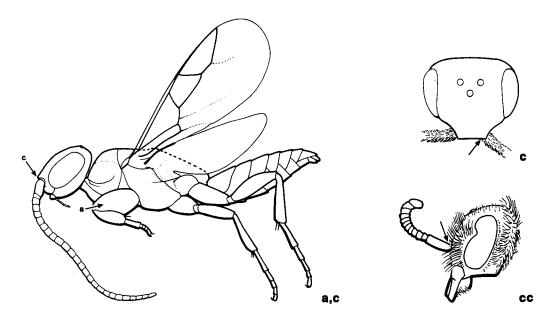
 aa. Fore wing with stigma
 18



<sup>5</sup> See note under couplet 14.

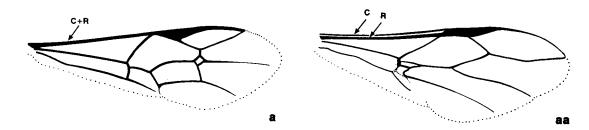
If distinguishing between tubular and nebulous veins is difficult, counting the number of closed cells may be confusing. Some latitude is built into the key to allow difficult specimens to key through either side of this couplet.

<sup>&</sup>lt;sup>4</sup> The presence of a stigma may be difficult to determine; species transitional for this character should key correctly on either side of this couplet.

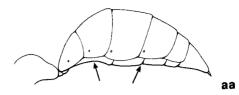


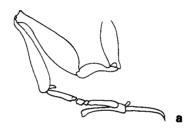
- 17(16) a. Profemur strongly widened, wider than or as wide as metafemur.
  - b. Antenna with 18 or more flagellomeres.

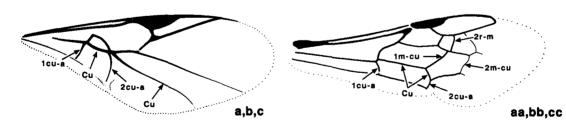
    - aa. Profemur smaller than metafemur.
    - bb. Antenna with 10 or more flagellomeres (usually 10-11 flagellomeres but many more in a few Ichneumonoidea).





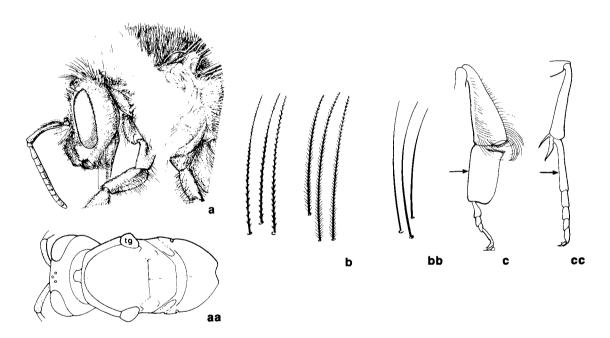






- a. Fore wing with vein Cu continuing nearly straight to wing margin (venation conspicuous in all species keying here).
  - b. Fore wing with vein 2cu-a as long as, or longer than, vein 1cu-a.
  - c. Fore wing without veins 2r-m and 2m-cu ...... some PROCTOTRUPOIDEA (p. 538)
  - aa. Fore wing with vein Cu deflected abruptly (angle of 30-90° or more) posteriorly, in step-like manner, at the base of 1m-cu.
  - bb. Fore wing with vein 2cu-a usually less than half as long as vein 1cu-a.

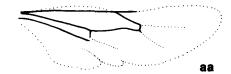


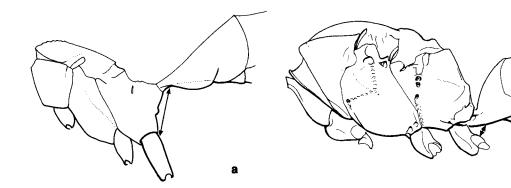


- 24(20, 23) a. Thoracic sutures around tegula so obscured by long dense hair that nearby sutures cannot be seen.
  - b. Body hairs,  $^6$  especially on propodeum, not smooth, but with short to long lateral branches (under magnification of  $40 \times \text{or more}$ ).
  - c. Hind leg with tarsomere 1 flattened from side to side, about four times as long as tarsomere 2 and twice as wide (metasomal tergum 2 without felt line) ..... (some Apiformes) APOIDEA (p. 308)
  - aa. Thoracic sutures visible around tegula (tg).
  - bb. Body hairs<sup>6</sup> variable in density and structure, usually sparse or short.

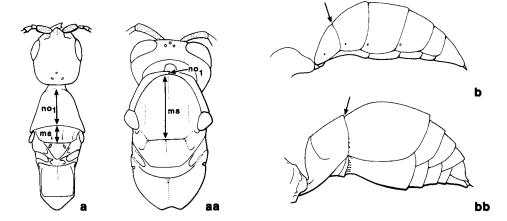
All bees (Apiformes) have at least a few hairs with short to long (plumose) branches, but they are often difficult to find on species with short or sparse hairs. Bees with sparse hair, or specimens in which the branched hairs cannot be seen, will key correctly below (couplets 29 and 30). Occasional male Mutillidae (Vespoidea) have some branched hairs, but the general body hair of these species does not obscure the view of the tegula and adjacent sutures; these individuals key to couplet 25.







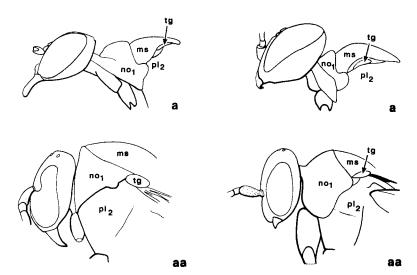
- a. Metasoma arising high on propodeum; distance between propodeal foramen and metacoxal cavity greater than width of either opening (ovipositor often conspicuous and long) . . . . . . . . . most EVANIOIDEA (p. 510)

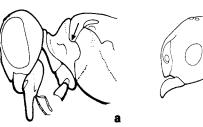


- 27(26) a. Pronotum (no<sub>1</sub>) (measured medially) more than half as long as mesoscutum (ms).

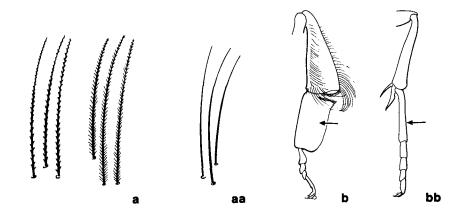
  - aa. Pronotum (no<sub>1</sub>) (measured medially) less than half as long as mesoscutum (ms).

aa



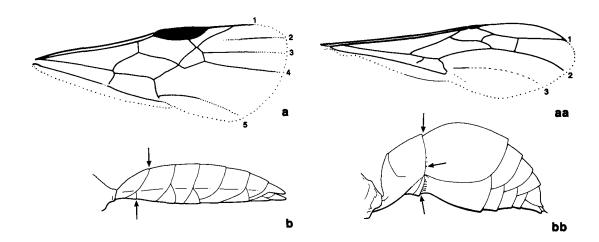


- aa
- - aa. Pronotum in lateral view with dorsal and posterior margins meeting in a rounded angle but without a conspicuous protruding rounded lobe on posterior margin; dorsal margin of pronotum forming a weakly concave to weakly convex curve  $(0-20^\circ)$  above posterior angle of pronotum ...... (some **FORMICIDAE**) VESPOIDEA (p. 217)



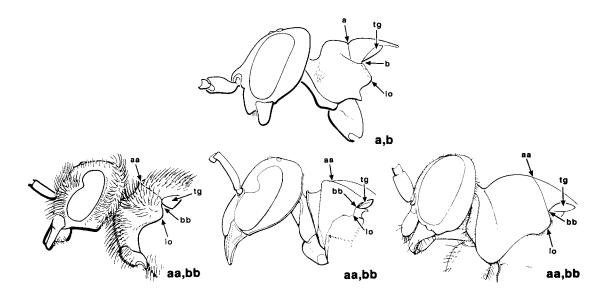
- a. Body hairs with short to long branches, especially on propodeum, near bases of wings, around coxae, or on margins of terga (use at least 40° magnification).
   b. Hind leg with tarsomere 1 flattened from side to side, about four times as long as tarsomere 2 and

  - aa. Body hairs thin and smooth, very rarely with short or long branches.

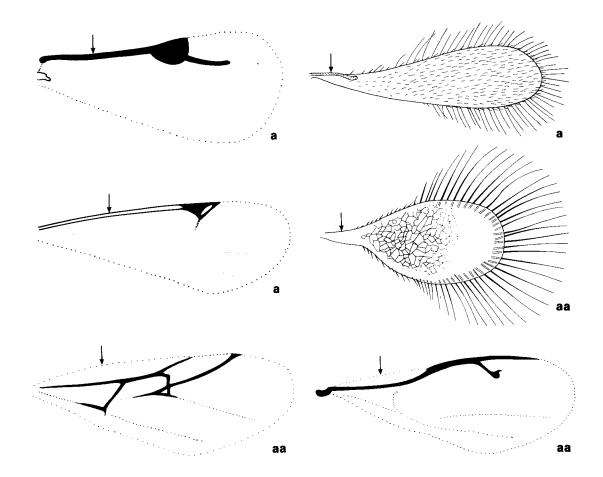


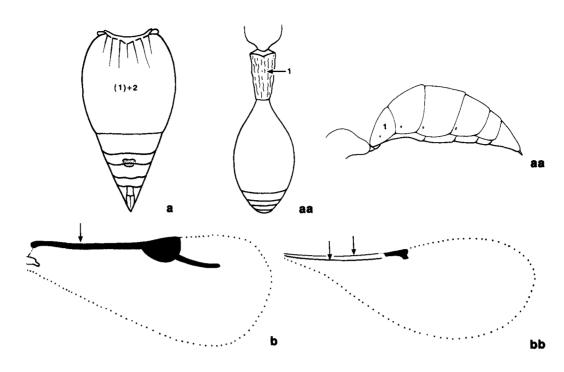
- 31(30) a. Fore wing with 4-5 veins approaching or touching apical margin beyond stigma.

  - aa. Fore wing with 3 (very rarely 4) veins approaching or touching apical margin beyond stigma (rarely, most venation crowded toward base of wing, but up to 3 transparent, convex, spectral veins can be seen stretching toward wing apex).

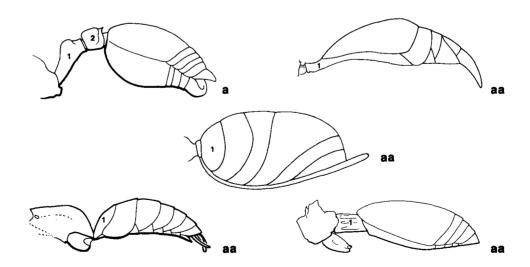


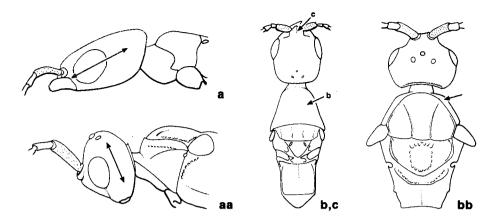
- a. Pronotum in lateral view with transverse median part meeting mesoscutum at a sharp angle or in a deep groove; posteromedial part of pronotal margin in dorsal view rather straight and meeting upper margin of posterior lobe in a sharp, approximately right-angled curve.
  - b. Tegula (tg) touching protruding lobe (lo) on posterior margin of pronotum . . . . . . . . . . . . . . a few APOIDEA (p. 279)
  - aa. Pronotum in lateral view with transverse median part blending smoothly to level of mesonotum, not elevated in a transverse roll-like lobe; posterior margin of pronotum often without lobe, the lobe defined by concave angles above and below; protruding lobe sometimes present but occurring completely below tegula; posterior margin of pronotum in dorsal view forming a comparatively uniform curve that continues back to the tegula or to a pointed lobe *above* it.
  - bb. Tegula (tg) touching pronotal margin, but point of contact above any protruding lobe (lo) that may be present on the posterior margin ....................... most VESPOIDEA (p. 162)

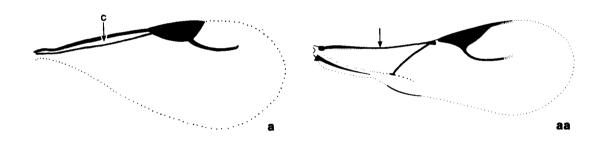


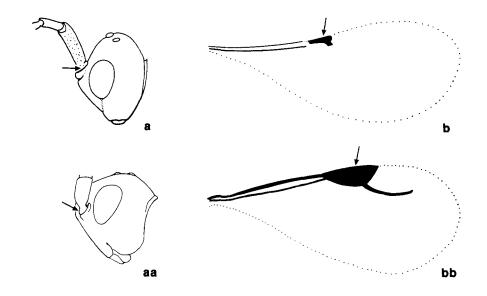


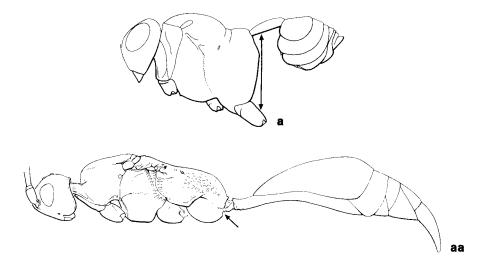
- a. Metasoma with apparent tergum 1 very large (true tergum 1 very small and invisibly fused into anterior of tergum 2), at least as wide as and as long as, or longer than, following terga combined.
  - b. Fore wing with only 1 vein on anterior margin ...... CERAPHRONOIDEA (p. 566)
  - aa. Metasoma with tergum 1 about the same length as, or shorter than, other metasomal terga, or much narrower than rest of metasoma.

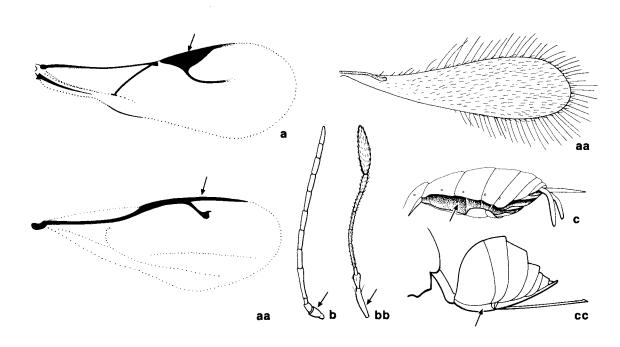






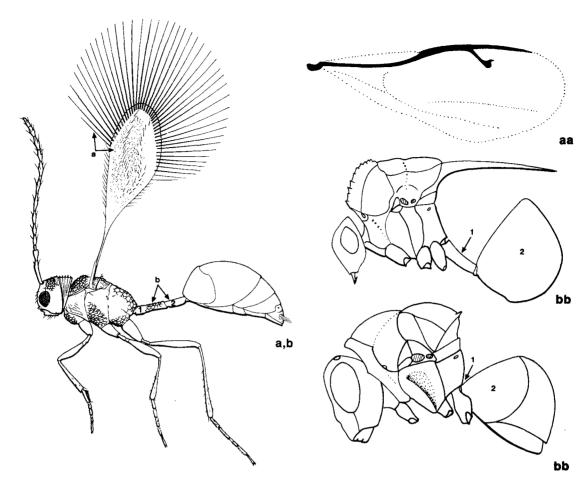






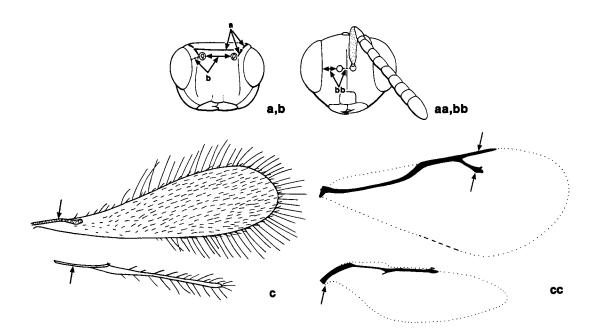
- 41(37) a. Fore wing with stigma.
  - b. Scape not more than twice as long as wide.

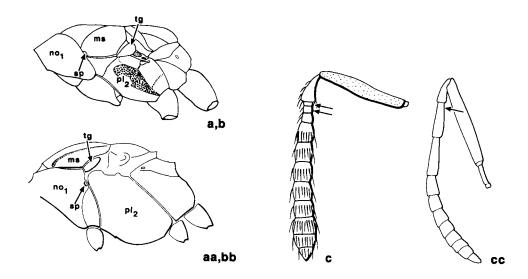
  - aa. Fore wing without stigma.
  - bb. Scape usually over three times as long as wide.



- 42(33, 41) a. Fore wing spoon-shaped, with long marginal hairs and reticulate membrane; hind wing minute and forked apically, without membrane ( $60 \times \text{magnification required}$ ).

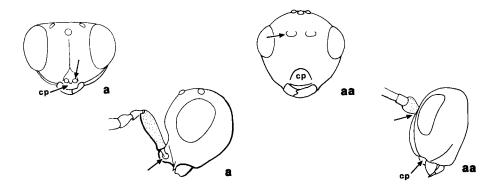
  - aa. Fore wing usually differently shaped, with or without long marginal hairs, but **if** with long marginal hairs **then** wing membrane not reticulate; hind wing longer and not forked apically, almost always with membrane.



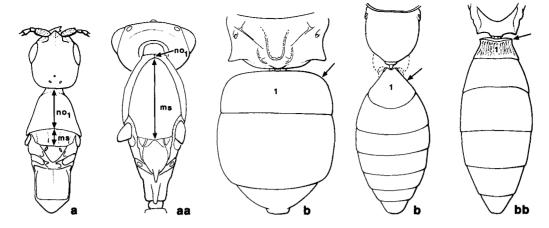


- 44(43) a. Pronotum (no<sub>1</sub>) in lateral view usually separated from tegula (tg).
  - b. Mesothoracic spiracle (sp) (not always visible) located between pronotum and lateral margin of mesoscutum (ms), far from anterior margin of mesopleuron (pl<sub>2</sub>).

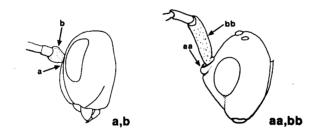
  - aa. Pronotum (no<sub>1</sub>) in lateral view usually extending posteriorly to tegula (tg).
  - bb. Mesothoracic spiracle (sp) located between pronotum and anterior margin of mesopleuron (pl<sub>2</sub>), separated from lateral margin of mesoscutum (ms) (or on pronotum in similar location).



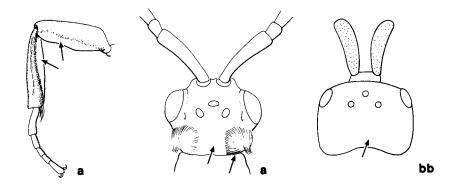
- - aa. Torulus separated by more than its own diameter from dorsal margin of clypeus (cp) . . . . . 47



- 46(45)
- a. Pronotum (no<sub>1</sub>) in dorsal view shaped like truncated pyramid; pronotal length measured along midline, as long as or longer than mesoscutum (ms).
- b. Metasomal segment 1 in dorsal view without angular anterolateral corners and with conical or bell-shaped outline . . . . . . . (some **BETHYLIDAE** and **CHRYSIDIDAE**) CHRYSIDOIDEA (p. 538)
- aa. Pronotum (no<sub>1</sub>) in dorsal view U-shaped, medially much shorter than mesoscutum (ms).
- bb. Metasomal segment 1 in dorsal view with distinct, angular anterolateral corners, subrectangular in outline ...... most PLATYGASTROIDEA (p. 558)

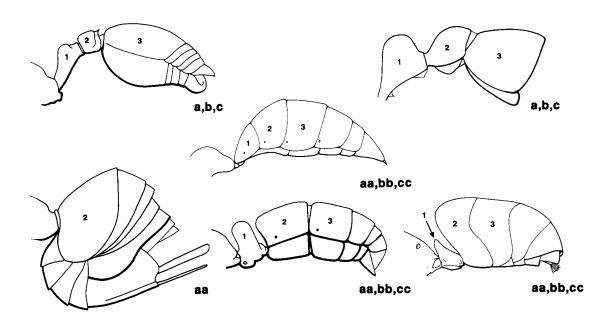


- 47(45)
- a. Head in lateral view with torulus facing forward at about middle of more or less flat face.
- b. Scape a little shorter than, to a little longer than, pedicel ..... most CYNIPOIDEA (p. 522)
- aa. Head in lateral view with torulus facing mostly upward on protruding shelf-like central part of face.



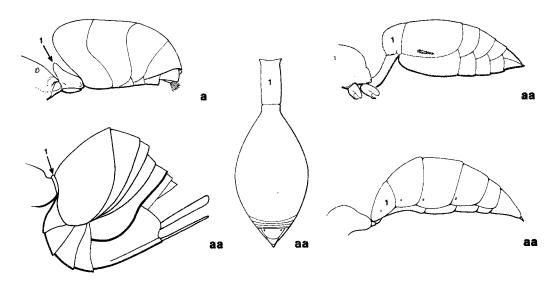
- **48(47)** a. Femora and tibiae frequently with leaf-like ventral lamina.
  - b. Head in dorsal view with large rectangular projection (narrower than width of head and bearing pallisade of fused hairs) extending from behind ocelli to pronotum.

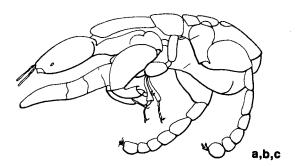
    (Indo-Australian region; rarely collected) . . . . (Loboscelidinae) CHRYSIDOIDEA (p. 138)
  - aa. Femora and tibiae more or less cylindrical and without ventral lamina.

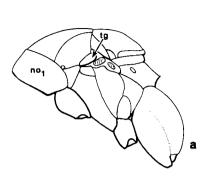


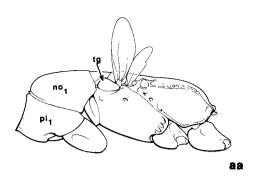
- 49(1) a. Metasomal segment 2 node-like (anterior and posterior diameters about the same, and central diameter greatest).
  - b. Metasomal segment 2 not longer than 1, usually distinctly shorter.

  - aa. Metasomal segment 2 usually tapered with anterior diameter less than posterior diameter and central diameter intermediate, or with posterior diameter about as large as maximum diameter of metasoma
  - bb. Metasomal segment 2 about as long as 1 or longer; segment 2 occasionally shorter than 1, but only if 1 is long, tapered and not node-like.



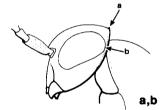


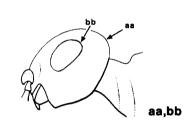




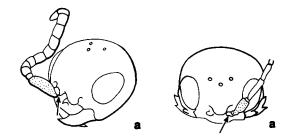
- 52(51) a. Pronotum  $(no_1)$  in lateral view not extending to tegula (tg).

  - aa. Pronotum (no<sub>1</sub>) in lateral view extending to tegula (tg) (propleuron (pl<sub>1</sub>) sometimes large and exposed, not to be confused with the pronotum), or thorax greatly modified and tegula absent.
  - bb. Integument thicker; body rarely collapsed in air-dried specimens (except for the ventral side of metasoma of Ichneumonoidea, which have a short scape and usually over 13 flagellomeres)

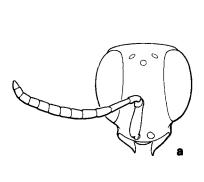


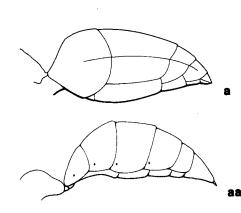


- 53(52) a. Vertex separated from occiput by acute and carinate angle.
  - b. Eye large, nearly touching posterior carinate angle of head.
  - c. Fore wing extending to base of metasoma; tegula present.
  - d. Body over 3 mm long; profemur extremely large; antenna with 10 or 11 flagellomeres . . . . . . . . . (one genus of **RHOPALOSOMATIDAE**) VESPOIDEA (p. 205)
  - aa. Vertex and occiput rounded at their junction and usually without carina.
  - bb. Eye various, usually small and far from posterior curvature of head.
  - cc. Wing remnants and tegula usually absent.

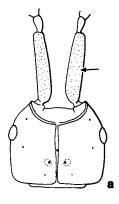


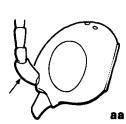






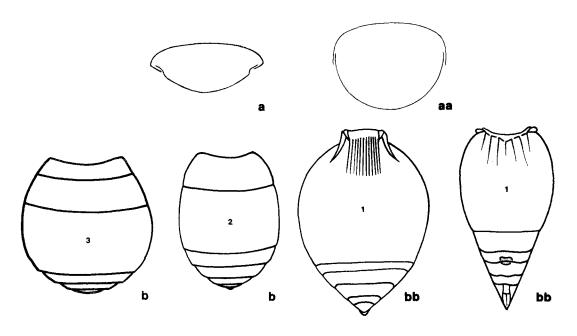
- a. Metasoma with 4-5 visible terga (body stout; head usually elongate below eye and with shallow depression above torulus) ..... (some CHRYSIDIDAE) CHRYSIDOIDEA (p. 135)
  - aa. Metasoma with 6-8 visible terga (head without depression above torulus) ...... 56



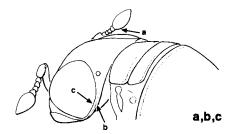


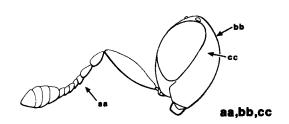


- 56(55) a. Scape at least five times as long as maximum width, more or less straight, and with radicle more or less parallel to long axis of scape.
  - b. Body under 3 mm long.
  - c. Metasoma without visible spiracles ...... 57
  - aa. Scape usually less than three times as long as maximum width, but if longer, then sinuate with radicle extending at right angles to long axis of scape.
  - bb. Body 2-30 mm long.



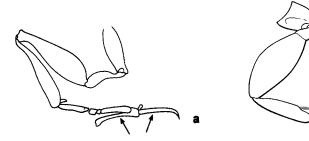
- a. Metasoma usually lens-shaped in cross section, wider than high, with sides usually sharply angulate.
  - b. Metasomal tergum 2 or 3 largest ...... some PLATYGASTROIDEA (p. 559)
  - aa. Metasoma not lens-shaped in cross section, about as wide as high, with sides rounded.



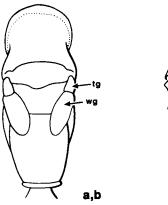


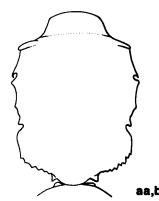
- **58(57)** a. Antenna with 5 flagellomeres.
  - b. Vertex separated from occiput by acute and carinate angle.

  - aa. Antenna with more than 5 flagellomeres.
  - bb. Vertex and occiput rounded at their junction or, at most, vertex subacute posteriorly.

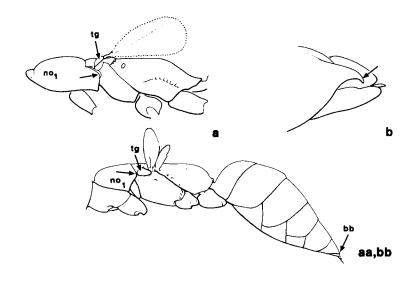


- 59(56)
  a. Fore leg of female with pincer formed by apical tarsomere and 1 very large tarsal claw (fore leg of male normal).
  b. Antenna with 8 flagellomeres . . . . . . . . . (some DRYINIDAE) CHRYSIDOIDEA (p. 139)
  - aa. Fore leg in either sex without pincer; apical tarsomere similar to others and both tarsal claws about same size.



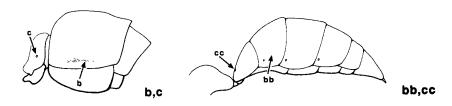


- - aa. Mesosoma without tegula and wing remnants.

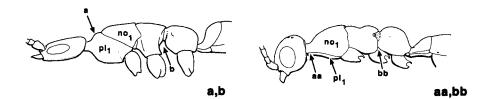


- a. Pronotum (no<sub>1</sub>) with widely angulate lateral lobe extending posterior to entire tegula (tg).

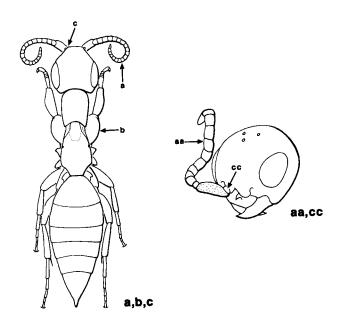
  - aa. Pronotum (no<sub>1</sub>) touching tegula (tg) but not extending posterior to it.



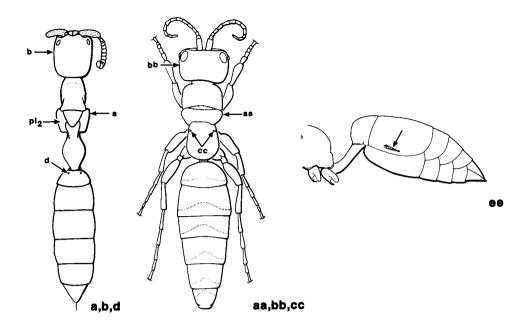
- a. Body sometimes coarsely punctate and with abundant long hair; body sometimes coriaceous (leather-like).
  - b. Metasomal tergum 2 often with lateral felt line.
  - aa. Body mostly coriaceous and comparatively smooth; with only sparse hair.
  - bb. Metasomal tergum 2 without felt line.



- 63(60) a. Propleura (pl<sub>1</sub>) fused dorsally and ventrally into a tubular neck protruding in front of pronotum
  - b. Junction between mesothorax and fused metathorax + propodeum very deeply constricted ventrally and laterally.
     (South American and southern African deserts; extremely rarely collected) . . . . . . . . . . . . . . . . . (female PLUMARIIDAE) (CHRYSIDOIDEA) (p. 133)
  - aa. Propleura (pl<sub>1</sub>) not fused to each other, not protruding in front of pronotum (no<sub>1</sub>).

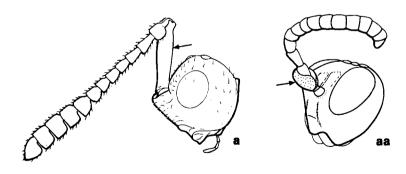


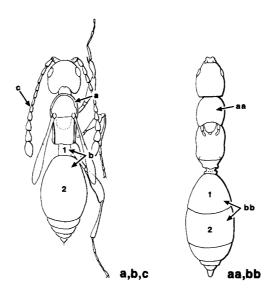
- **64(63)** a. Antenna with 15 or more flagellomeres.
  - b. Profemur strongly swollen, at least twice as wide as metafemur.
  - c. Toruli concealed in dorsal view under a transverse ledge that forms the anterior end of a prognathous head ............... (female SCLEROGIBBIDAE) CHRYSIDOIDEA (p. 139)
  - aa. Antenna with 10 or 11 flagellomeres (pedicel rarely hidden within scape).
  - bb. Profemur usually not wider than metafemur (rarely strongly swollen).



- a. Mesopleuron separated from mesonotum by a deep groove easily seen in dorsal view; mesosoma widest at mesopleura (pl<sub>2</sub>).
  - b. Head longer than wide and strongly prognathous; clypeus with median longitudinal carina.
  - c. Propodeal spiracles round or oval and closer to one another than to apex of propodeum.
  - d. Metasomal tergum 1 with spiracle dorsal.

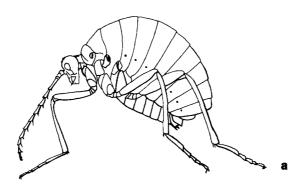
  - aa. Mesopleuron not separated from mesonotum or only weakly separated; mesosoma behind pronotum with sclerites usually fused into box-like structure (including propodeum) that may be widest at middle.
  - bb. Head usually as wide as long and rarely prognathous; clypeus sometimes with median carina.
  - cc. Propodeal spiracles usually slit-like and further from one another than from apex of propodeum.
  - dd. Metasomal tergum 1 with spiracle lateral.



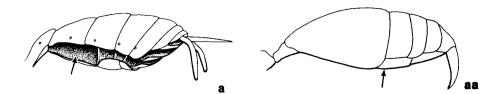


- a. Pronotum more or less U-shaped in dorsal view; medial length usually less than one-quarter as long as mesoscutum.
  - b. Metasomal tergum 2 several times as long as any other tergum and much wider than cylindrical segment 1.

  - aa. Pronotum more or less rectangular; medial length about as long as mesoscutum.
  - bb. Metasomal terga 1 and 2 about equally long and wide; metasomal segment 1 conical.
  - cc. Antenna with 8 flagellomeres ...... (EMBOLEMIDAE) CHRYSIDOIDEA (p. 146)

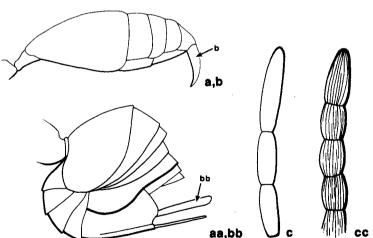


- **68(66)** a. Body without constriction between thorax and abdomen ..... TENTHREDINOIDEA (p. 105)



<b>69(68)</b>	a.	Metasoma with most sterna composed of several sclerites and much more weakly sclerotized		
	b.	than tergites; sterna folded and collapsed in air-dried specimens.  Antenna usually with more than 13 flagellomeres (sometimes as few as 9)		
	aa.			
	bb.	Antenna with 10–13 flagellomeres		
		8		
70(69)	a.	Metasomal segment 1 long conical, and with spiracle		

aa. Metasomal segment 1 short, cylindrical, and without spiracle.



b. Antenna with 10 flagellomeres ............... (a few **POMPILIDAE**) VESPOIDEA (p. 202)

# Chapter 6 Superfamilies Cephoidea, Megalodontoidea, Orussoidea, Siricoidea, Tenthredinoidea, and Xyeloidea

(Figs. 21-34)

Henri Goulet

## Superfamily CEPHOIDEA

(Fig. 21)

Included family (1): Cephidae.

Members of this family are easily keyed out, but to the untrained eye adults are very much like those of Ichneumonidae. However, they differ from Ichneumonidae by abdominal segment 1, which is clearly part of the abdomen rather than the thorax.

## **Family CEPHIDAE**

(Fig. 21)

**Diagnosis** Cenchri absent; slight dorsoventral constriction between abdominal segments 1 and 2.

Comments Members of Cephidae are sometimes called stem sawflies, because their larvae feed inside grass stems or twigs of woody plants. Those that bore within stems of cultivated cereals are major pests, e.g., *Cephus cinctus* Norton in wheat. They are unusually slender for sawflies, at first glance resembling ichneumonid wasps. The family contains about 100 species, mostly from Eurasia. One species is known from Madagascar. About 13

species occur in North America, including 10 in Canada.

References Benson (1946a) characterized the world genera, Muche (1981) keyed the world species, and Middlekauff (1969) the North American genera. Gussakovskij (1935) reviewed the Palaearctic species, Zhelokhovtsev (1988) reviewed the species of European USSR, Takeuchi (1938) the Japanese species, Benson (1951) the British species, Ries (1937) the North American species, and Smith (1988) the Neotropical species.

# Superfamily MEGALODONTOIDEA

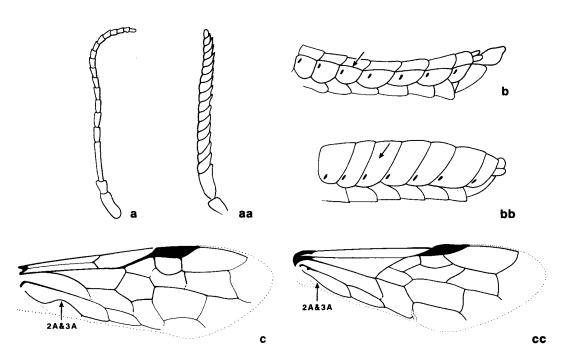
(Figs. 22, 23)

Included families (2): Megalodontidae, Pamphiliidae.

The very large, almost prognathous head, widest near the clypeus, is distinctive (see habitus

Fig. 22). The species are restricted to temperate regions of Eurasia and North America.

# Key to families of MEGALODONTOIDEA



- 1 a. Antenna thread-like.
  - b. Abdominal terga 2-8 sharply folded above spiracle.

  - aa. Antenna saw-like or comb-like.
  - bb. Abdominal terga 2–8 rounded above spiracle.

# Family MEGALODONTIDAE

(Fig. 22)

**Diagnosis** Distinguished from Pamphiliidae by antenna saw-like or comb-like and terga 2-5 not folded above spiracles.

**Comments** Larvae feed on herbaceous plants. Megalodontidae contains about 40 species and is restricted to temperate regions of Eurasia.

References Gussakovskij (1935) characterized the genera. Zhelokhovtsev (1988) reviewed the species of European USSR, and Takeuchi (1938) reviewed the Japanese species.

# Family PAMPHILIIDAE

(Fig. 23)

**Diagnosis** Distinguished from Megalodontidae by filiform or thread-like antennae and a longitudinal fold on abdominal terga 2-5 above spiracles.

**Comments** Larvae of these sawflies have the unusual habit of rolling leaves or spinning silk to form webs in which they feed. Some species are gregarious and live in large webs as do tent

caterpillars. A few species attack fruit trees and conifers and are sometimes pests. The family is an ancient one: fossils belonging to it have been found in rocks of Jurassic age, about 150 million years old. The family contains about 200 species in the temperate and boreal regions of Eurasia and North America. About 75 species occur in North America, including 55 in Canada.

References Benson (1945a) and Achterberg and Aartsen (1986) characterized the genera. Gussakovskij (1935) reviewed the Palaearctic species; Viitasaari (1982b) the Finnish species; Benson (1951) the British species; Zhelokhovtsev (1988) the species of European USSR; Achterberg and Aartsen (1986) the European species; Takeuchi

(1938) the Japanese species; Shinohara (1985a, 1985b, 1986a, 1986b, 1987) the Japanese and East Asian species of *Onycholyda*; and Middlekauff (1958, 1964) the North American genera and species. Smith (1988) revised the Neotropical species.

## Superfamily ORUSSOIDEA

(Fig. 24)

Included family (1): Orussidae.

Though rarely seen, members of Orussoidea play a pivotal role in deciphering major lineages of Hymenoptera, as discovered in the study of their unusual structures (Rasnitsyn 1988). Adults are cylindrical in cross section and have several spines around the median ocellus.

#### Family ORUSSIDAE

(Fig. 24)

**Diagnosis** Antenna inserted below the ventral margin of eye, generally under a distinct transverse ridge.

Comments Members of Orussidae are rare and morphologically unique. Although true sawflies. they have a very long thin ovipositor, as do some of the large ichneumonid wasps, and are parasitoids of wood-boring Coleoptera and Hymenoptera larvae. The long ovipositor is seen only when the female is actually ovipositing: at other times it is kept doubled up inside the body. Internally, it extends forward through the middle of the body, lying between the flight muscles in the centre of the thorax. Here it makes a loop up over the gut and returns again to the tip of the abdomen. Throughout it is enclosed in a pocket of tissue apparently derived from abdominal sterna 8 and 9. How the female unfolds and extrudes its ovipositor (which is at least twice as long as the insect) and gets it all back into the body and folded around the gut inside the thorax is unknown. Another unusual feature is the extremely long and slender eggs. They are longer than the body itself but are folded up

inside the ovarioles and only reach full length when passing down the ovipositor. A third unusual feature is the sawfly's ability to jump. The tergotrochanteral muscle is massive and replaces the dorsoventral flight muscle. Absence of the latter is unique within Hymenoptera. The family is ancient and is well represented as fossils. It contains about 70 usually rare species in all tropical and temperate regions, with the greatest diversity in Africa. Nine species occur in North America, including four in Canada.

References Benson (1955) characterized the world genera. Zhelokhovtsev (1988) reviewed the species of European USSR; Takeuchi (1938) the Japanese species; Benson (1951) the British species; Middlekauff (1983) the North and Central American species; Smith (1988) the Neotropical species; and Benson (1935, 1938b) the African and Australian species. Cooper (1953) described oviposition and genital anatomy of *Orussus*. Burke (1917) and Rawlings (1957) recorded hosts. Guiglia (1965) cataloged the world species.

# Superfamily SIRICOIDEA

(Fig. 25)

Included family (1): Siricidae.

These very characteristic and large wood-boring Hymenoptera are restricted to the northern

hemisphere, except for an accidentally introduced pest species in Australia and New Zealand.

## Family SIRICIDAE

(Fig. 25)

**Diagnosis** Last tergum in female or last sternum in male with a horn-like projection; pronotum transversely folded, collar-shaped.

Comments Members of Siricidae are brightly colored insects commonly called wood wasps or horntails. Adults are among the largest Hymenoptera, measuring up to 50 mm long. They use their drill-like ovipositor to insert their eggs and spores of a symbiotic fungus into dead or dying trees. The fungal spores are stored in special organs on the larvae and adult females. All larvae are wood borers, either in conifers or hardwood trees. They pupate in the bark just below the outer surface. Siricidae and related, now extinct, families were well represented in early Tertiary and

Mesozoic times. The family contains 93 species. Nineteen species occur in North America, including 14 in Canada.

References Benson (1943) reviewed the world fauna with keys to genera and to species of some genera. Ross (1937) and Smith (1975) characterized the North American genera and Benson (1951) the European genera. Gussakovskij (1935) reviewed the Palaearctic species, Zhelokhovtsev (1988) the species of European USSR, Viitasaari (1984) the Finnish species, Middlekauff (1960) the western North American species, and Smith (1988) the Neotropical species. Smith (1978) cataloged the world species. Stillwell (1965, 1966) described the symbiotic association between Siricidae and Fungi.

# **Superfamily TENTHREDINOIDEA**

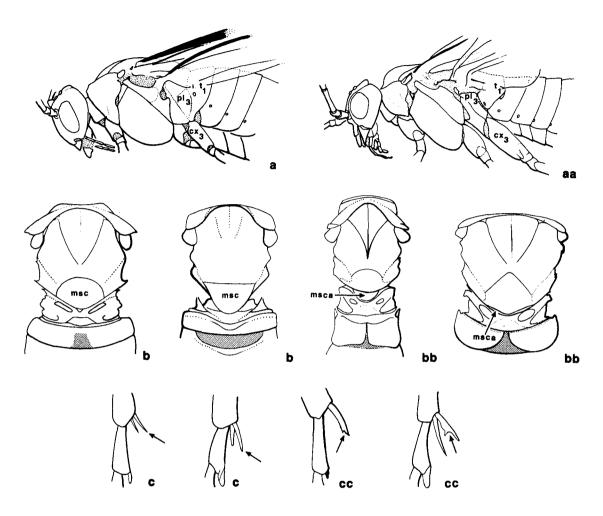
(Figs. 26-31)

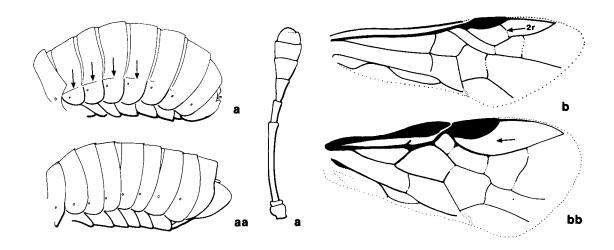
Included families (6): Argidae, Blasticotomidae, Cimbicidae, Diprionidae, Pergidae, Tenthredinidae.

Members of Tenthredinoidea are distinguished from other superfamilies and families of Symphyta by the markedly narrow pronotum medially, by the presence of two spurs at the apex of the protibia, and by the lack of a transscutal groove on the mesonotum. Larvae are all phytophagous and feed mainly on leaf tissue of ferns, horsetails, gymnosperms and angiosperms, and rarely in the pith of twigs or on catkins.

Most species of Symphyta belong to this superfamily. Over 7000 species occur around the world except for most oceanic islands. Tenthredinidae is the largest family.

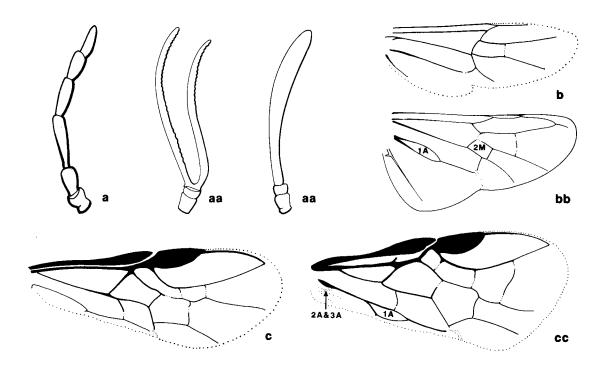
# **Key to families of TENTHREDINOIDEA**





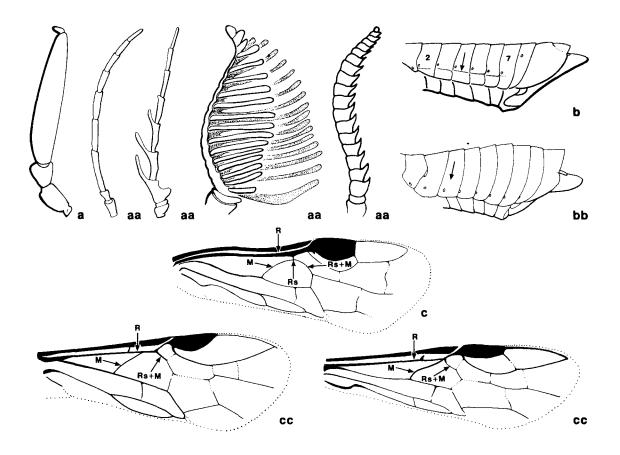
- 2(1) a. Abdominal terga 2-5 each usually folded above spiracle; flagellum club-like.
  - b. Fore wing with vein 2r.

  - aa. Abdominal terga 2-5 each rounded above spiracle; flagellum various but usually not club-like (only in some South American and Australian genera).
  - bb. Fore wing without vein 2r.

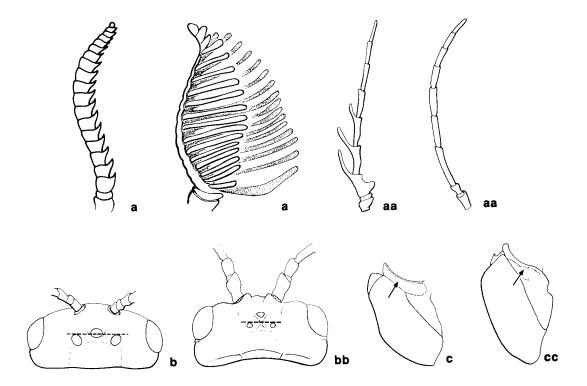


- 3(2) a. Antenna with 4-23 flagellomeres.
  - b. Hind wing without closed anal and medial cells.

- aa. Antenna with 1 flagellomere.
- bb. Hind wing usually with closed anal (1A) and medial (2M) cells.



- **4(1)** a. Antenna with 1 or 2 flagellomeres.
  - b. Abdominal terga 2–7 each clearly folded below spiracle.
  - c. Fore wing with vein M clearly joining Rs **not** R; veins M and Rs+M forming an evenly curved line ..... **BLASTICOTOMIDAE** (p. 108)
  - aa. Antenna with 5 or more flagellomeres (in a few species, apical flagellomeres counted even if fused, as long as delineated by a line).
  - bb. Abdominal terga each rounded below spiracle.



- **5(4)** a. Antenna with 15 or more flagellomeres.
  - b. Anterior margin of lateral ocellus level with middle of median ocellus.
  - c. Mesepimeron with upper portion not excavated along centre ...... **DIPRIONIDAE** (p. 109)
  - aa. Antenna with 5-10 flagellomeres.
  - bb. Anterior margin of lateral ocellus level with posterior margin of median ocellus or posterior to it.
  - cc. Mesepimeron with upper portion excavated along centre ..... **TENTHREDINIDAE** (p. 110)

#### **Family ARGIDAE**

(Fig. 26)

**Diagnosis** Antenna with 1 flagellomere; metapleuron fused with tergum 1.

Comments Many tropical species are brightly colored and may have striped or pictured wings. The larvae feed like caterpillars on foliage of many plants but seldom become abundant enough to cause much damage. The family is most diverse in tropical regions where about 800 species are found. About 70 species occur in North America, including about 15 in Canada.

References Benson (1938a) and Malaise (1941) characterized the genera. Gussakovskij (1935) reviewed the Palaearctic species; Zhelokhovtsev (1988) the species of European USSR; Benson (1951) the British species; Takeuchi (1939) the Japanese species; Smith (1969d, 1970, 1971b) the North American species (except *Arge*); Pasteels (1953) the African species; and Smith (1989, 1992) the New World species of *Arge* and the Neotropical Argidae.

# Family BLASTICOTOMIDAE

(Fig. 27)

**Diagnosis** Antenna with 1 or 2 flagellomeres; mesoscutellar appendage narrow; terga 2–5 sharply folded ventral to spiracles.

**Comments** Larvae are stem borers of ferns. The family contains three genera and nine species restricted to temperate regions of Eurasia.

**References** Gussakovskij (1935) characterized the genera and species. Zhelokhovtsev (1988) reviewed the species of European USSR, Togashi (1989) the

Japanese species, and Shinohara (1983) the Taiwanese species. Smith (1978) cataloged the world species.

#### Family CIMBICIDAE

(Fig. 28)

**Diagnosis** Antenna club-like; mesoscutellar appendage absent; terga usually folded dorsal to spiracles.

Comments Some members of Cimbicidae are among the largest Hymenoptera. One of them, Cimbex americana Leach, is a spectacular insect (adult about 3 cm long, larva 5 cm long) that attracts attention when found. The adult buzzes when picked up; when touched, the spines on its powerful legs generally cause pain that is intense enough to cause it to be dropped. The larva is the size of the little finger; it coils itself into a tight

spiral and drops when alarmed. Larvae are solitary and eat leaves of honeysuckle (*Lonicera*), willow (*Salix*), elm (*Ulmus*), snowberry (*Symphoricarpus*), and sometimes other plants. The family contains 130 species around the world. About 12 species occur in North America, including eight in Canada.

References Benson (1938a) characterized most genera and Ross (1937) those of North America. Gussakovskij (1947) reviewed the Palaearctic species, Zhelokhovtsev (1988) the species of European USSR, Takeuchi (1939) the Japanese species, and Smith (1988) the Neotropical species.

# **Family DIPRIONIDAE**

(Fig. 29)

**Diagnosis** Antenna with about 20 flagellomeres, comb-like in males, saw-like in females; tergum 1 separated from metapleuron in both sexes.

Comments Because the larvae attack and sometimes kill softwood trees they are considered major pests. Groups of striped or spotted caterpillar-like larvae are fairly common (sometimes much too common) on pine (*Pinus*) trees in early summer. Even though hundreds of entomologists and foresters have studied diprionids for over a century, many species still cannot be

clearly defined. The family contains about 90 species restricted to the Northern Hemisphere. About 45 species occur in North America, including 20 in Canada.

References Benson (1939a, 1945b) characterized the world genera and Smith (1974a) the Nearctic genera. Gussakovskij (1947) reviewed the Palaearctic species, Zhelokhovtsev (1988) the species of European USSR, Viitasaari (1987) the Finnish species, Takeuchi (1940) the Japanese species, and Smith (1988) the Neotropical species.

# **Family PERGIDAE**

(Fig. 30)

**Diagnosis** Antenna with 4 or more flagellomeres; fore wing without vein 2r and usually without anal cell; hind wing without anal cell; metapleuron fused with tergum 1.

Comments Larvae usually feed externally on leaves though some Australian species are leaf miners on *Eucalyptus*. Except for a small lineage in North America, species of Pergidae are restricted to Australia, and Central and South America, where they reach their greatest diversity. The family contains more than 400 species. At least four

species occur in North America, including three in Canada.

References Benson (1938) characterized the world subfamilies, Riek (1970) the Australian subfamilies, and Smith (1990) the New World subfamilies. Benson (1963) characterized the genera of Euryinae. Smith (1990) revised the species of most Neotropical genera. Benson (1939b, 1965) revised the species of *Perga*. Smith (1978) cataloged the world species.

## Family TENTHREDINIDAE

(Fig. 31)

**Diagnosis** Antenna with 5–9 flagellomeres (in some species the apical flagellomeres may be fused, but they are counted if a division is still visible); metapleuron clearly separated from tergum 1; mesoscutellar appendage long and clearly outlined (at least laterally).

**Comments** Adults are most common only for a few weeks in spring and early summer, but some are found throughout the summer and fall. Most species in temperate regions produce only one generation per year. In exceptional circumstances, some species produce two or more generations. Adults of Tenthredininae emerge comparatively late and are found in early and mid summer. Adults are usually black, most often with a color pattern of green, brown, yellow, red, or white. When alive, many species, especially among Tenthredininae and Nematinae, are strikingly bright and beautiful, but sadly for the collector most of the brilliant colors, especially the greens, fade rapidly to shades of yellow-brown after death. Most species feed singly on leaves, but some are borers in twigs and fruit, some (mainly Nematinae) are gall makers, and a few are leaf miners. Tenthredinidae is the dominant sawfly group in boreal and arctic regions as far north as vegetation occurs. The family consists of over 6000 species found mostly in temperate regions of the Northern Hemisphere. About 800 species occur in North America, including about 600 in Canada.

**References** Because of the large diversity of genera and species, the references are given by subfamily. Ross (1937) characterized the North American subfamilies. His concept is generally accepted and was partly reorganized by Smith (1969a, 1969b, 1969c, 1971a, 1974a, 1974b, 1979a, 1979b) and by Goulet (1986, 1992). Ross (1937) and Goulet (1992) reviewed the North American genera, Benson (1952) the British genera, and Takeuchi (1952) the Japanese genera.

• Allantinae Malaise (1963) characterized the world genera (his subfamily concept included the genera of Selandriinae and Heterarthrinae), and Smith (1979b) the Nearctic genera. Benson (1952) reviewed the British species, Zhelokhovtsev (1988) the species of European USSR, and Smith (1979b), the North American species.

- Blennocampinae Smith (1969c) characterized the North American genera. Benson (1952) reviewed the British species, Zhelokhovtsev (1988) the species of European USSR, and Smith (1969c) the North American species.
- Heterarthrinae Smith (1976c) characterized the North American genera of the subfamily and the world genera of Fenusini, and Takeuchi (1952) characterized the Japanese genera. Benson (1952) reviewed the British species, Zhelokhovtsev (1988) the species of European USSR, and Smith (1971a) the North American species.
- Nematinae Benson (1958) characterized the British genera, Zhelokhovtsev (1988) the species of European USSR, Takeuchi (1952) the Japanese genera, and Ross (1937) the North American genera. Smith (1974c) treated the genera of Cladiini and (1976b) those of the Pseudodineurini. Zhelokhovtsev (1988) reviewed the species of European USSR, and Benson (1958) the British species.
- Selandriinae (including Dolerinae) Malaise (1963) characterized the world genera (his subfamily concept included the genera of Heterarthrinae and Allantinae), and Smith (1969a) the Nearctic genera. Zhelokhovtsev (1988) reviewed the species of European USSR, Takeuchi (1941) the Japanese species, Smith (1969a) the North American species, Goulet (1986) the Nearctic Dolerini, Benson (1952) the British species, and Malaise (1945) the southeast Asian species.
- Susaninae The subfamily consists of one genus restricted to North America. Smith (1969b) revised the species, and Wong and Milliron (1972) added another species.
- Tenthredininae Malaise (1945) characterized the world genera, Benson (1946b) the European genera, and Ross (1937) and Goulet (1992) the North American genera. Benson (1952) reviewed the British species, Zhelokhovtsev (1988) the species of European USSR, and Malaise (1945) the southeast Asian species.

## **Superfamily XYELOIDEA**

(Fig. 32)

Included family (1): Xyelidae.

The superfamily consists of two subfamilies, four tribes, five genera, and 46 species. The extinct

fauna consists of four subfamilies, eight tribes, 40 genera, and 106 species. Most of the classification is based on extinct taxa.

#### Family XYELIDAE

(Fig. 32)

**Diagnosis** Antenna with an enormous flagellomere 1, followed by several short and narrow flagellomeres.

Comments Most species are 2-4 mm long and belong to the genus *Xyela*. The larvae feed in the springtime inside the pollen-producing cones of pines (*Pinus*). A few other species feed within buds and within developing shoots of fir (*Abies*) or on leaves of deciduous trees. Members of the genus *Xyela* are commonly found flying around cone-bearing branch tips of mature pines (*Pinus*), or visiting willow (*Salix*) blossoms or other pollen-bearing plants nearby during warm days in early spring; otherwise they are rarely found. Xyelidae are the earliest known Hymenoptera in

the fossil record. They have been found in the Triassic period (about 200 million years old). At that time they were the dominant group of Hymenoptera and must have occurred in far greater variety and abundance than they do now. The family contains 46 species. Twenty-four species occur in North America, including 13 in Canada.

References Ross (1937) characterized the genera. The species were reviewed by the following: Gussakovskij (1935), Palaearctic; Zhelokhovtsev (1988), European USSR; Viitasaari (1982b), Finland; Takeuchi (1938), Japan; Benson (1951), UK; Burdick (1961), North America; and Smith (1988), Neotropical. Smith (1978) cataloged the species.

# Family ANAXYELIDAE<sup>1</sup>

(Fig. 33)

**Diagnosis** Pedicel as long as flagellomere 1; pronotum with longitudinal medial groove or articulation.

**Comments** Adults oviposit in recently burnt cedar (*Juniperus*, *Libocedrus*, *Thuja*) and juniper (*Juniper*) trees in which their wood-boring larvae feed. Only one extant species is known, *Syntexis libocedrii* 

Rohwer, a living fossil found from California to south-central British Columbia. It is all that is left of a large Mesozoic fauna.

**References** Middlekauff (1974) described the biology of the only species. Smith (1978) cataloged the extant and fossil species.

# Family XIPHYDRIIDAE1

(Fig. 34)

**Diagnosis** Propleuron unusually long; head thus clearly separated from pronotum by a distinct "neck".

**Comments** These wood-boring sawflies attack small trunks and branches of deciduous trees. The family contains about 80 species around the world. Ten species occur in North America, including six in Canada.

References Benson (1954) characterized the world genera. The species were reviewed by the following: Gussakovskij (1935), Palaearctic; Zhelokhovtsev (1988), European USSR; Takeuchi (1938), Japan; Smith (1976a, 1983), North America; and Smith (1988), Neotropical. Deyrup (1984) described the biology of Xiphydria maculata Say, with notes on other species. Smith (1978) cataloged the world species.

<sup>&</sup>lt;sup>1</sup> Family unassigned to superfamily of Symphyta.

#### References to Symphyta

- Although most references are specifically mentioned under each family, some treat one or several aspects of Symphyta as a whole. Benson (1950) and Viitasaari (1982a) described their natural history. Yuasa (1922), and Lorenz and Kraus (1957) characterized the larvae of several
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  Transactions of the Royal Entomological Society of London 87(15):353–384.
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- genera for each family. Wright (1990) keyed the British genera. Abe and Smith (1991) listed all generic names with their type species, and references of major works listed by geographical region. Goulet (1992) keyed the Canadian genera.
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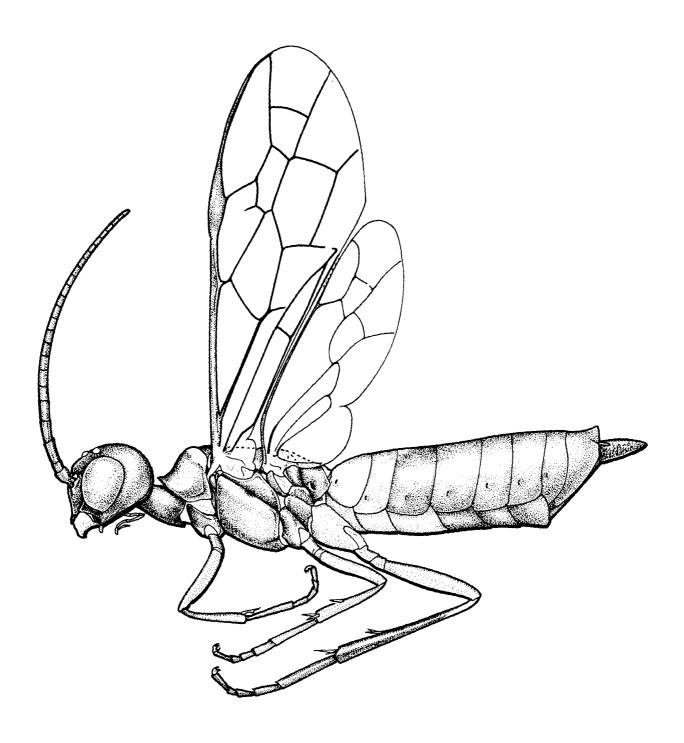


Fig. 21. Cephidae

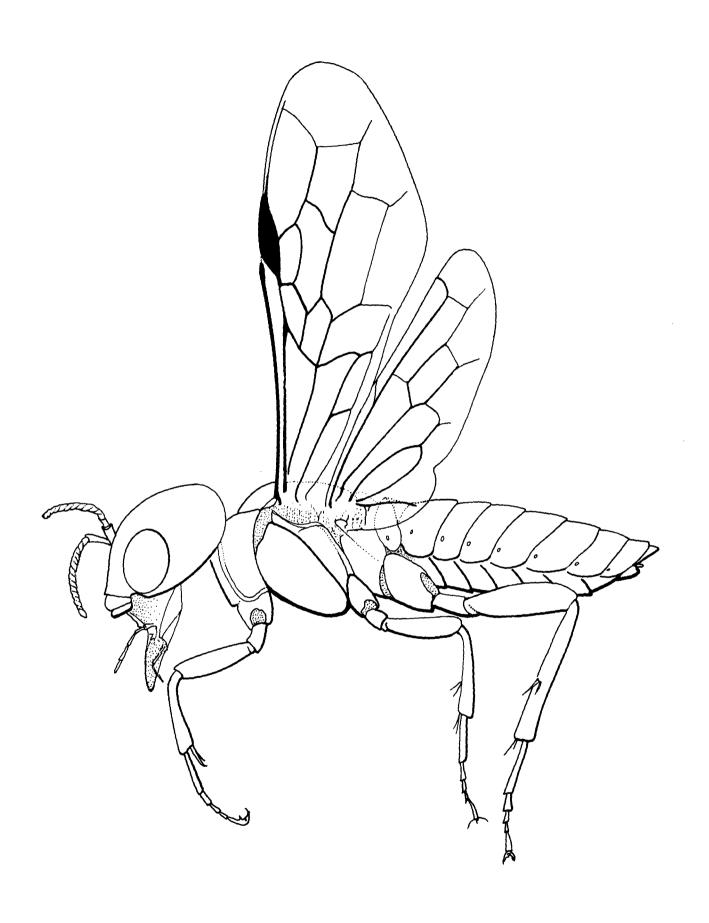


Fig. 22. Megalodontidae

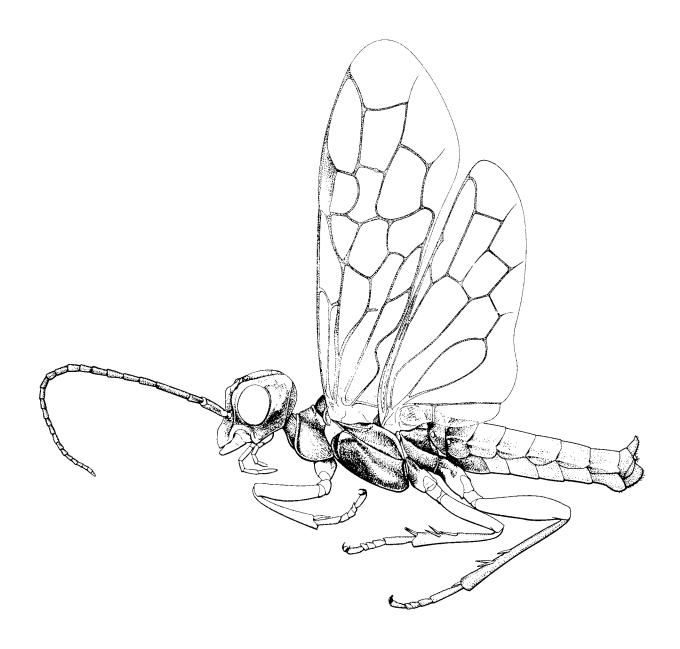


Fig. 23. Pamphiliidae

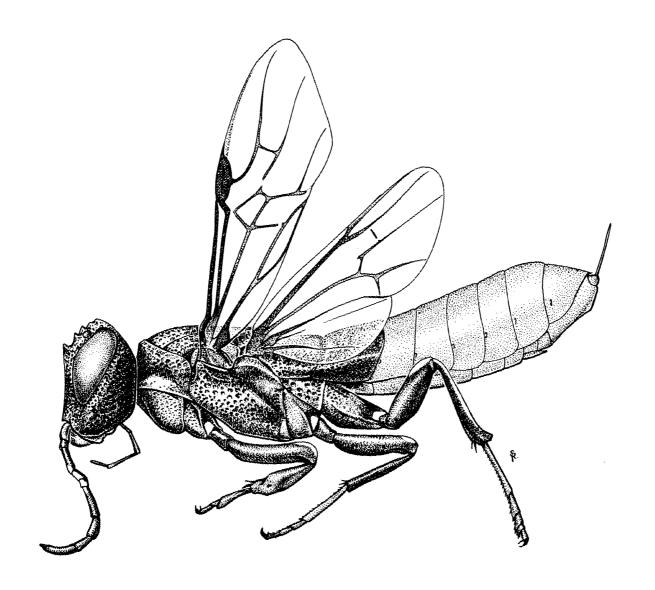




Fig. 25. Siricidae

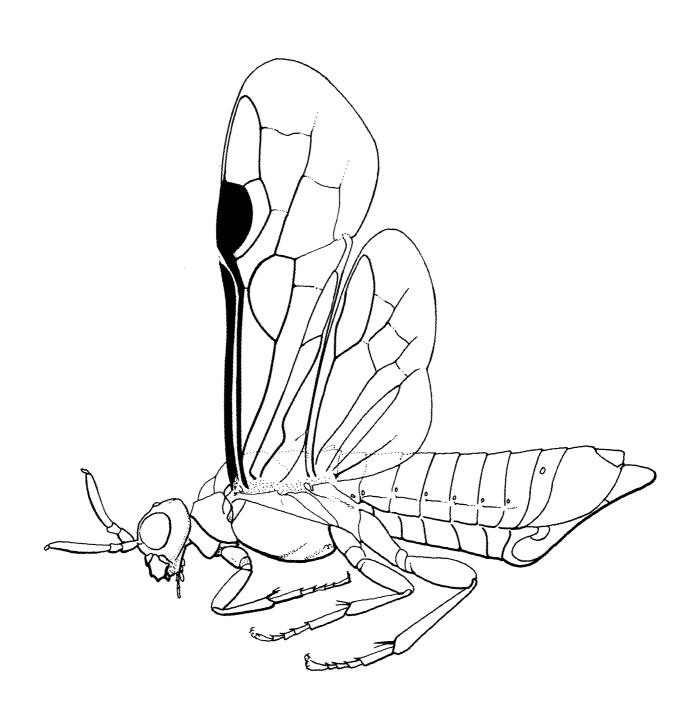


Fig. 27. Blasticotomidae

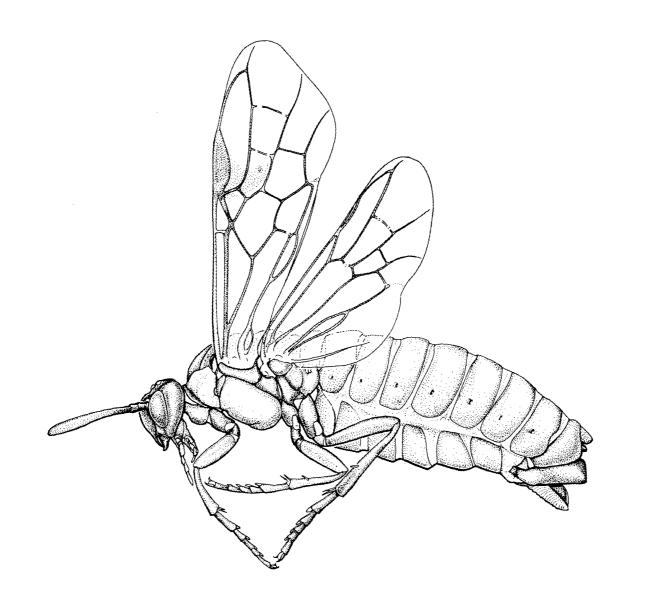


Fig. 26. Argidae

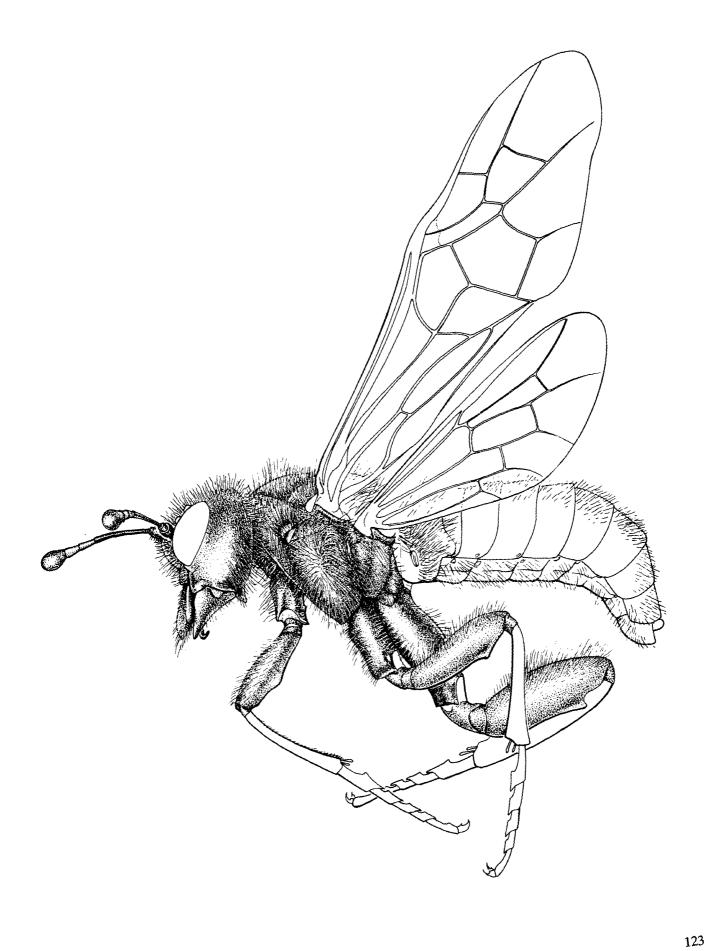


Fig. 28. Cimbicidae

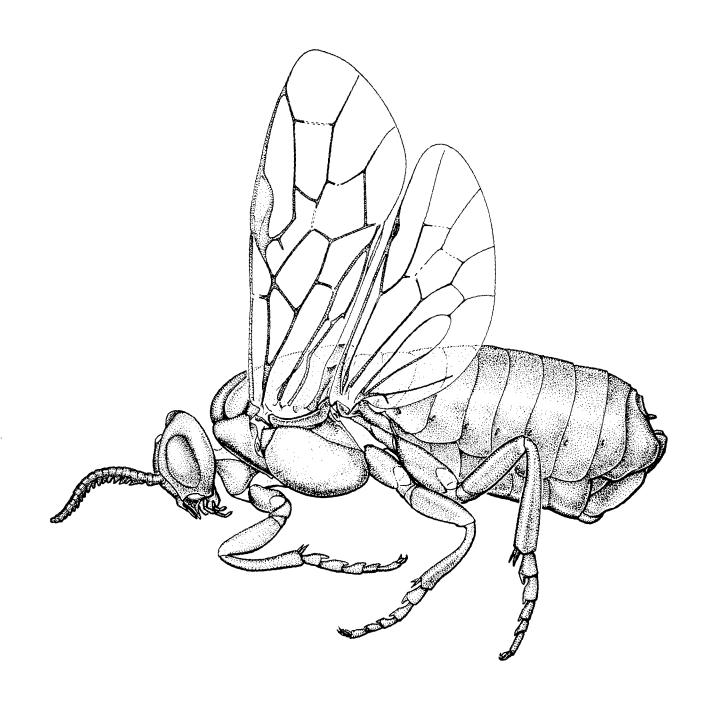


Fig. 29. Diprionidae

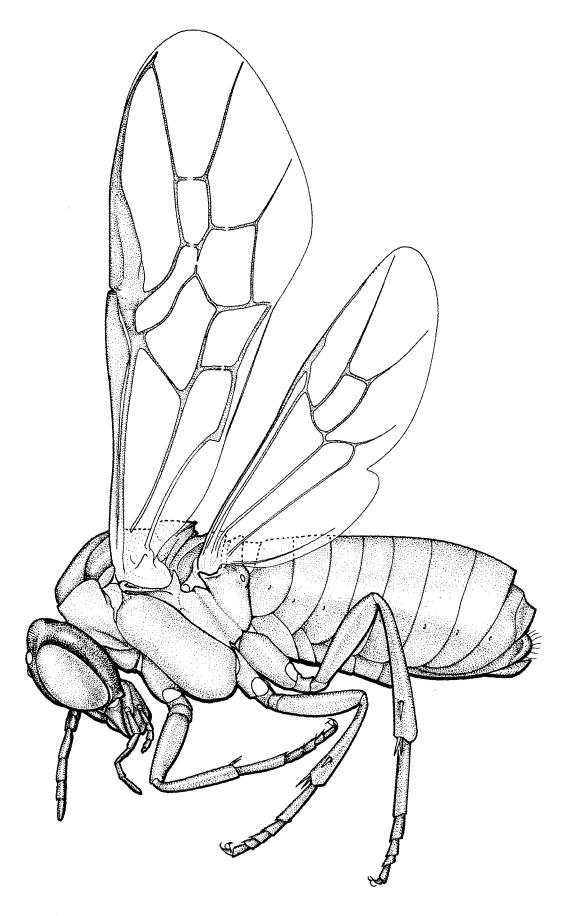


Fig. 30. Pergidae

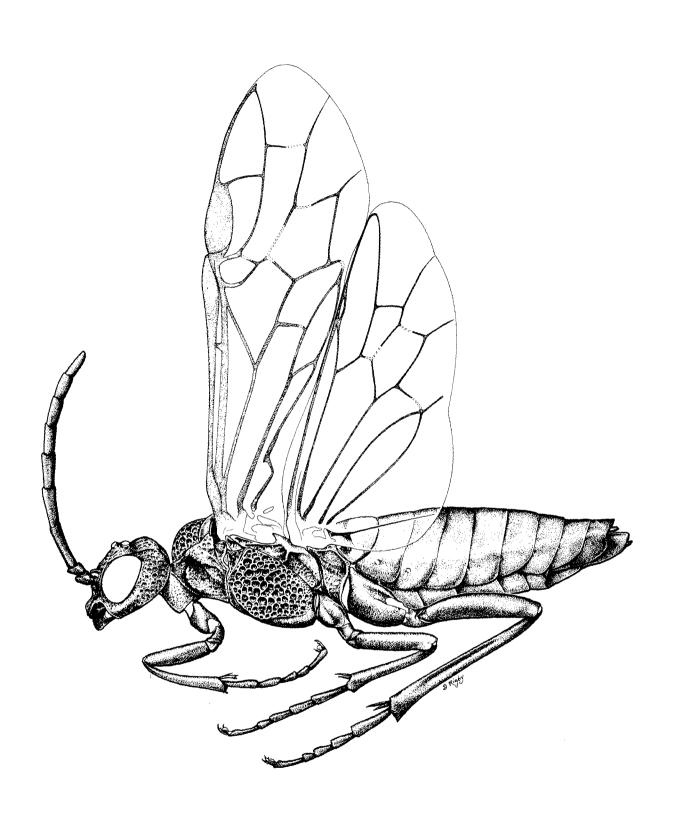


Fig. 31. Tenthredinidae



Fig. 32. Xyelidae

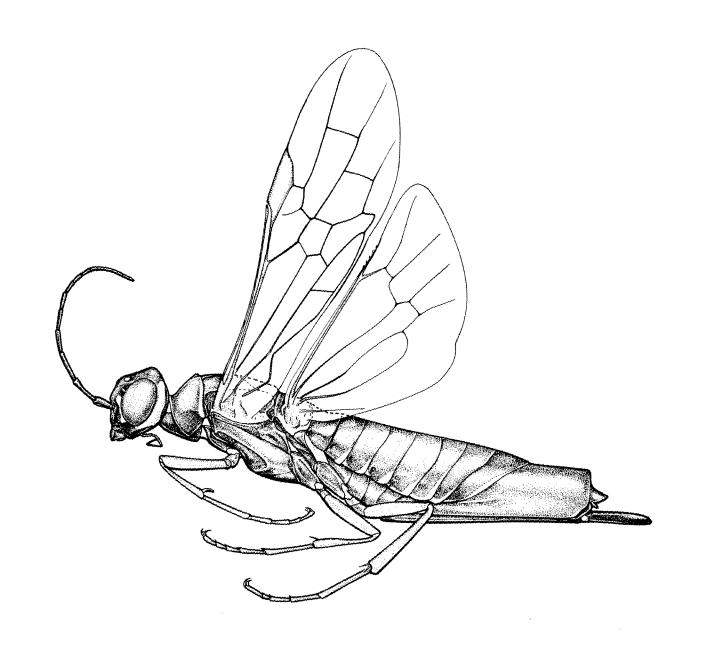


Fig. 33. Anaxyelidae



Fig. 34. Xiphydriidae

# Chapter 7 Superfamily Chrysidoidea

(Figs. 35-45)

Albert T. Finnamore and Denis J. Brothers

Included families (7): Bethylidae, Chrysididae, Dryinidae, Embolemidae, Plumariidae, Sclerogibbidae, Scolebythidae.

**Diagnosis** Antenna with same number of flagellomeres in both sexes, usually 8 or 11; pronotum with posterolateral apex usually reaching tegula but sometimes separated by distinct cuticular gap, with posterodorsal margin usually fairly shallowly concave, with posterolateral margin with lobe covering spiracle scarcely developed, and with lateroventral extremities broadly separated; metapostnotum short, transverse and fused with propodeum, sometimes exposed but not posteriorly expanded in middle; wing venation reduced, usually 3 or fewer closed cells in fore wing (rarely up to 8) and 1 or no closed cells in hind wing (rarely up to 3); hind wing without jugal lobe; metasomal sterna 1 and 2 not separated by constriction; female with articulation within gonocoxite 2 near base: ovipositor concealed at rest and usually modified as a sting; plumose setae absent. Sexual dimorphism slight to extreme: male macropterous but very rarely brachypterous or apterous; female usually macropterous but often apterous and rarely brachypterous.

Comments Chrysidoidea contains three large and common families (the first three listed above) and four small rare ones. Most chrysidoids are among the smallest of Aculeata; many are under 3 mm long. These parasitoids are often found in unusual situations for aculeates, e.g., in eggs of Cheleutoptera (= Phasmatodea), externally on Cicadellidae (Homoptera) and nymphal Embioptera, or on Coleoptera or Lepidoptera larvae beneath bark or in soil. Some are cleptoparasites in nests of other Aculeata. In some

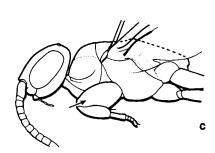
groups the females are wingless and often flattened, which facilitates host location in concealed habitats.

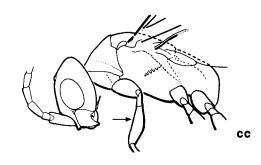
Except for Dryinidae and Chrysididae, chrysidoids form a poorly known pantropical group with relatively few northern representatives. The world fauna is estimated to be around 16 000 species, 70% of which are undescribed. About 550 described species occur in North America, including about 150 in Canada, predominantly in southern areas. The number of genera and species given below for each family and subfamily includes only those that are described, unless otherwise stated. Carpenter (1986) analyzed the relationships of the families. Brothers and Carpenter (1993) re-examined and extended that analysis.

The names of wing cells and veins used in the chapters on Chrysidoidea, Vespoidea, and Apoidea are those of Gauld and Bolton (1988). The following table gives the modified Comstock-Needham equivalents (for a discussion of wing venation see Chapter 3).

Gauld and Bolton (1988)	Modified Comstock-Needham
Marginal cell (M)	2R1
1st submarginal cell (1SM)	1R1
2nd submarginal cell (2SM)	1Rs
3rd submarginal cell (3SM)	2Rs
1st discal cell (1D)	1M
2nd discal cell (2D)	2M
1st subdiscal cell (1SD)	2Cu
subbasal cell (SB)	1Cu

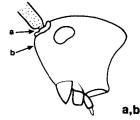
## Key to families of CHRYSIDOIDEA

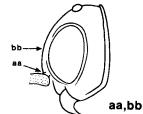


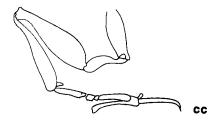


- a. Antenna with 13-37 flagellomeres.
  b. Female wingless.
  - c. Female with profemur greatly enlarged and swollen; male with profemur usually enlarged and swollen.

  - aa. Antenna with 8-11 flagellomeres.
  - bb. Female fully winged, short-winged, or wingless.
  - cc. Profemur usually not enlarged or swollen.
- - aa. Antenna with 10 or 11 flagellomeres .....

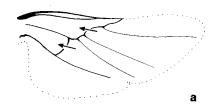






- a. Antenna inserted on low conical protuberance above middle of head, the torulus more than twice its width from dorsal margin of clypeus.
  - b. Head in lateral view strongly convex anteriorly.
  - c. Female protarsus unmodified, with 2 small equal-sized claws . . . . . EMBOLEMIDAE (p. 146)
  - aa. Antenna inserted on flat or concave surface below middle of head, the torulus less than its width from dorsal margin of clypeus.
  - bb. Head in lateral view concave to slightly convex anteriorly.

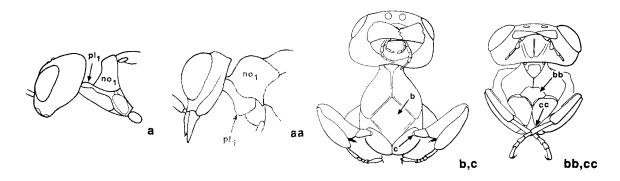
One species of Bethylidae also keys here (Strejček 1990), but it can be separated from Embolemidae and Dryinidae by having the head much longer than wide.



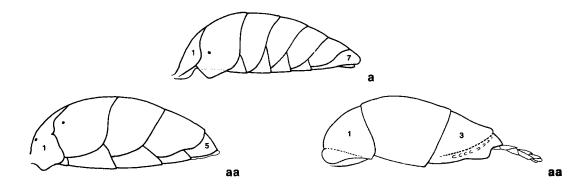


- a. Fully winged form (male): hind wing with at least 2 cells enclosed by tubular veins.
  - b. Wingless form (female): mesothorax separated from metathorax by strong ventral constriction.
  - c. Female pronotum without anterior flange, propleura thus exposed in dorsal view.

  - aa. Fully winged form (either sex): hind wing with 1 or no cells enclosed by tubular veins.
  - bb. Wingless or short-winged form (either sex): mesothorax not separated from metathorax by strong ventral constriction.
  - cc. Female pronotum usually with anterior flang, propleura thus concealed (not visible) in dorsal view; if pronotal flange not developed and propleura exposed in dorsal view then fully winged.
  - dd. Male flagellum with inconspicuous recumbent setae shorter than half the width of flagellomere



- a. Pronotum (no<sub>1</sub>) with anterior flange not developed, the propleuron (pl<sub>1</sub>) thus exposed in dorsal view; head distinctly separated from pronotum.
  - b. Prosternum large and diamond-shaped, exposed in ventral view.
  - c. Protrochanter originating from lateral surface of procoxa (procoxa produced posterior to origin of protrochanter) ...... SCOLEBYTHIDAE (p. 133)
  - aa. Pronotum (no<sub>1</sub>) with anterior flange well developed, the propleuron thus (pl<sub>1</sub>) concealed in dorsal view; head scarcely separated from pronotum.
  - bb. Prosternum small and more or less transverse, often concealed in ventral view.



- **6(5)** a. Metasoma with 6 or 7 exposed terga.
  - b. Pronotum usually touching tegula.
  - c. Head usually prognathous ...... BETHYLIDAE (p. 134)
  - aa. Metasoma with 5 or fewer exposed terga, rarely with indications of a 6th.
  - bb. Pronotum usually separated from tegula by a distinct cuticular gap.
  - cc. Head usually hypognathous ...... CHRYSIDIDAE (p. 137)

#### Family PLUMARIIDAE

(Fig. 35)

**Diagnosis** Antenna with 11 (rarely 10) flagellomeres, each usually with long erect setae; pronotum without anterior flange, propleuron thus partly exposed dorsally. Sexual dimorphism extreme: male macropterous, flagellomeres with numerous setae, pronotum vertical, hind wing with at least 2 cells enclosed by tubular veins; female apterous, head prognathous, flagellomeres with a few scattered setae, pronotum horizontal, mesothorax separated from metathorax by deep ventral (and lateral) constriction.

Comments Plumariidae contains four genera from arid and semiarid regions: two in South America (Ecuador to Chile and Argentina) and two in southern Africa (South Africa to Namibia and Zimbabwe). Fewer than 20 species have been described. Adults are black to pale brown. The few

very rare females have been collected under rocks or in pitfall traps, but the more commonly collected males come to lights (nocturnal species) or to Malaise traps (diurnal species). Nothing else is known about their biology.

References Brothers (1974) keyed three genera; Day (1984) subsequently recognized that *Heterogyna* was a member of Apoidea and placed it in Heterogynaidae. Evans (1966) described the first known female. Nagy (1973) keyed several Neotropical species, and Day (1977) described the fourth genus and discussed relationships. Janvier (1933) described the larva of a parasitoid of *Trachypus* sp. (Philanthidae), which he had identified as a *Plumarius*, but that identification is almost certainly incorrect and the species is probably a nocturnal mutillid.

# Family SCOLEBYTHIDAE

(Fig. 36)

**Diagnosis** Head obliquely hypognathous; antenna with 11 flagellomeres; pronotum substantially horizontal without anterior flange, propleuron thus partly exposed dorsally; prosternum large, diamond-shaped; hind wing without closed cells; protrochanter originating from lateral surface of procoxa. Sexual dimorphism slight: both sexes macropterous.

**Comments** Scolebythidae contains three monotypic genera, in Brazil, South Africa and Australia, and Madagascar. Adults are

predominantly black or dark brown. Little is known about their biology, but the larvae are probably gregarious external parasitoids of wood-boring Cerambycidae (Coleoptera). Pupation occurs in the host burrow.

**References** Evans (1963) described the family. Nagy (1975) and Evans, Kugler and Brown (1980) keyed the genera. Day (1977), Evans, Kugler and Brown (1980), and Brothers (1981) dealt with the biology.

#### **Family BETHYLIDAE**

(Figs. 37, 38)

**Diagnosis** Head usually prognathous; antenna with 11 (rarely 10 or 8) flagellomeres; pronotum with anterior flange, propleuron thus concealed in dorsal view; prosternum small, more or less transverse, often concealed in ventral view; metasoma with 6 or 7 exposed terga. Sexual dimorphism slight to extreme: male macropterous, rarely brachypterous; female macropterous,

brachypterous, or apterous; brachypterous and apterous forms without deep ventral constriction between mesothorax and metathorax.

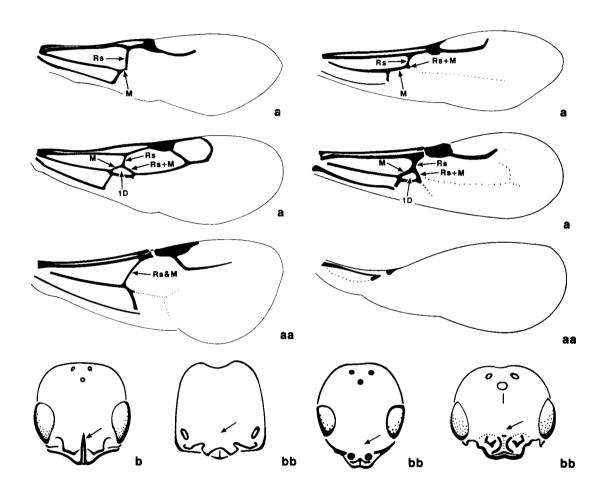
**Comments** Bethylidae is probably the largest family of chrysidoids and includes about 2200 species in four subfamilies: Bethylinae, Epyrinae, Mesitiinae, and Pristocerinae. The species are

particularly abundant in the tropics. Adults are predominantly black or dark brown, although several New World species are metallic green. The female stings and paralyses the host, usually a Lepidoptera or Coleoptera larva, lays several eggs on it, and either leaves it where it was found or

sometimes drags it into a crevice. In some species the female tends the eggs and developing larvae. Pupation occurs next to the host remains. The three North American subfamilies (199 species in 20 genera) extend to southern Canada, where 22 species (eight genera) occur.

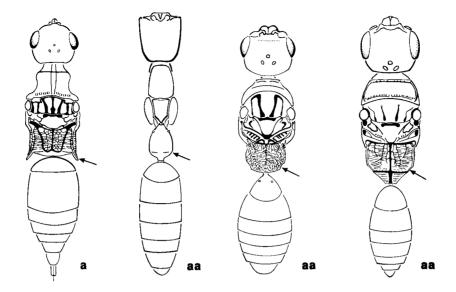
#### Key to subfamilies of BETHYLIDAE

(modified from Evans 1978)

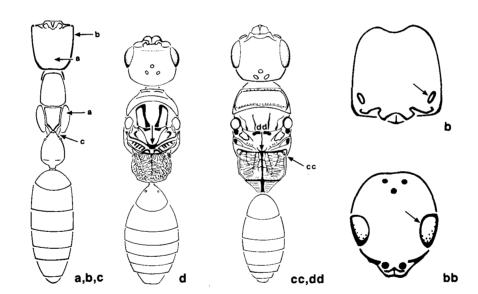


- a. Fore wing with veins Rs and M obtusely angled or giving rise to a vein or vein stub (Rs+M); 1st discal cell (1D) sometimes present.
  - b. Frons with longitudinal median carina or polished streak extending a short distance from clypeus.

  - aa. Fore wing with vein Rs&M simple and evenly arched, not angled or giving rise to any vein or stub, sometimes without vein Rs&M; 1st discal cell (1D) absent.
  - bb. Frons usually without median longitudinal carina or polished streak extending from clypeus.



- 2(1) a. Propodeum with dorsal posterolateral angle produced as a single large tooth ..... Mesitiinae



- a. Female wingless, without tegula or ocelli; male fully winged.
  - b. Female with eye small or absent, the eye height up to one-quarter of head width.
  - c. Female with propodeum often constricted anteriorly.

  - aa. Both sexes fully winged, short-winged, or wingless; if wingless then usually with tegula and ocelli.
  - bb. Female with eye height more than one-quarter of head width.
  - cc. Female with propodeum not constricted anteriorly.
  - dd. Both sexes with scutellum in contact with propodeum or nearly so; metanotum occasionally narrowly transverse but without pit opposite posterior apex of scutellum ...... Epyrinae

#### **Subfamily Pristocerinae**

(Fig. 37)

Females of this cosmopolitan subfamily are apterous and quite unlike the males, are rarely collected, and are very difficult to identify. The few records available indicate that the larvae are parasitoids of wood-boring and soil-dwelling Coleoptera larvae; a few have been found in ant colonies and are presumed to be parasitoids of myrmecophilous Coleoptera larvae. Sixty-one species (five genera) occur in North America, including four species (one genus) in Canada.

#### **Subfamily Epyrinae**

Adults of this cosmopolitan subfamily are mostly black, although some Neotropical adults are metallic green; sexual dimorphism is slight. Adults are parasitoids of Coleoptera larvae in concealed situations. Several genera are cosmopolitan, including parasitoids of pests in stored grain and occasionally in insect collections. Ninety-eight species (11 genera) occur in North America, including 13 species (five genera) in Canada.

#### Subfamily Bethylinae

(Fig. 38)

Adults of this cosmopolitan subfamily are mostly black; sexual dimorphism is slight. Larvae are parasitoids of Lepidoptera larvae in concealed

situations (budborers, casebearers, leafrollers) or parasitoids of exposed caterpillars, which are then concealed by the female wasp. Forty species (four genera) occur in North America, including five species (two genera) in Canada.

#### **Subfamily Mesitiinae**

This subfamily includes fewer than 200 species, all from the Old World. Many adults are black and reddish with pale markings on the dark folded wings and somewhat resemble Amiseginae (Chrysididae) or Mutillidae. Sexual dimorphism is marked. The only record indicates that the larvae are parasitoids of immature Clytrinae (Coleoptera: Chrysomelidae).

References Kieffer's (1914) difficult work is still the only comprehensive treatment of the world fauna. Evans (1964, 1978) keyed the New World genera, presented keys to species, and tabulated host records for the North American fauna. Richards (1939b) and Perkins (1976) dealt with the British species. Benoit (1963) dealt with some African Pristocerinae. Nagy (1974) and Argaman (1988a) proposed new subfamilies, which we consider to fall within the range of those recognized above. Móczár (1970, 1984) keyed the genera and some species of Mesitiinae. Clausen (1940), Doutt (1973), and Nagy (1969) dealt with biology. Hawkins and Gordh (1986) provided a bibliography of world literature, and Gordh and Móczár (1990) cataloged the world fauna.

## Family CHRYSIDIDAE

(Figs. 39-42)

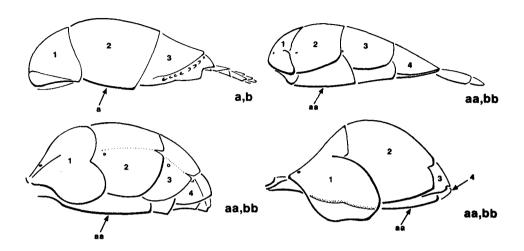
**Diagnosis** Head hypognathous; antenna with 11 flagellomeres; pronotum with anterior flange, thus propleuron concealed in dorsal view; pronotum with posterolateral apex usually well separated from tegula but sometimes touching; prosternum small; metasoma with 5 or fewer exposed terga, rarely with trace of a 6th. Sexual dimorphism usually very slight: both sexes macropterous, rarely brachypterous or apterous; brachypterous and apterous forms without deep ventral constriction between mesothorax and metathorax.

**Comments** Chrysididae includes about 3000 species in four subfamilies: Amiseginae,

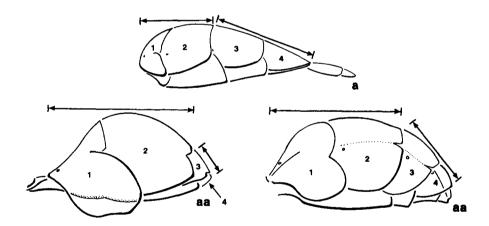
Chrysidinae, Cleptinae, and Loboscelidiinae. Their greatest diversity is in temperate deserts of both hemispheres. Adults are predominantly metallic green, violet and/or red, seldom brown or dull black, if brown or black then sometimes partly dull red. Larvae are parasitoids of the eggs or of the mature larvae of other insects or they are cleptoparasites in insect nests. Pupation occurs within the host egg, cocoon, or nest. The three North American subfamilies (about 231 species in 25 genera) extend to southern Canada where 59 species (11 genera) occur, mostly in the extreme south, although several occur in the boreal forest.

# Key to subfamilies of CHRYSIDIDAE

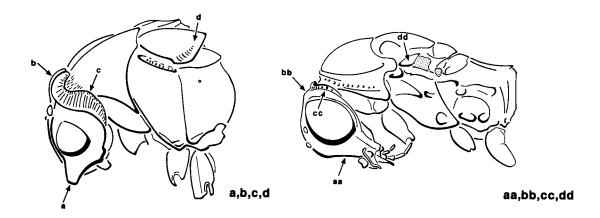
(modified from Bohart and Kimsey 1982)



- a. Metasoma concave ventrally, with sterna beyond sternum 1 not visible in lateral view.
  - b. Metasoma usually with up to 3 visible terga (male occasionally with 4 terga) ..... Chrysidinae
  - aa. Metasoma convex ventrally, with sterna visible in lateral view.



- 2(1) a. Metasomal terga 1 + 2 subequal to or shorter than terga 3 + 4.
  - b. Clypeus with ventrolateral margin concave and with narrow medical projection . . . . Cleptinae
  - aa. Metasomal terga 1 + 2 much longer than terga 3 + 4.
  - bb. . Clypeus with ventrolateral margin convex and without narrow medial projection ...... 3



- 3(2)
- a. Frons with frontal shelf.
- b. Vertex produced posteriorly.
- c. Gena laminate posteriorly (with wide, flat, fused setae); scape, femora, and tibiae often laminate ventrally.
- d. Tegula very large, posteriorly produced and recurved ..... Loboscelidiinae
- aa. Frons without frontal shelf.
- bb. Vertex not produced posteriorly.
- cc. Gena, scape, femora, and tibiae without laminae.
- dd. Tegula small or absent ...... Amiseginae

#### **Subfamily Cleptinae**

(Fig. 39)

This is a widespread subfamily (absent in Australia and subsaharan Africa). Adults are often only partly metallic. The larvae are ectoparasitoids on the prepupae of Tenthredinoidea within their cocoons. Seven species (one genus) occur in North America, including two species in Canada.

#### **Subfamily Amiseginae**

(Fig. 40)

This widespread, predominantly tropical subfamily includes species with adults that are often not metallic. The larvae are parasitoids in the eggs of Cheleutoptera (= Phasmatodea). Four species (three genera) occur in North America, including one species in Canada.

#### Subfamily Loboscelidiinae

(Fig. 41)

This tropical subfamily from the Oriental and Australian regions includes fewer than 20 species. Adults are shiny brown and not metallic. The larvae are apparently parasitoids in eggs of Cheleutoptera (= Phasmatodea).

#### **Subfamily Chrysidinae**

(Fig. 42)

This cosmopolitan group, the cuckoo wasps, is by far the largest subfamily. Adults are almost invariably brilliantly metallic, and have a concave metasomal venter, which permits them to roll into a ball when threatened. Larvae are usually cleptoparasites in the nests of solitary bees or wasps, the egg being laid in the host cell, usually before provisioning has been completed; the cuckoo-wasp larva kills the egg or recently hatched larva of the host and then feeds on the stored provisions. Some species are more typical parasitoids in that the larva feeds on the mature larva of the host within a cell or cocoon. Hosts include Vespidae, various Spheciformes, Megachilidae, and a few Lepidoptera. Two hundred and twenty species (21 genera) occur in North America, including 56 species (nine genera) in Canada, mostly in the south.

References Kimsey and Bohart (1990) revised the world genera, and Kimsey and Bohart (1981) keyed the Neotropical genera. Bohart and Kimsey (1982) revised and keyed the species of America north of Mexico. The Palaearctic species were treated in part by Morgan (1984) for Britain; Nikolskaya (1978) for European USSR; Balthasar (1951) for Palestine; and Tsuneki (1970a, 1970b, 1970c) for Japan. Edney (1940, 1947, 1952, 1953, 1954a, 1954b, 1962) revised the South African species. Zimmermann (1956) revised the species of

Madagascar. Kimsey (1986, 1987b) added to the Oriental and Neotropical Amiseginae, respectively. Krombein (1957, 1983) keyed the genera of Amiseginae, and revised Amiseginae and Loboscelidiinae of Sri Lanka, respectively. Maa and Yoshimoto (1961) revised and keyed the species of Loboscelidiinae, Day (1979) discussed their

placement, and Kimsey (1988) described new species and a second genus. Kimsey (1987a) reviewed the tribe Parnopini (Chrysidinae) and Kimsey (1985) keyed genera and species of the *Neochrysis* group of Chrysidini (Chrysidinae). Clausen (1940), Krombein (1967), Carpenter (1986), and Yamada (1987) discussed the biology.

## Family SCLEROGIBBIDAE

(Fig. 43)

**Diagnosis** Head obliquely hypognathous; antenna with 13–37 flagellomeres; pronotum with anterior flange, thus propleuron concealed in dorsal view. Sexual dimorphism extreme: male macropterous, profemur usually enlarged; female apterous, without deep ventral constriction between mesothorax and metathorax, with profemur strongly enlarged, and protibia wide, with ventral lamina overlying outer face of femur.

**Comments** Sclerogibbidae includes seven genera and 10 species distributed in the warmer areas of the world. Adults are predominantly black or dark

brown, sometimes partly reddish. The larvae are ectoparasitoids of Embioptera nymphs. Pupation occurs in the host web. Two species (one genus) occur in North America, neither in Canada.

**References** Argaman (1988b) recognized three subfamilies (the appropriateness of which awaits evaluation of further material), revised the world genera, and provided synonymies for most species. Richards (1939a) keyed the world species and Shetlar (1973) the American species. Krombein (1979a) treated the species of Sri Lanka. Callan (1939) dealt with the biology.

# **Family DRYINIDAE**

(Fig. 44)

**Diagnosis** Antenna with 8 flagellomeres and inserted near clypeus on more-or-less flat frons; pronotum with anterior flange, thus propleuron concealed in dorsal view; pronotum with posterolateral apex either well separated from tegula or touching it. Sexual dimorphism moderate to extreme: male macropterous or rarely brachypterous, the protarsus simple and unmodified; female macropterous, brachypterous, or apterous, the protarsus usually chelate but sometimes simple; brachypterous and apterous forms without deep ventral constriction between mesothorax and metathorax.

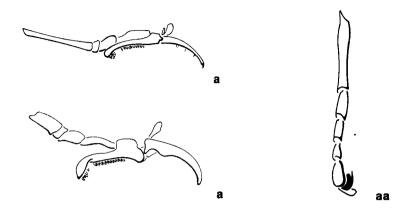
Comments Dryinidae is a cosmopolitan family including 58 genera and almost 1100 species in 11 subfamilies: Aphelopinae, Anteoninae, Apodryininae, Biaphelopinae, Bocchinae, Conganteoninae, Dryininae, Gonatopodinae, Plesiodryininae, Thaumatodryininae, and Transdryininae. Adults are usually dull black or

brown. Females are often apterous and ant-like in appearance and behavior, and usually have a chelate protarsus for clasping the host; the protarsus is modified by enlargement of one claw and lateral expansion of tarsomere 5. Dryinid larvae are parasitoids of immature and adult Homoptera-Auchenorrhyncha. They have been recorded from about 12 families, of which Cicadellidae, Delphacidae, and Flatidae are probably the most important. The larvae initially develop within the host body, but later instars form a characteristic sac (thylacium) bulging from the host abdomen and formed by the parasitoid's exuviae. Pupation occurs in the soil or on the host food plant. In rare cases, polyembryony occurs and the larvae develop entirely within the body of the host. Seven subfamilies containing 117 species in 27 genera occur in North America. Five subfamilies extend to Canada, where about 38 species in 14 genera occur in the south and several reach the Northwest Territories.

## Key to subfamilies of DRYINIDAE

(based on Olmi 1984, 1987a)

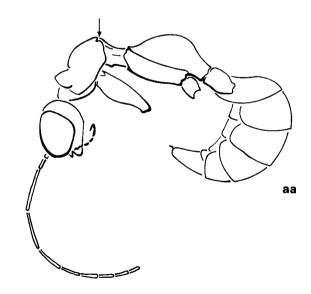
(Males of Transdryininae, Apodryininae, Biaphelopinae, and Plesiodryininae unknown.)



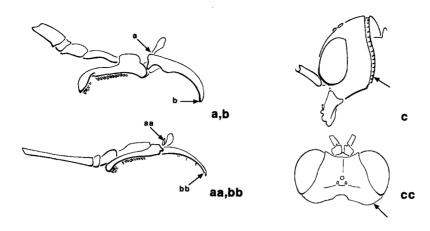
1a. Protarsus chelate; female2aa. Protarsus simple, unmodified; male or female10



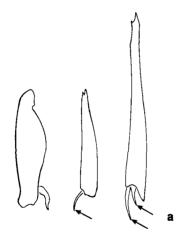
2(1) a. Ocelli absent aa. Ocelli present

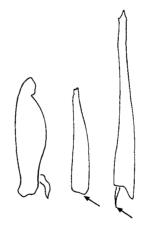


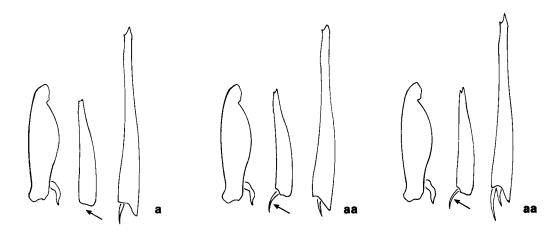
- a. Mesosomal dorsum with all segments fused, without sutures except between apparent pronotum and mesopleuron (Neotropical and Australian; three species known) . . . . . . female **Apodryininae** 
  - aa. Mesosomal dorsum with pronotum free; distinct sutures between pronotum and mesothorax (Neotropical; one species known) ...... female **Plesiodryininae**



- a. Protarsal chela without rudimentary claw (sometimes difficult to be sure because rudimentary claw often flattened against arolium and virtually indistinguishable even when present).
  - b. Enlarged claw of protarsus without preapical tooth or lamina and:
  - c. Head almost always with occipital carina complete and:
  - d. Fully winged or short-winged or with scale-like remnants of wings ...... 5
  - aa. Protarsal chela with rudimentary claw, this often flattened against arolium and virtually indistinguishable.
  - bb. Enlarged claw of protarsus with preapical tooth or lamina and/or:
  - cc. Head with occipital carina incomplete or absent and/or:



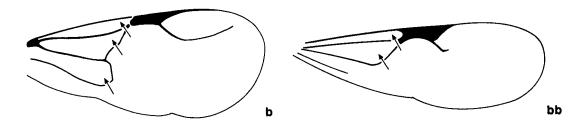






- **8**(7) a. Mandible with 4 apical teeth, these progressively larger from anterior to posterior.

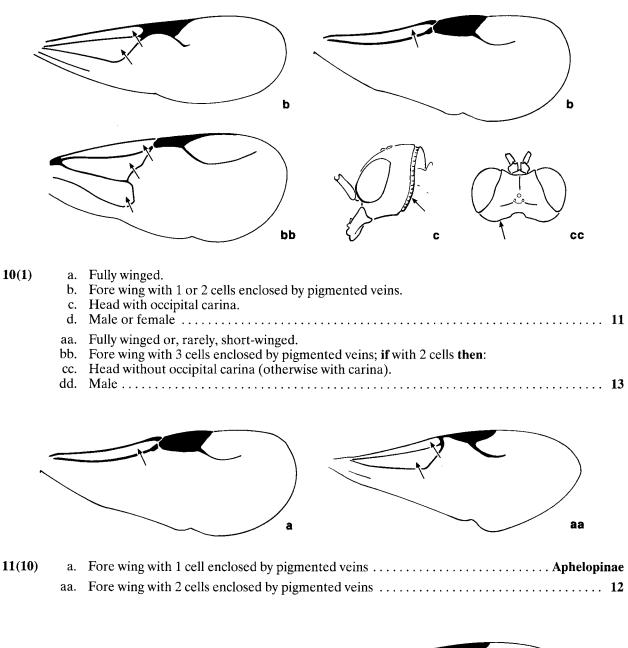
  - aa. Mandible with 1-4 apical teeth; **if** 4 **then** usually 3 large teeth and a rudimentary tooth between posterior teeth.

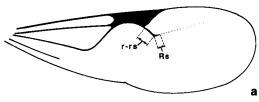


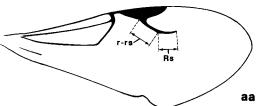
- 9(8) a. Fully winged or, rarely, short-winged; if fully winged then:
  - b. Fore wing with 3 cells completely enclosed by pigmented veins.

    (Widespread, except Neotropical; many species) ...... female **Bocchinae**
  - aa. Fully winged.
  - bb. Fore wing with 2 cells completely enclosed by pigmented veins.

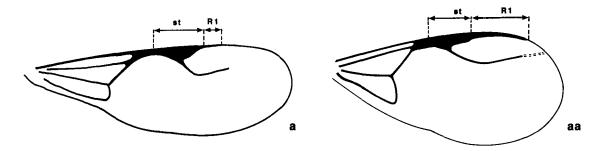
    (Palaearctic and Oriental; few species) ...... female Conganteoninae













a. Mandible with 1-4 apical teeth; if 3 then these not progressively increasing in size

### **Subfamily Aphelopinae**

15(13)

This widespread subfamily includes about 55 species in three genera. Larvae are parasitoids of Membracidae and some Cicadellidae; in one genus they are polyembryonic persistent endoparasitoids. Six known species (two genera) occur in North America, including five species (two genera) in Canada.

## **Subfamily Biaphelopinae**

This Palaearctic and Neotropical subfamily includes two species in one genus, known from females only. Habits are unknown.

#### **Subfamily Conganteoninae**

This Palaearctic, Oriental, and Afrotropical subfamily includes about eight species in three genera. Habits are unknown.

#### **Subfamily Plesiodryininae**

This monotypic subfamily is known from a female collected in Florida, USA. Habits are unknown.

#### **Subfamily Anteoninae**

This widespread subfamily includes about 250 species in five genera. Larvae are parasitoids of Cicadellidae. Twenty-two species (three genera) are known in North America, including 14 species (three genera) in Canada.

#### **Subfamily Bocchinae**

This widespread subfamily includes about 60 species in seven genera. The larvae are parasitoids of Issidae and some Cicadellidae. About 10 known species (one genus) occur in North America, including two species in Canada.

#### **Subfamily Thaumatodryininae**

This widespread subfamily includes 22 species in one genus. The larvae are parasitoids of Flatidae. The only North American species is not reported in Canada.

#### **Subfamily Dryininae**

This widespread subfamily includes about 190 species in eight genera. Larvae are parasitoids of a variety of Fulgoroidea. Sixteen species (four genera) occur in North America, including one modern species and one fossil species in Canada.

#### **Subfamily Transdryininae**

This Australian subfamily includes two monotypic genera known from females only. Habits are unknown.

#### **Subfamily Gonatopodinae**

(Fig. 44)

This widespread subfamily includes about 390 species in 23 genera. Larvae are parasitoids of some Cicadellidae and a variety of Fulgoroidea. About 60 species (15 genera) occur in North America, including 16 species (seven genera) in Canada.

#### **Subfamily Apodryininae**

This Neotropical subfamily includes three species in two genera, known from females only. Habits are unknown.

**References** Olmi (1984, 1986, 1987a, 1987b, 1987c, 1987d, 1991) revised the genera and species of the world. Olmi (1990) examined the distribution of species on the islands of the Pacific Ocean. Clausen (1940), Olmi (1984, 1989), and Waloff and Jervis (1987) surveyed the biology.

### Family EMBOLEMIDAE

(Fig. 45)

**Diagnosis** Antenna with 8 flagellomeres and inserted on low conical protuberance above middle of head, the torulus more than twice its width from dorsal margin of clypeus; pronotum with anterior flange, and with posterolateral apex touching tegula; propleuron concealed in dorsal view. Sexual dimorphism slight to extreme: male macropterous; female macropterous, brachypterous, or apterous, with protarsus unmodified; brachypterous and apterous forms without deep ventral constriction between mesothorax and metathorax.

**Comments** Embolemidae is a widespread family, including two genera and about 10 species. Several undescribed species are known. Adults are usually dull black or brown. Little is known of their biology,

but a Nearctic species has been reared from nymphs of Achilidae (Homoptera) which feed on subcortical fungi, the larva developing in a similar manner to those of Dryinidae. In the Palaearctic region, brachypterous females have been collected in ant nests and in burrows of small mammals. Both Nearctic species (two genera) probably occur in Canada, although only one has so far been recorded there

References The family has not been revised. Krombein (1979b) cataloged the two North American species. Donisthorpe (1927), Heim de Balsac (1935), Consani (1948), Bridwell (1958), Hirashima and Yamagishi (1975), Carpenter (1986), and Wharton (1989) discussed the biology.

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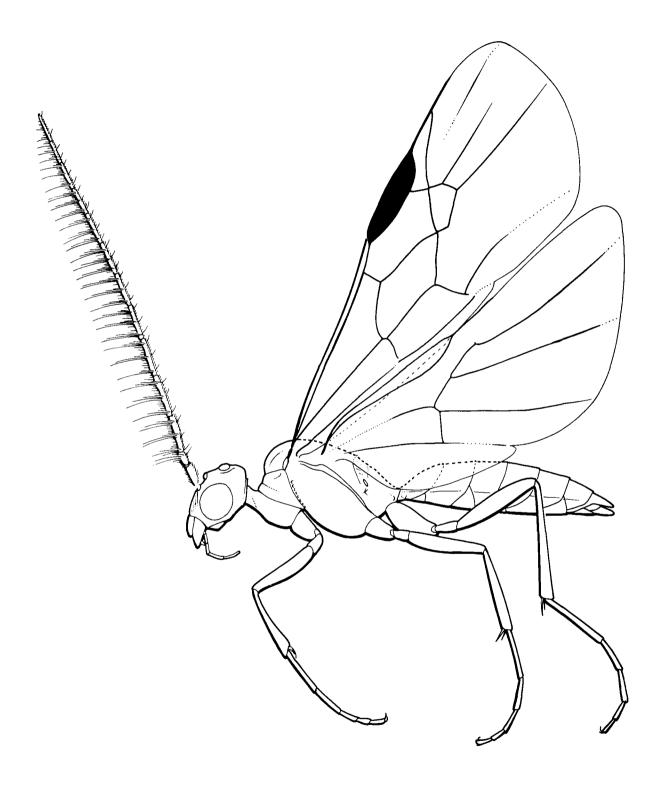


Fig. 35. Plumariidae

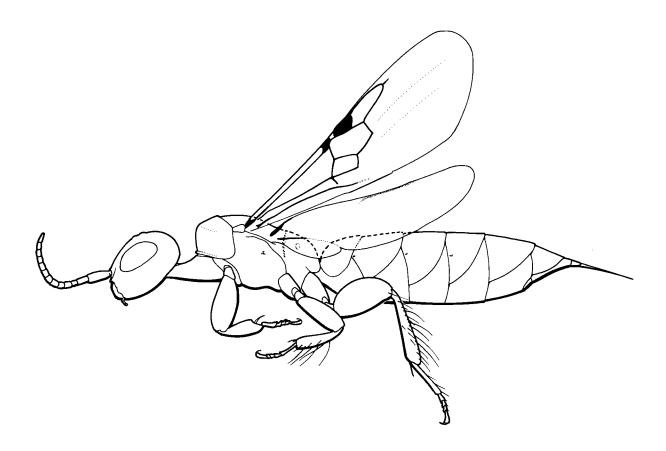


Fig. 36. Scolebythidae

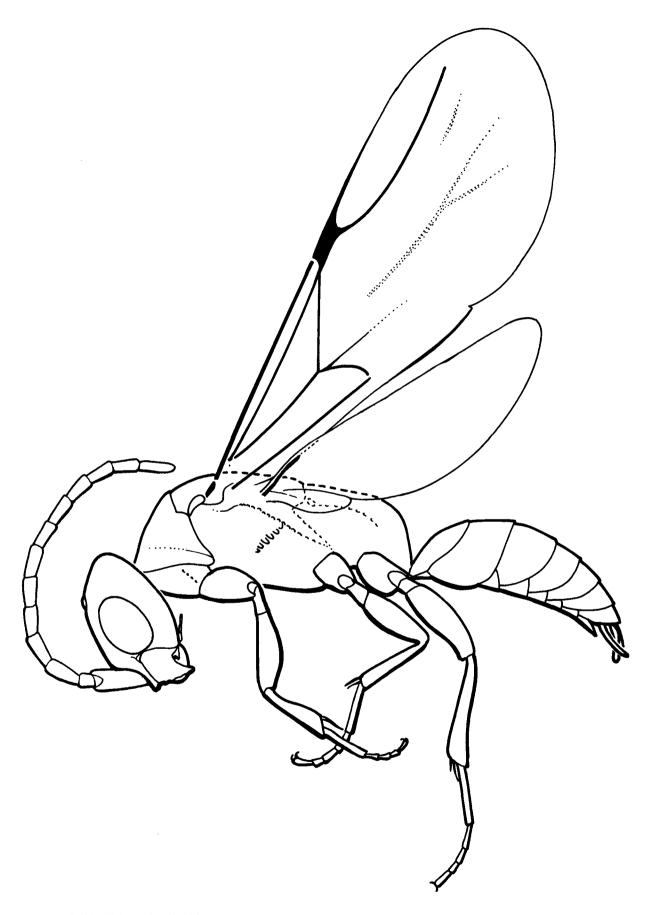


Fig. 37. Bethylidae: Pristocerinae (male)

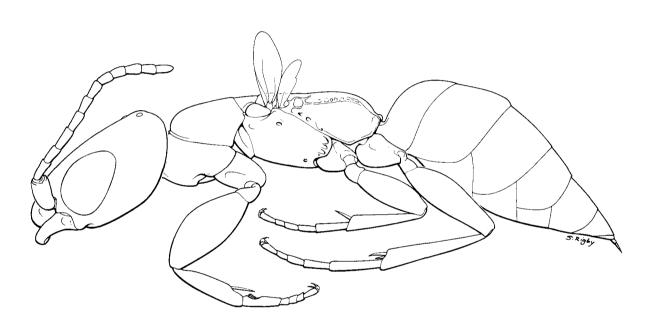


Fig. 38. Bethylidae: Bethylinae (female)

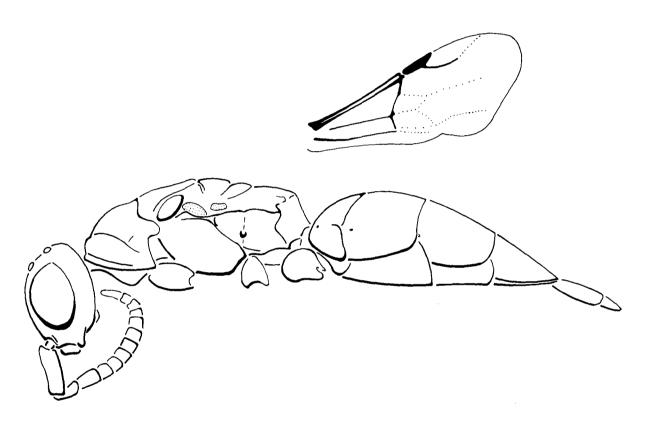
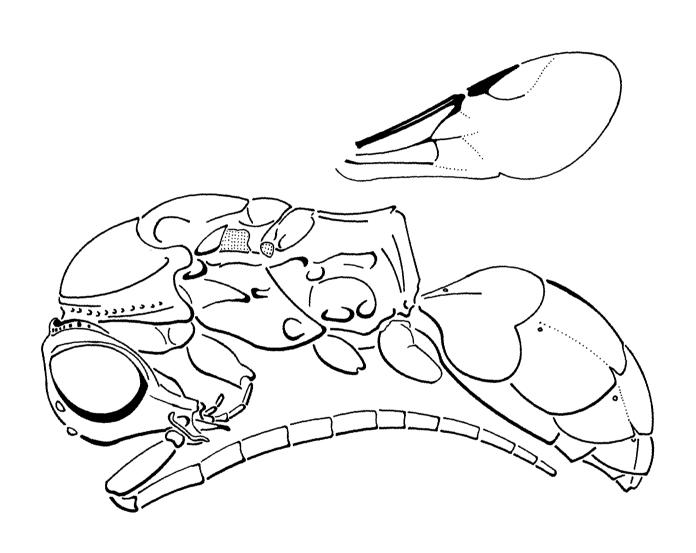


Fig. 39. Chrysididae: Cleptinae



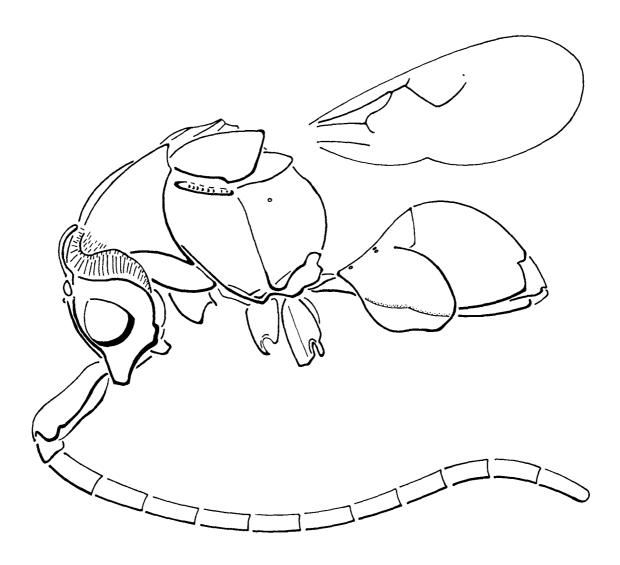


Fig. 41. Chrysididae: Loboscelidiinae

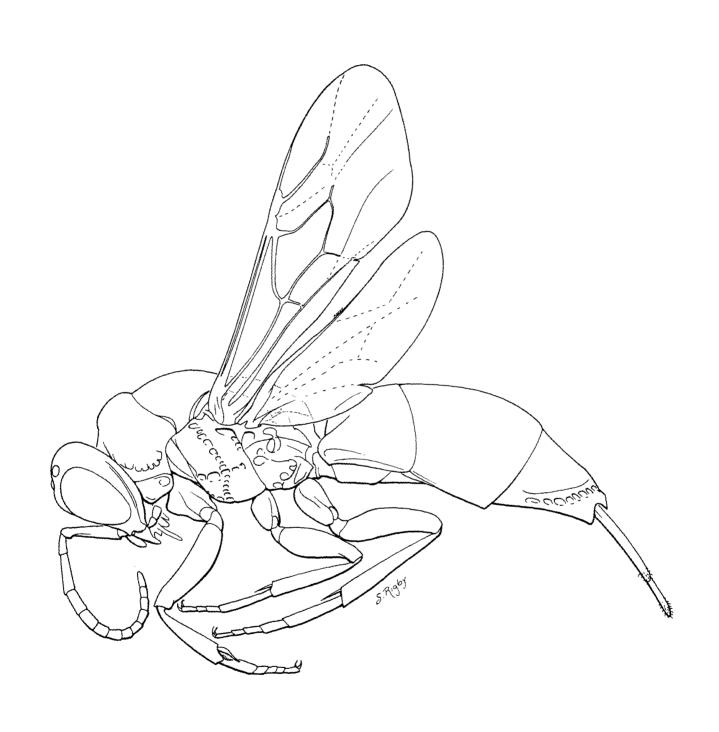


Fig. 42. Chrysididae: Chrysidinae

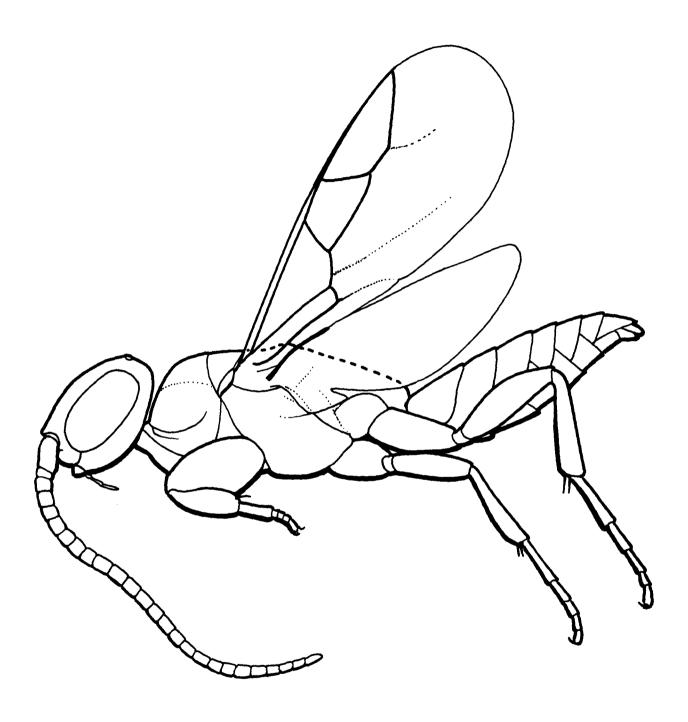


Fig. 43. Sclerogibbidae



Fig. 45. Embolemidae

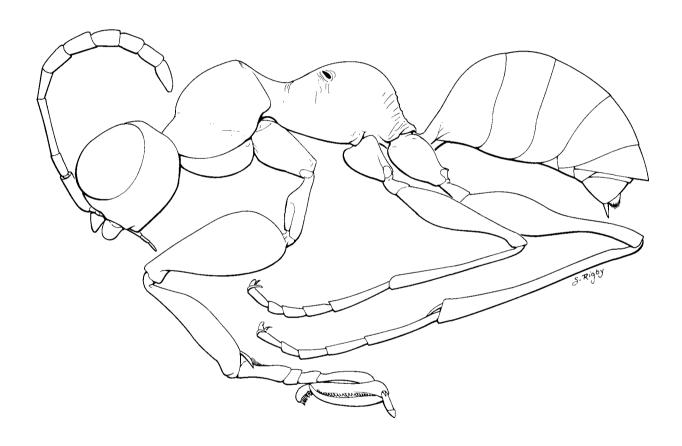


Fig. 44. Dryinidae: Gonatopodinae

## Chapter 8 Superfamily Vespoidea

(Figs. 46-92)

Denis J. Brothers and Albert T. Finnamore

Included families (10): Bradynobaenidae, Formicidae, Mutillidae, Pompilidae, Rhopalosomatidae, Sapygidae, Scoliidae, Sierolomorphidae, Tiphiidae, Vespidae.

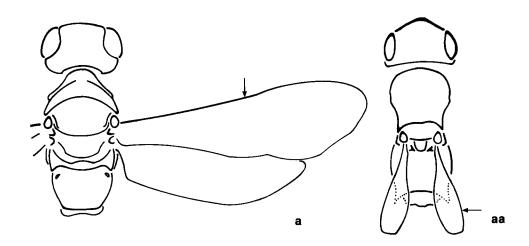
**Diagnosis** Antenna with 10 flagellomeres in female and 11 in male; pronotum with posterolateral apex reaching or exceeding tegula, the posterodorsal margin shallowly to very deeply concave but seldom broadly U-shaped, with lobe covering spiracle scarcely developed or only weakly convex and with lateroventral extremities broadly separated; metapostnotum short, transverse, fused with propodeum and sometimes exposed but not posteriorly expanded in middle; wing venation well developed, usually 10 or 9 closed cells in fore wing and 2 closed cells in hind wing (sometimes fewer); hind wing usually with jugal lobe; metasomal sterna 1 and 2 often separated by a constriction; female without an articulation within gonocoxite 2; ovipositor concealed at rest and modified as a sting; plumose setae usually absent. Sexual dimorphism slight to extreme: male macropterous but very rarely brachypterous or apterous; female usually macropterous but sometimes brachypterous or apterous.

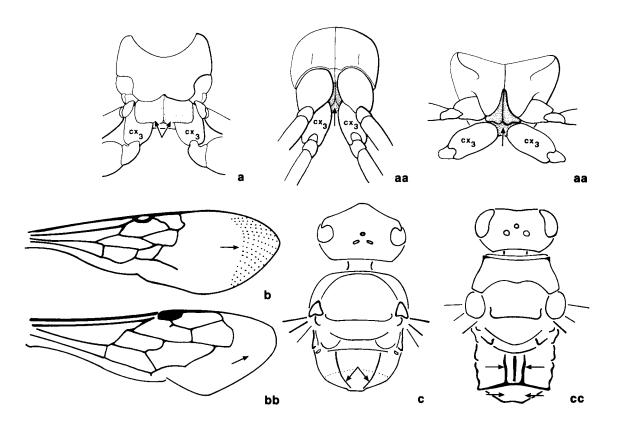
Comments Vespoidea includes two of the most frequently encountered groups of Aculeata, paper-nesting wasps and ants, both highly social. In addition, several groups of solitary predators or parasitoids comprise the vast majority of the wasp component of the superfamily. Species of Vespoidea exhibit a complete range of behavior, not only from parasitoid to predator, scavenger or specialized phytophage, but also from solitary to highly social with formation of large colonies and

morphological and behavioral caste differentiation. The parasitoid groups tend to parasitize the larvae of soil-dwelling Coleoptera or soil-nesting wasps and bees. Cleptoparasites generally parasitize colonies or nests of related genera within their respective families, although a few parasitize unrelated Hymenoptera. The predators and scavengers prey on a wide variety of other insects and spiders (Araneae), a female usually provisioning each cell with several prey as food for the larva. The plant-feeding groups tend to specialize on seeds, pollen or specially cultivated fungi.

Vespoidea is mainly tropical, with perhaps 48 000 species around the world, about half undescribed. About 1950 species occur in the Nearctic region, including about 312 species in Canada. The numbers of genera and species given below for each family and subfamily include only those that are described, unless otherwise indicated. Acceptance of Vespoidea as comprising the traditional Scolioidea, Pompiloidea, Vespoidea, and Formicoidea, as well as the delimitations of the various families, is based on the works of Brothers (1975), Carpenter (1982) and Brothers and Carpenter (1993), who reexamined and extended earlier analyses. The key to families is based on the world fauna. Because sexual or other dimorphism is common, especially with respect to degree of wing development and associated mesosomal adaptations, apterous and brachypterous specimens tend to be rather different from the macropterous forms and are keyed separately. In this chapter the wing vein and cell terminology of Gauld and Bolton (1988) is used. A table of updated Comstock-Needham equivalents is given in Chapter 7 (p. 130).

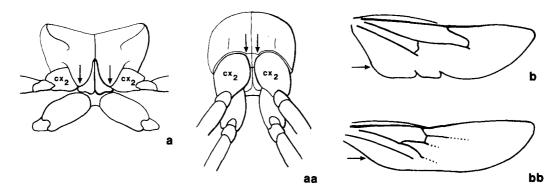
## **Key to families of VESPOIDEA**





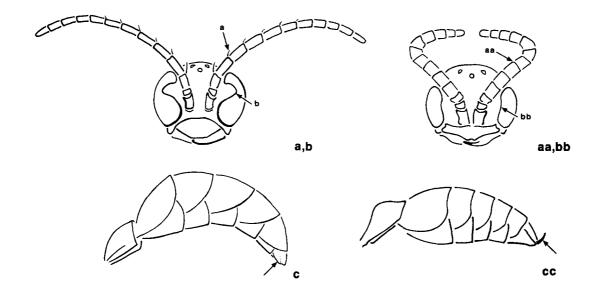
- a. Metacoxae (cx<sub>3</sub>) widely separated (rarely less so) by wide flat metasternum at same level as mesosternum; metacoxa partly concealed basally by wide lamina.
  - b. Wing membranes finely longitudinally wrinkled apically.

- aa. Metacoxae (cx<sub>3</sub>) almost contiguous; metasternum not wide and usually not at same level as mesosternum; metacoxa not concealed basally by lamina (i.e., metasternum not expanded posterolaterally).
- bb. Wing membranes without definite fine longitudinal wrinkles apically but with surface sometimes irregular.
- cc. Propodeum without 2 longitudinal grooves traversing both disc and declivity ........... 3



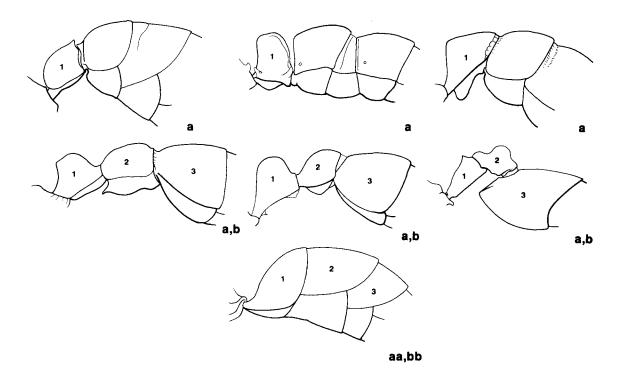
- 3(2) a. Mesosternum expanded posteromedially as a pair of small laminae overlying bases of mesocoxae  $(cx_2)$ .

  - aa. Mesosternum not expanded posteromedially over bases of mesocoxae (cx<sub>2</sub>), although sometimes acutely margined.

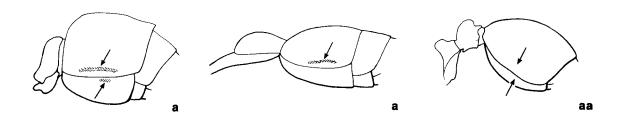


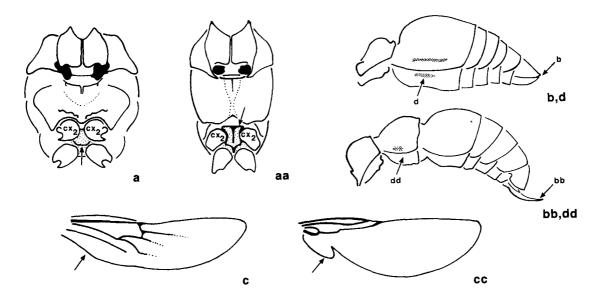
- 4(3) a. Antenna with apical spine-like setae on at least flagellomeres 5 and 6, at most on 1-6.
  - b. Eye with inner margin strongly emarginate.

  - aa. Antenna without apical spine-like setae on any flagellomere.
  - bb. Eye with inner margin convex or very shallowly sinuate, seldom broadly emarginate.
  - cc. Male with last visible metasomal sternum usually spine-like apically, often forming upcurved hook; sternum sometimes simple or partly concealed ...... most **TIPHIIDAE** (p. 178)



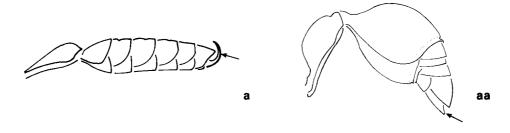
- a. Metasomal segment 1 node-like, in lateral view with tergum expanded in middle and more or less abruptly constricted at both ends.
  - b. Metasomal segment 2 sometimes node-like or with distinct dorsal and ventral constrictions between segments 2 and 3 and usually no constrictions between subsequent segments . . . . . 6
  - aa. Metasoma without node-like segments; tergum 1 in lateral view not markedly or abruptly constricted apically, although sometimes somewhat swollen in middle and/or tergum 2 sometimes narrowed anteriorly.





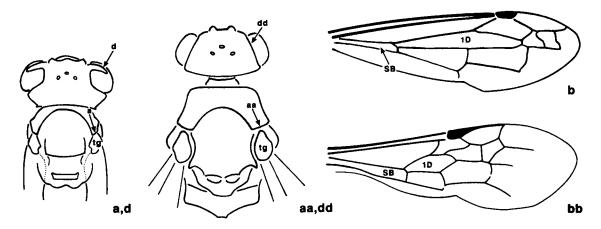
- a. Metasternum mostly concealed, not anteriorly produced but strongly depressed anteromedially to accommodate contiguous mesocoxae (cx<sub>2</sub>).
  - b. Metasoma with last visible sternum simple, bilobed, or emarginate apically, not hook-like.
  - c. Hind wing usually without jugal lobe, but sometimes with lobe.

  - aa. Metasternum conspicuous and slightly produced anteriorly between separated mesocoxae (cx<sub>2</sub>), not at all depressed.
  - bb. Metasoma with last visible sternum usually forming a strong medial upcurved hook; sternum sometimes simple.
  - cc. Hind wing usually with jugal lobe, but rarely without lobe.
  - dd. Metasomal sternum 2 without felt line ...... some male BRADYNOBAENIDAE (p. 207)



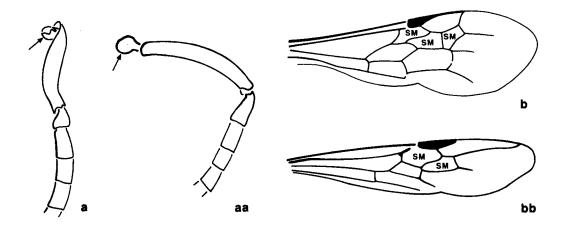
- **8(6)** a. Last visible metasomal sternum forming medial upcurved hook.

  - aa. Last visible metasomal sternum usually simple, never forming medial upcurved hook.



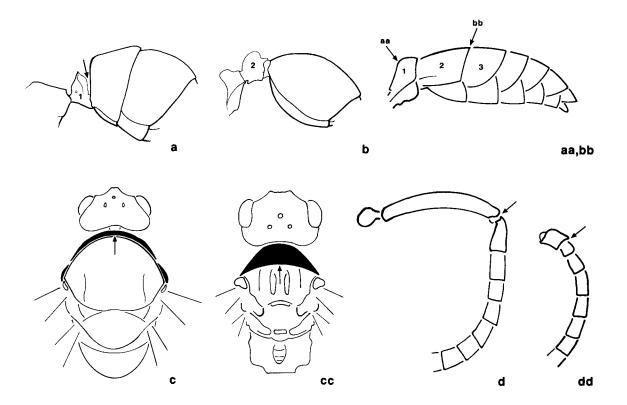
- **9(8)** a. Pronotum with posterolateral apex distinctly angulate or rectangular, extending slightly above and beyond anterior margin of tegula (tg).
  - b. Fore wing with first discal cell (1D) at least as long as subbasal cell (SB) but rarely shorter.
  - c. Fore wing usually folded longitudinally, but sometimes flat.

  - aa. Pronotum with posterolateral apex usually rounded or truncate, not extending beyond anterior margin of tegula (tg).
  - bb. Fore wing with first discal cell (1D) much shorter than subbasal cell (SB).
  - cc. Fore wing flat, not folded longitudinally.
  - dd. Eye with inner margin usually convex or shallowly sinuate, but rarely strongly emarginate



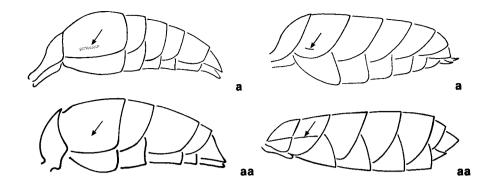
- a. Scape with radicle inserted at right angle to long axis of scape and usually concealed in basal depression of scape.

  - aa. Scape with radicle scarcely deviating from long axis of scape and not concealed in base of scape.



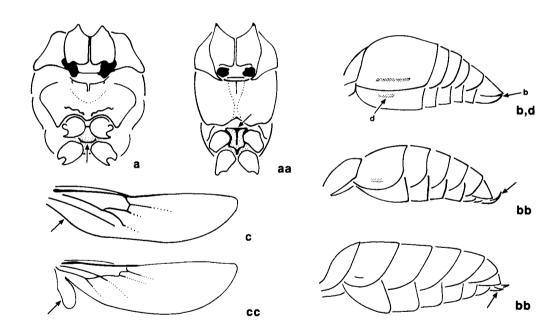
- a. Metasomal segment 1 strongly node-like with tergum very strongly constricted posteriorly, but very rarely weakly so.
  - b. Metasomal segment 2 sometimes node-like or with conspicuous dorsal and ventral constrictions between segments 2 and 3.
  - c. Pronotum with posterodorsal margin usually deeply concave and length of dorsal surface (measured medially excluding anterior flange) usually less than one-third the length of mesoscutum, but pronotum sometimes with posterodorsal margin shallowly concave and dorsal surface longer.

  - aa. Metasomal segment 1 scarcely node-like, with tergum weakly constricted posteriorly.
  - bb. Metasomal segments 2 and 3 without constriction between them.
  - cc. Pronotum with posterodorsal margin shallowly concave, with length of dorsal surface (measured medially excluding anterior flange) more than half the length of mesoscutum.



- a. Metasomal tergum 2 and/or sternum 2 laterally with felt line of dense recumbent setae or with deep lateral longitudinal groove (groove sometimes obscured by long hairs); if groove shallow and inconspicuous then separated from anterior margin and shorter than sclerite.
  - b. Last visible metasomal sternum sometimes with 3 spines apically, but sternum usually simple.

  - aa. Metasomal tergum 2 and sternum 2 without felt line and without lateral longitudinal groove; if fine groove present then extending from anterior margin to almost full length of sclerite.
  - bb. Last visible metasomal sternum usually simple, never with 3 spines apically.
  - cc. Fore wing with marginal and/or submarginal cells enclosed by tubular veins ...... 14



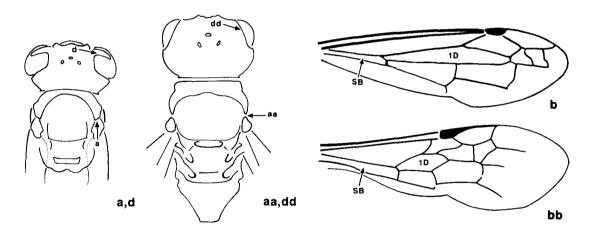
- a. Metasternum mostly concealed, not anteriorly produced but strongly depressed anteromedially to accommodate contiguous mesocoxae.
  - b. Metasoma with last visible sternum simple or emarginate apically, rarely with 2 weak spines but never with medial hook or 3 spines.
  - c. Hind wing usually without jugal lobe, rarely with lobe.

- aa. Metasternum conspicuous and slightly produced anteriorly between separated mesocoxae, not at all depressed.
- bb. Metasoma with last visible sternum usually with medial hook or with 3 strong spines apically, but sternum sometimes simple.
- cc. Hind wing usually with jugal lobe, but rarely without lobe.
- dd. Metasomal sternum 2 without felt line ...... some male **BRADYNOBAENIDAE** (p. 207)



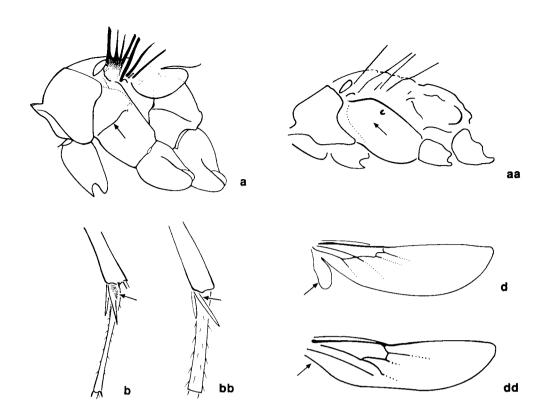
- 14(12) a. Last visible metasomal sternum forming medial upcurved hook.

  - aa. Last visible metasomal sternum usually simple, never forming medial upcurved hook.

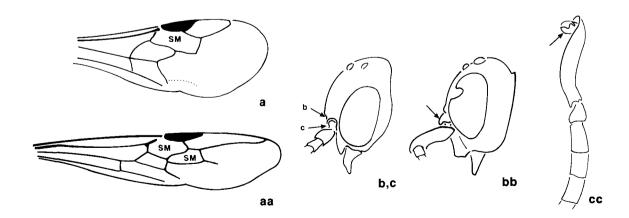


- a. Pronotum with posterolateral apex distinctly angulate or rectangular, extending slightly above and beyond anterior margin of tegula.
  - b. Fore wing with first discal cell (1D) at least as long as subbasal cell (SB), but rarely shorter.
  - c. Fore wing usually folded longitudinally, but sometimes flat.

  - aa. Pronotum with posterolateral apex usually rounded or truncate, not extending beyond anterior margin of tegula.
  - bb. Fore wing with first discal cell (1D) much shorter than subbasal cell (SB).
  - cc. Fore wing flat, but very rarely folded longitudinally.

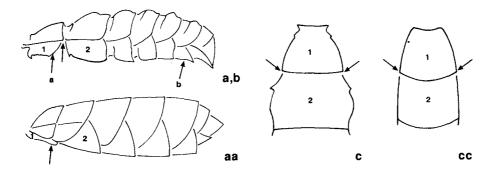


- 16(15) a. Mesepisternum with straight oblique groove traversing entire sclerite, but groove rarely absent.
  - b. Hind leg posterior (inner) tibial spur with tuft or row of fine brush-like setae basally, coadapted with highly setose brush-like region at base of tarsomere 1.
  - Legs usually conspicuously long and slender, with apex of metatibia often exceeding apex of metasoma.
  - d. Hind wing with jugal lobe ..... most **POMPILIDAE** (p. 203)
  - aa. Mesepisternum without straight oblique groove traversing entire sclerite, but sometimes with depression or pit.
  - bb. Hind leg posterior (inner) tibial spur without tuft or row of brush-like setae basally, although spur often entirely or predominantly finely setose; tarsomere 1 more or less evenly setose, without definite basal brush-like area.
  - cc. Legs not conspicuously long, with apex of metatibia not exceeding apex of metasoma.



a. Fore wing with only 1 submarginal cell (SM) enclosed by tubular veins, the cell virtually rectangular and as wide apically as basally.

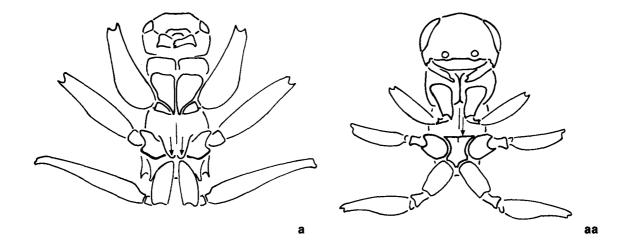
- b. Torulus on lower surface of slight medial swelling of frons and not partly concealed under well-defined transverse carina or laminate tubercle.
- c. Scape with radicle scarcely deviating from long axis of scape and not concealed in base of scape.
- d. Body weakly sculptured, mostly shining ..... most SIEROLOMORPHIDAE (p. 202)
- aa. Fore wing with 2 or more submarginal cells (SM) enclosed by tubular veins; if (rarely) only 1 cell, then cell irregularly triangular to pentagonal and much narrower apically than basally.
- bb. Torulus partly concealed under well-defined transverse carina or laminate tubercle.
- cc. Scape with radicle strongly deviating from long axis of scape and often concealed in basal depression of scape.

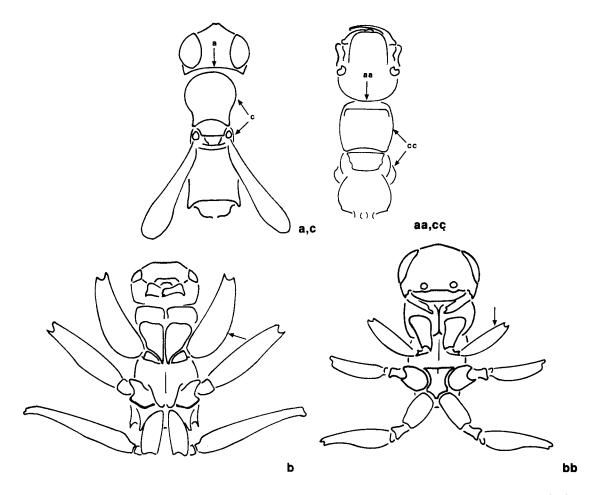


- **18(17)** a. Metasomal sternum 1 evenly and strongly depressed posteriorly, not overlapping sternum 2; in lateral view a strong constriction occurring between sterna 1 and 2.
  - b. Metasomal sternum 6 simple and transverse, not conical, ending well anterior to apex of metasoma.

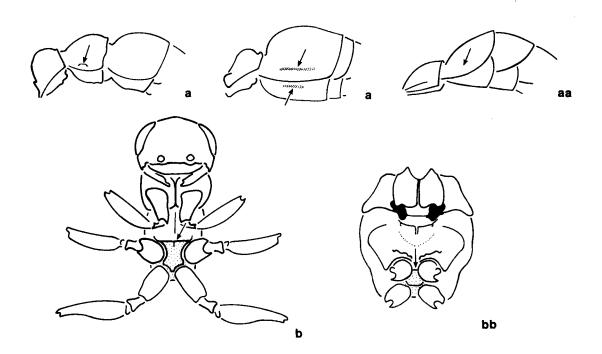
  - aa. Metasomal sternum 1 not depressed (except rarely at apical margin), overlapping sternum 2 slightly; in lateral view no strong constriction occurring between sterna 1 and 2.
  - bb. Metasomal sternum 6 sometimes conical, surrounding sting and extending beyond last tergum, but often simple and transverse and ending well anterior to apex of metasoma.
  - cc. Metasomal tergum 1 as wide as anterior of tergum 2, their sides forming an even contour ....

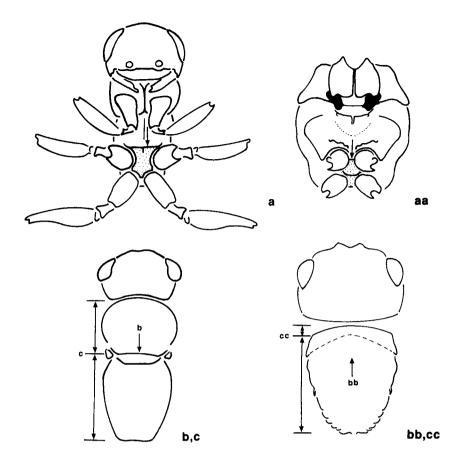
    SAPYGIDAE (p. 186)



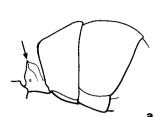


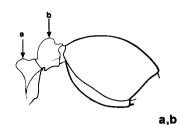
- 20(19) a. Head with entire posterior surface concave; vertex and gena bordered posteriorly by a continuous carina.
  - b. Profemur strongly swollen, much thicker than other femora.
  - c. Mesothorax narrower than prothorax ...... some **RHOPALOSOMATIDAE** (p. 205)
  - aa. Head with posterior surface convex or flat; vertex and gena without continuous carina.
  - bb. Profemur not swollen, no thicker than other femora.

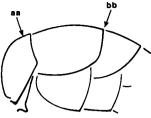




- a. Metasternum conspicuous, anteriorly extended between separated mesocoxae and not at all depressed.
  - b. Pronotum movable, articulating with mesothorax by distinct suture, and with posterodorsal margin straight or only slightly concave.
  - c. Pronotal length (measured medially excluding anterior flange), at least two-thirds dorsal length of fused mesonotum-propodeum ................ female BRADYNOBAENIDAE (p. 206)
  - aa. Metasternum mostly concealed, not anteriorly extended but strongly depressed anteromedially to accommodate contiguous mesocoxae.
  - bb. Pronotum usually indistinguishably fused with mesothorax, and sometimes with suture demarcating deeply concave posterodorsal margin.

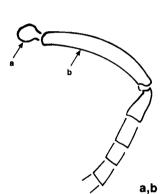


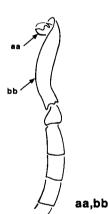


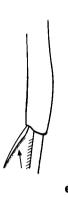


- aa,bb
- a. Metasoma with segment 1 node-like, in lateral view tergum 1 expanded in middle and more or less abruptly constricted at both ends.

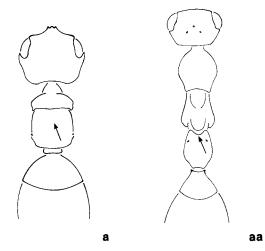
  - aa. Metasoma without node-like segments; in lateral view tergum 1 not markedly or abruptly constricted apically, although sometimes somewhat swollen in the middle **and/or** tergum 2 sometimes narrowed anteriorly.





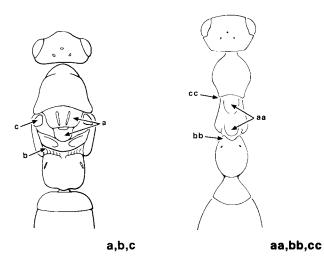


- 24(23)
- a. Scape with radicle not deviating much from long axis of scape and not concealed in basal depression of scape.
- b. Scape more than five times as long as wide.
- c. Metasomal segment 2 sometimes node-like or with distinct dorsal and ventral constrictions between segments 2 and 3.
- d. Suture between mesonotum and metanotum sometimes distinct, but often indistinct or absent.
- aa. Scape with radicle inserted at right angles to long axis of scape, usually concealed in basal depression of scape.
- bb. Scape less than four times as long as wide.
- cc. Metasomal segments 2 and 3 without constriction between them.
- dd. Suture between mesonotum and metanotum never distinct.



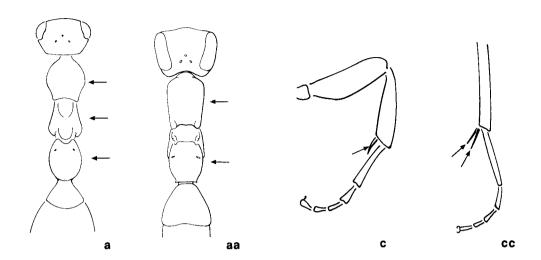
- a. Suture between mesonotum and metanotum not distinct; dorsum of mesosoma comprising at most 2 distinct regions.
  - b. Mesosoma squat, usually less than twice as long as wide.

  - aa. Suture between mesonotum and metanotum distinct, often movable; dorsum of mesosoma comprising 3 or more distinct regions, very rarely only 2 regions.
  - bb. Mesosoma usually elongate, often at least three times as long as wide.



- a. Mesonotum with conspicuous and well-differentiated scutum and scutellum; mesothorax slightly larger than propodeal region.
  - b. Metanotum separated from metapostnotum by distinct articulating suture; metapostnotum forming distinct depressed area along anterior margin of propodeum.
  - c. Tegula well developed.

  - aa. Mesonotum with scutum and scutellum usually poorly differentiated; mesothorax usually distinctly smaller than propodeal region, but sometimes same size.
  - bb. Metanotum indistinguishably fused to propodeum; metapostnotum not visible.
  - cc. Tegula usually absent or minute, but rarely well-developed.



27(26)

- a. Mesosoma divided into 3 distinct regions (prothorax, mesothorax, and metathorax–propodeum), with strong constriction laterally between mesothorax and metathorax.
- b. Mesepisternum without oblique transverse groove.
- c. Metatibia often with 1 apical spur, sometimes with 2 . . . . . . a few female **TIPHIDAE** (p. 178)
- aa. Mesosoma divided into 2 distinct regions (prothorax and mesothorax-metathorax-propodeum), without constriction laterally between mesothorax and metathorax.
- bb. Mesepisternum often with straight oblique groove traversing entire sclerite, but groove sometimes absent.

## Family TIPHIIDAE

(Figs. 46-54)

**Diagnosis** Dorsal rim of torulus usually simple but often tuberculate or produced as a transverse ridge or swelling of frons; eye with inner margin convex or more or less straight, seldom emarginate. Pronotum with posterodorsal margin usually weakly concave but sometimes U-shaped, and with posterolateral apex usually rounded but sometimes truncate anterior to tegula; mesosternum with laminate expansions on each side of midline covering bases of contiguous mesocoxae, the expansions rarely reduced to small teeth; metacoxae contiguous; hind wing with distinct claval and jugal lobes; female usually with mesotibia and metatibia stout and heavily spined. Metasoma usually sessile but sometimes briefly petiolate; metasomal segment 1 without a true node, although sometimes approaching it; metasomal sternum 1 usually separated from sternum 2 by a deep constriction but sometimes without any constriction; male metasomal sternum 8 (hypopygium) usually forming a single strong acute upcurved hook, the hypopygium sometimes simple or with 2-5 spines, and usually entirely exposed but

sometimes partly concealed. Sexual dimorphism slight to extreme: male macropterous; female usually macropterous or apterous, sometimes brachypterous; brachypterous and apterous forms with mesosoma different from that in macropterous form, the pronotum freely articulating, the mesonotum and propodeum (at least) also distinct.

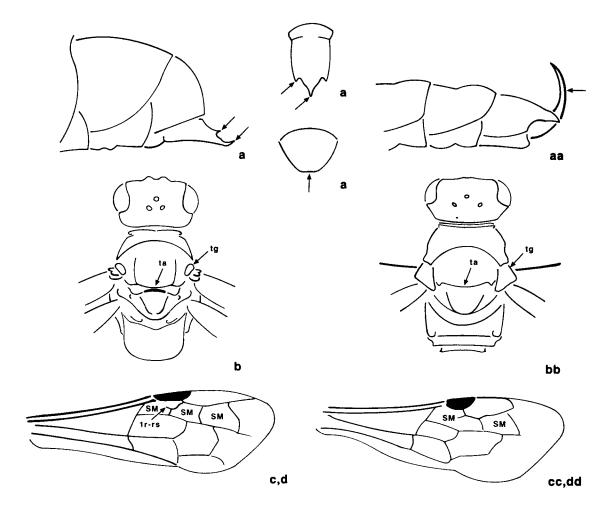
Comments Tiphiidae is a varied, cosmopolitan, but predominantly tropical family containing about 1500 species in seven subfamilies: Anthoboscinae, Brachycistidinae, Diamminae, Methochinae, Myzininae, Thynninae, and Tiphiinae. Adults generally are predominantly black, sometimes marked with yellow or red. Sex associations are often very difficult, especially in groups with seldom-collected apterous females. All species are solitary. The larvae are usually ectoparasitoids of the larvae of soil-dwelling Coleoptera, pupation occurring within the substrate occupied by the host. The five North American subfamilies (about 220 species in 21 genera) extend to southern Canada, where about 26 species (about six genera) occur.

# Key to subfamilies of TIPHIIDAE

#### Denis J. Brothers

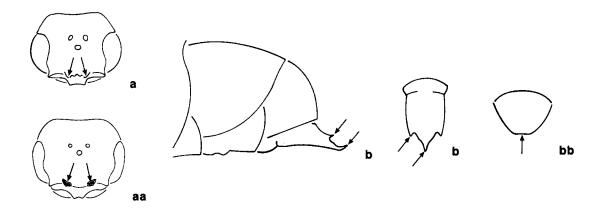
(For characters of Diamminae see account of Thynninae, below.)

1 Fully winged or short-winged (fore wing usually at least as long as mesosoma). b. Male or female ..... aa. Wingless (fore wing completely absent or no longer than tegula). aa aa 2(1) Male: metasoma with 7 exposed terga; antenna with 11 flagellomeres (fl) (pedicel sometimes Female: metasoma with 6 exposed terga; antenna with 10 flagellomeres (fl) (pedicel sometimes dd 3(2) Tarsal claws simple and smooth ventrally. Mesotibia with 1 apical spur. Body pale to dark brown, rarely black, without bright markings. Ocelli usually conspicuously enlarged, seldom small ...... male Brachycistidinae Tarsal claws toothed or cleft ventrally. Mesotibia usually with 2 apical spurs, but rarely only 1. cc. Body usually black, often with red or yellow markings. dd. Ocelli small, but rarely conspicuously enlarged .....

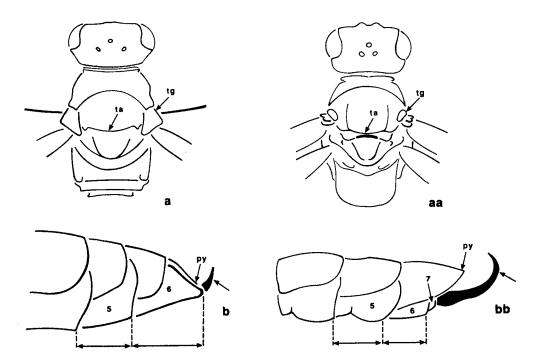


- a. Metasomal sternum 8 (hypopygium) with apex simple, or bluntly produced, or variously spine-like; if hypopygium 8 with a single strong acute upcurved hook then the hook dorsoventrally flattened and flanked by lateral teeth basally or issuing from ventral surface before apex; sternum 6 not enlarged.
  - b. Tegula (tg) short and semicircular, exposing humeral and median plates and ending well anterior to level of transscutal articulation (ta).
  - c. Fore wing with 3 submarginal cells (SM) enclosed by tubular veins.

  - aa. Entire metasomal sternum 8 (hypopygium) modified as a single strong acute upcurved hook, the hook often exposed but sometimes partly or entirely concealed by enlarged sternum 6.
  - bb. Tegula (tg) sometimes elongate or nearly circular, concealing humeral and median plates and ending at or posterior to level of transscutal articulation (ta), but often short and semicircular, exposing humeral and median plates and ending well anterior to level of transscutal articulation.
  - cc. Fore wing sometimes with 2 submarginal cells (SM) enclosed by tubular veins, but often with 3.

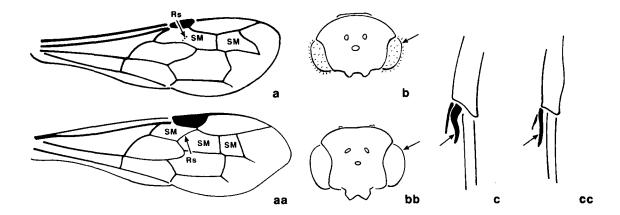


- a. Torulus partly or entirely concealed from above under well-defined transverse carina or laminat tubercle; if torulus exposed from above then from slightly obliquely swollen above toruli, and with a strong vertical carina between toruli.
  - b. Metasomal sternum 8 (hypopygium) with apex often bluntly produced or variously spine-like, but sometimes simple and rounded ....................... male Thynninae and Diamminae
  - aa. Torulus entirely exposed from above; frons flat or more or less evenly convex.
  - bb. Metasomal sternum 8 (hypopygium) with apex simple and rounded ..... male Anthoboscinae

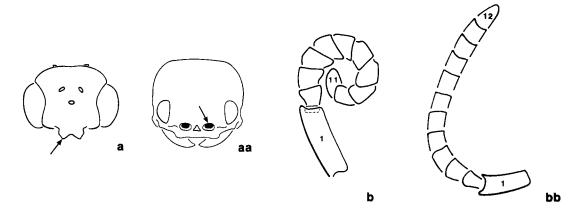


- a. Tegula (tg) elongate or nearly circular, concealing humeral and median plates and ending at or posterior to level of transscutal articulation (ta).

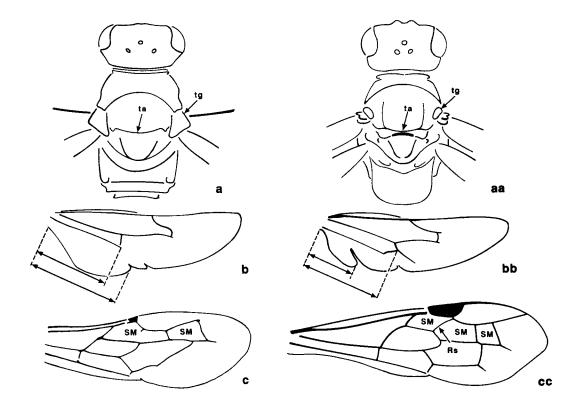
  - aa. Tegula (tg) short and semicircular, exposing humeral and median plates and ending well anterior to level of transscutal articulation (ta).



- a. Fore wing apparently with only 2 submarginal cells (SM) enclosed by tubular veins, vein Rs between true first and second submarginal cells reduced or absent, at least anteroapically.
  - b. Eye covered with conspicuous long setae.
  - c. Metatibia with posterior (inner) apical spur distinctly S-shaped ..... male Methochinae
  - aa. Fore wing with 3 submarginal cells (SM) enclosed by tubular veins, vein Rs between first and second cells complete.
  - bb. Eye bare, without any setae.
  - cc. Metatibia with posterior (inner) apical spur more or less straight .......... male Myzininae

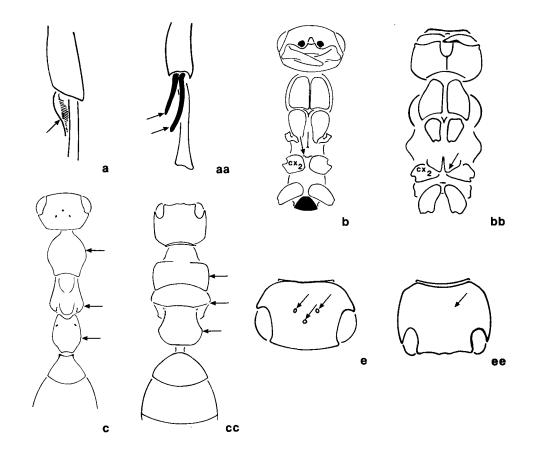


- a. Torulus partly or entirely concealed from above under well-defined transverse carina or laminate tubercle formed by elaboration of from above and/or between toruli.
  - b. Antenna usually apparently with 11 segments (pedicel reduced and concealed in apex of scape), but rarely with 12 distinct segments ....... most female Myzininae
  - aa. Torulus entirely exposed from above; frons flat or more or less evenly convex.
  - bb. Antenna with 12 distinct segments (pedicel not concealed in apex of scape) ............

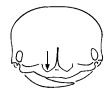


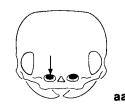
- a. Tegula (tg) elongate or nearly circular, concealing humeral and median plates and ending at or posterior to level of transscutal articulation (ta).
  - b. Hind wing with jugal lobe longer than subbasal cell.

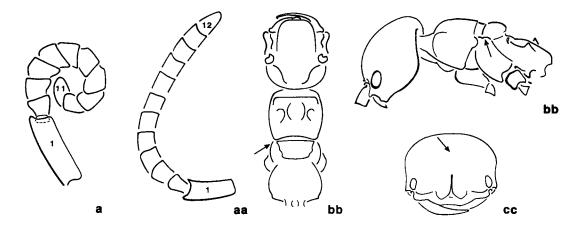
  - aa. Tegula (tg) short and semicircular, exposing humeral and median plates and ending well anterior to level of transscutal articulation (ta).
  - bb. Hind wing with jugal lobe shorter than subbasal cell.
  - cc. Fore wing with 3 submarginal cells (SM) enclosed by tubular veins, vein Rs between first and second cells complete ...... female Anthoboscinae



- a. Metatibia with 1 apical spur, the spur S-shaped and finely comb-like dorsally; mesotibia with 1 apical spur, the spur comb-like dorsally.
  - b. Mesocoxa (cx<sub>2</sub>) entirely exposed, with mesosternum having at most a minute transverse tooth posteromedially.
  - c. Prothorax, mesothorax, and metathorax-propodeum forming three distinct, similar, and almost equal regions separated by marked constrictions; metathorax-propodeum almost globose.
  - d. Legs long and slender, with femora and tibiae elongate and subcylindrical.
  - e. Ocelli present ..... female Methochinae
  - aa. Metatibia usually with 2 apical spurs, rarely 1, the spurs fairly straight and smooth dorsally; mesotibia usually with 2 but sometimes 1 apical spur, the spurs smooth dorsally.
  - bb. Mesocoxa (cx<sub>2</sub>) usually partly concealed basally by posteromedial laminate expansion of mesosternum overlying coxa, but mesocoxa rarely partly exposed.
  - cc. Prothorax, mesothorax, and metathorax-propodeum neither similar nor almost equal, with some regions not separated by marked constrictions; metathorax-propodeum not almost globose, its margin(s) often angled.
  - dd. Legs usually short and stout with femora and tibiae squat and/or flattened, but rarely slender.







- a. Antenna apparently with 11 segments (pedicel not visible from above but reduced and concealed in apex of scape).
  - b. Tegula distinctly present.

  - aa. Antenna with 12 distinct segments (pedicel visible from above and not entirely concealed in apex of scape).
  - bb. Tegula usually absent, but rarely present and indistinct.
  - cc. Ocelli absent, but rarely represented by nonfunctional traces . . . . . . most female **Thynninae**



- **13(11)** a. Tarsal claws simple and smooth ventrally.
  - b. Mesonotum and mesopleuron entirely fused, the suture between them indistinct or absent.

  - aa. Tarsal claws usually toothed or cleft ventrally, but rarely simple and smooth.
  - bb. Mesonotum and mesopleuron not entirely fused, the suture between them distinct.

#### **Subfamily Anthoboscinae**

(Fig. 46)

This widespread subfamily, which is absent from the Oriental region, includes several species in six genera. Sexual dimorphism is slight; both males and females are usually predominantly black without extensive bright markings. The larvae are probably ectoparasitoids on the larvae of Scarabaeoidea (Coleoptera). The only North American species, found in the western United States, may also occur in Canada in the dry valleys of southern British Columbia.

### **Subfamilies Thynninae and Diamminae**

(Figs. 47, 48)

This austral group, found in the Australian and Neotropical regions, includes many species in 51 genera. Sexual dimorphism is extreme; males are usually predominantly dark but often with extensive bright markings, especially yellow or white, and females are generally mostly dark without bright markings. The larvae are ectoparasitoids on the larvae of Scarabaeoidea (Coleoptera); one species parasitizes Gryllotalpidae (Grylloptera). A few species have been used for biological control. Kimsey (1991) recognized a separate subfamily, Diamminae, for the gryllotalpid parasitoid. Females are recognized by their metallic bluish body color and the reduction of the metapleuron to a strip hidden by the mesopleuron, except at its dorsal extremity; males have veins 1m-cu and 2m-cu both received by submarginal cell 2 (in Thynninae received by submarginal cells 1 and 2 respectively or with 2m-cu rarely aligned with 2 rs-m), and the hypopygium is thickened and obtusely rounded apically (rarely so in Thynninae where the hypopygium is usually variously spined).

### Subfamily Myzininae

(Fig. 49)

This widespread subfamily includes many species in 12 genera. Sexual dimorphism is moderate to extreme; males are usually predominantly dark but often with extensive bright markings, especially yellow, and females are generally mostly dark with less extensive bright markings; adults of some species are extensively red or even metallic green. The larvae are usually ectoparasitoids on the larvae of soil-dwelling

Scarabaeoidea, but a few parasitize the larvae of Cicindelinae or timber-dwelling Cerambycidae (all Coleoptera). Fourteen species in two genera occur in North America, including one species in Canada.

### **Subfamily Methochinae**

(Figs. 50, 51)

This widespread subfamily, which is absent from the Australian region, includes few species in two genera. Sexual dimorphism is extreme; males are usually black, and females are mostly black and/or red. The larvae are ectoparasitoids on the larvae of soil-dwelling Cicindelinae (Coleoptera). Four species in one genus occur in North America, including one species in Canada.

### **Subfamily Tiphiinae**

(Fig. 52)

This cosmopolitan subfamily includes many species in nine genera. Sexual dimorphism is slight to moderate; both males and females are usually black but sometimes with red appendages and seldom with bright yellow markings. The larvae are ectoparasitoids on the larvae of Scarabaeoidea (Coleoptera). A few species have been used for biological control. One hundred and forty-two species in five genera occur in North America, including 20 species in two genera in Canada.

### **Subfamily Brachycistidinae**

(Figs. 53, 54)

This Nearctic subfamily, which is restricted to arid regions of western North America, includes several species in 13 genera. Sexual dimorphism is extreme; both males and females are generally pale to dark brown. The adults are usually nocturnal, and the larvae are probably ectoparasitoids on the larvae of Scarabaeoidea (Coleoptera). Sixty-one species in 12 genera (six including only males, five only females, and one both sexes) occur in North America, including three species in one genus in southwestern Canada.

**References** Pate (1947a) keyed the world subfamilies, and Brothers (1975), Kimsey (1991) and Brothers and Carpenter (1993) revised the subfamily divisions. Tobias (1978b) keyed the species of European USSR, and Gorbatovski (1981) those of far eastern USSR. Krombein (1982)

revised the species of Sri Lanka. Turner (1912) reviewed the world Anthoboscinae, and Genise (1984) treated the Neotropical species. Turner (1910) treated the world genera of Thynninae, and Given (1954) provided a catalog of the Thynninae of the Australian region. Krombein (1937, 1938) keyed the world genera of Myzininae, and those of North America and the Nearctic species of Myzinum, respectively. Brown (1985) revised the Myzininae of Australia. Krombein (1979b) keyed the world genera and subgenera of Methochinae.

Allen (1966, 1968, 1971, 1972) revised the North American species of *Tiphia* and *Paratiphia*, and keyed the New World genera of Tiphiinae. Arbouw (1985) cataloged Tiphiinae. Mickel and Krombein (1942) keyed the genera of Brachycistidinae for females, and Pate (1947a) keyed them for both sexes; Wasbauer (1968) presented an updated key to genera of males. Bischoff (1927), Clausen (1940), Pate (1947a), and Krombein (1968) gave information on biology.

# Family SAPYGIDAE

(Figs. 55, 56)

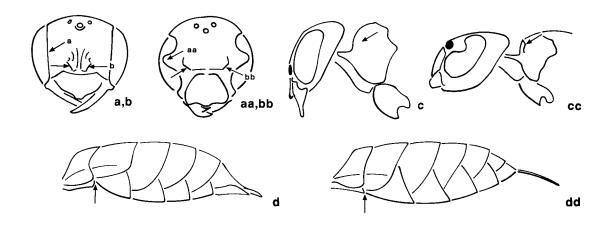
**Diagnosis** Dorsal rim of torulus elaborated as a small tubercle or transverse ridge; eye with inner margin more or less straight or strongly emarginate. Pronotum with posterodorsal margin weakly concave and with posterolateral apex rounded anterior to tegula; mesocoxae and metacoxae contiguous; hind wing without distinct claval lobe but with distinct jugal lobe; metacoxa with dorsal longitudinal carina. Metasoma sessile; metasomal sternum 1 usually not separated from sternum 2 by any constriction but weak constriction sometimes present; female metasomal sternum 6 conical and imbricate, with sides overlapping each other dorsally and extending posteriorly beyond tergum 6; male metasomal sternum 8 (hypopygium) simple,

entirely exposed. Sexual dimorphism slight: both male and female macropterous.

Comments Sapygidae is a widespread family that is absent from the Australian region and contains about 80 species in two subfamilies: Fedtschenkiinae and Sapyginae. Adults are generally predominantly black, often marked with yellow or white. All species are solitary. The larvae are cleptoparasites or ectoparasitoids of the larvae of Megachilidae, Anthophoridae, and Eumeninae, pupation occurring within the cell constructed by the host. Both subfamilies (17 species in three genera) occur in North America, including about six species in two genera in southern Canada.

# Key to subfamilies of SAPYGIDAE

Denis J. Brothers



- a. Eye with inner margin very weakly sinuate.
  - b. Toruli close together, separated by a space about as wide as a torulus.
  - c. Pronotum with dorsal anterolateral extremity (humeral angle) rounded.
  - d. Metasomal sternum 1 separated from sternum 2 by a shallow constriction . . . . . Fedtschenkiinae

- aa. Eye with inner margin deeply emarginate.
- bb. Toruli far apart, separated by a space at least twice as wide as a torulus.
- cc. Pronotum with dorsal anterolateral extremity (humeral angle) acute and carinate.
- dd. Metasomal sternum 1 not separated from sternum 2 by a constriction ....... Sapyginae

### Subfamily Fedtschenklinae

(Fig. 55)

This Holarctic subfamily, which is restricted to arid areas, includes very few species in one genus. Adults are usually black. The larvae are ectoparasitoids on the larvae of soil-nesting Eumeninae. One species occurs in North America; it may occur in southwestern Canada although it has not yet been recorded there.

### Subfamily Sapyginae

(Fig. 56)

This widespread subfamily, which is absent from the Australian region, includes several species

in a few genera. Adults are usually black with yellow or white markings. The larvae are cleptoparasites or ectoparasitoids of the larvae of Megachilidae, Anthophoridae, and Eumeninae. Sixteen species in two genera occur in North America, including six species in two genera in Canada.

References Tobias (1965) keyed the subfamilies, and he and Bradley (1955) discussed Fedtschenkiinae. Pate (1947b) provided keys to the New World genera. Arnold (1929) revised the African species, and Kurzenko (1986) revised those of the USSR. Krombein (1979c) summarized information on biology.

# Family MUTILLIDAE

(Figs. 57-68)

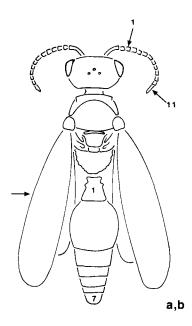
**Diagnosis** Dorsal rim of torulus elaborated as a strong convex tubercle; eye with inner margin convex, more or less straight or emarginate in male, convex or more or less straight in female. Pronotum with posterodorsal margin usually V-shaped but sometimes weakly concave, the posterolateral apex usually truncate but sometimes rounded anterior to tegula; mesocoxae and metacoxae contiguous; hind wing without distinct claval lobe, usually without, but rarely with, distinct jugal lobe. Metasoma usually sessile but sometimes with a short petiole; metasomal segment 1 without a true node although sometimes approaching it; metasomal sternum 1 separated from sternum 2 by a deep constriction; metasomal segment 2 usually with longitudinal felt line or with felted pit on tergum and/or sternum but sometimes without; male metasomal sternum 8 (hypopygium) usually simple or rarely with apex emarginate, usually entirely exposed but rarely concealed. Sexual dimorphism usually extreme but rarely slight: male usually macropterous, sometimes brachypterous or apterous; female apterous; brachypterous and apterous forms with mesosoma different from that in macropterous form, with pronotum usually fused to mesothorax but rarely freely articulating, and mesonotum and metanotum-propodeum usually indistinguishably fused but the suture rarely discernible.

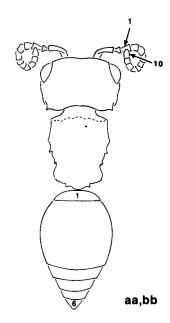
**Comments** Mutillidae (velvet ants) is a cosmopolitan but predominantly tropical family

containing about 5000 species in seven subfamilies: Mutillinae, Myrmillinae, Myrmosinae, Pseudophotopsidinae, Rhopalomutillinae, Sphaeropthalminae, and Ticoplinae. We believe that Kudakrumiinae, described by Krombein (1979a) and redefined by Lelej (1981a), is better regarded as a tribe within Myrmosinae. Adults are generally densely pubescent and predominantly black, brown, or reddish, often marked with bright spots or bands that are usually white, yellow, or red; some species from the Australian region are brilliantly metallic in shades of bronze, green, blue, or purple; the wings are usually dark. The integument is usually extremely thick and hard, and the females often have a very powerful sting. Sex associations are very difficult and usually depend on captures in copulo or rearings from a single host. The male is very much larger than the female in some species and may then carry the female before mating, or true phoretic copulation may occur. All species are solitary. The larvae are ectoparasitoids of the enclosed immatures (usually larvae or pupae) of other insects, especially Aculeata but also Cyclorrhapha (Diptera), Lepidoptera, Coleoptera, and Blattodea (Dictuoptera). Pupation occurs within the cell, cocoon, or ootheca constructed by the host. About 435 species (20 genera in three subfamilies) occur in North America, including about 25 species in southwestern Canada and three in eastern Canada.

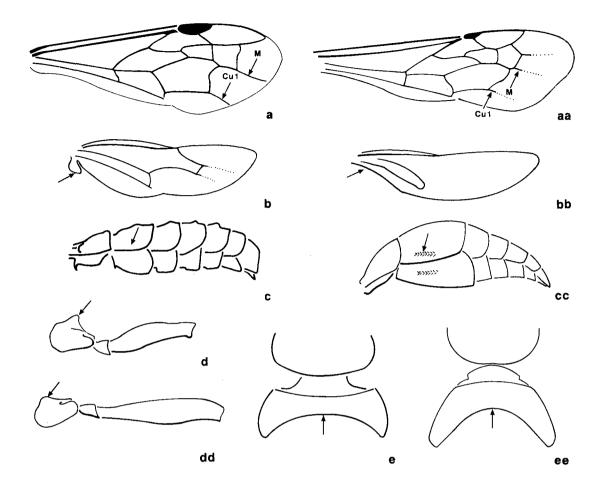
# Key to subfamilies of MUTILLIDAE

Denis J. Brothers

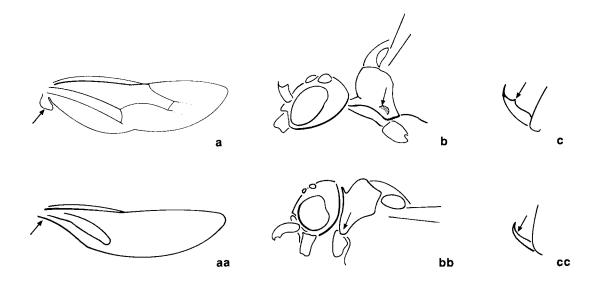


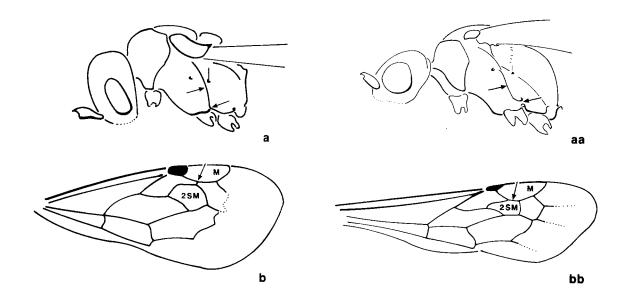


- - bb. Usually female: metasoma with 6 visible terga, the antenna usually with 10 flagellomeres, rarely 11; sometimes male: metasoma with 7 visible terga, the antenna with 11 flagellomeres . . . . . . . . 8

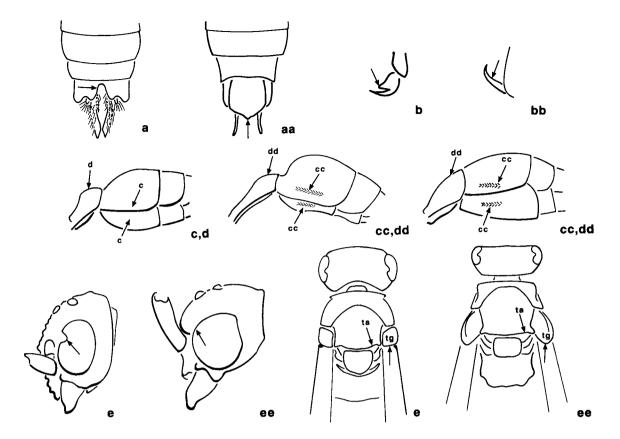


- 2(1) a. Fore wing with tubular veins M and Cu1 extending to apical margin.
  - b. Hind wing usually with jugal lobe, but rarely without lobe.
  - c. Metasomal segment 2 without any trace of felt line.
  - d. Metacoxa with laminate basal process dorsally, but rarely a weakly reflexed carina there.
  - e. Pronotum with posterodorsal margin shallowly concave ..... male Myrmosinae
  - aa. Fore wing with tubular veins M and Cu1 ending far from apical margin, the remnants sometimes visible in apical membrane but not tubular.
  - bb. Hind wing usually without jugal lobe, but rarely with lobe.
  - cc. Metasomal segment 2 usually with, but sometimes without, felt line on tergum and/or sternum.
  - dd. Metacoxa smoothly rounded, or with a low basal carina dorsally.



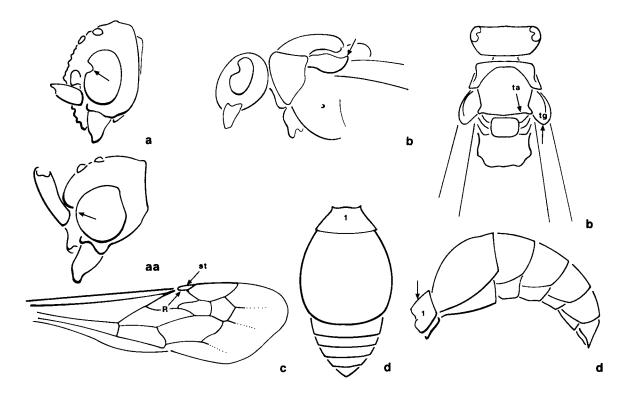


- a. Mesopleuron with posterior margin convex, especially over ventral half, and not fused with metapleuron.
  - b. Fore wing with second submarginal cell (2SM) petiolate anteriorly—i.e., not sharing a common vein with marginal cell (M) but connected to it by a crossvein; if (rarely) only 1 submarginal cell enclosed by tubular veins then the cell much shortened apically ...... most male **Ticoplinae**
  - aa. Mesopleuron with posterior margin distinctly sinuate, concave at about mid height and usually below, and fused with metapleuron at ventral bridge at least.



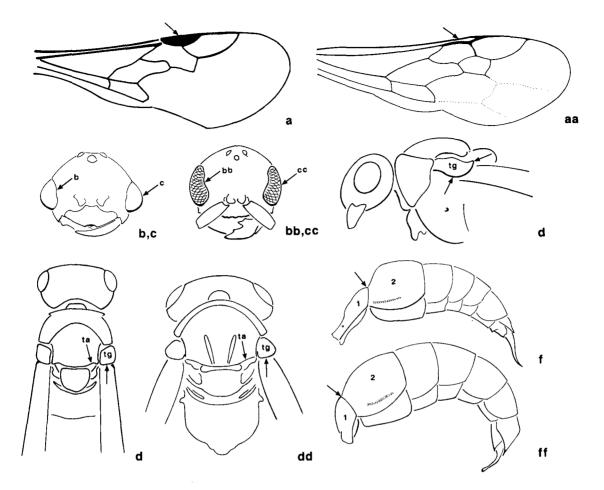
- 5(4) a. Last visible sternum strongly emarginate apically, usually with a narrow ventrally projecting lobe on each side.
  - b. Tarsal claws with basal laminate tooth ventrally.
  - c. Metasomal segment 2 without felt line.
  - d. Metasomal segment 1 petiolate and almost node-like.

  - aa. Last visible sternum straight or convex apically, without narrow ventrally projecting lobe on each side, but rarely emarginate.
  - bb. Tarsal claws simple and smooth ventrally.
  - cc. Metasomal segment 2 usually with, but rarely without, felt line on tergum and/or sternum.
  - dd. Metasomal segment 1 sessile, or petiolate and/or almost node-like.



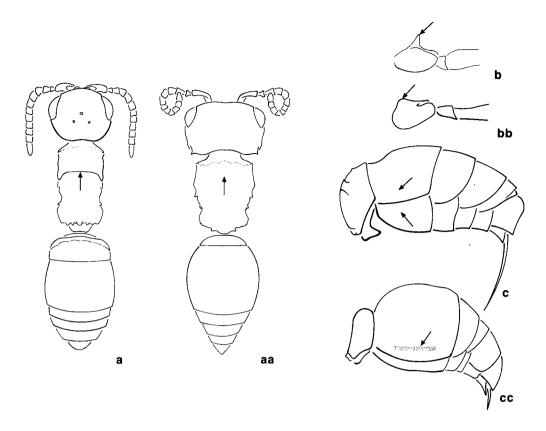
- a. Eye with inner margin deeply and abruptly emarginate; if eye shallowly emarginate then notch distinctly above mid height.
  - b. Tegula (tg) distinctly reflexed or flattened posteriorly or with distinct longitudinal angle anteriorly, usually ending well posterior to level of transscutal articulation (ta) but sometimes shorter.
  - c. Fore wing with stigma (st) unsclerotized and cell-like, with distinct bounding veins (especially in ventral view), or stigma absent, rarely with stigma apparently well sclerotized through thickening of vein R.

  - aa. Eye with inner margin usually convex, but sometimes sinuate or shallowly emarginate at about mid height.
  - bb. Tegula usually entirely convex and ending at or anterior to level of transscutal articulation; if tegula slightly recurved posteriorly and/or ending more posteriorly then inner margin of eye not at all emarginate.
  - cc. Fore wing with stigma not entirely cell-like, usually well sclerotized and distinct, but sometimes reduced or absent.

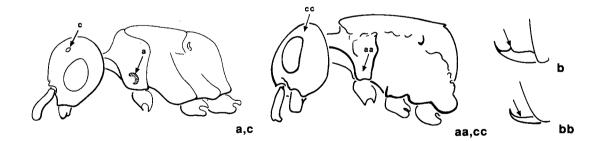


- a. Fore wing with stigma well developed and completely sclerotized; if stigma reduced and poorly sclerotized then metasomal tergum 1 petiolate and/or almost node-like.
  - b. Eye round with inner margin usually strongly convex, but sometimes sinuate.
  - c. Eye often protruding markedly, almost hemispherical and smooth-surfaced, but sometimes protruding little and/or surface distinctly faceted.
  - d. Tegula (tg) usually ending at level of transscutal articulation (ta) and entirely convex, but sometimes extending further posteriorly and/or recurved posteriorly.
  - e. Plumose hairs sometimes present in addition to simple hairs.

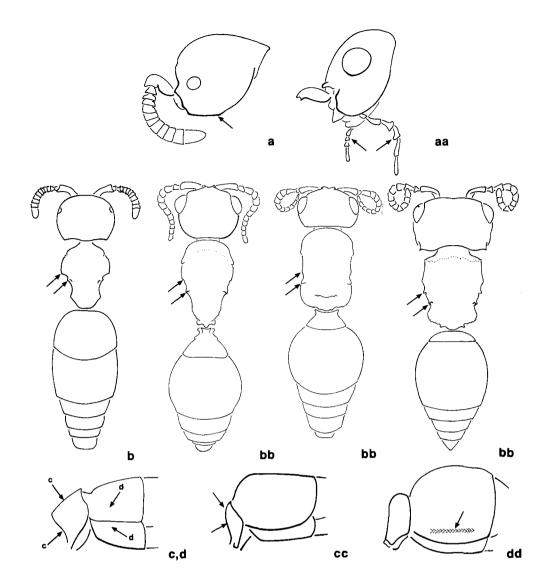
  - aa. Fore wing with stigma much reduced and poorly sclerotized or unsclerotized, not bounded basally **and** metasomal tergum 1 sessile.
  - bb. Eye oval with inner margin weakly convex, sinuate, or shallowly emarginate.
  - cc. Eye protruding little, the surface distinctly faceted.
  - dd. Tegula (tg) ending at or anterior to transscutal articulation (ta), the tegula not recurved posteriorly.
  - ee. Plumose hairs absent.



- **8(1)** a. Pronotum with posterodorsal margin straight or scarcely concave, articulating with mesothorax; dorsum of remainder of mesosoma without sutures.
  - b. Metacoxa with laminate basal process dorsally.
  - c. Metasomal segment 2 without any trace of felt line or felted pit ...... female Myrmosinae
  - aa. Pronotum with posterodorsal margin moderately to deeply concave or indiscernible, usually fused with mesothorax; if pronotum articulating then dorsum of remainder of mesosoma with distinct sutures.
  - bb. Metacoxa smoothly rounded or with a low basal carina dorsally.

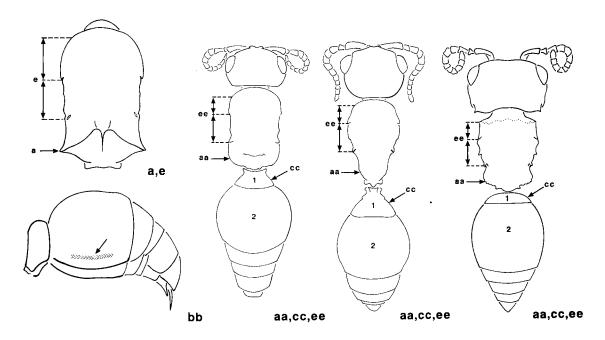


- **9(8)** a. Pronotum with felted pit ventrolaterally.
  - b. Tarsal claws with small acute tooth ventrally beyond mid length.
  - c. Female only: ocelli often present but sometimes absent ..... female Pseudophotopsidinae
  - aa. Pronotum without felted pit.
  - bb. Tarsal claws simple and smooth ventrally.

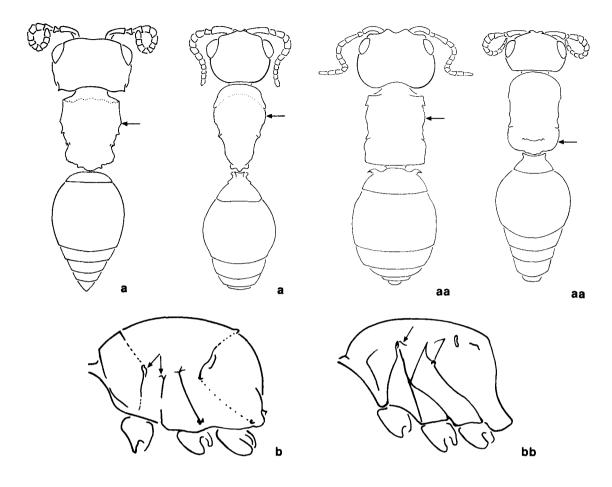


**10(9)** a. Maxillary and labial palpi minute and usually concealed, each with 2 segments or fewer.

- b. Mesosoma in dorsal view with sides abruptly and strongly concave from widest point (on mesothorax) to propodeal spiracle; female only.
- c. Metasomal tergum 1 with distinct dorsal and anterior surfaces; dorsal surface at least half as long as wide, with sides only slightly diverging, parallel, or slightly converging posteriorly.
- d. Metasomal segment 2 without felt line or felted pit . . . . . female Rhopalomutillinae
- aa. Maxillary and labial palpi long and exposed, with 6 and 4 segments respectively.
- bb. Mesosoma in dorsal view with sides usually more or less straight or convex immediately anterior to propodeal spiracle, at most gradually and weakly concave in female, but sometimes fairly strongly concave in male and then mesosoma not widest across mesothorax.
- cc. Metasomal tergum 1 usually without distinct dorsal and anterior surfaces; if dorsal surface distinct then usually much less than half as long as wide with sides usually diverging posteriorly but sometimes parallel.

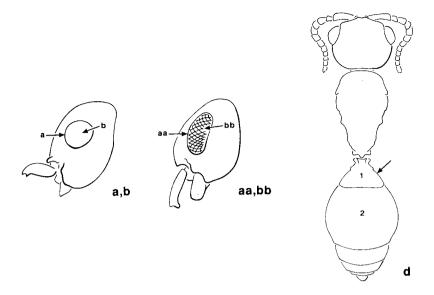


- a. Mesosoma in dorsal view widest (excluding length of any spines) at level of acute spine or tooth halfway down posterolateral margin of propodeum.
  - b. Metasomal tergum 2 without felt line or felted pit.
  - c. Metasomal tergum 1 almost as wide as tergum 2, sessile, and forming an even contour with it.
  - d. Pronotum with posterolateral margin indistinguishably fused with mesopleuron in female and in male with nonarticulating pronotum; margin distinct in male with articulating pronotum.
  - e. Distance from dorsal anterolateral extremity (humeral angle) of pronotum to pronotal spiracle at least as long as distance between pronotal and propodeal spiracles in female and in male with nonarticulating pronotum; distance often different in male with articulating pronotum.
  - f. Eye sometimes densely setose, but often bare ..... female and a few male Ticoplinae
  - aa. Mesosoma in dorsal view rarely widest posteriorly (excluding length of any spines); if widest posteriorly then usually widest at higher point and/or without strong tooth or spine halfway down posterolateral margin (sometimes with tooth or spine on posterodorsal angle).
  - bb. Metasomal tergum 2 usually with felt line or felted pit; if without then mesosoma definitely not widest posteriorly.
  - cc. Metasomal tergum 1 usually less than two-thirds width of tergum 2, petiolate or not forming an even contour with it, but tergum 1 rarely almost as wide as tergum 2, sessile and forming an even contour with it.
  - dd. Pronotum with posterolateral margin usually distinct although fused with mesopleuron in female and male with nonarticulating pronotum, but margin sometimes indistinguishable; margin distinct in male with articulating pronotum.
  - ee. Distance from dorsal anterolateral extremity (humeral angle) of pronotum to pronotal spiracle much shorter than distance between pronotal and propodeal spiracles in female and in male with nonarticulating pronotum; distance often different in male with articulating pronotum.
  - ff. Eye bare, not setose ...... 12

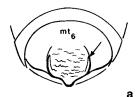


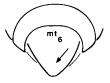
- 12(11) a. Mesosoma in dorsal view distinctly widest across mesothorax or pronotal spiracle, usually narrowest posteriorly, with sides convex or sinuate; male rarely with mesosoma widest anterior to pronotal spiracle.

  - aa. Mesosoma in dorsal view not widest across mesothorax or pronotal spiracle, widest posteriorly or anterior to pronotal spiracle or parallel-sided, with sides more or less straight or concave; male never with mesosoma widest anterior to pronotal spiracle.

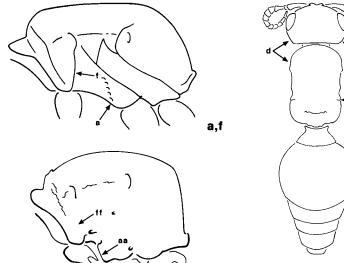


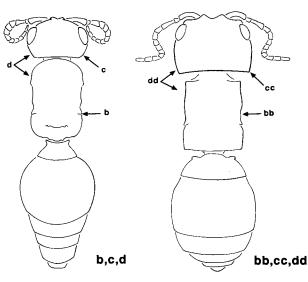
13(12) a. Eye round or longer than high but rarely slightly higher than long, with inner margin usually strongly and evenly convex but rarely weakly sinuate. b. Eye often smooth (i.e., facets indistinct on surface) and strongly projecting, but sometimes distinctly faceted and/or weakly projecting. Plumose hairs sometimes present in addition to simple hairs. Female with metasomal tergum 1 markedly narrower than 2, short and sessile or petiolate but not cvlindrical. e. Female mesosoma with dorsolateral margin sometimes multiply dentate, but often rounded or with a single tooth. Tegula, if present, scarcely longer than wide and entirely convex ...... ..... female and a few male Sphaeropthalminae aa. Eye distinctly higher than long with inner margin weakly and/or unevenly convex, sinuate or bb. Eye distinctly faceted and weakly projecting. cc. Plumose hairs absent. dd. Female with metasomal tergum 1 short and scarcely narrower than 2, or cylindrical and much narrower than 2. ee. Female mesosoma with dorsolateral margin rounded or at most with a single tooth behind pronotal spiracle, dorsolateral margin not multiply dentate. Tegula, if present, distinctly longer than wide and slightly recurved posteriorly ..... ..... some female and a few male Mutillinae 14(12) aa. 15(14) Eye with inner margin distinctly emarginate and/or tegula distinctly longer than wide and aa. Eye with inner margin weakly convex or sinuate; tegula (if present) scarcely longer than 



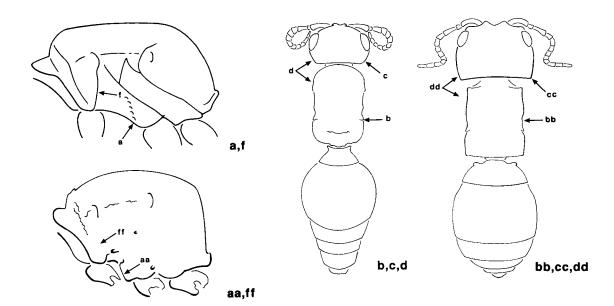


aa





- a. Mesopleural carina usually not raised ventrally anterior to mesocoxa, but sometimes with weak carina present there.
  - b. Mesosoma in dorsal view usually more or less parallel-sided, but sometimes widest anteriorly or posteriorly.
  - c. Head in dorsal view rounded or oval, with sides convex and converging behind eyes and with posterolateral apex widely rounded.
  - d. Head area in dorsal view usually less (rarely greater) than mesosomal area.
  - e. Mesosoma with pleura usually more or less flat or weakly convex, but pleura rarely concave.
  - f. Pronotum with posterolateral margin usually distinct, but margin rarely not discernable ......
    most female Mutillinae
  - aa. Mesopleural carina usually raised ventrally as a strong carina or tooth anterior to mesocoxa, but sometimes without carina there.
  - bb. Mesosoma in dorsal view more or less parallel-sided or widest posteriorly, but very rarely widest anteriorly at prominent dorsal anterolateral externity (humeral angle).
  - cc. Head in dorsal view often almost square, with sides more or less straight and parallel behind eyes and with posterolateral apex narrowly rounded, but the head sometimes rounded or oval.
  - dd. Head area in dorsal view usually greater (rarely less) than mesosomal area.
  - ee. Mesosoma with pleura usually concave, but pleura sometimes more or less flat.



- a. Mesopleural carina usually not raised ventrally anterior to mesocoxa, but sometimes with weak carina present there.
  - b. Mesosoma in dorsal view usually more or less parallel-sided or widest anteriorly, but rarely widest posteriorly.
  - c. Head in dorsal view rounded or oval, with sides convex and converging behind eyes and with posterolateral apex widely rounded.
  - d. Head area in dorsal view usually less (rarely greater) than mesosomal area.
  - e. Mesosoma with pleura usually more or less flat or weakly convex, but pleura rarely concave.
  - f. Pronotum with posterolateral margin usually distinct, but margin rarely not discernable.

  - aa. Mesopleural carina usually raised ventrally as a strong carina or tooth anterior to mesocoxa, but the carina sometimes absent there.
  - bb. Mesosoma in dorsal view widest posteriorly or more or less parallel-sided.
  - cc. Head in dorsal view almost square, with sides more or less straight and parallel behind eyes and with posterolateral apex angulate or narrowly rounded, but the head sometimes rounded or oval.
  - dd. Head area in dorsal view usually greater (rarely less) than mesosomal area.
  - ee. Mesosoma with pleura usually concave, but pleura sometimes more or less flat.
  - ff. Pronotum with posterolateral margin usually not discernible, but margin rarely distinct.
  - gg. Body length usually less than 10 mm, but sometimes greater ..... most female Myrmillinae

# **Subfamily Myrmosinae**

(Figs. 57, 58)

This Holarctic and Oriental subfamily includes fewer than 50 species in about eight genera. Males are usually uniformly black and females are usually brown or reddish; they are generally diurnal. Sexual dimorphism is always extreme, and true phoretic copulation occurs in some species, but the male does not generally carry the female. Fifteen species

in three genera occur in North America, including two species in two genera in southern Canada.

#### **Subfamily Pseudophotopsidinae**

(Fig. 59)

This Palaearctic and Afrotropical subfamily includes fewer than 30 species in one genus. Males and females are usually uniformly brown or reddish; they are generally nocturnal or crepuscular. Sexual

dimorphism is always extreme, but the male probably does not carry the female.

### **Subfamily Ticoplinae**

(Fig. 60)

This Palaearctic, Afrotropical, and Oriental subfamily includes fewer than 100 species in about three genera. Males are usually uniformly black or black and reddish brown, and females are usually black and reddish brown; they are generally diurnal. Sexual dimorphism varies from extreme to slight (species with apterous males), and the male probably does not carry the female.

#### Subfamily Rhopalomutillinae

(Figs. 61, 62)

This Afrotropical and Oriental subfamily includes fewer than 50 species in about four genera. Males are usually uniformly black, and females are usually brown; they are diurnal. Sexual dimorphism is always extreme and true phoretic copulation is the rule.

#### Subfamily Sphaeropthalminae

(Figs. 63, 64)

This cosmopolitan subfamily includes about 2500 species in about 80 genera. Color varies greatly, from uniformly black or brown to brilliantly marked or metallic; adults are usually diurnal but many desert species are nocturnal or crepuscular. Sexual dimorphism is extreme to slight (species with apterous males), the male usually does not carry the female, and true phoretic copulation does not occur. About 360 species in about 15 genera occur in North America, including 20 species in about five genera in Canada.

#### Subfamily Myrmillinae

(Figs. 65, 66)

This Palaearctic, Afrotropical, and Oriental subfamily includes about 400 species in about 20 genera. Males are usually uniformly black or black and red, and females are usually brown or black and red without striking markings; they are diurnal. Sexual dimorphism is extreme to slight (species

with apterous males), and the male probably does not carry the female.

### **Subfamily Mutillinae**

(Figs. 67, 68)

This cosmopolitan subfamily (richest in the Old World but absent from most of Australia) includes about 1800 species in about 40 genera. Males are usually black, brown, or black and red without striking markings, and females are usually black and red with conspicuous pale spots; they are usually diurnal, but a few desert species are nocturnal or crepuscular. Sexual dimorphism is extreme to marked (species with brachypterous males), and the male sometimes carries the female, but true phoretic copulation does not occur. About 60 species in two genera occur in North America, including three species in two genera in Canada.

**References** Brothers (1975) revised the family and subfamily classification, and Mickel (1970) presented a bibliography. Bingham (1897) surveyed the Indian species, André (1899–1903) revised the European species, Bischoff (1920–21) revised the Afrotropical species, and Nonveiller (1980a, 1980b) reviewed the African fauna. Olsoufieff (1938) and Krombein (1972) revised the Madagascan species, Giner Marí (1944) the Spanish species, Invrea (1964) the Italian species, Lelej (1985) the fauna of the USSR, and Chen (1957) that of China. Mickel (1934) surveyed the species of the Philippines and the Pacific islands, and Mickel (1935b, 1952) keyed the genera and reviewed the species of northern South America, respectively. Cameron (1894–1899) dealt with the Central American and Mexican species, and Nonveiller (1990) cataloged the Neotropical and Mexican species. Krombein (1940) reviewed the world Myrmosinae, Suárez (1960, 1988) revised the Moroccan species and the species from the Iberian Peninsula, respectively, Wasbauer (1973) keyed the Nearctic species, and Krombein (1979a) described the Kudakrumiinae (here regarded as a tribe of the Myrmosinae). Schuster (1958) and Mickel (1935a, 1936) treated Nearctic Sphaeropthalminae. Mickel (1937) and Schuster (1951, 1956) treated Nearctic Mutillinae, and Mickel (1938), Schuster (1949), and Casal (1968, 1969a, 1969b, 1970) treated Neotropical species. Bischoff (1927), Mickel (1928), Ferguson (1962). Nonveiller (1963) and Brothers (1972, 1984, 1989) surveyed the information on biology.

# Family SIEROLOMORPHIDAE

(Fig. 69)

**Diagnosis** Dorsal rim of torulus simple but from evenly swollen above it; eye with inner margin more or less straight. Pronotum with posterodorsal margin weakly concave and with posterolateral apex rounded anterior to tegula; mesocoxae and metacoxae contiguous; hind wing without distinct claval or jugal lobes; metacoxa with weak dorsal longitudinal carina. Metasoma sessile; metasomal segment 1 without true node although sometimes approaching it; metasomal sternum 1 separated from sternum 2 by deep constriction; male metasomal sternum 8 (hypopygium) simple but reduced, mostly concealed. Sexual dimorphism slight to marked: both sexes usually macropterous but female sometimes brachypterous or apterous; brachypterous and apterous forms with mesosoma

similar to that in macropterous form, with pronotum freely articulating, and with mesonotum, metanotum, and propodeum distinct.

Comments Sierolomorphidae is a Northern Hemisphere family containing about 10 species in one genus. Adults are black or dark brown. All species are solitary. The larvae are probably ectoparasitoids of other insects, but nothing is known about the biology. The six New World species are distributed from the Yukon in Canada to Panama and Hawaii; two species occur across Canada.

**References** Evans (1961) keyed the Nearctic species and Nagy (1971) described the two Palaearctic species.

# Family POMPILIDAE

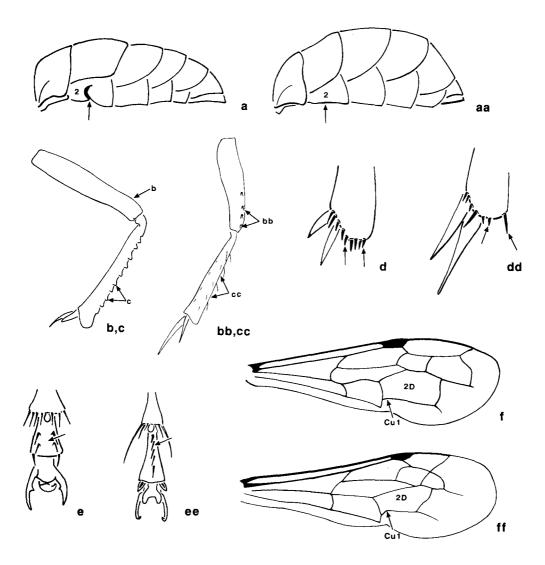
(Figs. 70-72)

**Diagnosis** Dorsal rim of torulus simple: eve with inner margin usually more or less straight, rarely emarginate. Pronotum with posterodorsal margin usually weakly but sometimes moderately concave, with posterolateral apex rounded anterior to tegula; mesepisternum with straight oblique groove, rarely without; mesocoxae and metacoxae contiguous; hind wing without distinct claval lobe but with distinct jugal lobe; legs usually conspicuously elongate; posterior (inner) spur of metatibia modified as a calcar. Metasoma usually sessile but rarely more or less petiolate; metasomal sternum 1 not separated from sternum 2 by any constriction; male metasomal sternum 8 (hypopygium) simple, entirely exposed. Sexual dimorphism slight: both sexes usually macropterous, rarely brachypterous or apterous; brachypterous and apterous forms with mesosoma usually somewhat different from that in macropterous form, with pronotum freely articulating, and with at least mesonotum and propodeum also distinct.

**Comments** Pompilidae (spider wasps) is a cosmopolitan but predominantly tropical family containing about 4200 species in three subfamilies: Ceropalinae, Pepsinae, and Pompilinae. Adults are predominantly black, often with red, white, or vellow areas or markings. All species are solitary. Usually each larva develops on a single paralyzed spider (Araneae), very rarely another order of Arachnida, in a cell constructed and provisioned by the female, although a preexisting cavity may sometimes be used; the larva is rarely an ectoparasitoid of an active spider or a cleptoparasite in a cell provisioned by another pompilid. About 282 species in 40 genera occur in North America, including about 75 species in 20 genera in Canada that are found mostly in the southwest, although several reach the southern fringes of the Arctic.

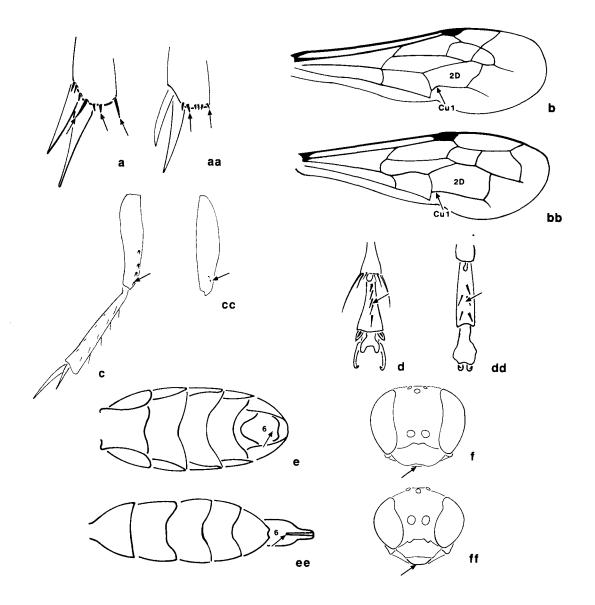
## Key to subfamilies of POMPILIDAE

(modified from Townes 1957)



- a. Metasomal sternum 2 with distinct sharp transverse groove, but male often without sharp groove.
  - b. Mesofemur and metafemur without subapical spine-like setae set in grooves or pits.

- c. Metatibia often with a series of teeth along dorsal margin, but sometimes without such teeth.
- d. Metatibia with apical spine-like setae of more or less uniform length, the setae not splayed.
- e. Tarsomere 5 ventrally without distinct median row of setae, but sometimes with pair of submedian rows of setae.
- aa. Metasomal sternum 2 without distinct sharp transverse groove, but sometimes with wide shallow transverse depression.
- bb. Mesofemur and metafemur usually with 1 or more subapical dorsal spine-like setae set in grooves or pits, but sometimes without such setae.
- cc. Metatibia usually without a series of teeth along dorsal margin, but rarely with such teeth.
- dd. Metatibia with apical spine-like setae usually of different lengths and splayed, but the setae sometimes of uniform length and not splayed.
- ee. Tarsomere 5 often with a distinct median ventral row of setae, but sometimes without setae or with setae otherwise arranged.



- a. Metatibia with apical spine-like setae long, of irregular lengths and spacing, the setae distinctly splayed.
  - b. Fore wing with vein Cu1 usually distinctly deflected downward at base (second discal cell (2D) with a posterior "pocket"), but vein rarely not deflected.
  - c. Mesofemur and metafemur usually with 1 or more distinct subapical dorsal spine-like setae set in grooves or pits, but rarely without such setae.
  - d. Tarsomere 5 with ventral preapical setae often forming a distinct median row, but the setae sometimes absent.
  - e. Female metasomal sternum 6 (subgenital plate) without median longitudinal carina or sharp
  - f. Labrum often concealed below clypeus, but labrum sometimes exposed ...... Pompilinae
  - aa. Metatibia with apical spine-like setae short, of more or less uniform length and spacing, not splayed.
  - bb. Fore wing with vein Cu1 simple at base, without any definite downward deflection (second discal cell (2D) without a posterior "pocket").
  - cc. Mesofemur and metafemur usually without subapical spine-like setae set in grooves or pits; if femora with such setae then these setae small and inconspicuous.
  - dd. Tarsomere 5 with ventral preapical setae usually not forming a distinct median row, differently arranged, with setae sometimes absent.

- ee. Female metasomal sternum 6 (subgenital plate) with distinct median longitudinal carina or sharp fold, at least apically.

#### **Subfamily Pepsinae**

(Fig. 70)

This cosmopolitan subfamily includes over 2000 species in about 100 genera. It includes some of the largest pompilids; many are black with orange-red wings. About 115 species in 13 genera occur in North America, including 24 species in seven genera in Canada.

### **Subfamily Pompilinae**

(Fig. 71)

This cosmopolitan subfamily includes about 2000 species in about 100 genera. It includes some of the smallest pompilids; many are black and gray. A few species are ectoparasitoids of living spiders (Araneae). About 142 species in 24 genera occur in North America, including about 46 species in 11 genera in Canada.

#### **Subfamily Ceropalinae**

(Fig. 72)

This cosmopolitan subfamily includes about 200 species in a few genera. Adults are generally black, usually with yellow or white markings. Most species are cleptoparasites of other pompilids, but some are ectoparasitoids of living spiders

(Araneae). About 25 species in three genera occur in North America, including five species in two genera in Canada.

**References** Haupt (1927) surveyed the family for central, northern, and eastern Europe, Day (1988) for Britain, Tobias (1978c) for European USSR, Tsuneki (1989) for Taiwan, Harris (1987) for New Zealand, and Arnold (1932-1937) for the Afrotropical region. Wahis (1986) cataloged the western European species. Dreisbach (1952) keyed the New World genera of Pepsini (Pepsinae), and Townes (1957) presented keys to the Nearctic genera and species of Pepsinae and Ceropalinae. Evans (1973) treated the Neotropical genera of Auplopodini (Pepsinae), Evans (1966) the Central American and Mexican species of Pompilinae (including keys to tribes and North and Central American genera), and Evans (1950, 1951a, 1951b) the Nearctic species of Pompilini (Pompilinae). Bradley (1944) keyed the New World species of Aporini (Pompilinae). Day (1981) restricted the genus Pompilus to seven Old World species and suggested that the American subgenera be distributed among the taxa used in modern Palaearctic treatments. Day (1988) analyzed morphology and relationships. Bischoff (1927), Evans (1953), Olberg (1959), Grandi (1961), Evans and Yoshimoto (1962), Grout and Brothers (1982), and Day (1988) surveyed the information on biology.

# Family RHOPALOSOMATIDAE

(Fig. 73)

**Diagnosis** Dorsal rim of torulus simple; eye with inner margin more or less straight or deeply emarginate; apices of 2 or more flagellomeres usually with spines but spines rarely absent; pronotum with posterodorsal margin weakly or deeply concave, and with posterolateral apex weakly truncate anterior to tegula; mesosternum with small laminate expansions on each side of midline covering bases of contiguous mesocoxae; metacoxae contiguous; fore wing with costal cell virtually obliterated through fusion of veins C and Sc except near stigma; hind wing with distinct claval and jugal lobes; posterior (inner) spur of metatibia modified as a calcar. Metasoma sessile or petiolate; metasomal segment 1 without a true node although sometimes approaching it; metasomal sternum 1 separated from sternum 2 by a slight constriction; male metasomal sternum 8 (hypopygium) simple, entirely exposed. Sexual dimorphism slight: both

sexes usually macropterous, sometimes both brachypterous or apterous; brachypterous and apterous forms with head carinate and concave posteriorly, with mesosoma different from that in macropterous form, with pronotum freely articulating, and with at least mesonotum and propodeum also distinct.

Comments Rhopalosomatidae is a widespread family, predominantly tropical, absent from the Palaearctic region, and containing about 34 species in four genera. Adults are usually uniformly tawny or brownish, seldom black and then often with reddish or yellowish markings. Macropterous forms are usually nocturnal, but the brachypterous and apterous ones are usually diurnal. All species are solitary. The larvae are ectoparasitoids of nymphal Gryllidae (Grylloptera), forming sac-like structures similar to those produced by Dryinidae and

pupating in a sheltered spot. Three species in three genera occur in North America, including one species in Canada, in extreme southern Ontario.

**References** Townes (1977) revised and keyed the genera and species of the world. Gurney (1953) dealt with the biology.

# Family BRADYNOBAENIDAE

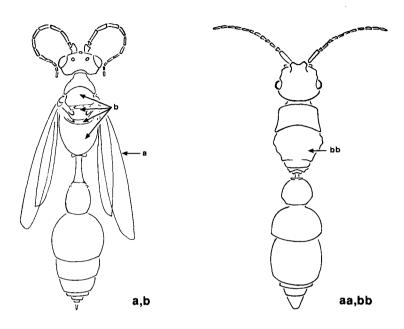
(Figs. 74-76)

**Diagnosis** Dorsal rim of torulus usually elaborated as a strong convex tubercle but sometimes weakly tuberculate or simple; eye with inner margin convex, more or less straight or sinuate in male, convex or more or less straight in female: pronotum with posterodorsal margin usually U-shaped but sometimes weakly concave. and with posterolateral apex usually rounded anterior to tegula but sometimes rounded below tegula; mesocoxae slightly separated by metasternum; metacoxae contiguous; hind wing usually without but rarely with distinct claval lobe, usually with but rarely without distinct jugal lobe. Metasoma usually petiolate but sometimes sessile; metasomal segment 1 usually without a true node but sometimes strongly node-like; metasomal sternum 1 separated from sternum 2 by a deep constriction; metasomal segment 2 usually with longitudinal felt line on tergum but sometimes merely with longitudinal cuticular groove; male metasomal sternum 8 (hypopygium) entirely exposed, usually with 3 spines, the middle spine generally forming a single strong acute upcurved hook, but hypopygium sometimes simple. Sexual dimorphism extreme: male usually macropterous, very rarely slightly brachypterous; female apterous; apterous form with mesosoma different from that in macropterous and brachypterous forms, with pronotum freely articulating, and with mesonotum, metanotum, and propodeum usually indistinguishably fused but the sutures between them sometimes distinct.

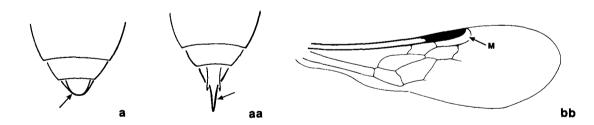
Comments Bradynobaenidae is a widespread family, predominantly tropical, absent from the Australian region, and containing about 155 species in four subfamilies: Apterogyninae, Bradynobaeninae, Chyphotinae, and Typhoctinae. Adults are often fairly densely hairy and predominantly black, brown, reddish, or bicolored (black and reddish), sometimes marked with pale bands. The integument is often extremely thick and hard, and the females may have a very powerful sting. Sex associations are very difficult and usually depend on captures in copulo or on correlations of distribution. All species are apparently solitary. Information on a single somewhat atypical species indicates that the larvae are ectoparasitoids of Solifugae (Arachnida), pupation occurring within the shelter of the host. About 48 species (two genera in two subfamilies) occur in North America, including one species in western Canada.

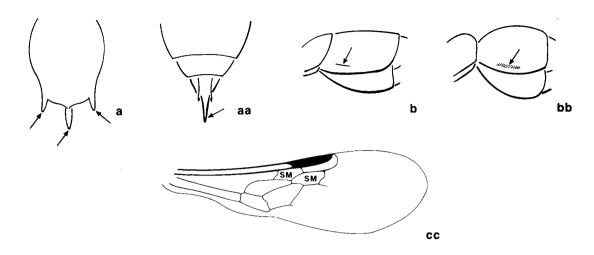
# Key to subfamilies of BRADYNOBAENIDAE

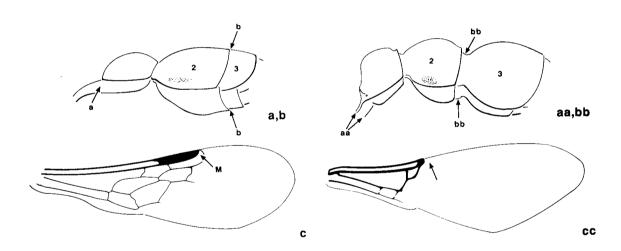
#### Denis J. Brothers

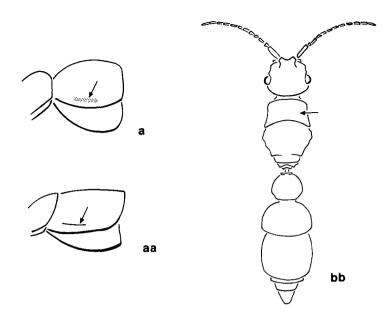


1	a.	Wings usually fully developed, rarely short-winged.	
	b.	Mesoscutum, mesoscutellum, metanotum, and propodeum distinct and usually articulating.	
	c.	Male only	2
	aa.	Wings absent.	
1	bb.	Mesoscutum, mesoscutellum, metanotum, and propodeum indistinct and fused.	
	cc.	Female only	5

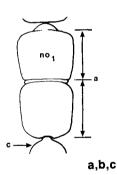


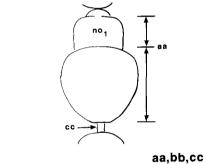




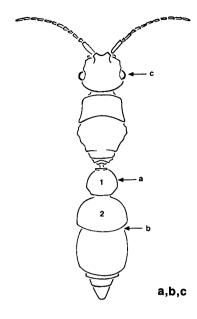


- 5(1) a. Metasomal tergum 2 with lateral felt line of short fine recumbent setae.
  - b. Pronotum in dorsal view narrowed posteriorly or parallel-sided; if parallel-sided then at least as long as wide and/or forming a discontinuous profile with rest of mesosoma in dorsal view ..... 6
  - aa. Metasomal tergum 2 without felt line, but with lateral longitudinal groove.





- **6(5)** a. Mesosoma in dorsal view with pronotum  $(no_1)$  about as long as remainder of mesosoma.
  - b. Pronotum in dorsal view at least as wide as subrectangular remainder of mesosoma.
  - c. Metasomal segment 1 without anterior stalk, the tergum extending to base ...... female **Typhoctinae**
  - aa. Mesosoma in dorsal view with pronotum (no<sub>1</sub>) no more than half as long as remainder of mesosoma.
  - bb. Pronotum in dorsal view less than two-thirds width of more or less spherical remainder of mesosoma.
  - cc. Metasomal segment 1 with cylindrical anterior stalk formed by sternum only ...... female Chyphotinae



- 7(5) a. Metasomal segment 1 about or less than half width of 2, strongly node-like and constricted posteriorly.
  - b. Metasomal segment 2 constricted posteriorly, usually node-like.
  - c. Head hypognathous, not depressed.
  - d. Body dull and heavily sculptured ...... female Apterogyninae
  - aa. Metasomal segment 1 at least two-thirds width of 2, not at all node-like, and not constricted posteriorly.
  - bb. Metasomal segment 2 not at all constricted posteriorly, not node-like.
  - cc. Head prognathous, depressed.
  - dd. Body shining and very sparsely sculptured, smooth ...... female **Bradynobaeninae**

## **Subfamily Typhoctinae**

This Nearctic and Neotropical subfamily includes about 10 species in four genera. Males are usually uniformly black, and females are usually black or reddish, sometimes with pale markings; they are diurnal. Larvae of *Typhoctes* have been found on immature Solifugae (Arachnida). Three species in one genus occur in North America, possibly including one in southwestern Canada.

#### Subfamily Chyphotinae

(Fig. 74)

This Nearctic subfamily includes about 55 species in one genus. Males and females are usually uniformly brownish; adults are nocturnal. Hosts are unknown. Forty-five species occur in North America, one in southwestern Canada.

# **Subfamily Apterogyninae**

(Figs. 75, 76)

This Afrotropical, Palaearctic, and Oriental subfamily includes about 80 species in two genera.

Males are usually uniformly black or brownish, and females are usually brownish or black and reddish; they are diurnal or nocturnal. Hosts are unknown.

#### **Subfamily Bradynobaeninae**

This Neotropical subfamily includes about 10 species in one genus. Males are usually uniformly black, or black and reddish, and females are usually brownish, or black and reddish; they are diurnal. Hosts are unknown.

References Brothers (1975) established the family and subfamily limits, and Nonveiller (1990) cataloged the Neotropical species. Mickel (1967) revised Chyphotinae and Genise (1986) Bradynobaeninae. Krombein and Schuster (1957) reviewed the North American species of Typhoctinae, and Invrea (1951, 1957) the northern and southern African Apterogyninae, respectively. The little information on biology is still unpublished.

# Family SCOLIDAE

(Figs. 77, 78)

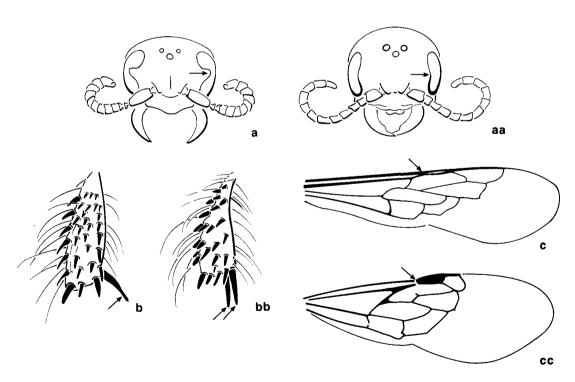
**Diagnosis** Dorsal rim of torulus usually simple but sometimes widely tuberculate; eye with inner margin usually deeply emarginate but sometimes weakly sinuate. Pronotum with posterodorsal margin U-shaped and with posterolateral apex truncate and weakly produced above anterior margin of tegula; mesosternum with small laminate expansions on each side of midline covering bases of widely separated mesocoxae; metasternum with laminate expansions covering bases of widely separated metacoxae; wings with dense fine longitudinal wrinkles near apices; hind wing without distinct claval lobe but with distinct jugal lobe; female usually with mesotibia and metatibia stout and heavily spined. Metasoma sessile; metasomal segment 1 without a true node, although sometimes approaching it; metasomal sternum 1 separated from sternum 2 by a deep constriction; male metasomal sternum 8 (hypopygium) partly

concealed, usually forming 3 straight apical spines, but hypopygium sometimes bluntly trilobed. Sexual dimorphism slight to moderate: both sexes macropterous.

Comments Scoliidae is a cosmopolitan but predominantly tropical family, containing about 300 species in two subfamilies: Proscoliinae and Scoliinae. Adults are often predominantly black, but commonly marked with yellow, white, or red. Sex associations are sometimes difficult because color patterns frequently differ between the sexes. All species are solitary. The larvae are ectoparasitoids of the larvae of Coleoptera, usually Scarabaeoidea but rarely Curculionoidea, pupation occurring within the substrate occupied by the host. About 21 species in five genera occur in North America, including two species in Canada.

# Key to subfamilies of SCOLIIDAE

(modified from Day, Else, and Morgan 1981)



- 1 a. Eye with inner margin deeply emarginate.
  - b. Mesotibia with 1 apical spur.
  - c. Fore wing without break or articulation between stigma and prestigma ....... Scoliinae
  - aa. Eye with inner margin almost straight, weakly sinuate.
  - bb. Mesotibia with 2 apical spurs.

## **Subfamily Proscoliinae**

(Fig. 77)

This Palaearctic subfamily includes two species in one genus. Males are uniformly black and females uniformly reddish; they are diurnal. Hosts are unknown.

#### Subfamily Scoliinae

(Fig. 78)

This cosmopolitan subfamily includes about 300 species in several genera. Males are usually predominantly black but often marked with yellow, white, or red, females are usually predominantly black with fewer markings, and the wings are often iridescent; they are diurnal. Larvae are ectoparasitoids of larval Scarabaeoidea or Curculionoidea (Coleoptera). About 21 species in

five genera occur in North America, including two species in Canada.

**References** Rasnitsvn (1977) reviewed the subfamily classification and Day, Else, and Morgan (1981) keyed the subfamilies and revised the species of Proscoliinae. Grissell (1977) keyed the Nearctic genera, MacKay (1987) keyed the species of southwestern United States, and Bradley (1957, 1964) keyed the New World subgenera of Campsomeris. Betrem (1928, 1935, 1941) revised the species of Indo-Australia, of the western Palaearctic region, and of China and Japan, respectively. Tobias (1978a) keyed the species of European USSR and Lelej (1981b) those of far eastern USSR. Krombein (1963, 1978) revised the species of the Papuan subregion and those of Sri Lanka, respectively. Betrem and Bradley (1972) revised the Campsomerini of Africa. Bradley (1959) treated some African groups of Scoliini. Pagliano (1987) revised the Italian Scoliidae. Bischoff (1927) and Clausen (1940) surveyed the biology.

# **Family VESPIDAE**

(Figs. 79-84)

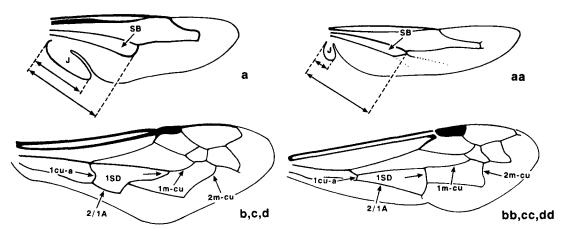
Diagnosis Dorsal rim of torulus simple; eye with inner margin deeply emarginate. Pronotum with posterodorsal margin V-shaped, and with posterolateral apex acute and strongly produced above anterior margin of tegula: mesocoxae and metacoxae contiguous; fore wing usually longitudinally folded but sometimes not folded; hind wing without distinct claval lobe, and usually with distinct jugal lobe but sometimes without; posterior (inner) spur of metatibia weakly modified as a calcar. Metasoma sessile or petiolate; metasomal segment 1 without a true node although sometimes approaching it; metasomal sternum 1 separated from sternum 2 by a deep constriction; male metasomal sternum 8 (hypopygium) simple, not concealed. Usually no sterile worker caste. Sexual dimorphism slight: both sexes macropterous.

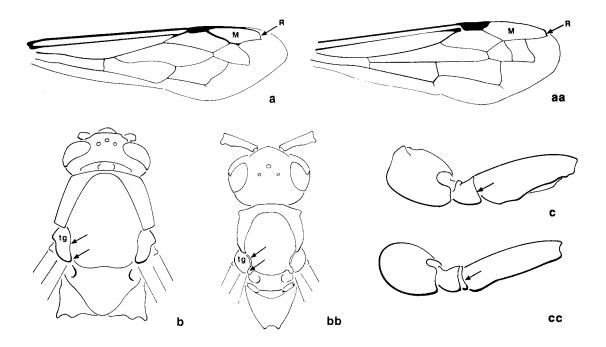
**Comments** Vespidae is a cosmopolitan but predominantly tropical family, containing about 4000 species in six subfamilies: Eumeninae,

Euparagiinae, Masarinae, Polistinae, Stenogastrinae, and Vespinae. The group was often divided into three separate families (Masaridae, Eumenidae, and Vespidae) in the past. Adults are generally predominantly black or brown but are often extensively marked with yellow or white. Most species are solitary, but many are social. In solitary species the larva is usually predatory on other insects, particularly caterpillars, in a cell constructed and provisioned by the adult female; the larva is rarely supplied with a mixture of pollen and nectar instead. In social species the larva is progressively fed by adult females on masticated insects or rarely predominantly on glandular secretions. A few are cleptoparasites in the nests of social species. Pupation occurs within the cell. About 315 species in about 31 genera (in five subfamilies) occur in North America, including 62 species in 14 genera (and perhaps an additional 27 species) in Canada.

# Key to subfamilies of VESPIDAE

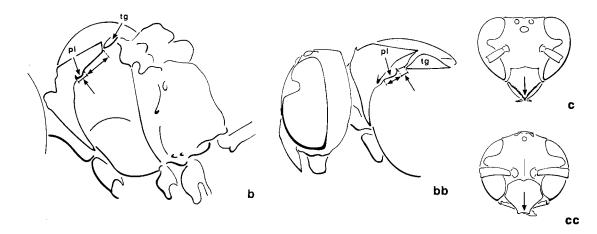
(modified from Carpenter 1981)



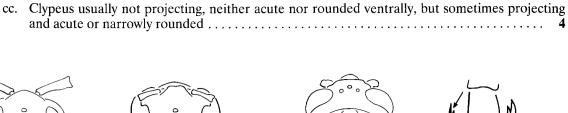


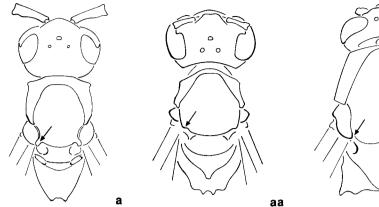
- a. Fore wing with apex of marginal cell (M) widely separated from anterior margin of wing, the apical free section of vein R at least as long as width of stigma.
  - b. Mesoscutum without lateral longitudinal carina opposite tegula (tg), and without projecting lobe at posterolateral apex.

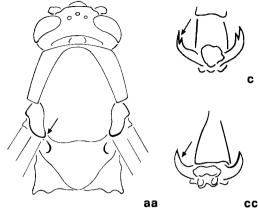
  - aa. Fore wing with apex of marginal cell (M) narrowly or not separated from anterior margin of wing, the apical free section of vein R less than half as long as width of stigma or absent.
  - bb. Mesoscutum with a lateral longitudinal carina opposite tegula (tg) or with a projecting lobe at posterolateral apex.

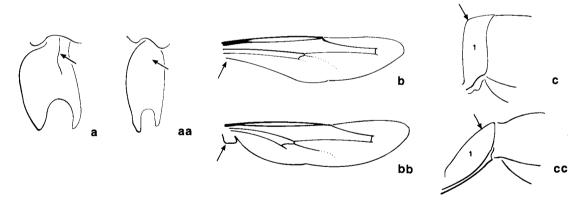


- a. Fore wing not longitudinally folded at rest, not reaching beyond metasomal segment 3.
  - b. Pronotal lobe (pl) separated from tegula (tg) by a distance greater than length of lobe.
  - c. Clypeus projecting and acute or narrowly rounded ventrally ...... Stenogastrinae
  - aa. Fore wing longitudinally folded at rest, usually reaching at least to posterior margin of metasomal segment 4.
  - bb. Pronotal lobe (pl) usually separated from tegula (tg) by a distance equal to or less than length of lobe, but distance rarely greater.









## Subfamily Euparagiinae

(Fig. 79)

This Nearctic subfamily includes about 10 species in one genus. Adults are small and compact with a sessile metasoma. All species are solitary. Burrows in the soil are provisioned with Coleoptera larvae. None occurs in Canada.

#### **Subfamily Masarinae**

(Fig. 80)

This cosmopolitan subfamily, most speciose in the Southern Hemisphere, includes about 220 species in 18 genera. Adults are small to moderate, with a sessile metasoma. All species are solitary. Burrows in the soil or exposed mud nests are provisioned with a mixture of pollen and nectar. About 15 species in one genus occur in North America, including two species in southwestern Canada.

#### **Subfamily Eumeninae**

(Fig. 81)

This cosmopolitan subfamily includes about 3000 species in about 150 genera. Adults are small to large and compact to elongate with a sessile to strongly petiolate metasoma. All species are solitary or sometimes subsocial. Burrows in the soil or wood, or exposed mud nests, are provisioned with the larvae of Lepidoptera, Coleoptera, or Symphyta. About 250 species in 23 genera occur in North America, including 42 species in nine genera in Canada.

#### Subfamily Stenogastrinae

(Fig. 82)

This Oriental subfamily includes about 50 species in about six genera. Adults are fairly small to moderate, and elongate with a strongly petiolate metasoma. They are weakly social and construct loose paper or mud nests in sheltered places. The larvae are fed on glandular secretions and masticated insects.

#### Subfamily Vespinae

(Fig. 83)

This Holarctic and Oriental subfamily (yellow-jackets and hornets) includes about 80 species in four genera. Adults are moderate to very large and compact with a sessile metasoma. They are eusocial and construct annual or perennial compact paper nests, which are usually multicombed and covered with a paper envelope,

suspended in the open, in sheltered positions or underground. The larvae are fed on masticated insects or even flesh from dead vertebrates. A few are cleptoparasites in the nests of other Vespinae. Eighteen species in two genera occur in North America, including 16 species in two genera in Canada as far north as the treeline and even up to 70 km beyond.

#### **Subfamily Polistinae**

(Fig. 84)

This cosmopolitan subfamily (paper wasps), most speciose in the Neotropical region, includes about 700 species in about 25 genera. Adults are small to large and compact to elongate with a sessile to petiolate metasoma. They are eusocial and construct annual or perennial compact paper nests, which are sometimes multicombed and covered with a paper or mud envelope but are often single-combed and exposed, suspended in the open or in sheltered positions. The larvae are fed on masticated insects, especially caterpillars, but may also be fed stored termite (Termitodea, Dictuoptera) or ant reproductives, or honey. Twenty-two species in four genera occur in North America, including two species in two genera in southern Canada.

**References** Carpenter (1981, 1987, 1988, 1989) revised the higher classification and presented a key to subfamilies, and analyzed the phylogeny of the genera of Vespinae, Stenogastrinae, and Gayellini (Masarinae). Tobias (1978d) keyed the species of European USSR, and Li (1985) reviewed the species of China. Cardale (1985) cataloged the Australian species. Richards (1962, 1978a, 1978b) revised Euparagiinae and Masarinae, the New World Polistinae, and the Australian Polistinae and Vespinae, respectively. Snelling (1981) keyed the genera of Stenogastrinae, Vespinae, and Polistinae. Carpenter (1986) presented a checklist of genus-group names in Eumeninae. Carpenter and Cumming (1985) reviewed and keyed the Nearctic genera of Eumeninae, and Menke and Stange (1986) updated that key. Van der Vecht and Fischer (1972) cataloged the Palaearctic Eumeninae, Giordani Soika (1978) and Guichard (1980) keyed the genera of Europe, and Kurzenko (1981) keyed the genera of the USSR. Archer (1989) keyed the world species of Vespinae, and Akre et al. (1981) and Miller (1961) keyed the Nearctic Vespinae. Das and Gupta (1989) revised the Vespinae, Polistinae, and Stenogastrinae of the Indian subregion. The biology has been treated by many authors, including Bischoff (1927), Michener and Michener (1951), Richards (1953), Olberg (1959), Grandi (1961), Krombein (1967), Evans and West Eberhard (1970), Wilson (1971), Matsuura and Yamane (1984), Gess and Gess (1989), Turillazzi (1989), and Ross and Matthews (1991).

# Family FORMICIDAE

(Figs. 85-92)

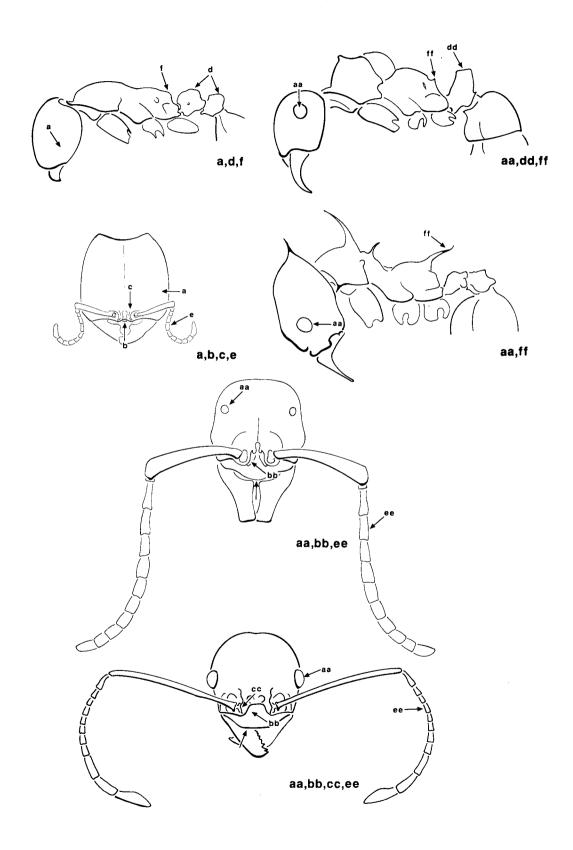
Diagnosis Dorsal rim of torulus often tuberculate or concealed under vertical laminate carina of frons, rim sometimes simple; eye with inner margin more or less straight or convex. Pronotum with posterodorsal margin weakly concave to U-shaped and with posterolateral apex truncate anterior to tegula; metapleural gland usually opening above metacoxa, the opening and/or gland rarely absent: mesocoxae and metacoxae contiguous; hind wing usually without distinct claval lobe but claval lobe rarely indicated, and usually without distinct jugal lobe but jugal lobe rarely present; posterior (inner) spur of metatibia modified as a calcar. Metasoma petiolate; metasomal segment 1 usually strongly constricted at each end, forming a true node, but rarely unconstricted posterodorsally; metasomal sternum 1 separated from sternum 2 by a deep constriction; male metasomal sternum 8 (hypopygium) simple, not concealed. Sterile worker caste present but rarely absent. Sexual dimorphism slight to extreme: reproductives of both sexes usually macropterous, but female rarely brachypterous or sometimes apterous (often dealate) and male rarely apterous; sterile female apterous; apterous form with mesosoma somewhat different from that in macropterous and brachypterous forms, with pronotum usually freely articulating but sometimes fused with mesothorax, with mesonotum and metanotum - propodeum rarely articulating but usually fused with the suture

between them often distinct, and with mesosomal sclerites sometimes entirely fused with all sutures indistinguishable.

Comments Formicidae (ants) is a cosmopolitan but predominantly tropical family, containing about 8800 species in 10 subfamilies: Aneuretinae, Dolichoderinae, Dorylinae (including Aenictini and Ecitonini), Formicinae, Leptanillinae, Myrmeciinae, Myrmicinae, Nothomyrmeciinae, Ponerinae (including Cerapachyini), and Pseudomyrmecinae; the recognition of more subfamilies as suggested in recent publications awaits more general acceptance. Many species are widespread or cosmopolitan as a result of introductions by humans. Adults are generally more or less uniformly black, brown, reddish, or vellowish. All are highly social, but some are slave makers or social parasites in which the worker caste has been lost, and a few have laving workers instead of queens. The larvae are fed by the workers on a wide variety of substances of animal or vegetable origin, in chambers constructed by the workers. Pupation occurs within the chamber, and adult eclosion from the cocoon (when present) usually cannot take place without assistance from workers. About 590 species in about 73 genera (six in subfamilies) occur in North America, including 111 species in about 28 genera in Canada.

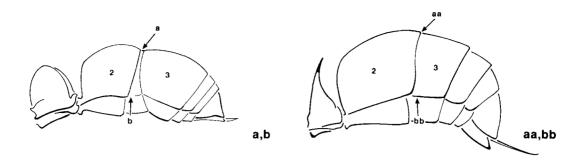
# Key to subfamilies of FORMICIDAE (workers)

(modified from Snelling 1981)

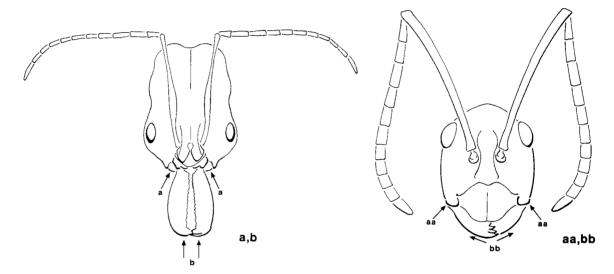


1 a. Eye vestigial or absent. Clypeus short, the antenna thus inserted near anterior margin of head. Frontal carina short and vertical, not covering torulus. Metasoma usually with 2 anterior nodes. Antenna usually short. Propodeum usually without spines ..... f. Eye fully developed and/or: aa. Clypeus long, the antenna thus inserted far from anterior margin of head and/or: cc. Frontal carina long and oblique, covering torulus and/or: dd. Metasoma with 1 anterior node and/or: ee. Antenna long and/or: ff. Propodeum with spines ..... aa,cc 2(1) Body at most 2.5 mm long and markedly elongate and slender; groove between pronotum and mesonotum distinct. Maxillary palpus not segmented or with 2 segments; labial palpus not segmented. Metasoma with 2 anterior nodes ...... Leptanillinae Body more than 3 mm long, usually not markedly elongate and slender, and/or groove between pronotum and mesonotum weak or not discernible. Maxillary and labial palpi each with 2 or 3 segments. aa 3(1) Metasoma with 1 anterior node .....

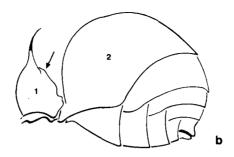
Metasoma with 2 anterior nodes ......



- 4(3) Metasoma with distinct constriction between segments 2 and 3. Metasomal segment 3 with tergum and sternum fused anteriorly . . . . . . . some **Ponerinae** Metasoma without distinct constriction between segments 2 and 3. aa.
  - bb. Metasomal segment 3 usually with tergum and sternum free but sometimes fused anteriorly ..... 5

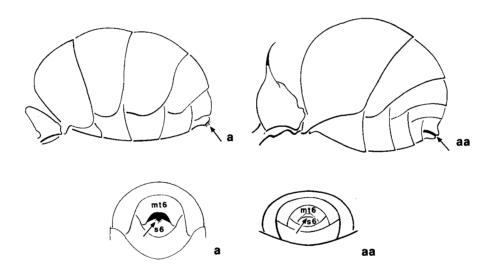


- 5(4) a. In anterior view, mandibles originating close together near middle of anteroventral margin of head. b. Mandibles parallel to each other when closed, forming a straight line when fully open. Metasomal segment 3 with tergum and sternum fused anteriorly . . . . . . . some **Ponerinae** In anterior view, mandibles originating a distance apart, at lateral extremities of anteroventral margin of head. Mandibles usually distinctly converging when closed, forming an acute or obtuse angle when fully bb.
  - cc. Metasomal segment 3 with tergum and sternum free ...... 6

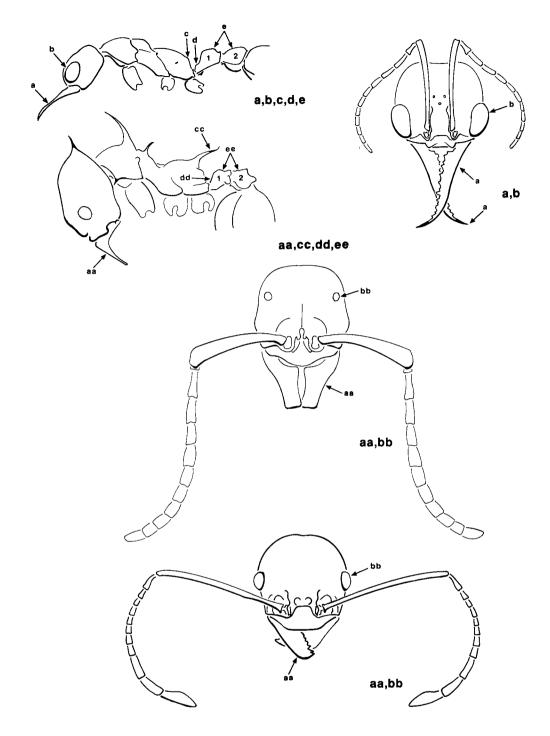


- **6(5)** a. Sting absent or vestigial.

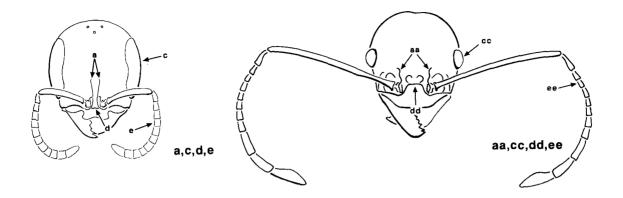
  - aa. Sting fully developed and protrusible.



- 7(6) a. Opening at apex of metasoma formed by last sternum (s<sub>6</sub>); opening terminal, semicircular to circular, usually nozzle-like and/or surrounded by a fringe of hairs.
  - b. If opening at apex of metasoma concealed by last tergum then antenna inserted well posterior to posterior clypeal margin (otherwise antenna at posterior clypeal margin) ...... Formicinae
  - aa. Opening at apex of metasoma formed by last tergum  $(mt_6)$  and sternum  $(s_6)$ ; opening terminal or subterminal, slit-like and without a fringe of hairs.
- **8(6)** a. Clypeus with anteroventral margin emarginate in middle.
  - b. Eye small, positioned below mid height of lateral margin of head.
  - c. Propodeum angulate in lateral view, with strong spine at posterodorsal angle . . . . Aneuretinae
  - aa. Clypeus with anteroventral margin convex in middle.
  - bb. Eye large and convex, positioned slightly above mid height of lateral margin of head.
  - cc. Propodeum rounded in lateral view, without spines ...... Nothomyrmeciinae



- **9(3)** a. Mandible very long, more or less straight, narrow, apically acute and toothed along entire inner margin.
  - b. Eye positioned slightly below mid height of lateral margin of head.
  - c. Propodeum without spines.
  - d. Metasomal segment 1 gradually swollen and often with narrow anterior stalk.
  - e. Metasomal segment 2 cup-shaped or bell-shaped and larger than 1 ........... Myrmeciinae
  - aa. Mandible short and/or curved and/or wide and/or apically truncate and/or not toothed along entire inner margin and/or:
  - bb. Eye positioned above mid height of lateral margin of head and/or:
  - cc. Propodeum with spines and/or:
  - dd. Metasomal segment 1 abruptly swollen and/or without narrow anterior stalk and/or:



- **10(9)** a. Frontal
  - a. Frontal carinae usually close together, narrow, and not covering toruli.
  - b. Body markedly elongate, often very slender.
  - c. Eye very large and elongate.
  - d. Clypeus with dorsal margin rounded, not produced dorsally between frontal carinae.

  - aa. Frontal carinae usually well-separated, large, and covering toruli.
  - bb. Body compact and/or:
  - cc. Eye small and rounded and/or:
  - dd. Clypeus with dorsal margin narrow and produced dorsally between frontal carinae and/or:

# **Subfamily Myrmeciinae**

(Fig. 85)

This Australian subfamily (bulldog ants) includes about 90 species in one genus. Adults are moderate to large predators; female reproductives are macropterous, and workers can sting. Nests are permanent and in the soil.

# **Subfamily Pseudomyrmecinae**

(Fig. 86)

This cosmopolitan subfamily (tree ants) includes about 150 species in two genera; some authorities consider the Cerapachyini to constitute a separate subfamily. Adults are small to moderate-sized predators; female reproductives are macropterous, and workers can sting. Nests are permanent and in hollow stems or thorns of trees or other plants. Five species in one genus occur in North America, none in Canada.

#### **Subfamily Ponerinae**

(Fig. 87)

This cosmopolitan subfamily includes about 600 species in about 55 genera. Adults are small to large predators; female reproductives are

macropterous or apterous, and workers can sting. Nests are permanent and are usually constructed in the soil or rotting logs. Thirty-three species in 16 genera occur in North America, including four species in about three genera in Canada.

#### **Subfamily Dorylinae**

(Fig. 88)

This cosmopolitan subfamily of army and driver ants includes about 170 species in about seven genera; some authorities consider the Aenictini and the Ecitonini to comprise separate subfamilies. Adults are small to large predators or rarely phytophagous; female reproductives are apterous, and workers can usually sting. Colonies are nomadic, and the workers usually establish bivouacs in the soil or in sheltered places above ground. Twenty-five species in three genera occur in North America, none in Canada.

# **Subfamily Leptanillinae**

This Australian, Oriental, and southern Palaearctic subfamily includes about 20 species in four genera. Adults are minute to small and probably predacious; female reproductives are apterous, and workers can sting. Nests are constructed in the soil.

#### **Subfamily Myrmicinae**

(Fig. 89)

This cosmopolitan subfamily includes about 2000 species in about 140 genera. Adults are small to moderate-sized predators, granivores, or fungivores; female reproductives are macropterous, and workers can or cannot sting. Nests are permanent and are usually constructed in the soil, in rotting wood, under objects, or in trees (including carton-making species); some species are social parasites. About 310 species in 35 genera occur in North America, including 37 species in about 15 genera in Canada.

#### **Subfamily Nothomyrmeciinae**

This Australian subfamily includes one monotypic genus. Adults are moderate-sized predators; female reproductives are brachypterous, and workers can sting. Nests are permanent and are constructed in the soil.

## **Subfamily Aneuretinae**

This Oriental subfamily includes one monotypic genus. Adults are small predators; female reproductive are macropterous, and workers can sting. Nests are permanent and are constructed in the soil.

#### **Subfamily Dolichoderinae**

(Fig. 90)

This cosmopolitan subfamily includes about 230 species in about 22 genera. Adults are small to moderate-sized and polyphagous; female reproductives are macropterous, and workers cannot sting. Nests are permanent and are usually constructed in the soil, in rotting wood, or under objects. About 17 species in six genera occur in North America, including three species in two genera in Canada.

#### **Subfamily Formicinae**

(Figs. 91, 92)

This cosmopolitan subfamily, which is commonest in temperate regions, includes about 1400 species in about 50 genera. Adults are small to moderate-sized and mostly phytophagous; female reproductives are macropterous, and workers cannot sting. Nests are permanent and are usually constructed in the soil, in rotting wood, or under objects; a few species are social parasites. About 200 species in 12 genera occur in North America, including 67 species in about eight genera in Canada.

**References** The best general work on ants is by Hölldobler and Wilson (1990), which includes comprehensive regional keys to the world genera, a discussion of ant morphology, and detailed coverage of all aspects of ant biology. Wheeler (1922), Taylor (1978), Snelling (1981), Wheeler and Wheeler (1972, 1985), and Bolton (1990a, 1990b. 1990c.) evaluated and/or keved the subfamilies. Wheeler (1922) keyed and Brown (1973) listed the world genera and their distributions. The fauna was revised as follows: Creighton (1950) for North America, Smith (1936) for Puerto Rico, Snelling and Hunt (1976) for Chile, Bernard (1968) for Europe, Bolton and Collingwood (1975) for Britain, Arnold (1915-1926) for South Africa, Wilson and Taylor (1967) for Polynesia, and Brown (1958) for New Zealand. Wheeler and Wheeler (1990) keyed the Nearctic genera, Kusnezov (1978) keyed the genera of Argentina, and Bolton (1973) those of West Africa. Chapman and Capco (1951) provided a checklist of the Asian species. Kempf (1972) cataloged the Neotropical species, and Taylor and Brown (1985) the Australian species. Ogata and Taylor (1991) reviewed Myrmeciinae. Wheeler and Wheeler (1976) surveyed the larvae. Ant biology has been studied by numerous authors and was surveyed by Wheeler (1910) and Wilson (1971). Peeters and Crozier (1988) analyzed the concept of caste, Baroni Urbani (1989) evaluated biological features as related to phylogeny, and Smith (1979) summarized biological and taxonomic information for the Nearctic species. Schneirla (1971) treated the biology of Dorylinae, and Weber (1972) that of Attini (Myrmicinae).

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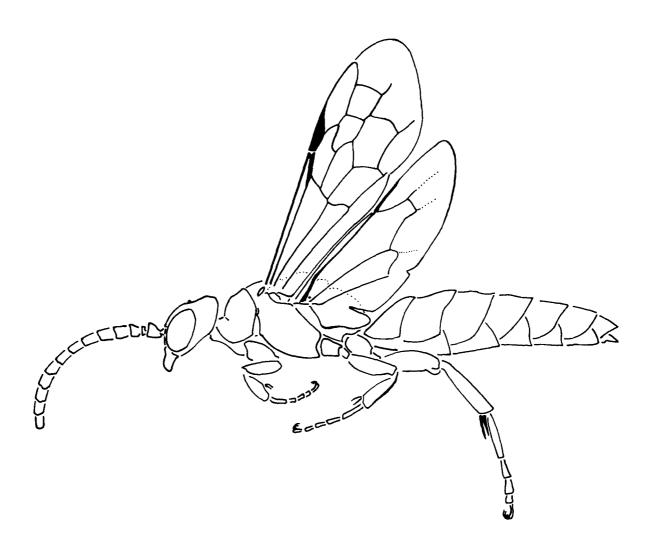
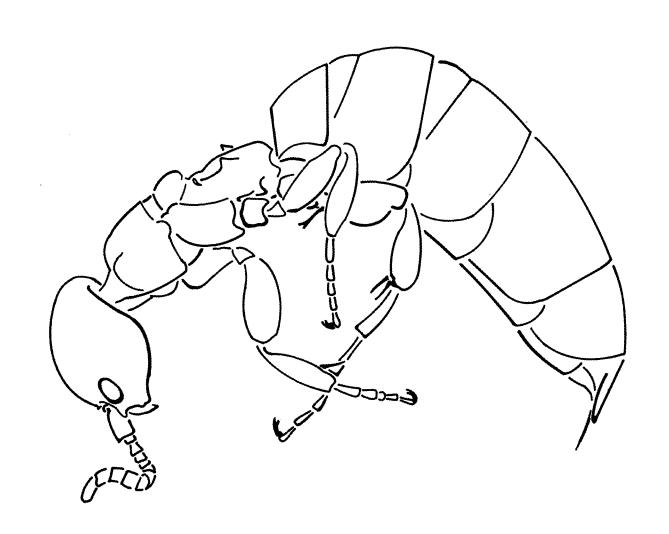


Fig. 46. Tiphiidae: Anthoboscinae



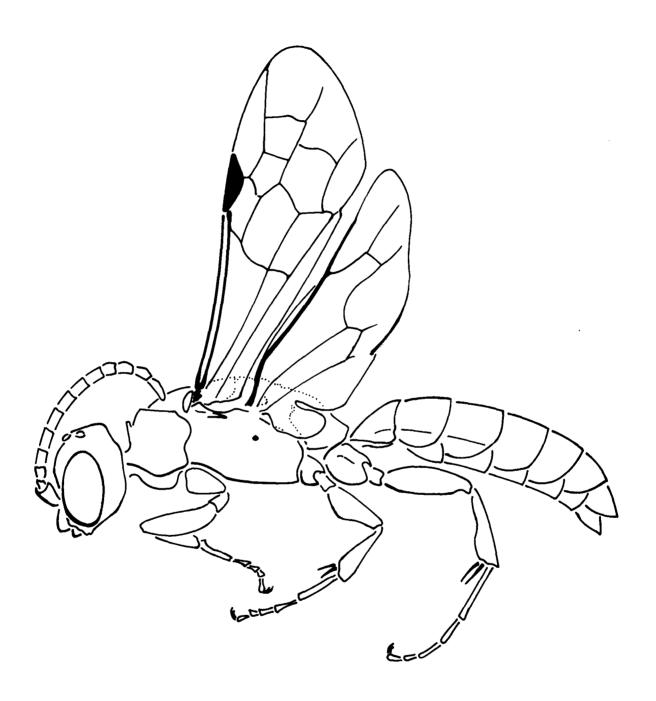


Fig. 48. Tiphiidae: Thynninae (male)

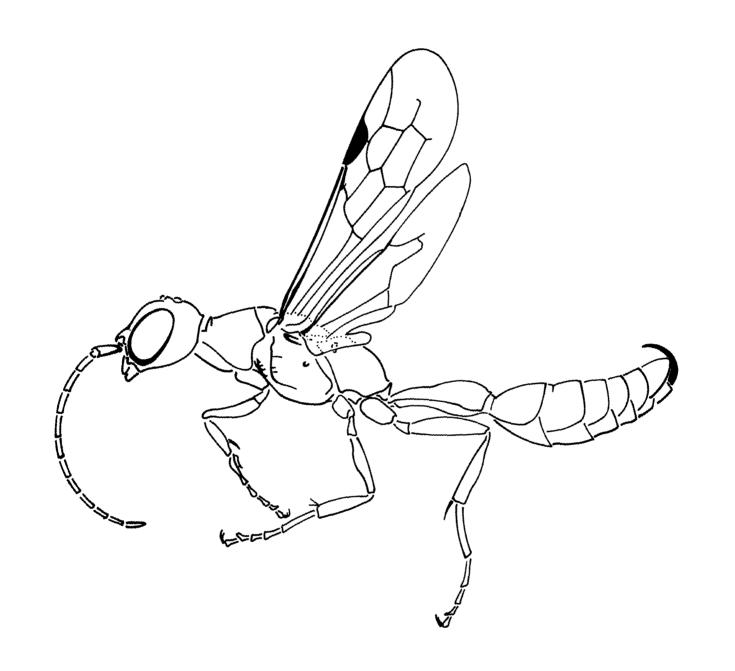


Fig. 49. Tiphiidae: Myzininae

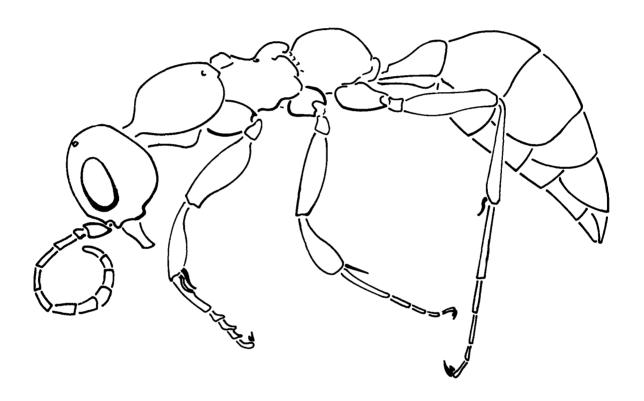


Fig. 50. Tiphiidae: Methocinae (female)

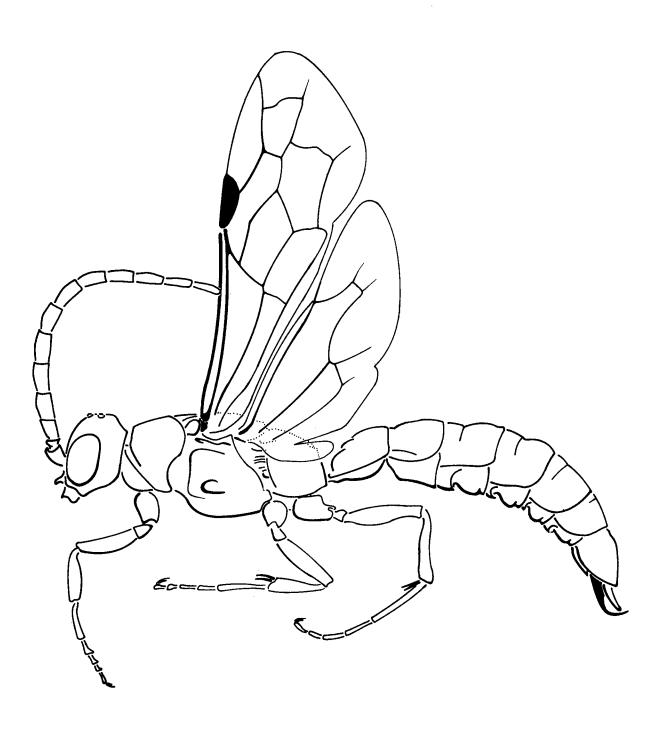


Fig. 51. Tiphiidae: Methocinae (male)



Fig. 52. Tiphiidae: Tiphiinae

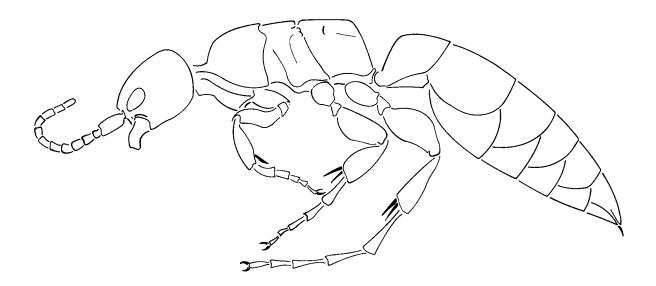


Fig. 53. Tiphiidae: Brachycistidinae (female)

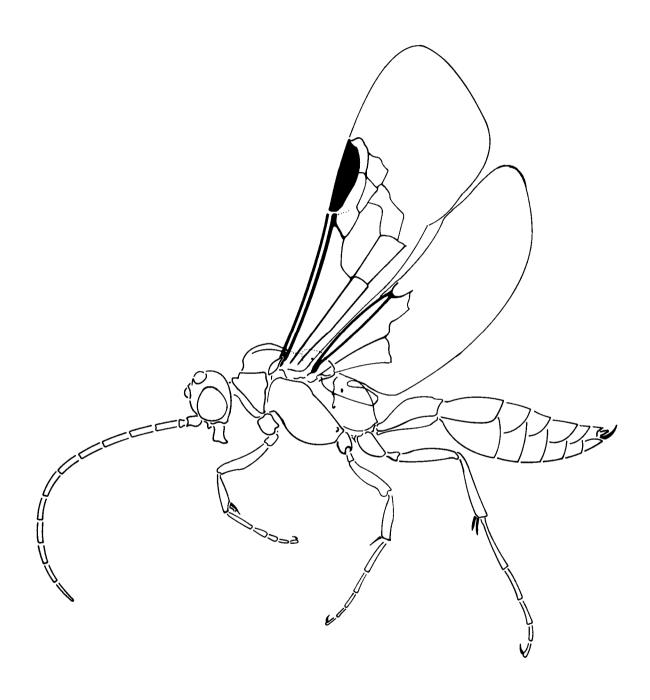


Fig. 54. Tiphiidae: Brachycistidinae (male)

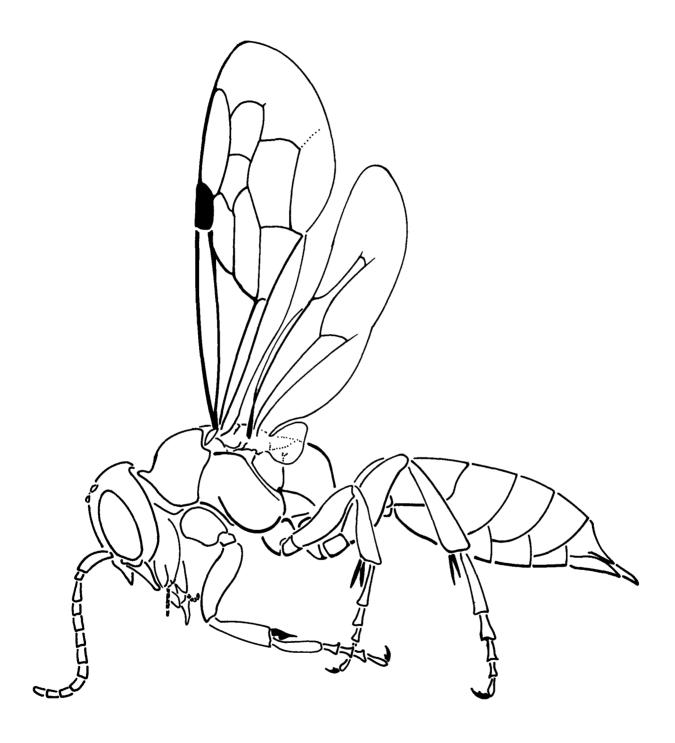


Fig. 55. Sapygidae: Fedtschenkiinae

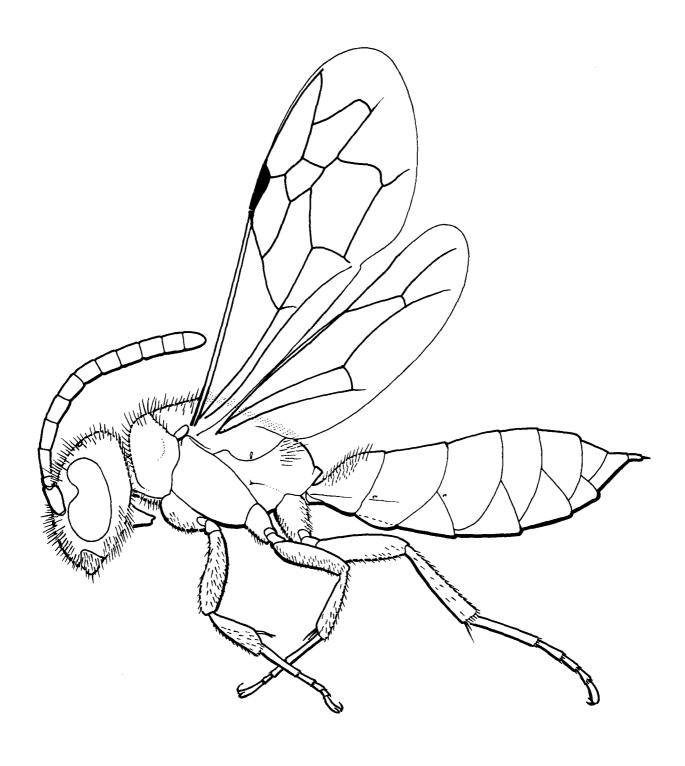


Fig. 56. Sapygidae: Sapyginae

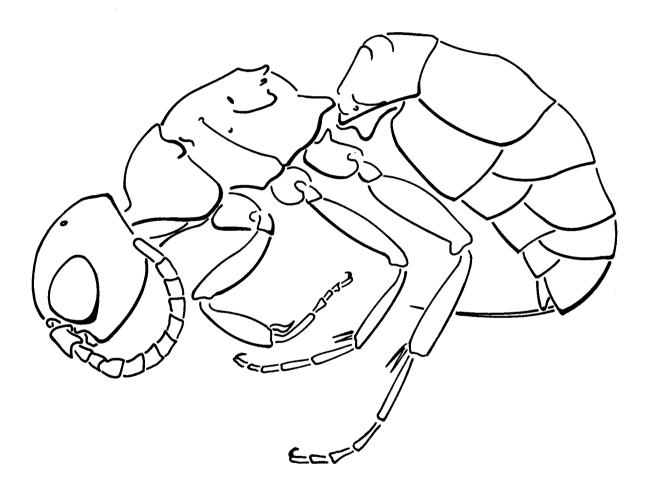


Fig. 57. Mutillidae: Myrmosinae (female)

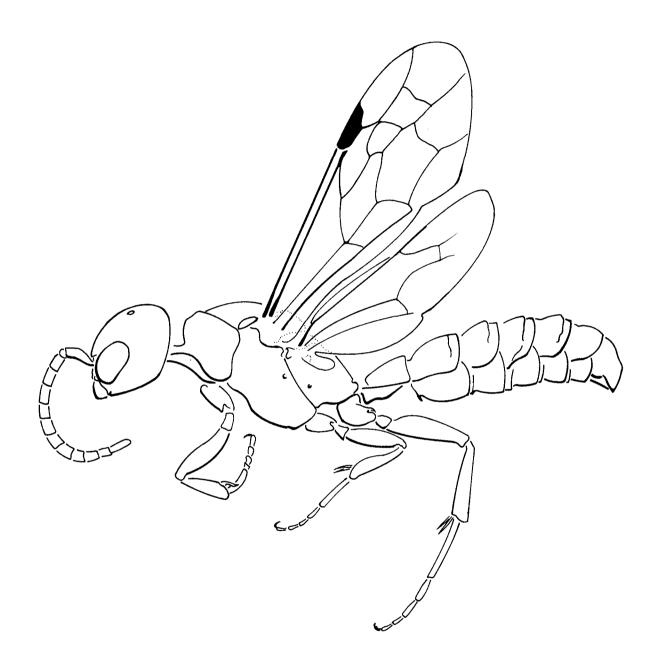


Fig. 58. Mutillidae: Myrmosinae (male)

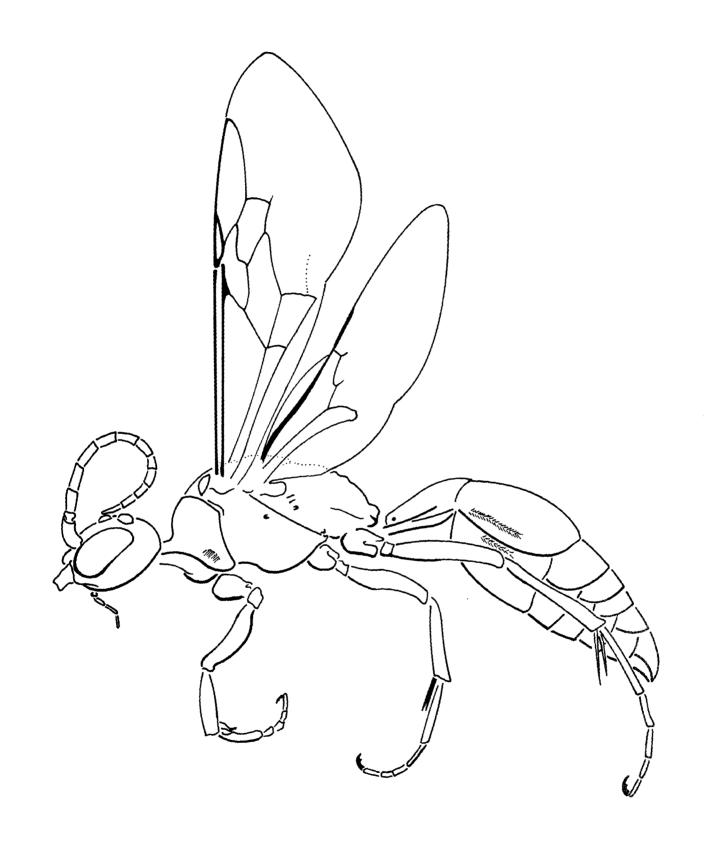


Fig. 59. Mutillidae: Pseudophotopsidinae

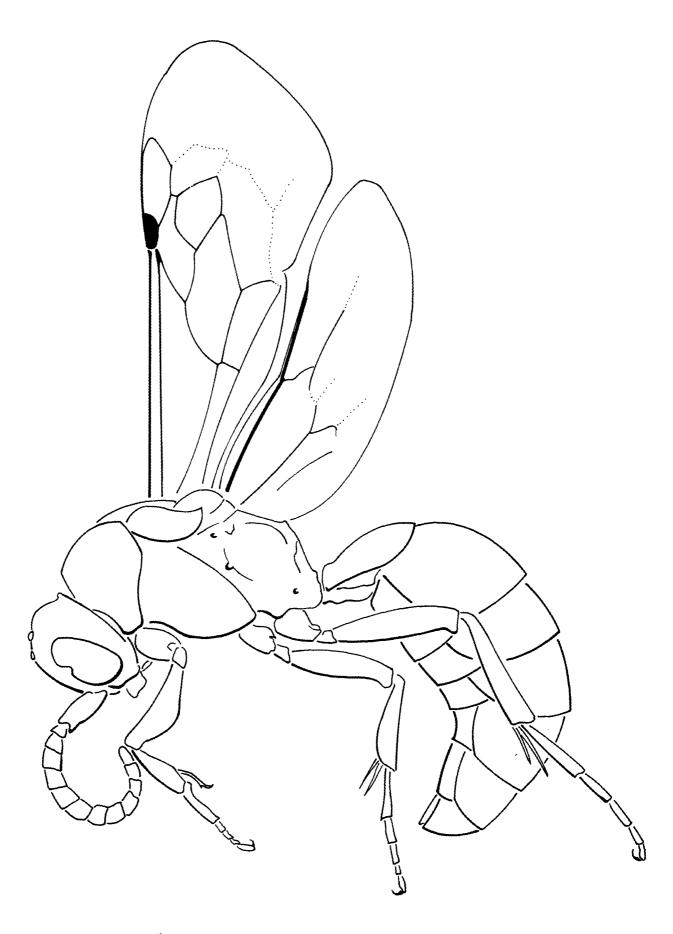


Fig. 60. Mutillidae: Ticoplinae

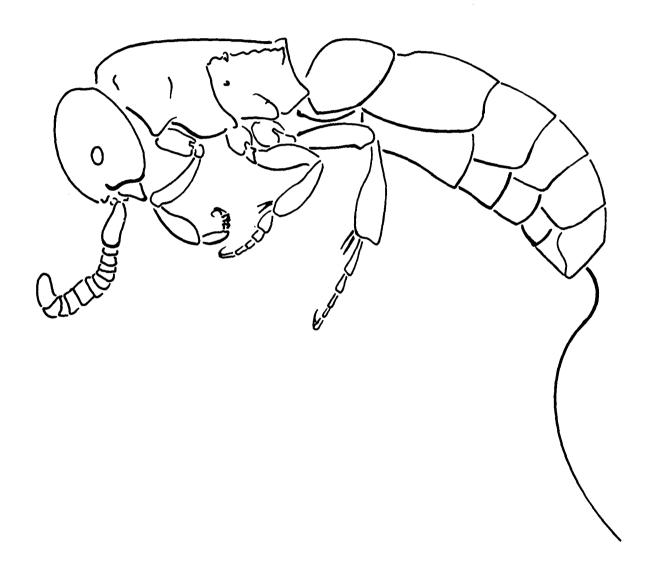


Fig. 61. Mutillidae: Rhopalomutillinae (female)

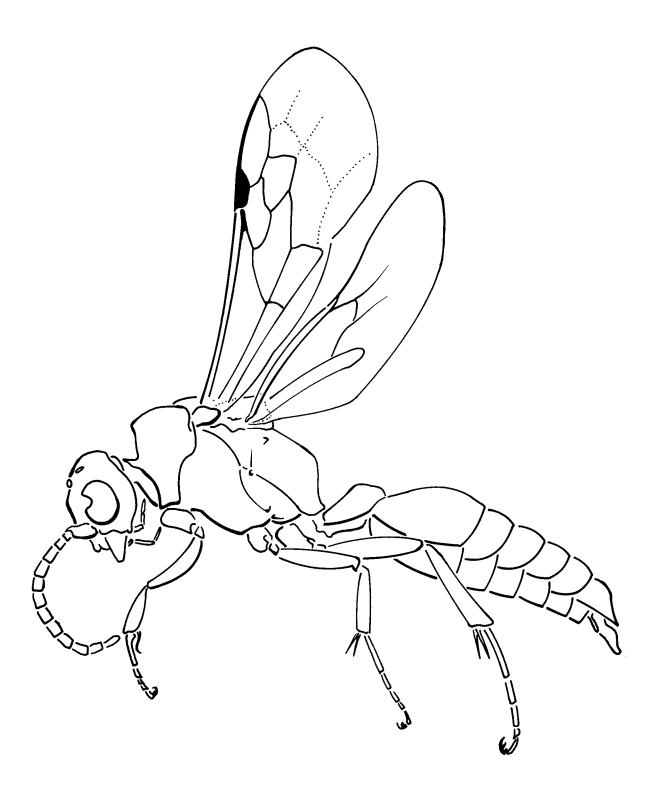


Fig. 62. Mutillidae: Rhopalomutillinae (male)

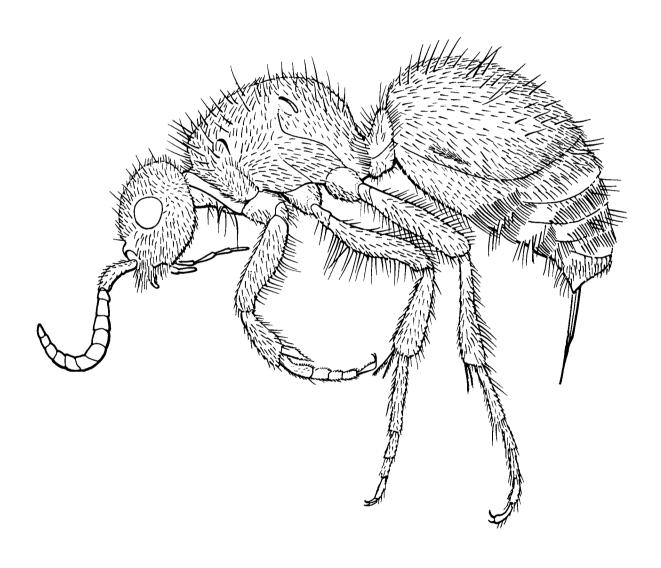


Fig. 63. Mutillidae: Sphaeropthalminae (female)

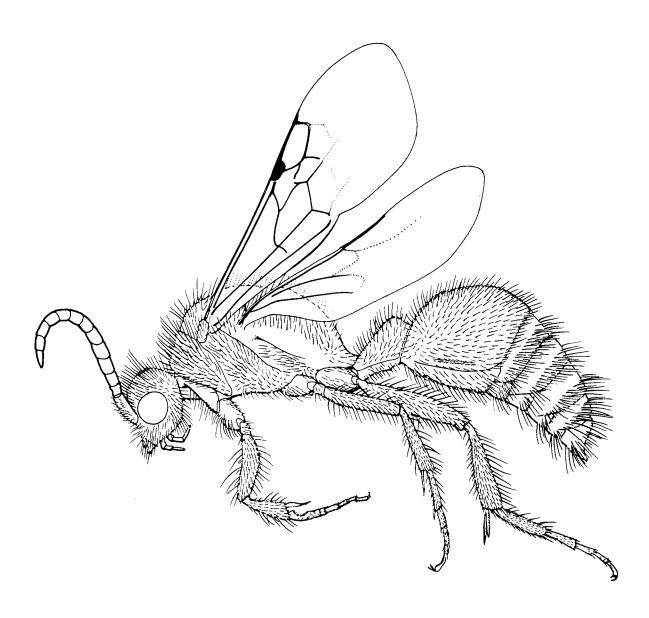


Fig. 64. Mutillidae: Sphaeropthalminae (male)

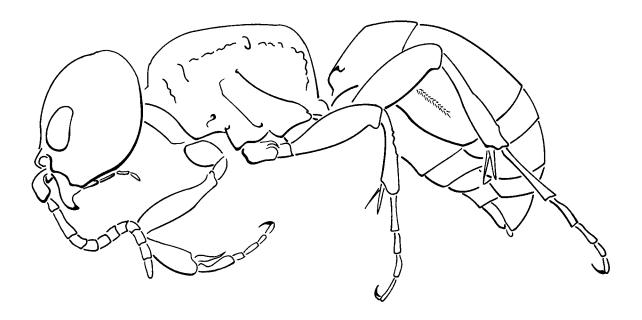


Fig. 65. Mutillidae: Myrmillinae (female)

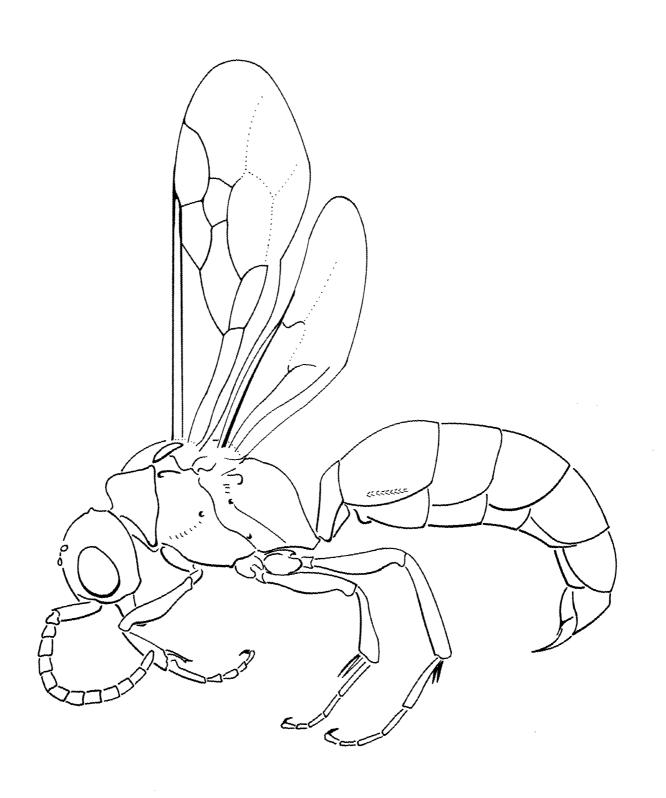


Fig. 66. Mutillidae: Myrmillinae (male)

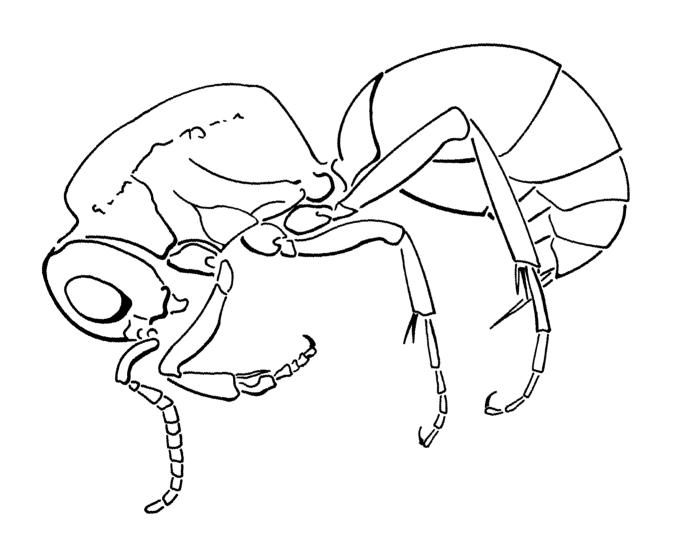


Fig. 67. Mutillidae: Mutillinae (female)

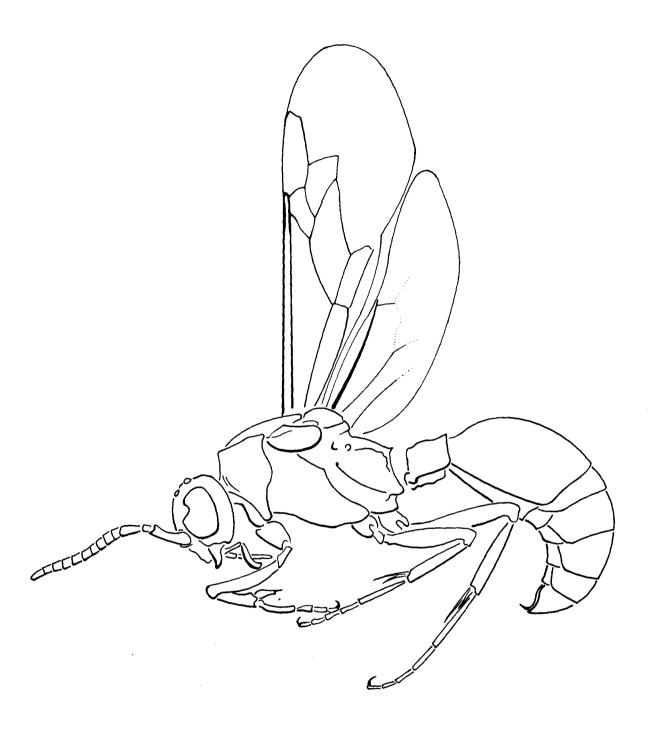


Fig. 68. Mutillidae: Mutillinae (male)

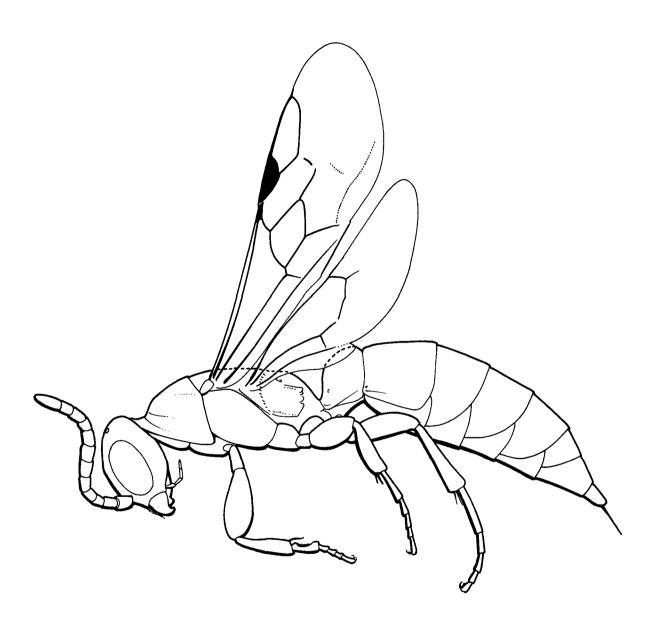


Fig. 69. Sierolomorphidae

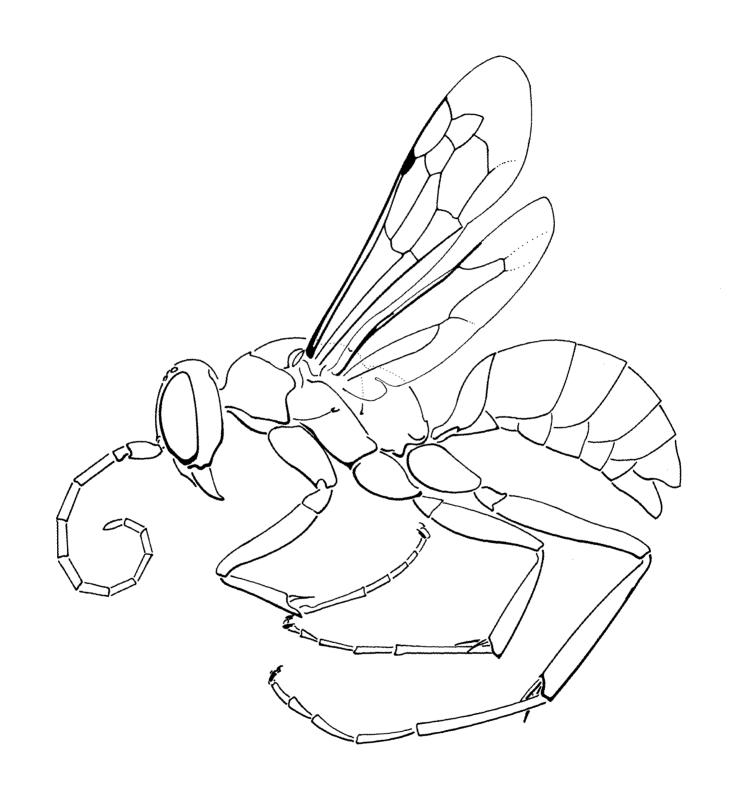


Fig. 70. Pompilidae: Pepsinae

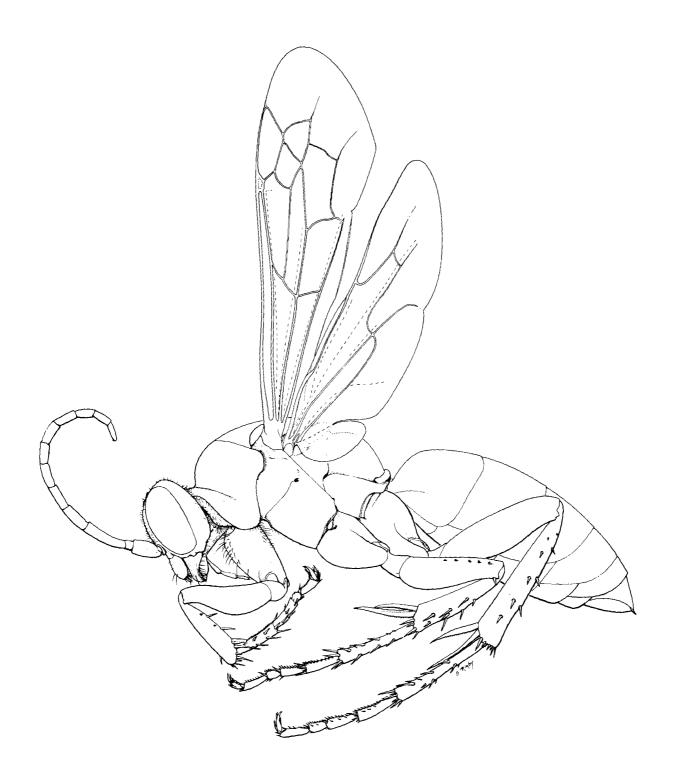


Fig. 71. Pompilidae: Pompilinae

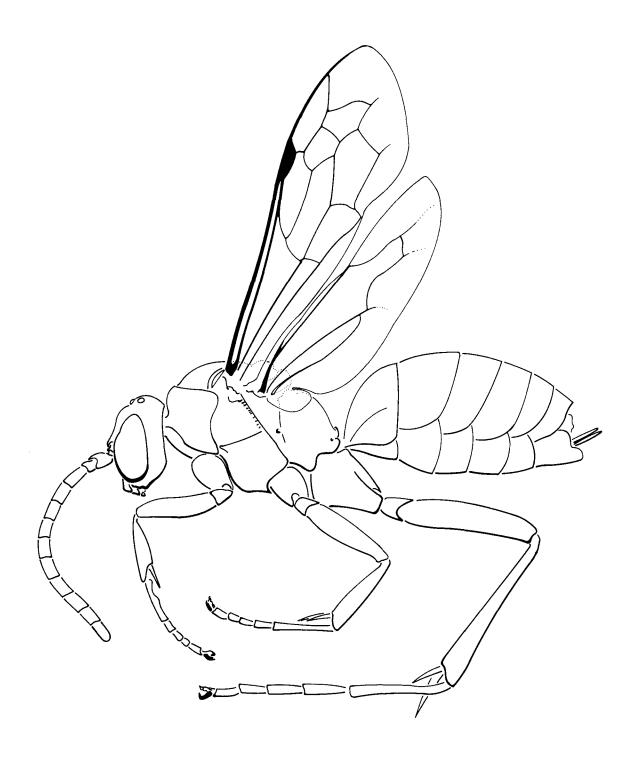


Fig. 72. Pompilidae: Ceropalinae

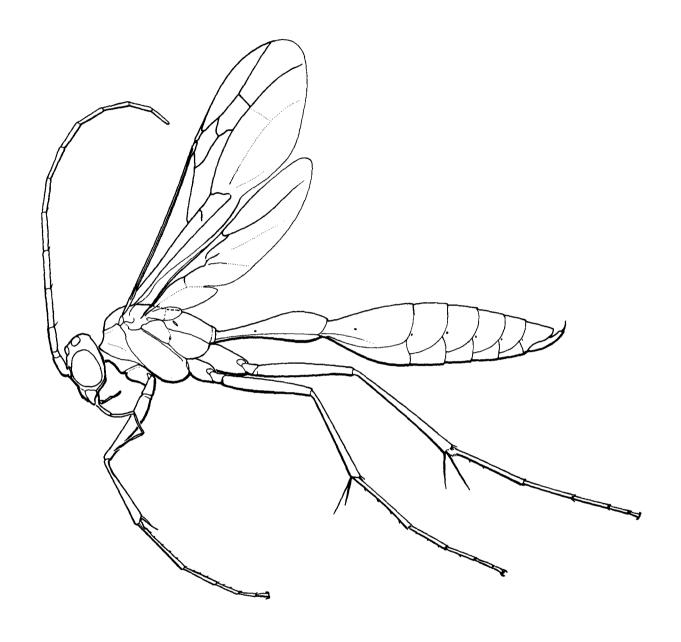


Fig. 73. Rhopalosomatidae

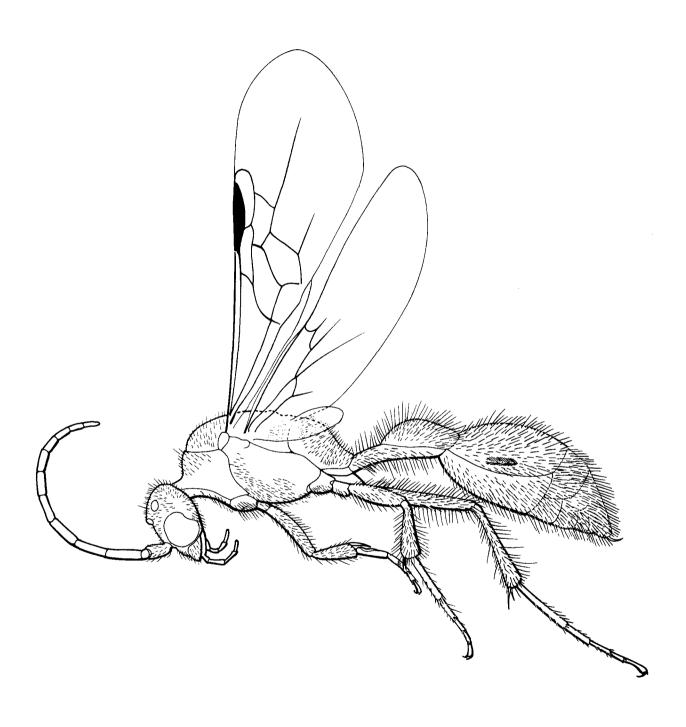


Fig. 74. Bradynobaenidae: Chyphotinae

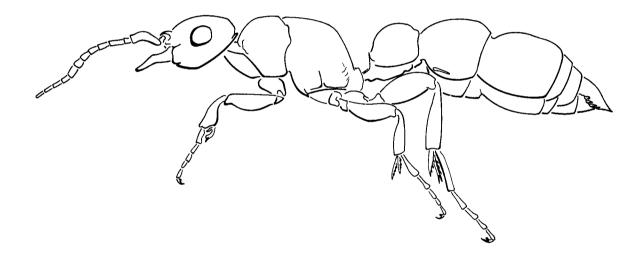


Fig. 75. Bradynobaenidae: Apterogyninae (female)

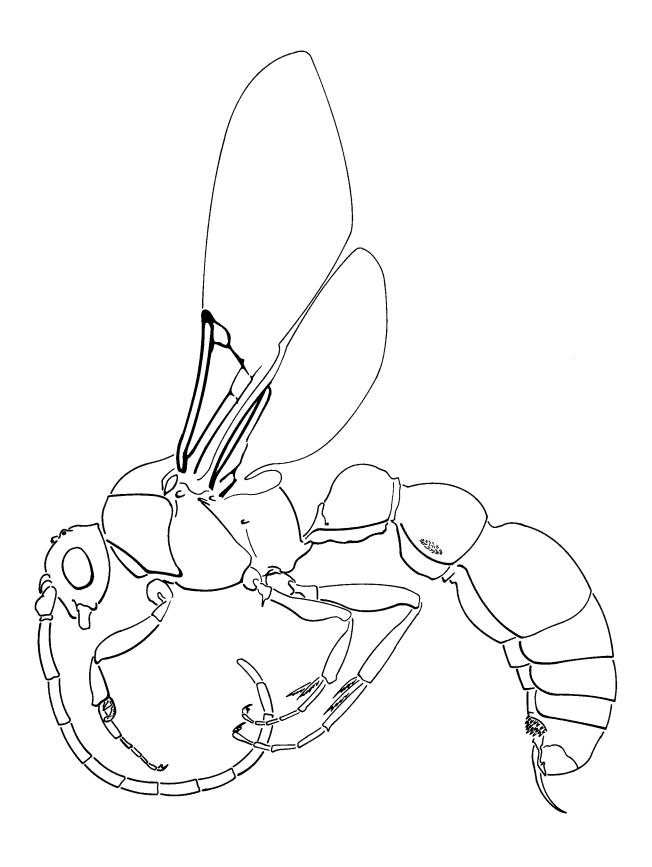


Fig. 76. Bradynobaenidae: Apterogyninae (male)

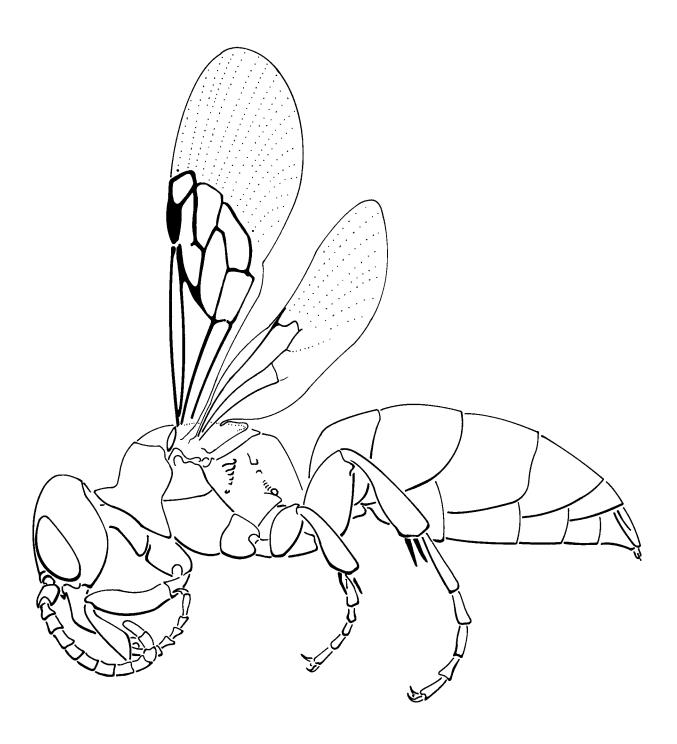


Fig. 77. Scoliidae: Proscoliinae



Fig. 78. Scoliidae: Scoliinae



Fig. 79. Vespidae: Euparagiinae

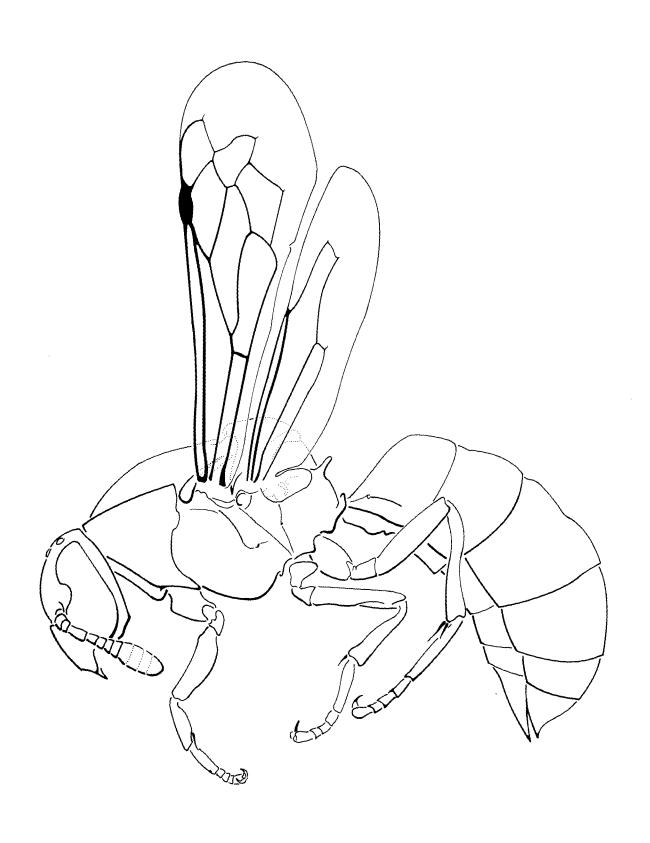


Fig. 80. Vespidae: Masarinae

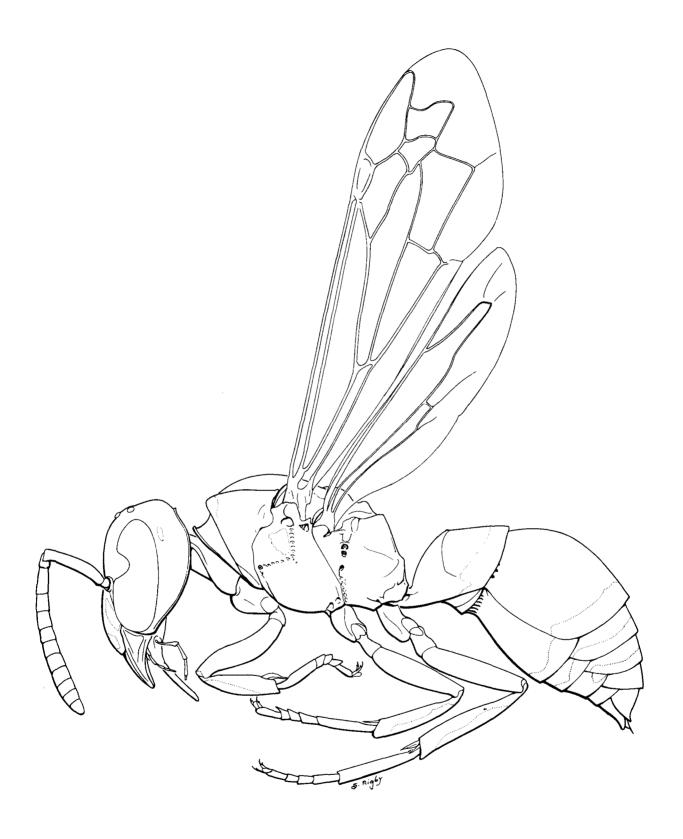


Fig. 81. Vespidae: Eumeninae

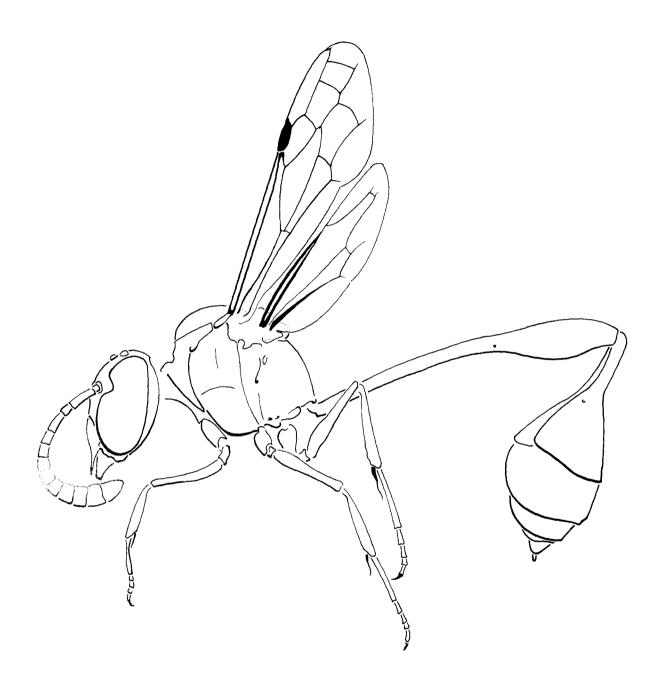


Fig. 82. Vespidae: Stenogastrinae

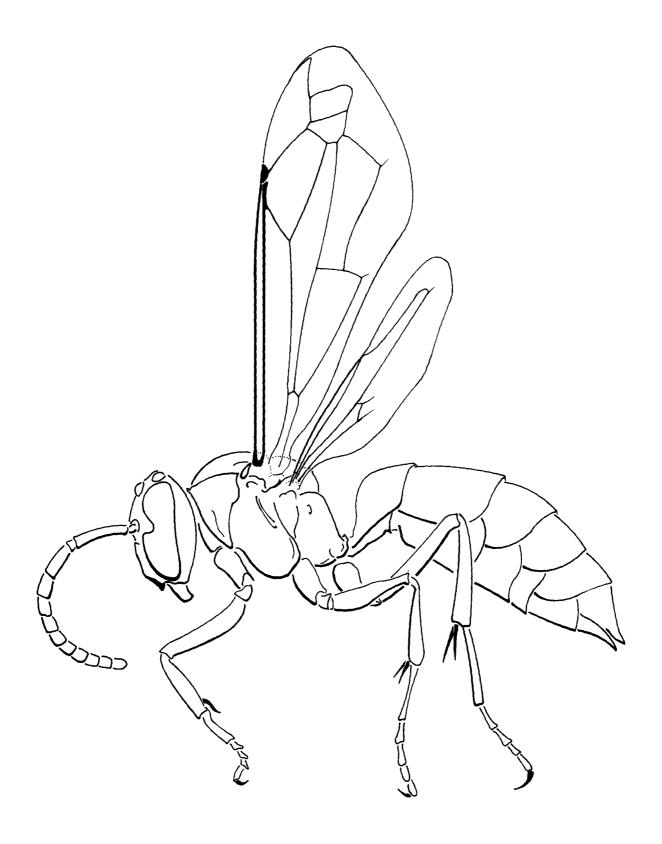


Fig. 83. Vespidae: Vespinae

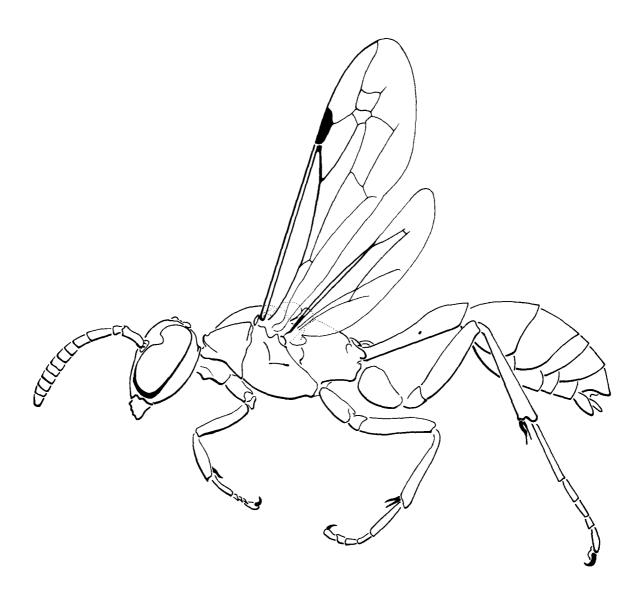


Fig. 84. Vespidae: Polistinae

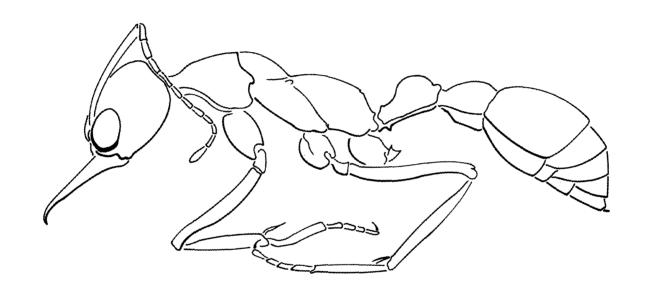


Fig. 85. Formicidae: Myrmeciinae

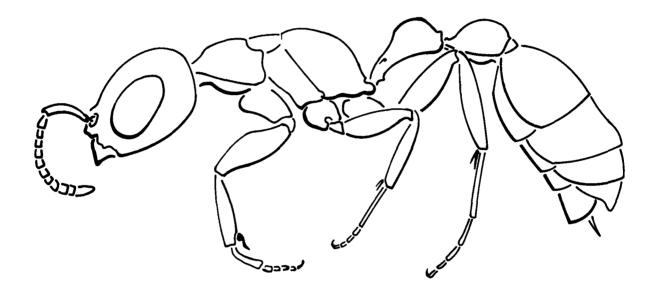


Fig. 86. Formicidae: Pseudomyrmeciinae

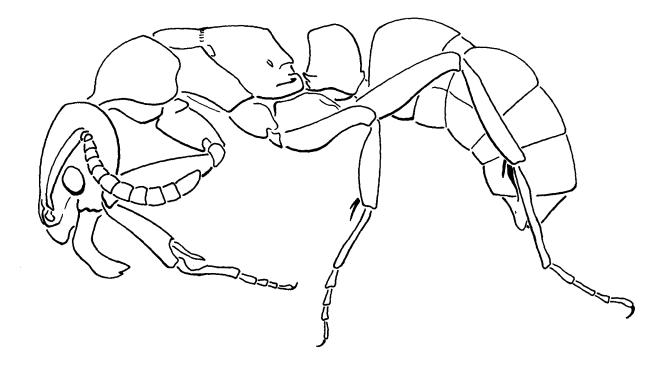


Fig. 87. Formicidae: Ponerinae

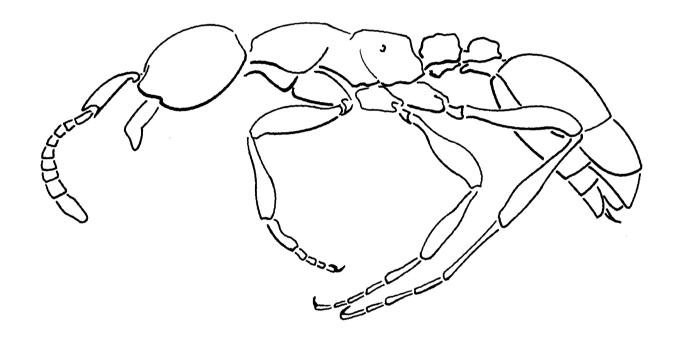


Fig. 88. Formicidae: Dorylinae

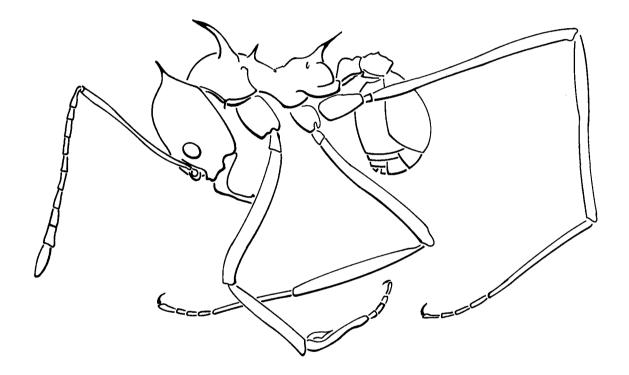


Fig. 89. Formicidae: Myrmicinae

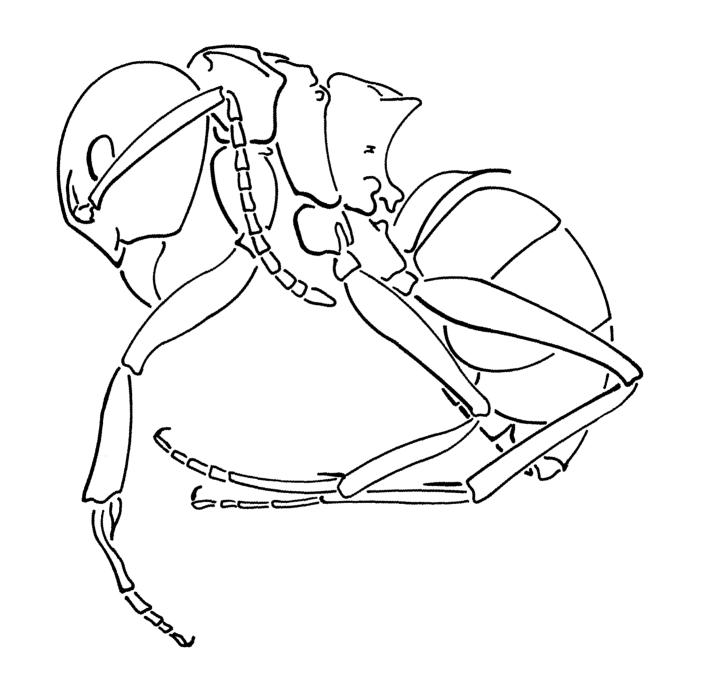


Fig. 90. Formicidae: Dolichoderinae

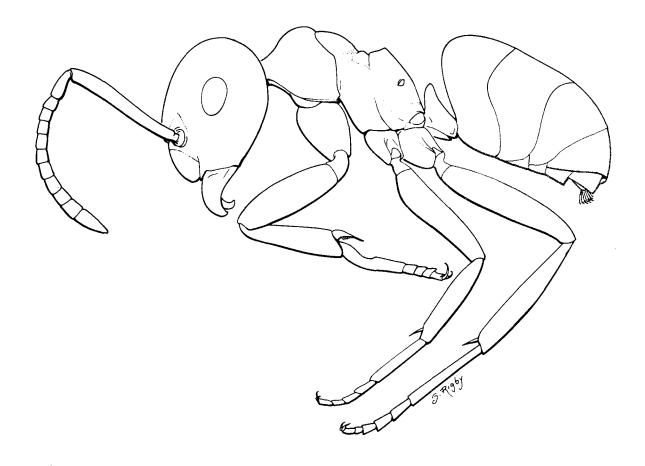


Fig. 91. Formicidae: Formicinae (worker)

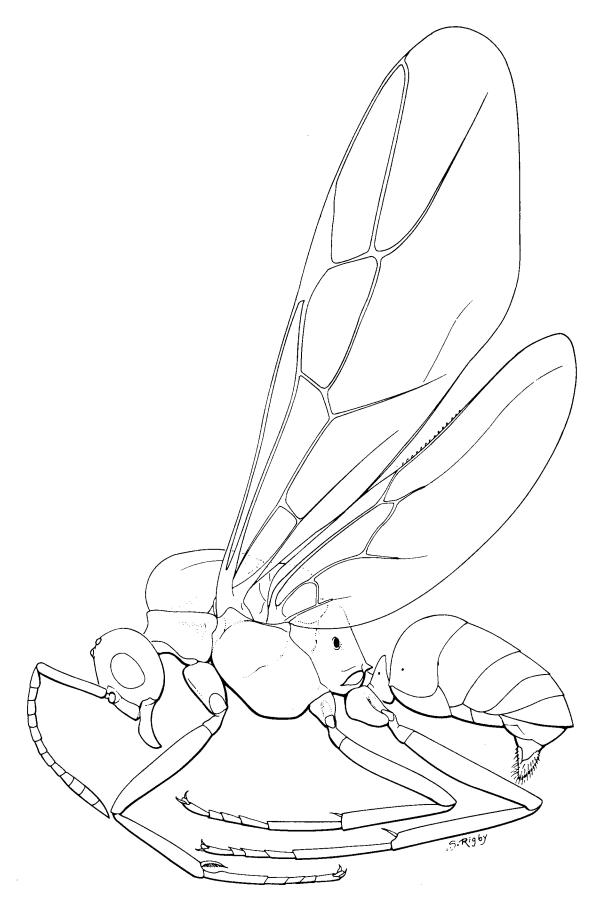


Fig. 92. Formicidae: Formicinae (male)

# **Chapter 9 Superfamily APOIDEA**

(Figs. 93-124)

Albert T. Finnamore and Charles D. Michener

Included families (20): Spheciformes: Ampulicidae, Astatidae, Crabronidae, Heterogynaidae, Mellinidae, Nyssonidae, Pemphredonidae, Philanthidae, Sphecidae. Apiformes: Andrenidae, Anthophoridae, Apidae, Colletidae, Ctenoplectidae, Fideliidae, Halictidae, Megachilidae, Melittidae, Oxaeidae, Stenotritidae.

**Diagnosis** Antenna with 10 flagellomeres in female and 11 in male; pronotum with posterolateral apex separated from tegula by a distinct cuticular gap (seldom reaching tegula), with posterodorsal margin broadly U-shaped, with posterolateral margin with lobe covering spiracle very strongly convex (often almost circular), and with lateroventral extremities contiguous; metapostnotum long, fused with propodeum, and exposed and posteriorly expanded in middle; wing venation well developed, usually 10 or 9 closed cells in fore wing and 2 closed cells in hind wing (sometimes fewer); hind wing usually with jugal lobe; meta-somal sterna 1 and 2 not separated by a constriction: female without an articulation within gonocoxite 2; ovipositor concealed at rest and modified as a sting; plumose setae often present. Sexual dimorphism slight to moderate; both sexes macropterous.

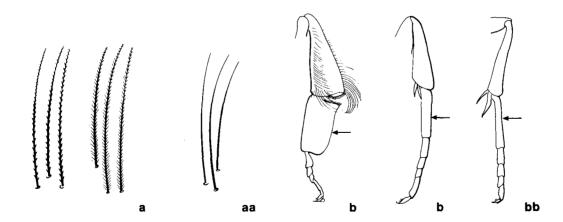
**Comments** Apoidea includes both sphecoid wasps, which provide animal matter as food for the

larvae, and bees, which provide pollen and nectar. They are treated here as two informal series, Spheciformes and Apiformes, respectively, following the classification suggested by Brothers (1975). The use of the name Apoidea instead of Sphecoidea follows Michener (1986b), who confirmed the priority of the name Apoidea. Members of this superfamily are associated primarily on the basis of the enlarged metapostnotum (propodeal triangle) (Brothers 1976), the broadly U-shaped posterodorsal margin of the pronotum, and the posterior production of the lateral angle of the pronotum forming a lobe below but not reaching the tegula, all attributes considered by Brothers (1975) to be unique synapomorphies.

Apoidea is a large group of 20 families with about 28 000 species around the world (8000 Spheciformes and 20 000 Apiformes). About 4650 species in 16 families are known in North America, including about 845 species in 15 families in Canada. The number of genera and species given for each family and subfamily includes only those that are described.

Wing cell and vein nomenclature follows Gauld and Bolton (1988). A table of updated Comstock-Needham equivalents is given in Chapter 7 (p. 130).

## **Key to series of APOIDEA**



- a. Body setae branched, often feather-like, at least a few such setae on dorsolateral area of propodeum.
- b. Hind leg with tarsomere 1 wider than following tarsomeres ......... APIFORMES (p. 308)
- aa. Body setae simple, unbranched

1

#### Series SPHECIFORMES

(Figs. 93-113)

#### Albert T. Finnamore

The sphecoid wasps lack a single common name but include such groups as digger wasps, sand wasps, thread-waisted wasps, and mud-dauber wasps. The group shows extreme variation in size. appearance, nesting site and choice of prey, so that generalizations are difficult. Many are brightly colored, conspicuous, and fast moving. In most species, females make nests for their young, use those of other wasps, or use preexisting cavities. Males generally play no role in nesting, but in a few species, such as some Trypoxylon (Crabronidae), males may act as nest guards preventing entry of parasitoids while females forage. All, except for a few eleptoparasites, find and capture prey, which they usually sting to paralyze it and then place it in the nest with the wasp egg. The prey of any particular species may vary according to locality or season, or both, but host utilization is generally limited taxonomically and physically. For example, a wasp may use various Cicadellidae (Homoptera) but no other prey, whereas a related species may prey only on Cercopidae or Fulgoridae (both Homoptera). Others may use almost any kind of spider (Araneae) but always within a particular size range. Members of a few highly specialized groups, such as Microbembex (Nyssonidae), will take almost any arthropod of suitable size, dead or alive, but such a broad range of prey selection is rare. Members of the more primitive wasp groups tend to prey on Hemimetabola and more advanced ones on Holometabola. In the tropics numerous generations

may occur per year, but in Canada usually one to a few occur.

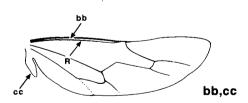
The Spheciformes are a highly diverse assemblage treated as a single family by some authors (Bohart and Menke 1976, Gauld and Bolton 1988) or as a series of nine families, as presented here. Both systems are likely incorrect; provision of a natural classification awaits critical cladistic analysis. The families presented here correspond for the most part to the subfamilies recognized in Bohart and Menke's (1976) revision of world genera; they are raised to family level to make the classification comparable to that widely accepted in the Apiformes. About 1200 species occur in the Nearctic region, and about 283 species in eight families occur in Canada. The total Canadian fauna may be closer to 400 species.

References Bohart and Menke (1976) revised the world genera. Alexander (1992b) presented a preliminary cladistic analysis of the group. Cardale (1985) cataloged the Spheciformes of Australia. The Palaearctic species were keyed by Richards (1980) for UK, Lomholdt (1975–1976) for northeastern Europe, Tobias (1978) for European USSR, and Kazenas (1978) for Kazakhstan and Middle Asian USSR. Finnamore (1982) keyed the species of eastern Canada. Alayo (1976) keyed the species of Cuba. Krombein (1979a) cataloged the North American species. Only major references later than Bohart and Menke (1976) are given in the following sketches.

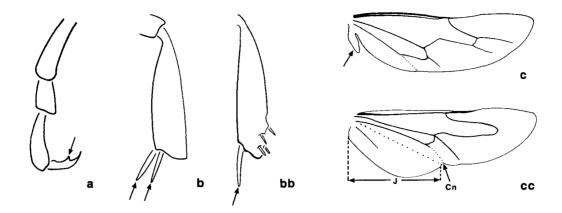
## Key to families of SPHECIFORMES

(modified from Bohart and Menke 1976)

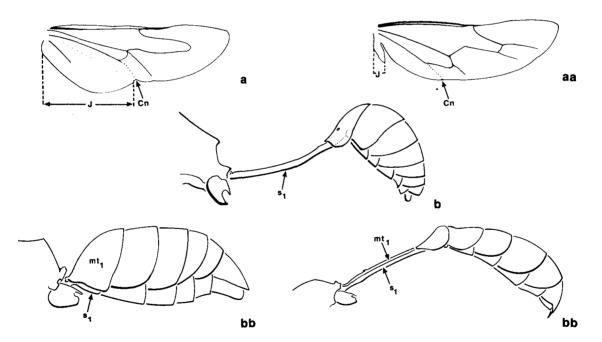




- a. Female short-winged; fore wing without closed cells.
  - b. Male hind wing without trace of costal cell.
  - c. Hind wing without jugal lobe ...... HETEROGYNAIDAE (p. 290)
  - aa. Female fully winged; fore wing with closed cells.
  - bb. Male hind wing with costal cell complete or represented by membrane anterior to vein R

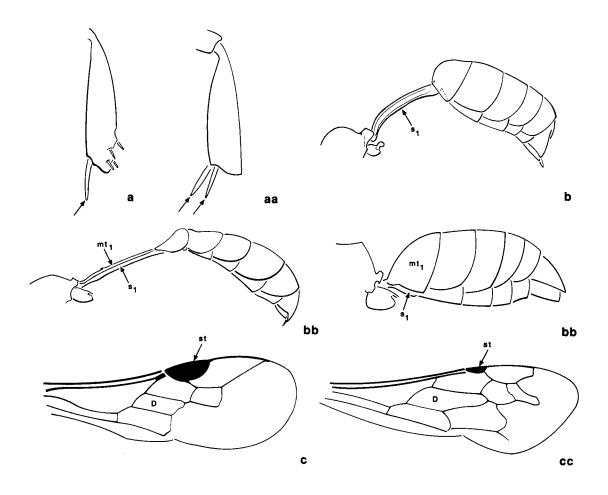


- **2(1)** a. Tarsal claws toothed along inner margin or cleft.
  - b. Mesotibia with 2 apical spurs.
  - c. Hind wing with jugal lobe small or absent ...... AMPULICIDAE (p. 291)
  - aa. Tarsal claws usually simple; if claws toothed or cleft then without preceding combination.
  - bb. Mesotibia with 2, 1, or no apical spurs.



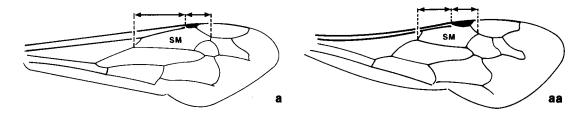
- 3(2) a. Hind wing with jugal lobe (J) large, more than half length of area posterior to claval notch (Cn) and:
  - b. Metosoma petiolate, the petiole composed of sternum only  $(s_1)$  ..... SPHECIDAE (p. 292)
  - aa. Hind wing with jugal lobe (J) less than half length of area posterior to claval notch (Cn) and/or:
  - bb. Metasoma sessile or, if petiolate, the petiole composed of both tergum (mt<sub>1</sub>) and sternum (s<sub>1</sub>)

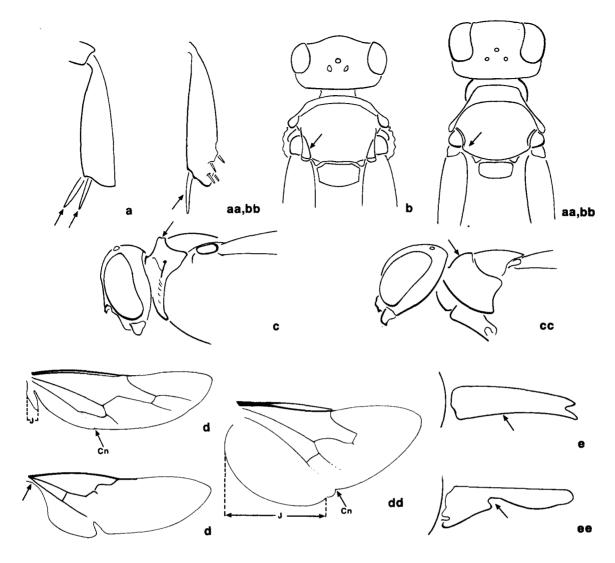
    4



- **4(3)** a. Mesotibia with 1 apical spur.
  - b. Metasoma petiolate (petiole sometimes wider than long), petiole composed of sternum (s<sub>1</sub>) only and/or:

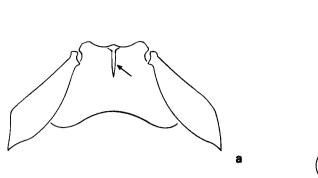
  - aa. Mesotibia with 2, 1, or no apical spurs.
  - bb. Metasoma sessile to petiolate, the petiole composed of both tergum  $(mt_1)$  and sternum  $(s_1)$  and:

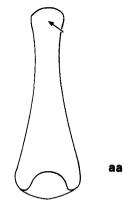




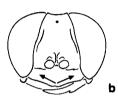
**6(5)** a. Mesotibia with 2 apical spurs **and/or**:

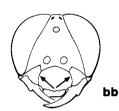
- b. Mesoscutum with oblique scutal carina posterolaterally.
- c. Pronotal collar short and transverse.
- d. Hind wing without or with jugal lobe (J); if lobe present then less than half length of area posterior to claval notch (Cn).
- aa,bb. Mesotibia with 1 apical spur and mesoscutum without oblique scutal carina; if mesotibia with 2 mesotibial spurs, then:
- cc-ee. Pronotal collar long and rounded in lateral view, or jugal lobe (J) more than half length of area posterior to claval notch (Cn), or mandible emarginate or stepped externoventrally ...... 8

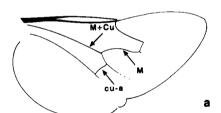


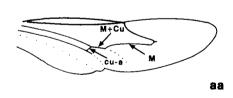










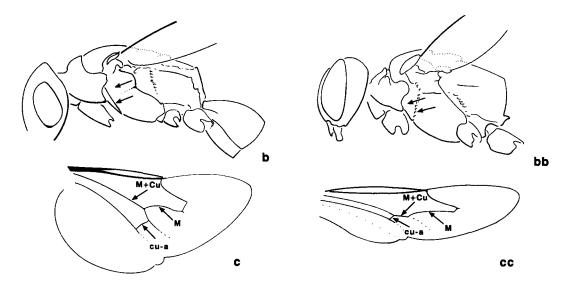


aa. Hind wing with vein M diverging from M+Cu beyond (apical to) vein cu-a ............. 10



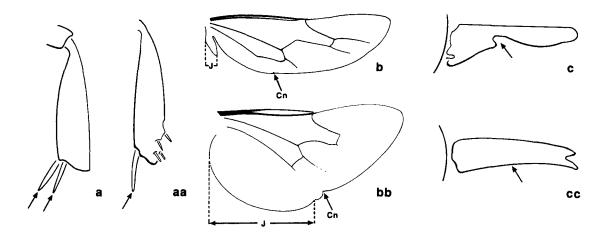






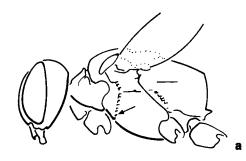
- 11(8) a. With following combination:
  - b. Mesopleuron with epicnemial carina and without episternal groove.

  - aa. Without preceding combination.
  - bb. Mesopleuron with or without epicnemial carina and with or without episternal groove.
  - cc. Hind wing with vein M diverging from M+Cu before or beyond vein cu-a ...... 12



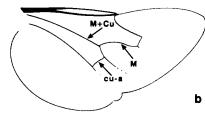
- **12(11)** a. Mesotibia with 2 apical spurs; if mesotibia without spurs then:
  - b. Hind wing with jugal lobe (J) less than half length of area posterior to claval notch (Cn) and:

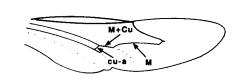
  - aa. Mesotibia with 1 apical spur; if mesotibia without spurs then:
  - bb. Hind wing with jugal lobe (J) more than half length of area posterior to claval notch (Cn) or:



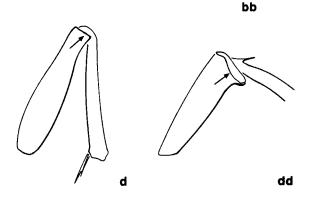


13(12) a. Mesopleuron with episternal groove reaching ventral region ..... most ASTATIDAE (p. 295)





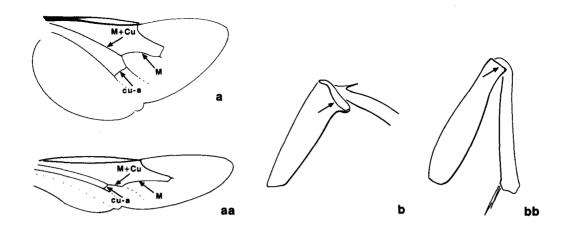


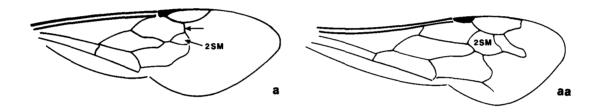




- With following combination:
  - Hind wing with vein M diverging from M+Cu before vein cu-a.
  - Mandible stepped or notched externoventrally.
  - Metafemur not truncate apically ...... a few ASTATIDAE (p. 295)
  - Without preceding combination.
  - bb. Hind wing with vein M diverging from M+Cu before or beyond vein cu-a.
  - cc. Mandible entire or notched externoventrally.

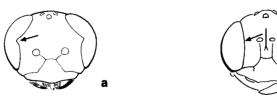
14(12)

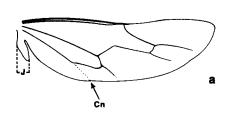


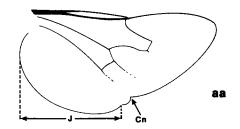


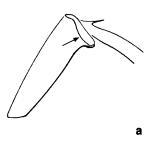


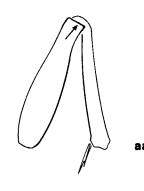
- - aa. Eyes with inner orbits converging above ...... a few PHILANTHIDAE (p. 304)

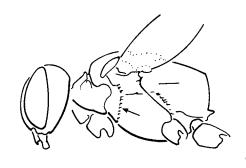


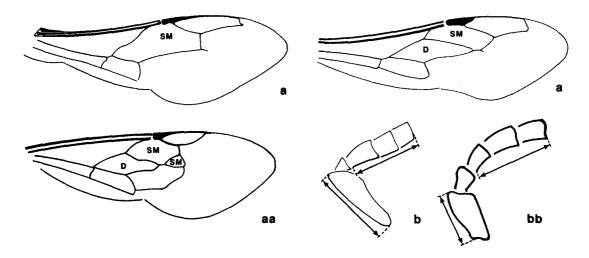




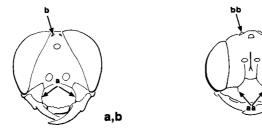








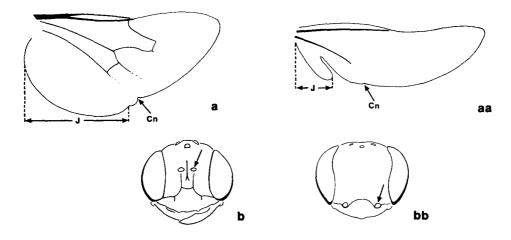
- a. Fore wing with 1 submarginal cell (SM) confluent with first discal cell (D) or, if not confluent, then:
  - b. Scape at least as long as basal 3 flagellomeres combined .... many CRABRONIDAE (p. 297)
  - aa. Fore wing usually with 2 or 3 submarginal cells (SM); if fore wing with 1 submarginal cell then not confluent with first discal cell (D) and:



- 23(22) a. Clypeus divided into three parts by complete longitudinal lines.

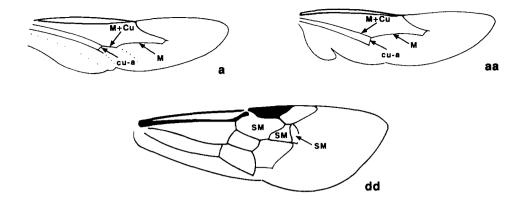
aa,bb

- aa. Clypeus not divided into three parts; if longitudinal lines present then lines incomplete.



- 24(23) a. Hind wing with jugal lobe (J) much more than half length of area posterior to claval notch (Cn).

  - aa. Hind wing with jugal lobe (J) not much more than half length of area posterior to claval notch (Cn).



- 25(24) a. Hind wing with vein M, when present, diverging from M+Cu beyond cu-a.
  - b. Maxillary palpus with 6 segments; labial palpus with 4 segments.
  - c. Mandibular socket usually open, continuous with oral cavity; if socket closed then fore wing with 1 submarginal cell.
  - d. Fore wing with 3, 2, 1 or no submarginal cells ..... some **CRABRONIDAE** (p. 297)
  - aa. Hind wing with vein M diverging from M+Cu at cu-a.
  - bb. Maxillary palpus with 5 segments; labial palpus with 3 segments.
  - cc. Mandibular socket closed, separated from oral cavity.
  - dd. Fore wing with 3 submarginal cells (SM) ...... a few **PHILANTHIDAE** (p. 304)

## Family HETEROGYNAIDAE

(Fig. 93)

**Diagnosis** Mesotibia with 2 apical spurs; male hind wing with 2 closed cells or fewer, without costal cell remnant or jugal lobe. Female brachypterous, fore wing without closed cells.

**Comments** The five rare species in this family occur in Madagascar, Botswana, and the eastern Mediterranean region. Their biology is unknown.

Brothers (1974) considered *Heterogyna* to represent a distinct subfamily of Plumariidae (Chrysidoidea), but Day (1984) provided evidence for treating the genus as a primitive family of Spheciformes.

**References** Day (1984) revised the family and keyed the species.

## Family AMPULICIDAE

(Figs. 94, 95)

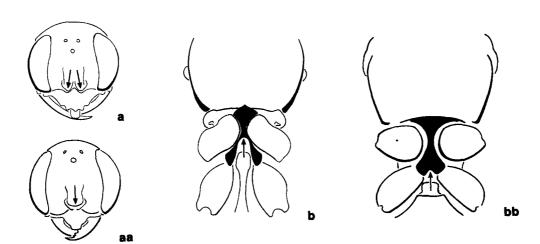
**Diagnosis** Tarsal claws toothed or cleft along inner margin; mesotibia with 2 apical spurs; hind wing with jugal lobe small or absent; metasoma sessile or with petiole composed of tergum and sternum.

**Comments** Ampulicidae is principally a tropical family of 167 species in two subfamilies: Ampulicinae and Dolichurinae. The family is

considered to be among the most primitive of the Spheciformes. Adults of many tropical species are metallic green and can be up to 33 mm long. Prey consists of Blattodea (Dictuoptera). The female wasp stings the prey to induce paralysis, and then drags it to a preexisting cavity where an egg is laid. One host is provided per cell. Four species occur in North America, including two in Canada.

## Keys to subfamilies of AMPULICIDAE

(modified from Bohart and Menke 1976)



- 1 a. Toruli each with an overhanging frontal lobe.
  - b. Metasternum Y-shaped with arms directed posteriorly.

  - aa. Toruli unmodified or both overlain by a single median frontal lobe.
  - bb. Metasternum somewhat emarginate posteriorly but not Y-shaped.

### **Subfamily Dolichurinae**

(Fig. 94)

This widely distributed subfamily contains about 50 species and five of the six genera in the family. Adults of many species are inconspicuous and ant-like in behavior, and have banded wings; others are dark metallic blue green. Two species in two genera occur in North America, including one in southeastern Canada.

#### **Subfamily Ampulicinae**

(Fig. 95)

This widespread, primarily tropical subfamily contains about 118 species in one genus. Adults are small to large, and many are metallic green to blue. Two species occur in North America, including one in southeastern Canada.

**References** Krombein (1979b) treated the species of Sri Lanka. Pagliano (1986) keyed the genera and species of Italy.

## **Family SPHECIDAE**

(Figs. 96-98)

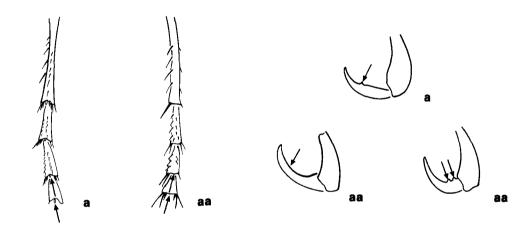
**Diagnosis** Fore wing with 3 (rarely 2) submarginal cells; mesotibia usually with 2 apical spurs, sometimes 1; tarsal claws toothed or not along inner margins; hind wing with jugal lobe large, more than half length of anal area; metasomal sternum 1 forming cylindrical petiole.

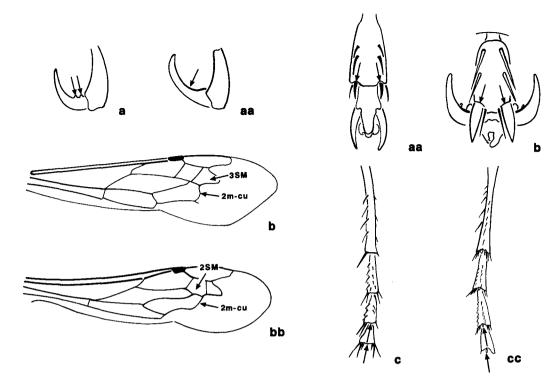
**Comments** Sphecidae (mud-dauber and thread-waisted wasps) is a cosmopolitan family of 660 species in three subfamilies: Ammophilinae, Sceliphrinae, and Sphecinae. Adults are medium to

large, some tropical specimens reaching 52 mm in length. The mud-daubers (Sceliphrinae) often build their nests from mud. Adults of other subfamilies nest in preexisting cavities or, more often, construct a nest in the ground. Within the family, a broad range of behavior exists, ranging from parasitoid-like to primitive social. Prey includes Araneae, orthopteroids, or Lepidoptera larvae. About 102 species in 11 genera occur in North America, including 34 species in 10 genera in Canada.

## Key to subfamilies of SPHECIDAE

(modified from Bohart and Menke 1976)





- a. Tarsal claws with 2 or more teeth.
  - b. Fore wing with vein 2m-cu received by third submarginal cell (3SM), but if not then tarsal claws with at least 3 teeth or apicoventral setae of metatarsomere 5 wide, the setae separated at base by no more than 1.5 setal widths.
  - c. Tarsi without plantar lobes ...... Sphecinae
  - aa. Tarsal claws usually simple or with 1 tooth; if tarsal claws with 2 teeth (Old World species) then apicoventral setae of metatarsomere 5 narrow, the setae separated at base by at least 3 setal widths.
  - bb. Fore wing with vein 2m-cu usually received by second submarginal cell (2SM).

### **Subfamily Sceliphrinae**

(Fig. 96)

Adults of this widespread group exhibit a broad range of behavior, from parasitoid-like (Chlorion) to primitively social (mud-nest building Trigonopsis). Adults of most species prey on orthopteroids, but two cosmopolitan genera prey on Araneae. Color tends to be black and red or yellow, although adults of some species in several genera are metallic green or blue. The 135 species are distributed among all zoogeographic regions. Eight species in four genera occur in North America, including three species in three genera in Canada.

#### **Subfamily Sphecinae**

(Fig. 97)

Adults of this widespread subfamily of about 230 species are fossorial or nest in preexisting cavities. Prey are orthopteroids, mainly Tettigoniidae (Grylloptera) and Acrididae

(Orthoptera). These robust wasps tend to be black or black and red, although a few species have metallic blue reflections. Thirty-four species in four genera occur in North America, including 10 species in three genera in southern Canada.

### **Subfamily Ammophilinae**

(Fig. 98)

With about 300 species, Ammophilinae is the largest subfamily of Sphecidae. Adults of most species are fossorial, although members of one genus nests in preexisting cavities in wood. Prey usually consists of Lepidoptera or Symphyta larvae. These slender, usually black and red wasps are found in all regions. Eighty-one species in three genera occur in North America, including 21 species in three genera in Canada, with several species occurring north of the Arctic Circle.

**References** No major works have been published since that of Bohart and Menke (1976).

## Family PEMPHREDONIDAE

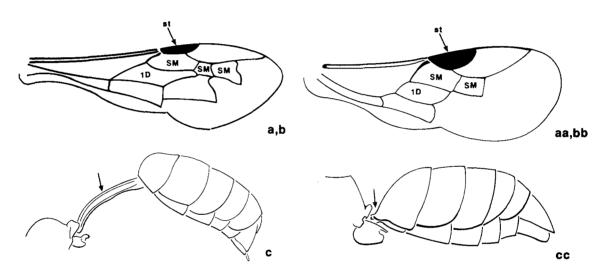
(Figs. 99, 100)

**Diagnosis** Fore wing with 3, 2, 1, or no submarginal cells; mesotibia with a single apical spur; stigma of fore wing enlarged, at least nearly as large as first discal cell and/or metasomal sternum 1 forming a petiole that may be short, wider than long; jugal lobe of hind wing small, less than half length of anal area.

**Comments** Pemphredonidae is a cosmopolitan family of about 860 species in two subfamilies: Pemphredoninae and Pseninae. Hundreds more species await description from the New and Old

World tropics. Adults are usually black, black and red or yellow, and occasionally metallic blue green or bronze. Adults are among the smallest of the Spheciformes, seldom reaching 10 mm in length, with members of some genera averaging 2 mm long. Behavior ranges from solitary to social (*Microstigmus*). Nests are constructed in twigs or soil or suspended from leaves and are usually provisioned with Homoptera, although Thysanoptera and Collembola are preyed upon in some genera.

### Key to subfamilies of PEMPHREDONIDAE



- a. Fore wing with 3 submarginal cells (SM).
  - b. Fore wing with stigma (st) smaller than first discal cell (1D).

  - aa. Fore wing with 2, 1, or, rarely, no submarginal cells (SM).
  - bb. Fore wing with stigma (st) often larger than first discal cell (1D).

#### **Subfamily Pseninae**

(Fig. 99)

1

Adults of this subfamily tend to construct ground nests, although some members of *Psenulus* use hollow twigs or stems. Prey consists of Homoptera, usually Cicadellidae, Cercopidae, and Fulgoridae, but Membracidae and Psyllidae are also preyed upon. The subfamily contains about 460 species in 11 genera. About 90 species in seven genera occur in North America, including 25 species in five genera in Canada.

### **Subfamily Pemphredoninae**

(Fig. 100)

Adults construct nests in twigs or in soil. Prey usually consists of Aphidae (Homoptera) or Thysanoptera, but Collembola are preyed upon by members of at least one genus. The family contains about 400 species in 18 genera. About 90 species in 12 genera occur in North America, including about 20 species in five genera in Canada.

**Reference** Finnamore (1987) analyzed the genera of Pseninae, described a new genus, and keyed the world genera.

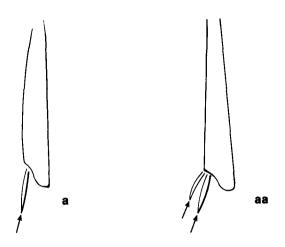
## **Family ASTATIDAE**

(Fig. 101)

**Diagnosis** Fore wing with 2 or 3 submarginal cells; hind wing vein M diverging before vein cu-a; hind wing with jugal lobe usually subequal to anal area but sometimes half its length; mesotibia usually with 2 apical spurs, sometimes with 1 or none; if mesotibia with 1 spur then mandible with an externoventral notch; if mesotibia without spurs on apex then hind wing jugal lobe equal to about half length of anal area; metasoma sessile.

Comments This family occurs in all regions except the Australian and contains about 150 species (six genera) in three subfamilies: Astatinae, Dinetinae, and Laphyragoginae. Adults are ground nesters that construct single or multicellular nests. Cells are provisioned with various Hemiptera. About 36 species in three genera occur in North America, including about nine species in three genera in Canada.

## Key to subfamilies of ASTATIDAE



a. Mesotibia with 1 apical spur aa. Mesotibia with 2 apical spurs or none 2

### **Subfamily Astatinae**

(Fig. 101)

This subfamily contains the majority of species (about 137 in four genera) and is found in all zoogeographic regions except the Australian. Adults are black, black and red, or metallic blue. This is the only subfamily of Astatidae found in the Western Hemisphere. Prey consists of various Hemiptera.

### **Subfamily Dinetinae**

This subfamily of eight species is found in the southern part of the Palaearctic region, from

northeastern India to Morocco. Prey consists of various Hemiptera.

### Subfamily Laphyragoginae

This subfamily of six species is found for the most part across the southern Palaearctic region. Adults have distinctive red and yellow banded metasomata. Nothing is known of their biology.

**References** No comprehensive treatments have been published since that of Bohart and Menke (1976).

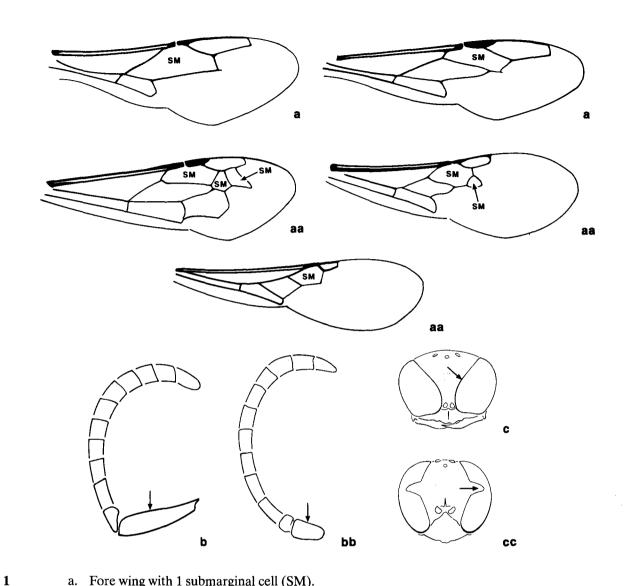
## Family CRABRONIDAE

(Figs. 102, 103)

**Diagnosis** Labrum transverse, wider than long; lateral ocelli usually normal; if ocelli deformed or represented by scars then appearing either oval, elliptic, or comma-shaped; mesotibia with 1 apical spur; fore wing with 3, 2, 1, or no submarginal cells; if fore wing with 3 submarginal cells then vein 2m-cu received by second submarginal cell; hind wing vein M almost always diverging after cu-a; mesosoma without oblique scutal carina; metasoma sessile or with petiole composed of both sternum and tergum.

Comments Crabronidae is the largest of the spheciform families, with about 3400 species around the world in two subfamilies: Crabroninae and Larrinae. Nesting behavior is variable; members of Larrinae tend to be ground nesters although Trypoxylonini (Larrinae) nest in preexisting cavities or construct tubular mud nests. Adults of Crabroninae usually nest in preexisting cavities or in twigs, although many are ground nesters. Prey consists of an exceptionally wide range of insects and spiders (Araneae): 12 orders of insects are known to be preyed upon.

### Key to subfamilies of CRABRONIDAE



- a. Fore wing with 1 submarginal cell (SM).
  - Scape about half as long as flagellum.

  - Fore wing with 3, 2, 1, or no submarginal cells (SM); if fore wing with 1 submarginal cell then either bb or cc.
  - bb. Scape much less than half length of flagellum.

### **Subfamily Larrinae**

(Fig. 102)

This widespread subfamily contains over 2000 species. Its members show considerable diversity in color, size, and shape; adults of many species are large and robust, others are among the smallest of

the Spheciformes. The sand nesting species are commonly called digger wasps. Adults of Larrinae provision their nests with orthopteroids or Hemiptera; those of Trypoxylonini prey upon Araneae. About 250 species in 14 genera occur in North America including 46 species in seven genera in Canada.

### **Subfamily Crabroninae**

(Fig. 103)

This widespread subfamily contains over 1300 species, which show considerably more uniformity in color, size, and shape than do members of Larrinae. Adults are usually black or black with yellow or white markings. They provision their nests with Diptera. About 200 species in 14 genera occur in North America, including about 75 species in nine genera in Canada.

References Since Bohart and Menke's (1976) world generic revision a considerable number of regional generic treatments have been published. Among the more encompassing are Menke (1977), which includes a revised key to the genera of Miscophini; Menke and Vardy (1980), which treats the genera and species of Scapheutini; and Lomholdt (1985), which provides a reclassification of the larrine tribes and a revision of the Miscophini of southern Africa and Madagascar.

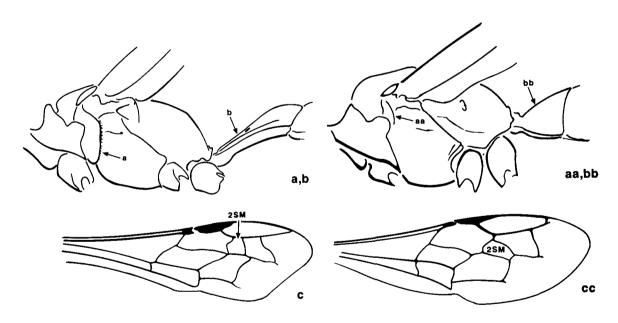
## Family MELLINIDAE

(Fig. 104)

**Diagnosis** Mesotibia with 2 apical spurs; fore wing with 3 submarginal cells; hind wing jugal lobe less than half length of anal area; metasomal sternum 1 simple anteriorly, without median or submedian anterior ridges.

Comments This small, primarily Holarctic family contains 13 species in two subfamilies: Mellininae and Xenosphecinae. Adults are gregarious ground nesters that construct multicellular nests. Cells are provisioned with Diptera. Seven species occur in North America, including two in Canada.

## Key to subfamilies of MELLINIDAE



- 1 a. Mesopleuron with episternal groove extending to ventral region.
  - b. Metasoma pedunculate.
  - c. Fore wing with second submarginal cell (2SM) trapezoidal ...... Mellininae
  - aa. Mesopleuron with episternal groove short, evident only on dorsal region.
  - bb. Metasoma sessile.
  - cc. Fore wing with second submarginal cell (2SM) petiolate or triangular ...... Xenosphecinae

### **Subfamily Xenosphecinae**

This Nearctic subfamily is known from three species (one genus) and fewer than 100 specimens. Adults are black and white. They have been observed preying on Bombyliidae (Diptera). The group has been collected only from the southwestern United States.

Nearctic. Adults are black and white, yellow, or red. They prey on muscoid Diptera, mainly around dung. Two species occur in Canada.

**References** No revisions more recent than those listed in Bohart and Menke (1976) have been published.

### **Subfamily Mellininae**

(Fig. 104)

This subfamily contains 10 species (one genus): three Palaearctic, three Neotropical, and four

### Family NYSSONIDAE

(Figs. 105-109)

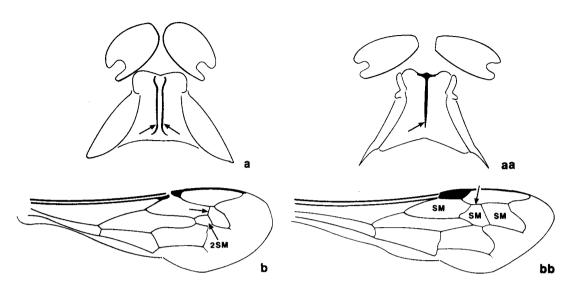
**Diagnosis** Mesotibia usually with 2 apical spurs; if mesotibia with 1 spur then fore wing with prestigmal length of first submarginal cell much more than half length of cell or oblique scutal carina absent; fore wing with 2 or 3 submarginal cells; hind wing jugal lobe less than half length of anal area; metasomal sternum 1 with a anterior median carina or submedian carinae; metasoma usually sessile but occasionally petiolate.

**Comments** Nyssonidae is the second largest of the spheciform families, with almost 1500 species in seven subfamilies: Alyssoninae, Bembicinae,

Entomosericinae, Gorytinae, Heliocausinae, Nyssoninae, and Stizinae. Adults of all species are ground nesters. Nesting behavior varies from solitary to high-density nesting aggregations. Prey is highly variable, including seven orders of insects. Adults of one genus provision their nests with any dead arthropods. Some species are cleptoparasites on other Nyssonidae. About 260 species in 35 genera occur in North America, including about 45 species in 21 genera in Canada.

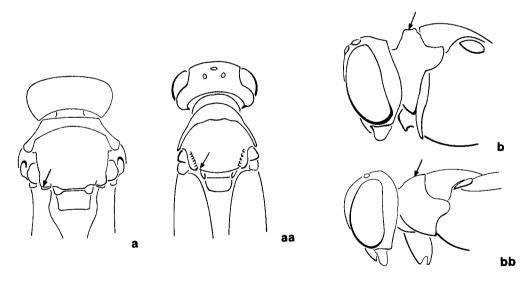
## Key to subfamilies of NYSSONIDAE

(modified from Bohart and Menke 1976)



- a. Metasomal sternum 1 with 2 carinae diverging posteriorly from between metacoxae or a single carina forking toward middle of sternum.

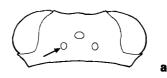
  - aa. Metasomal sternum 1 with a single, often anterior carina, the carina not bifurcating posteriorly

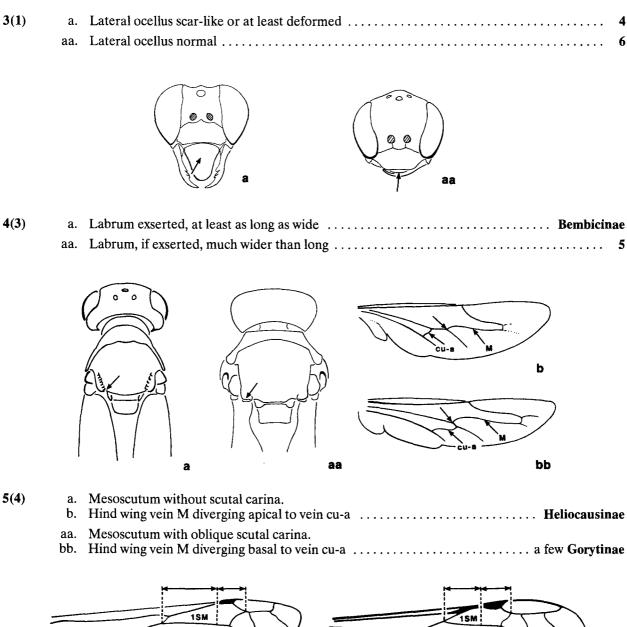


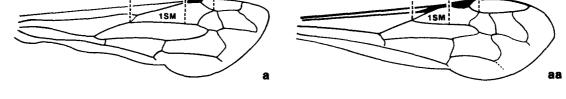
- **2(1)** a. Mesoscutum with oblique scutal carina.

  - aa. Mesoscutum without scutal carina.







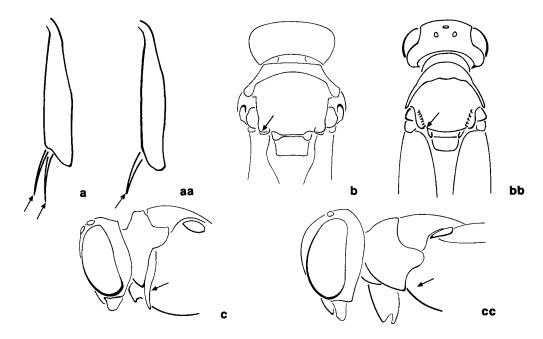


a. Fore wing with prestigmal length of first submarginal cell (1SM) much more than half cell length

Stizinae

aa. Fore wing with prestigmal length of first submarginal cell (1SM) not much more than half cell length

7



- 7(6) a. Mesotibia with 2 apical spurs and/or:
  - b. Mesoscutum with oblique scutal carina.
  - c. Mesopleuron usually with epicnemial carina ..... most Gorytinae
  - aa. Mesotibia with 1 apical spur and:
  - bb. Mesoscutum without scutal carina.
  - cc. Mesopleuron without epicnemial carina ..... Entomosericinae

#### **Subfamily Entomosericinae**

Bohart and Menke (1976) placed this subfamily outside Nyssonidae; it is here classified within the Nyssonidae on the basis of the median carina on metasomal sternum 1, an attribute shared with the Nyssonidae. Entomosericinae is a southern Palaearctic group of two species in one genus. Nothing is known of their biology.

#### **Subfamily Heliocausinae**

This is a southern Neotropical subfamily of nine species in one genus. Adults are black, often with red or yellow. Nesting is gregarious; prey are believed to be immature Orthoptera although records of Cicadellidae (Homoptera), Hemiptera, and Araneae also exist.

### **Subfamily Alyssoninae**

(Fig. 105)

This subfamily of 56 species is found in all regions except the Australian and Neotropical. Adults are usually black or black and red, often with a pair of white spots on metasomal tergum 2. Prey

are usually Cicadellidae, although Cercopidae and Fulgoridae (all Homoptera) are also reported. Sixteen species in two genera occur in North America, including six species in two genera in Canada.

### **Subfamily Nyssoninae**

(Fig. 106)

This widespread subfamily of about 220 species are cleptoparasites of Gorytinae or Larrinae. The heavily armored integument of these black or reddish wasps is believed to be a consequence of their cletoparasitic habits. About 60 species in seven genera occur in North America, including five species in five genera in Canada.

#### **Subfamily Gorytinae**

(Fig. 107)

This widespread subfamily of about 420 species exhibits the greatest diversity in the family. Adults are black or black and yellow, usually small to medium, but occasionally large. Prey are Homoptera, usually Cicadellidae, Cercopidae,

Membracidae, Psyllidae, Fulgoridae, and, occasionally, Cicadidae. About 90 species in 15 genera occur in North America, including about 20 species in nine genera in Canada.

### **Subfamily Stizinae**

(Fig. 108)

This is a widespread subfamily of over 300 species. Adults are medium-small to large and black, black and red, or black and yellow. Prey are Orthoptera or Mantodea (Dictuoptera), although members of one genus are cleptoparasitic on Sphecidae and possibly Bembicinae. Eleven species in three genera occur in North America, including one species in Canada.

#### **Subfamily Bembicinae**

(Fig. 109)

With over 460 species, this subfamily is the largest in the Nyssonidae. Adults are medium to large and marked with white or yellow on the metasoma. Nests vary from solitary to high-density aggregations. Prey consists of a wide range of insects including Hemiptera, Diptera, Lepidoptera, Hymenoptera, Homoptera, Odonata, and Neuroptera. Adults of *Microbembex* prey upon a variety of living or dead arthropods. Over 80 species in eight genera occur in North America, including nine species in five genera in Canada.

References Fritz and Toro (1977) treated the species of Heliocausinae. Bohart and Gillaspy (1985) keyed the North American genera and species of the bembicine tribe Stictiellini. Krombein (1984, 1985) revised the Sri Lankan species of Stizinae and Alyssoninae, Nyssoninae, and Gorytinae, respectively.

### Family PHILANTHIDAE

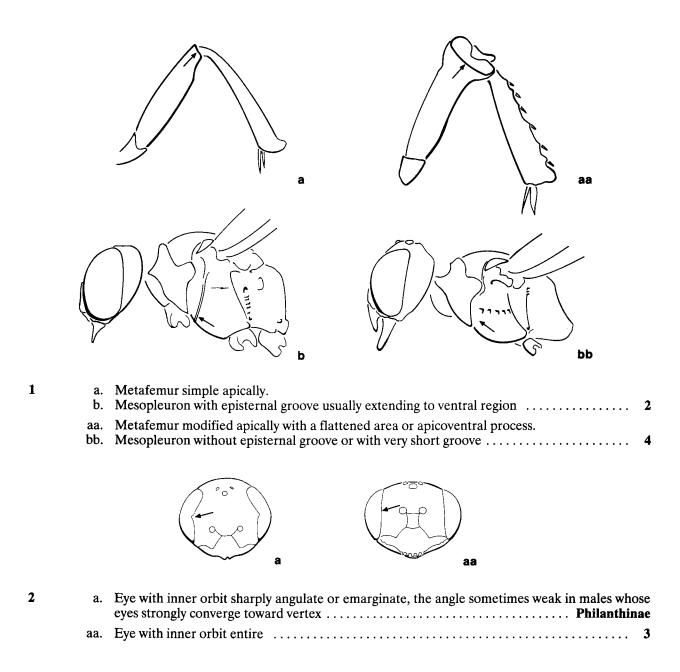
(Figs. 110-113)

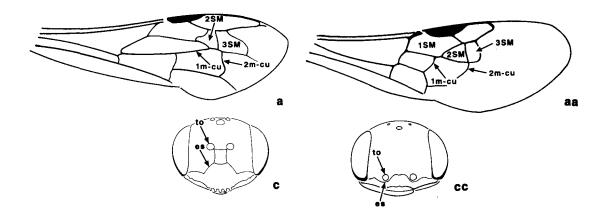
Diagnosis Torulus almost always placed well above frontoclypeal suture; mesosoma without epicnemial carina; mesotibia with 1 apical spur; fore wing with 3 submarginal cells, the second and third usually each receiving an m-cu vein; prestigmal length of first submarginal cell less than half length of cell; lateral ocelli usually normal; if lateral ocelli deformed then hind wing with vein M diverging before vein cu-a; metasoma usually sessile; if metasoma petiolate then metasomal segment 1 composed of both tergum and sternum; epicnemial carina absent.

Comments The family contains about 1100 species in six subfamilies: Aphilanthopinae, Cercerinae, Eremiasphecinae, Odontosphecinae, Philanthinae, and Pseudoscolinae. The results of a cladistic analysis of the family by Alexander (1992a) were published too late for inclusion here. These colorful black and yellow or red wasps are common around flowers. Adults construct multicellular nests in the ground. Prey includes adult Hymenoptera and adult Coleoptera. About 145 species in six genera occur in North America, including about 40 species in five genera in Canada.

## Key to subfamilies of PHILANTHIDAE

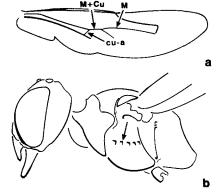
(modified from Bohart and Menke 1976)

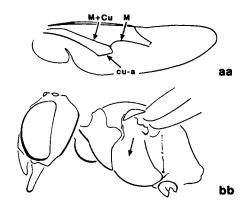




- a. Fore wing with vein 1m-cu received by second submarginal cell (2SM) and with vein 2m-cu received by third submarginal cell (3SM).
  - b. Maxillary palpus with 6 segments; labial palpus with 4 segments.

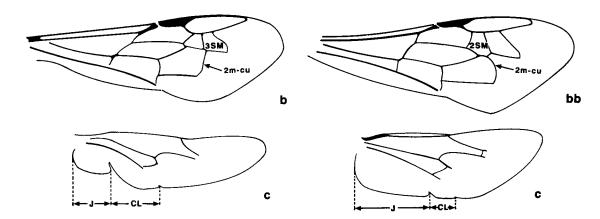
  - aa. Fore wing with vein 1m-cu received by first submarginal cell (1SM), or between first and second submarginal cells and with vein 2m-cu received by second submarginal cell (2SM), or between second and third submarginal cells (3SM).
  - bb. Maxillary palpus with 5 segments; labial palpus with 3 segments.
  - cc. Torulus (to) almost touching epistomal suture (es) ..... Eremiasphecinae





- 4(1) a. Hind wing with vein M diverging from M+Cu beyond vein cu-a.

  - aa. Hind wing with vein M diverging from M+Cu before vein cu-a.



- 5(4)
- a. Hind ocelli normal.
- b. Fore wing with vein 2m-cu received by third submarginal cell (3SM).
- c. Hind wing with jugal lobe (J) at most half as long as claval lobe (CL) ...... Pseudoscoliinae
- aa. Hind ocelli vestigial.
- bb. Fore wing with vein 2m-cu received by second submarginal cell (2SM).
- cc. Hind wing with jugal lobe (J) much longer than claval lobe (CL) . . . . . Odontosphecinae

### **Subfamily Eremiasphecinae**

(Fig. 110)

This subfamily contains seven species from the southern Palaearctic region. Adults are small, with white or yellow markings, sometimes predominantly white or yellow. Nothing is known of their biology.

### **Subfamily Philanthinae**

(Fig. 111)

Known from all regions except the Australian, these colorful wasps are common around flowers. Prey generally consists of adult Apiformes in several families (including *Apis mellifera* L.), hence the common name "bee-wolf" applied to members of this group. Over 150 species in two genera occur around the world. Thirty-two species in one genus occur in North America, including 17 species in Canada.

#### **Subfamily Aphilanthopinae**

(Fig. 112)

This is a small subfamily of 17 species (four genera) from the southern Palaearctic and Nearctic Regions. Adults are medium-sized and black with yellow or red markings. Prey consists exclusively of Formicidae, which in species where the behavior has been studied can be restricted to a single species or to a single caste of a genus, e.g., winged queens of the genus *Formica*. Thirteen species in three genera occur in North America, including three species in two genera in Canada.

#### **Subfamily Odontosphecinae**

This subfamily contains four species from northwest Africa, Saudi Arabia, and the Neotropical region (Bolivia, Argentina). Nothing is known of their biology.

### **Subfamily Pseudoscoliinae**

The 19 species (one genus) of this subfamily are all Palaearctic. A single prey record indicates that they may provision their nests with Halictidae.

#### **Subfamily Cercerinae**

(Fig. 113)

This is by far the largest subfamily, with almost 900 species in two genera. The huge genus *Cerceris* contains about 850 species and is found in every zoogeographic region. Prey are usually adult Coleoptera, although a few records of adult Hymenoptera are also known. About 100 species occur in North America, including 18 in Canada.

References Bohart and Grissell (1975) keyed the Nearctic genera and species of Philanthidae, except for *Cerceris* and *Eucerceris*, where only the California species were treated. Ferguson (1984) provided an annotated synonymic list of *Cerceris* for North America and the Caribbean region. Krombein (1981) keyed the species of Philanthidae of Sri Lanka.

### Series APIFORMES

(Figs. 114-124)

Charles D. Michener

This group includes bees, probably the group of insects most beneficial to humans. Not only is the domestic honey bee important, but also hundreds of species of other bees whose pollinating activities ensure that our fruit, nut, and berry crops are fertilized and that seeds of many vegetable, fiber, and forage crops (clover, alfalfa, beans, sunflowers for instance) are formed. In fact, bees and flowering plants have co-evolved since the Cretaceous age, and without the work of bees the world would be a very different place.

Apiformes differ from Spheciformes in that they have at least some branched hairs. These hairs may be widespread on the body and legs, for many bees are hairy so that they look even more robust than their real body form. Some bees, however, are slender and wasp-like and in some such bees (e.g., Hylaeus in Colletidae) the branched hairs are hard to find. When the hairs are scarce, they can usually be found at least on the vertical surfaces of the propodeum. It is often easier to recognize the Apiformes by the hind tarsomere 1 (basitarsus), which is almost always wider than the following tarsomeres. The lower part of the face is rarely covered with short, silvery hairs. Metasomal tergum 7 of the female is completely divided into lateral plates (hemitergites) associated with the sting apparatus, and sternum 7 of the male is completely invaginated and often elaborately modified, not at all like an apical ventral plate.

Like their relatives, the spheciform wasps, bees visit flowers for the sugar and water in nectar, but unlike their relatives, most bees gather pollen as a high-protein source for their young. None gather insect or spider prey as do the Spheciformes. The Ctenoplectridae and some Melittidae and Anthophoridae collect floral oils instead of nectar to mix with pollen for larval food, but their energy source for adults is nectar, as with other bees. A few stingless bees use carrion as food. Other bees that do not gather pollen either steal it from other bees, as in two genera of Meliponinae (Apidae), or are parasitic on other bees, as described below. Bees are abundant all over the world but are much more numerous in dry sunny climates; thus there are many more species in western than in eastern North America.

The majority of bees are solitary, that is, each female makes her own nest, provisions the cells, lays an egg in each, and dies. Most bees in temperate climates produce one generation per year. Scattered widely among the families are communal species in which several females live in the same nest, each making and provisioning her own cells and laying eggs in them. In Halictidae,

Anthophoridae, and Apidae eusocial species are found in which female castes (queens and workers) exist. Such castes may differ principally in physiology and behavior; or they may also differ strikingly in size, as in some *Bombus* (Apidae); or they may also differ in structure in the highly social bees that form large, long-lived colonies (Meliponinae and Apinae of Apidae).

Most bee nests, like most spheciform nests, are burrows in the soil. Others are in pithy or hollow stems, or are excavated into wood. Some are constructed of resin or mud, often with pebbles. Cell linings are secreted or constructed with leaf fragments, petals, resin, and other such materials. Members of Apidae nest in large cavities or sometimes in exposed situations, using secreted wax, often mixed with pollen, resin, or mud for construction.

In addition to nest-making bees, there are parasitic forms (cleptoparasites and social parasites) that depend on nest-making bees to feed their larvae. Such bees ordinarily lack the pollen-carrying scopal hairs characteristic of most female bees. Parasitic forms are found in Halictidae, Ctenoplectridae, Megachilidae, Anthophoridae, and Apidae. The cleptoparasitic female enters the nests of the host and lays an egg in any cell that is in the appropriate stage, often returning to the nest repeatedly to parasitize other cells as they are constructed and provisioned. The host egg or young larva is killed either by the adult parasite, as in Sphecodes (Halictidae), or by the young larva of the parasite (as in parasitic Megachilidae and Anthophoridae). Most of the cleptoparasites are slender, brightly colored, without long hairs, and therefore wasp-like in appearance. The social parasite female, unlike a cleptoparasite, usurps the host nest and colony, becoming in effect the queen of a colony that includes the host workers. The hosts are social bees with a worker caste; the parasites lack a worker caste.

The world fauna of Apiformes has at least 20 000 species. About 3500 species occur in North America, including at least 1000 in Canada.

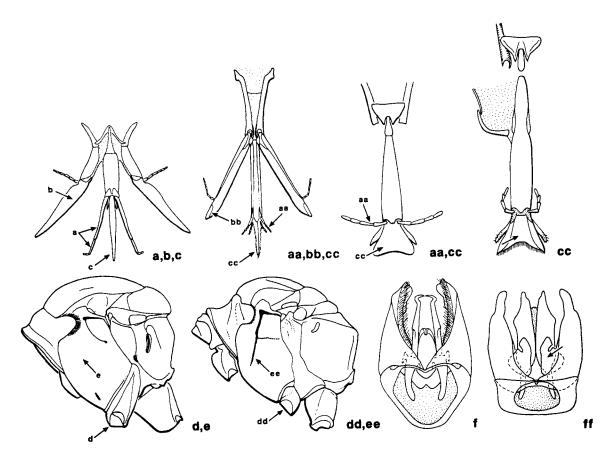
References Michener (1944) treated the classification of bees. The genera and species of Apiformes of North America are keyed by Mitchell (1960, 1962) for most of the area east of the Mississippi River and the genera by Stephen et al. (1969) for the area west of the Rocky Mountains and north of California. McGinley (1981) gave a phenetic analysis of Apoidea larvae. Michener (1954) classified the bees of Panama and Michener

(1965) the Australian and South Pacific regions. Osychnyuk, Panfilov, and Ponomareva (1978) keyed the Apoidea of European USSR. Roubik (1989) listed the genera and subgenera of the world and illustrated many of them. Michener, McGinley, and

Danforth (1993) gave an account of the genera of bees of North and Central America, with keys to genera.

The keys and revisions cited by Hurd (1979) are not listed but more recent keys are cited.

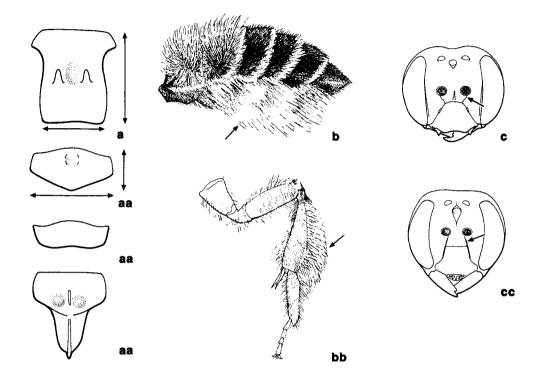
# Key<sup>1</sup> to families of APIFORMES (bees)



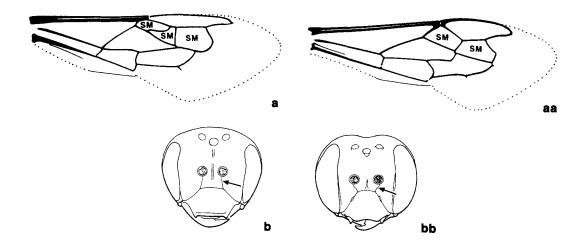
- a. Labial palpus with segments 1 and 2 long, flattened and sheath-like; segments 3 and 4 small, short, directed laterally, not sheath-like, rarely absent, or rarely segment 3 flat and not directed laterally.
  - b. Galea with postpalpal part greatly elongated, usually longer than stipes.
  - c. Glossa elongated and pointed, usually longer than prementum.
  - d. Mesocoxa usually over two-thirds as long as distance from its summit to base of hind wing.
  - e. Mesopleuron usually without episternal groove ventral to scrobal groove.

Because this key uses many characters of the mouthparts (proboscis), it is often difficult to use. The proboscis should be extended while the specimen is soft. This is unnecessary or is easily done for specimens killed with ethyl acetate. From dry specimens with the proboscis retracted, it can be dissected, partly cleared, and preserved for study in glycerin as one does for genitalia. For purposes of orientation, the proboscis is considered to project downward. Thus the anterior surface is the surface that would be dorsal if the proboscis were extended forward.

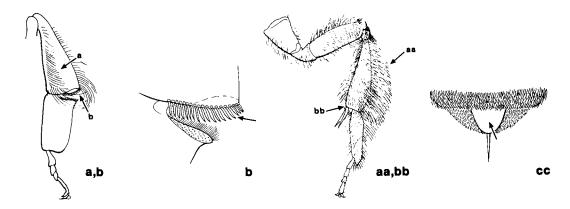
- aa. Labial palpus with segments 1 and 2 not flattened and sheath-like, similar in form to segments 3 and 4, or sometimes segment 1 much elongated and somewhat sheath-like.
- bb. Galea with postpalpal part usually much shorter than stipes.
- cc. Glossa usually shorter than prementum.
- dd. Mesocoxa (or at least exposed part) much shorter than distance from its summit to base of hind wing.
- ee. Mesopleuron usually with episternal groove ventral to scrobal groove.



- a. Labrum longer than wide, widened at base to broad articulation with clypeus; apex broadly rounded or truncate.
  - b. Scopa, when present, on metasomal sterna.
  - c. Face with subantennal groove usually directed toward outer margin of torulus .......
  - aa. Labrum wider than long or, if longer than wide, then narrowed at base to narrow articulation with clypeus; apex of labrum often a slender process sometimes making the labrum longer than wide
  - bb. Scopa, when present, on hind leg (principally the tibia).
  - cc. Face with subantennal groove usually directed toward inner margin or middle of torulus ..... 4



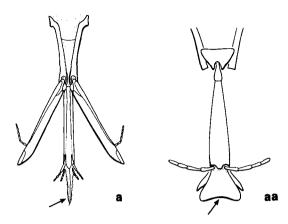
- a. Fore wing with vein 1r-m, resulting in 3 submarginal cells (SM).<sup>2</sup>
  - b. Face with subantennal groove directed toward middle of torulus . . . . . FIDELIIDAE (p. 319)
  - aa. Fore wing without vein 1r-m, resulting in 2 submarginal cells (SM).2



- a. Scopa, when present, consisting of fringes around large, flat or concave shining area forming corbicula on outer surface of metatibia.
  - b. Female metatibia (except for parasites and queens, as well as some minute tropical species) with posterior (inner) apical margin with comb of short, stiff setae (rastellum).

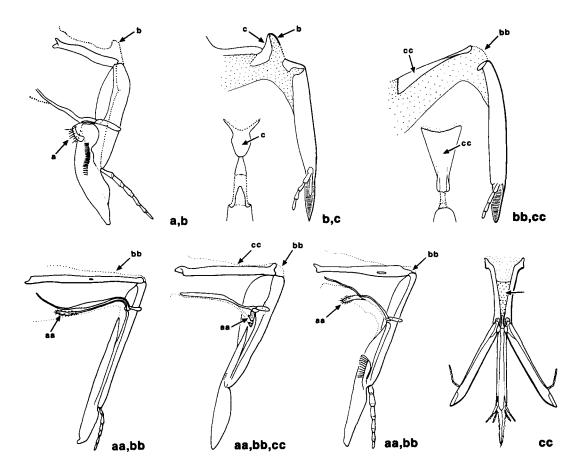
  - aa. Scopa not forming corbicula.
  - bb. Metatibia with apical margin without comb of short setae.

The three submarginal cells (SM) of most aculeate Hymenoptera are 1R1, 1Rs, and 2Rs in the modified Comstock-Needham system. When the number is reduced to two, it is sometimes impossible to know whether the missing vein is the 2nd abcissa of Rs (2/Rs) or 1r-m. It is therefore not always practical to use the terms for cells found elsewhere in this work, and the term submarginal cell is widely used.



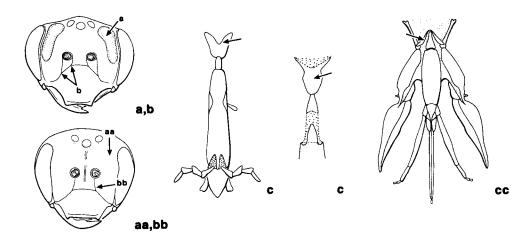
5(1)	a.	Glossa pointed
	aa.	Glossa bluntly rounded, truncate, or bilobed (pointed in males of three Australian genera havin
		2 submarginal cells, <sup>2</sup> the second much shorter than the first, having a complete episternal groove
		and lacking pygidial and basitibial plates)

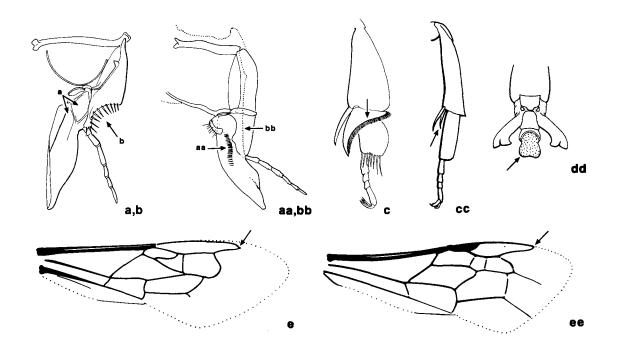
<sup>&</sup>lt;sup>2</sup> See note under couplet 2.



- a. Lacinia present as scale-like lobe with hairs, near base of galea.
  - b. Mentum and submentum (lorum) together forming a lobe projecting posterior to labiomaxillary tube (base of proboscis).

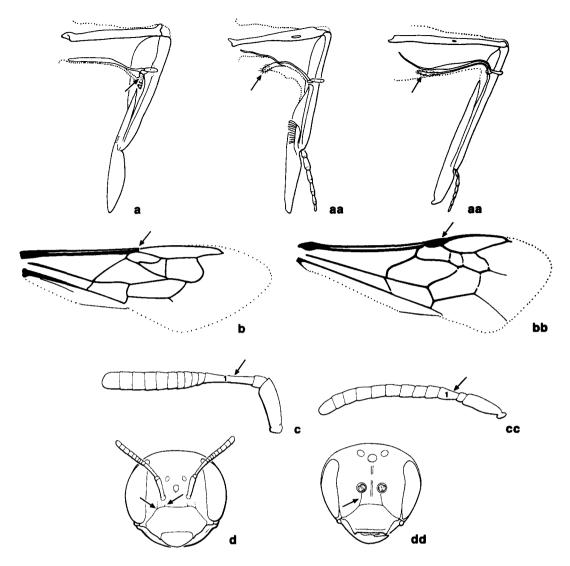
  - aa. Lacinia inconspicuous or displaced, not easily identifiable.
  - bb. Mentum and submentum (lorum) not forming a lobe projecting posterior to labiomaxillary tube; mentum membranous or membrane partly sclerotized.



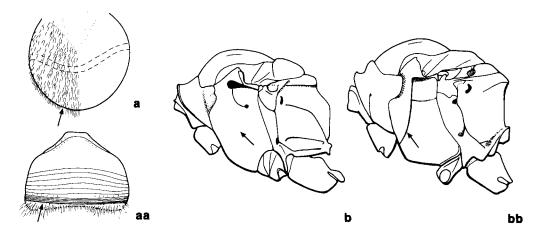


- **8**(7) a. Galea without comb.
  - b. Stipes with comb, in strong concavity of posterior stipital margin.
  - c. Female metatibia with inner spur usually greatly widened basally, crescentic, deeply and finely comb-like.
  - d. Pretarsi without arolia.

  - aa. Galea with comb (rarely reduced to 2 or 3 bristles).
  - bb. Stipes without comb.
  - cc. Female metatibia with inner spur not wide, not crescentic, and not finely comb-like.
  - dd. Pretarsi usually with arolia.
  - ee. Fore wing with apex of marginal cell on or near wing margin ...... MELITTIDAE (p. 319)



- 9(6) a. Lacinia a small hairless sclerite near base of galea but hidden between expanded stipites.
  - b. Fore wing with stigma virtually absent.
  - c. Flagellomere 1 as long as or longer than scape.
  - d. Face with 2 subantennal grooves ventral to each torulus ..... OXAEIDAE (p. 318)
  - aa. Lacinia dissociated from rest of maxilla and represented by small hairy lobe on anterior surface of labiomaxillary tube dorsal to rest of maxilla.
  - bb. Fore wing with stigma well developed.
  - cc. Flagellomere 1 much shorter than scape.
  - dd. Face with 1 subantennal groove ventral to each torulus ...... HALICTIDAE (p. 318)



- 10(5) a. Glossa with apex bluntly rounded, without preapical fringe.

  - aa. Glossa with apex subtruncate to emarginate, the females and some males with preapical fringe on anterior side separating basal annulate surface from nonannulate hairy apical lobes. (Glossa pointed in males of 3 genera from Australia; glossa rounded or truncate, with median lobe and no preapical fringe in males of 2 genera from Australia.)

#### Family COLLETIDAE

(Fig. 114)

**Diagnosis** Glossa widely truncate or bilobed except pointed in males of the Australian genera *Hemirhiza*, *Meroglossa*, and *Palaeorhiza* (Michener and Brooks 1984); glossa with transverse preapical fringe on anterior (dorsal) surface separating transversely annulate area from apical hairy lobes; preepisternal groove usually present and extending well below scrobal groove. North American species without basitibial and pygidial plates except for rare southern Diphaglossinae and *Eulonchopria* in Colletinae.

Comments Although the wide, truncate or bilobed glossa of this family suggests that of wasps, it is likely to be a derived feature rather than a plesiomorphy retained from Speciformes. It is used by colletids to apply the cellophane-like coating of the cells in which young develop. This waterproof coating holds the liquid (nectar plus pollen) provisions provided for larval food by many colletids.

The family contains perhaps 2000 species around the world. About 150 species occur in North America, including 45 in Canada. There are five subfamilies: Colletinae, Hylaeinae (both common), Diphaglossinae, Xeromelissinae, and Euryglossinae. The subfamily Hylaeinae is found around the world but is most abundant and diverse in Australia. It is represented in North America by

the genus Hylaeus, which contains small, slender, black (in the Western Hemisphere) species with two submarginal cells (probably 1R1+1Rs and 2Rs), usually with yellow markings at least on the face. The body is only sparsely hairy and because the female lacks a pollen-carrying scopa, pollen is carried to the nest along with nectar in the crop. Most species nest in dead hollow or pithy stems. The subfamily Colletinae occurs around the world but is diverse only in the southern continents. It is represented in North America principally by Colletes. This genus contains hairy bees, without yellow markings, and with three submarginal cells (1R1, 1Rs, 2Rs). The body form suggests that of Andrena or Halictus; the strongly convergent eyes and rather heart-shaped face usually distinguish Colletes from superficially similar bees in Halictidae, Andrenidae, and Melittidae. Also Colletes, the only colletine genus north of Mexico and southern Arizona, differs from all other bees in having the posterior half of fore wing vein 2m-cu distinctly arcuate toward the wing margin. Females carry pollen externally, on the well-developed scopa of the hind legs (trochanter to tibia). Nests are in burrows in the ground.

In the southern United States and Latin America large, hairy bees of the subfamily Diphaglossinae exist; North American species are in the genera *Caupolicana* and *Ptiloglossa*. In Latin America small *Hylaeus*-like bees of the subfamily Xeromelissinae are also found; they have a small scopa on the hind legs and basal metasomal sterna for external pollen transport, unlike Hylaeinae. One genus, *Chilicola*, extends north as far as central Mexico. Euryglossinae is endemic in Australia. Members resemble Hylaeinae but usually have a wide face with the clypeus not extending much above the level of the tentorial pits.

References In addition to the citations in Hurd (1979), Michener (1986a) reviewed Diphaglossini and Dissoglottini. Snelling (1985) reviewed the Hylaenae of the Ethiopian region. Houston (1975, 1981) revised the Australian Hylaeinae. Dathe (1980) revised Hylaeus of Europe, and Warncke (1978) revised the West Palaearctic Colletes. McGinley (1981) reviewed the larvae of Colletidae. Ikudome (1989) revised the Colletidae of Japan.

### Family STENOTRITIDAE

(Fig. 115)

**Diagnosis** Glossa bluntly rounded without apical point or specialization and without a transverse preapical fringe as in Colletidae; preepisternal groove absent below scrobal groove.

**Comments** This family is limited to Australia. Its few species constitute two genera of large, hairy

bees resembling superficially the colletid subfamily Diphaglossinae.

**References** McGinley (1980) raised this group to family rank.

### Family ANDRENIDAE

(Fig. 116)

**Diagnosis** Almost always with 2 subantennal sutures defining subantennal area below each torulus, these sutures conspicuous if integument is pale but often almost invisible if integument is black; glossa acute, short or long; labial palpus with segments similar or first (rarely second) segment elongate; pygidial plate present in females and many males.

**Comments** This family contains well over 2000 species. About 1200 species occur in North America, including 250 in Canada. The family consists of two subfamilies: Andreninae and Panurginae. Andreninae, whose members have the apex of the marginal cell (2R1) pointed on the wing margin (except in one Peruvian genus), includes the enormous Holarctic and African genus Andrena and four small genera from xeric areas of the Western Hemisphere. In all North American species the females can be distinguished from the superficially similar Colletinae, Halictidae, and Melittidae by the wide facial foveae, covered with short pale or silvery hairs. With a little experience this character can be seen without a microscope. Females carry pollen on the hind legs (trochanter to tibia) and usually also on the sides of the propodeum. Except for the face in some species, the body nearly always lacks yellow or white integumental markings.

The subfamily Panurginae has the apex of the marginal cell (2R1) truncate or at least bent strongly away from the wing margin (obliquely truncate). It is found primarily in the Western Hemisphere, although a small panurgine fauna occurs in the Palaearctic and African regions. The facial foveae of females are narrow depressions or grooves, not lined with short hairs as in Andreninae. Most species are more sparsely haired than those of Andreninae, and the scopa is restricted to the hind tibia. Nearly all species have yellow or white markings at least on the face of the male. Often such markings are widespread on the body and in a few species of the enormous genus *Perdita* the whole body is white or yellow.

Nests of all Andrenidae are burrows in the soil. Most andrenids are solitary, but some in both subfamilies are communal; none is parasitic.

References In addition to the citations in Hurd (1979), Hirashima (1952) keyed the subgenera of Palaearctic Andrena and Hirashima (1966) revised the Andrena of Japan. Warncke (1968) keyed the West Palaearctic subgenera. LaBerge (1986, 1987, 1989 and earlier papers) keyed the subgenera of Andrena and revised the genus Andrena of the Western Hemisphere. Osychnyuk (1977) revised the family for the Ukraine.

### **Family OXAEIDAE**

(Fig. 117)

**Diagnosis** Large bees without pale integumental markings and with subantennal areas as in Andrenidae; glossa rather short, pointed; preepisternal groove absent below scrobal groove; ocelli low on face, near antennal bases; basitibial and pygidial plates present.

**Comments** These large hairy bees are represented by two genera and nearly 20 species, including four species in North America. Members of *Oxaea* have

a green banded metasoma and occur in tropical America; members of *Protoxaea* occur in the Argentine region, in Mexico, and from Texas to Arizona. The dense scopa is on the hind leg of the female, from the coxa to the tibia. Nests consist of deep burrows in the soil, occupied by single females or by several females living communally.

**References** Hurd and Linsley (1976) revised the family.

### Family HALICTIDAE

(Fig. 118)

**Diagnosis** Lacinia consisting of a small lobe separated by membrane from rest of maxilla; glossa short to long, pointed; basitibial plate present in nonparasitic females and many males; pygidial plate present in females but commonly hidden under tergum 5; pygidial plate reduced in parasitic genera. Preepisternal groove present (complete, i.e., extending ventral to scrobal groove) in common groups except Nomiinae, including all Canadian species.

**Comments** In most places in the world the halictids are the commonest bees except for the Apidae. The family contains perhaps 3500 species around the world. Perhaps 500 species occur in North America, including 150 in Canada. The family consists of three subfamilies: Halictinae. Nomiinae, and Rophitinae. The largest and most common subfamily, the worldwide Halictinae, contains such familiar genera as Halictus and Lasioglossum, as well as the bright green Augochlora and its allies, and Agapostemon. Halictinae is easily recognized among the superficially similar Colletinae, Andreninae, and Melittidae by the strongly curved (rather than gently curved or straight) 1st abscissa (1/M) of vein M (basal vein) of the fore wing and in females by having metasomal tergum 6 hidden beneath tergum 5, which has, in nonparasitic species, a longitudinal median zone of distinctive, minute hairs (and sometimes a slit) dividing the hairy fimbria of tergum 5. Except for the sparsely haired parasitic species, such as Sphecodes (often with a glabrous red metasoma), females have a pollen-carrying scopa on the hind legs, usually from trochanter to tibia but in the Rophitinae largely restricted to the metatibia. Some females also carry pollen on the metasomal sterna.

The Nomiinae are a diversified group in the Old World. In North America there are only about

20 species in two genera, *Nomia* and *Dieunomia*. One species, *Nomia melanderi* Cockerell, the alkali bee, is important in alfalfa pollination. The subfamily is recognized by the lack of the preepisternal groove below the scrobal groove.

Rophitinae (formerly Dufoureinae), recognized by the small clypeus and large labrum, the two often being similar in length, are mostly Holarctic and African, although there is one Chilean genus. A few species of the genus *Dufourea* occur in Canada.

Halictid nests are burrows in the soil, except for a few Halictinae that burrow in rotting wood. Many species are solitary, but some Nomiinae and Halictinae are communal and some Halictinae are eusocial with behaviorally distinct female castes. All intergradations between solitary and fully eusocial exist among the few species so far studied.

**References** Numerous revisional studies have been published other than those cited by Hurd (1979). Blüthgen (1926) revised the Indo-Malayan Halictinae. Ebmer (1984) revised Dufourea, and Ebmer (1987) revised Halictus and Lasioglossum of Europe with keys to genera. Eickwort (1969) revised the genera of Augochlorini. Hirashima (1961) revised the Nomiinae of Japan. McGinley (1986) revised the New World Lasioglossum s.s. Michener (1978) reviewed the tribes and revised certain Old World genera. Moure and Hurd (1987) cataloged the Western Hemisphere species. Pesenko (1983) revised the Nomioidini of the USSR, Pesenko (1984) revised the subgenera of Halictus s.s., and Pesenko (1986) keyed the Palaearctic Lasioglossum s.s. Roberts and Brooks (1987) revised the genera related to Agapostemon. Pauly (1984) reviewed the African genera of Nomiinae.

### **Family MELITTIDAE**

(Fig. 119)

**Diagnosis** Mentum long and tapering basally, and lorum V-shaped, as in long-tongued bees, but segments of labial palpus similar; galeal comb present and stipital comb absent; glossa rather short and pointed; preepisternal groove and most of scrobal groove absent; basitibial and pygidial plates present in female.

Comments This family contains over 100 species around the world. About 30 species occur in North America, including three in Canada. Except for the subfamily Meganomiinae consisting of large African bees with extensive yellow integumental markings, this family contains two subfamilies of small to moderate-sized Holarctic and African species superficially resembling Colletinae, Halictidae, and Andreninae.

Members of the American Dasypodinae (genus *Hesperapis*) differ from superficially similar bees in their soft integument, so that they feel soft when

picked up for pinning. They have two submarginal cells (probably 1R1 and 1Rs+2Rs), the base of the second (2nd abscissa of vein Rs) being at right angles to vein M. Members of the American Melittinae have either 2 or 3 submarginal cells; those with 3 cells differ from superficially similar bees like *Andrena* in that the 3rd submarginal cell (2Rs) is pointed at its apex on vein M. The three melittid species known in Canada belong to this subfamily.

Melittid nests are burrows in the soil. Females carry pollen on the hind legs, in a scopa that is largely limited to the tibia as in panurgine Andrenidae, rophitine Halictidae, Ctenoplectridae, and many long-tongued bees.

**Reference** Michener (1981) reviewed Meganomiinae and treated the genera of the family worldwide.

### Family CTENOPLECTRIDAE

(Fig. 120)

**Diagnosis** Mentum and lorum as in Melittidae; galeal comb absent and stipital comb present, as in many long-tongued bees; and glossa moderately long, pointed, with long flabellum; segments of labial palpus similar to one another; preepisternal suture absent ventral to scrobal groove; basitibial and pygidial plates present in female.

Comments This family contains about 20 species of rather robust, medium-sized to small bees. It is found in Africa and tropical and eastern Asia, south to northernmost Australia. Nests are in preformed burrows in wood or in old mud nests of wasps.

**References** Michener and Greenberg (1980) reviewed the family relationships.

# Family FIDELIIDAE

(Fig. 121)

**Diagnosis** Long-tongued bees with labrum longer than wide; mandible multidentate and not wide; fore wing with 3 submarginal cells; scopa on metasomal sterna but hind legs with long hairs that do not carry pollen; basitibial and pygidial plates absent.

**Comments** This family contains about 15 species. It is often and perhaps best regarded as a primitive

subfamily of Megachilidae. The nests consist of burrows in the soil and do not involve foreign materials. The species are placed in three genera. Distribution is limited to southern Africa, Morocco, and central Chile.

**References** There is no comprehensive treatment.

### Family MEGACHILIDAE

(Fig. 122)

**Diagnosis** Long-tongued bees with labrum longer than wide; mandible of nearly all females and many males wide apically, with apical margin ordinarily forming 3 or more teeth; fore wing with 2

submarginal cells (i.e., vein 1r-m absent); scopa absent on hind legs, when present restricted to metasomal sterna; basitibial plate absent; pygidial

plate of female absent or represented by spine and pygidial plate of male usually absent.

**Comments** This is a large, worldwide family with many genera and several thousand species. About 610 species occur in North America, including more than 200 in Canada. The family consists of two subfamilies: Megachilinae and Lithurginae. The large and rather quadrate head, especially of females, together with the wide mandibles, makes most species recognizable on sight as megachilids. The small subfamily Lithurginae, represented in North America only by the genus Lithurge, contains a few species that superficially resemble Megachile. Megachilinae contains the usually yellow and black species of the tribe Anthidiini as well as black (sometimes with the metasoma red) to brilliantly metallic blue or green Megachilini. In both tribes cleptoparasitic as well as nest-making genera are known.

Nests may consist of burrows in soil, in pithy stems, or occur in preformed cavities such as burrows of Coleoptera in wood. They may also be constructed in the open on rocks, stems, or even leaves. Unlike cells of other bees, cells of Megachilidae are made of foreign materials brought into the nest, or at least used to divide a burrow into segments that function as cells. The foreign materials may be leaf pieces (used by *Megachile* species), chewed leaf pulp, plant hairs (used by *Anthidium* species), resin, or mud or sometimes mixtures of the preceding and sometimes supplemented with pebbles.

References In addition to the citations by Hurd (1979), Mitchell (1943, 1973, 1980) revised the Neotropical *Megachile*, the subgenera of *Coelioxys* for the Western Hemisphere, and the genera of Megachilini for the Western Hemisphere with a key to world genera, respectively. Pasteels (1965, 1968, 1984) revised various genera for the Ethiopian region, and Pasteels (1969) Anthidiinae for the Old World. Warncke (1977, 1980) treated the genera *Anthidium* and *Dioxys*, respectively, for the west Palaearctic region.

# Family ANTHOPHORIDAE

(Fig. 123)

**Diagnosis** Long-tongued bees with pygidial plate present in almost all females, with basitibial plate present in most nonparasitic females (both plates absent or difficult to recognize, however, in some common bees like *Ceratina*). Scopa (absent in parasites) largely restricted to metatibia. Labrum (except in a few parasitic forms) wider than long.

Comments This family contains several thousand species around the world. About 920 species occur in North America, including about 100 in Canada. Anthophoridae is an unsatisfactory unit and its classification will eventually be modified, either by subdividing it or by uniting it with the Apidae. Anthophoridae contains all the long-tongued bees that do not possess the derived features of any other family.

Three subfamilies are recognized: Nomadinae, Anthophorinae, and Xylocopinae. Nomadinae contains generally wasp-like, short-haired parasitic forms without scopae. Many either have a red metasoma or widespread yellow or white integumental markings. In size they vary from minute to large; the body is usually somewhat slender. Most species of the large genus Nomada are cleptoparasites of Andrena. A diversity of other bee genera are parasitized; for example, species of Epeolus are parasites of Colletes, species of Triepeolus are mostly parasites of eucerine Anthophorinae, and species of Neolarra are parasites of Perdita, a panurgine andrenid.

Most of the Anthophorinae are robust, hairy, pollen-collecting (i.e., nonparasitic) bees, although

parasitic tribes that lack scopae exist (Melectini, Ericrocidini). Nests of nearly all species consist of burrows in the soil, although a widespread Canadian species (*Anthophora terminalis* Cresson) burrows in rotten wood or stems. Some species are communal, several females using the same nest.

The subfamily Xylocopinae contains both the large, robust bees of the tribe Xylocopini and the small, slender, sparsely hairy bees in three other tribes. Of these only *Ceratina* in the tribe Ceratinini occurs in North America. Nests of nearly all species are constructed in wood or in stems. Some nests of many species contain small colonies of two to several adults, sometimes with behaviorally recognizable castes.

Each subfamily occurs in all continents, although the Nomadinae are rare in Australia.

References In addition to the citations by Hurd (1979), Brooks (1988) revised Anthophorini. Hirashima (1971) reviewed the genus *Ceratina* for Asia and the West Pacific. Hurd and Moure (1963) revised Xylocopini. Iuga (1958) revised Anthophorinae of Romania. Michener (1975) revised African allodapine bees. Snelling (1984) revised American Centridini. Snelling and Brooks (1985) reviewed some genera of Ericrocidini. Timberlake (1980) reviewed *Exomalopsis* for North America. Warncke (1983) treated the genus *Pasites* for the west Palaearctic region. Snelling (1986) and Alexander (1991) treated the genus *Nomada*.

# **Family APIDAE**

(Fig. 124)

**Diagnosis** Long-tongued bees without pygidial or basitibial plates. Scopa (absent in queens of highly social species and in parasitic and robber genera) restricted to metatibia and consisting of fringe of long hairs surrounding large smooth area, thus forming a corbicula. Labrum wider than long.

Comments This family contains about 1000 species including all the highly social bees as well as some solitary and primitively social forms. Forty-seven species occur in North America, and all also occur in Canada. There are four major groups, here called subfamilies: Euglossinae, Bombinae, Meliponinae, and Apinae. Except for most Meliponinae they are robust, hairy bees.

Euglossinae, or orchid bees, of the American tropics are mostly solitary, although some live in small groups; none has a distinct caste organization. Most species are brilliantly metallic, green, blue, and brassy red, among other colors. Others are hairy and resemble large bumble bees. Two genera are parasitic and lack corbiculae, but otherwise females have very wide corbiculae. The males are the pollinators of many orchid species.

Members of Bombinae are the familiar bumble bees. Two genera have been recognized, one (*Psithyrus*) parasitic in the nests of the other (*Bombus*). The subfamily is primarily Holarctic and abundant in cool temperate regions, but it ranges south to southern South America and, in the Orient, to Java. *Bombus* species occur even in the northern parts of the Arctic Archipelago, and one species there is parasitic, as is *Psithyrus* farther south. Colonies are annual, established each spring by overwintered queens working alone in soil cavities, in old nests of mice, voles, or birds, or under masses of dead vegetation. Each colony consists of a large queen and a few to hundreds of morphologically similar but smaller workers.

Members of Meliponinae, or stingless honey bees, are pantropical in distribution. They are among the commonest bees in the American tropics and southeast Asia, and are easily recognized by the reduced wing venation. A few hundred species have been described; major genera are Melipona and *Trigona*. Two robber genera lack corbiculae. They range in size from larger than honey bees to the smallest of all bees (body length 1.9 mm). Colonies are perennial and reproduce by sending out a "bud" (workers) to make a new nest; a young queen will join later to establish a new colony. Queens and workers differ greatly in morphology, and colonies range from a few dozen to many thousands of individuals. Colonies are found in cavities in trees, in the soil, or in exposed nests, depending on the species.

Apinae contains the familiar honey bees (Apis). One species, A. mellifera Linnaeus, which has been carried to all parts of the world by humans, originally ranged from northern Europe to southernmost Africa. The other species are found in southern and eastern Asia. Colonies are perennial and reproduce by swarming, the old queen leaving the nest with a mass of workers. Queens and workers differ greatly in morphology. Colonies ordinarily contain thousands of bees and occur in hollow trees, rock or soil cavities, and, in southern Asia, on exposed combs of cells hanging from tree branches or ledges.

References Maa (1953) reviewed the Apidini. Richards (1968) reviewed the subgenera of *Bombus*. Schwarz (1939, 1948) revised the Meliponinae of the Indomalayan region and of the Western Hemisphere, respectively. Michener (1990) reviewed the classification of the entire family.

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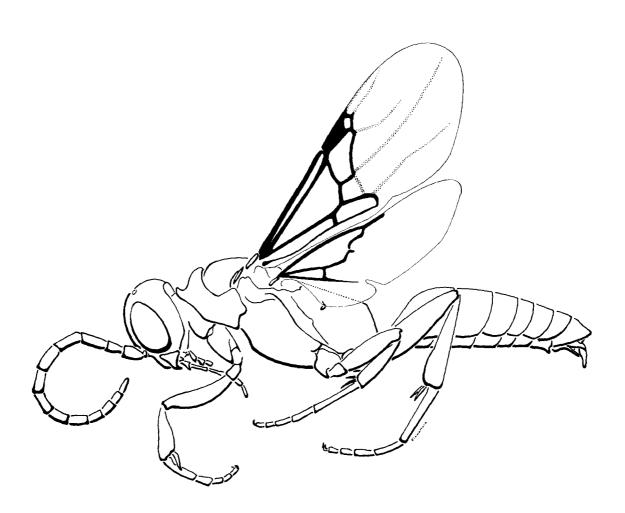


Fig. 93. Heterogynaidae

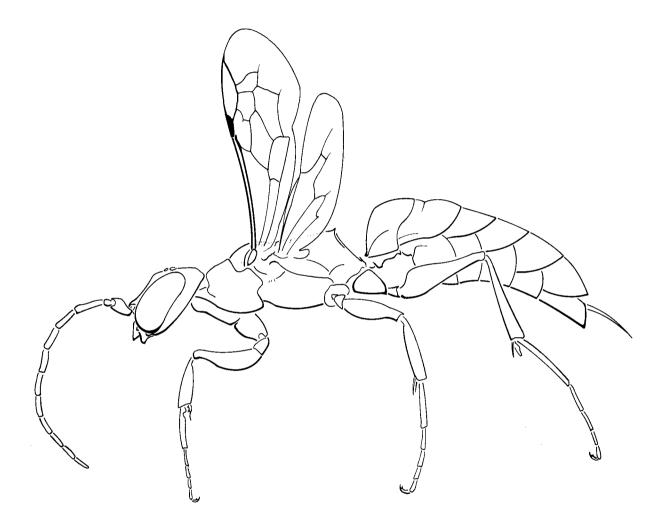


Fig. 94. Ampulicidae: Dolichurinae

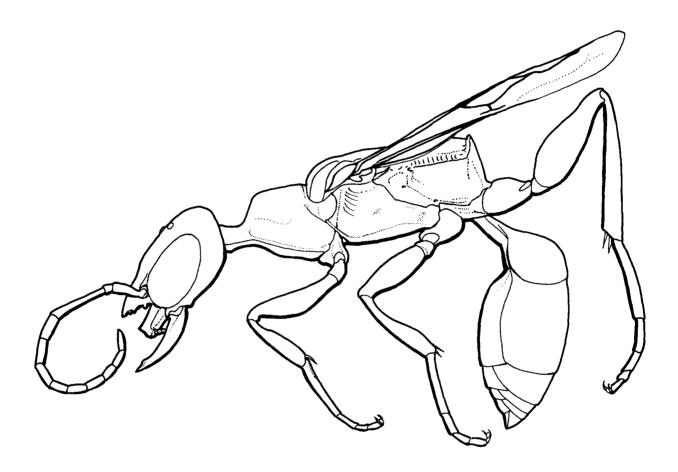


Fig. 95. Ampulicidae: Ampulicinae

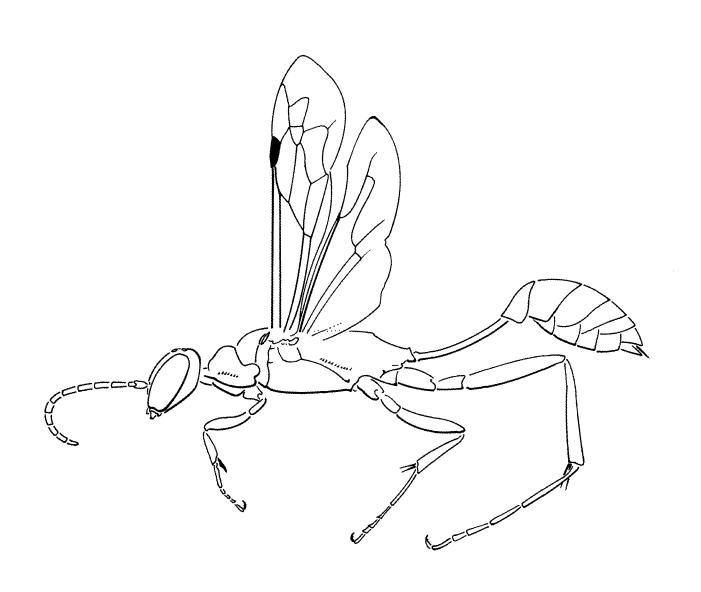




Fig. 97. Sphecidae: Sphecinae

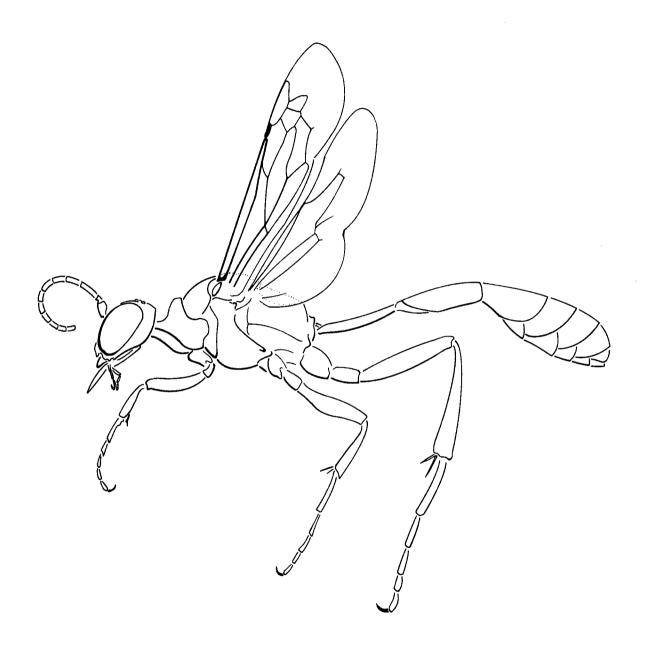


Fig. 98. Sphecidae: Ammophilinae



Fig. 99. Pemphredonidae: Pseninae

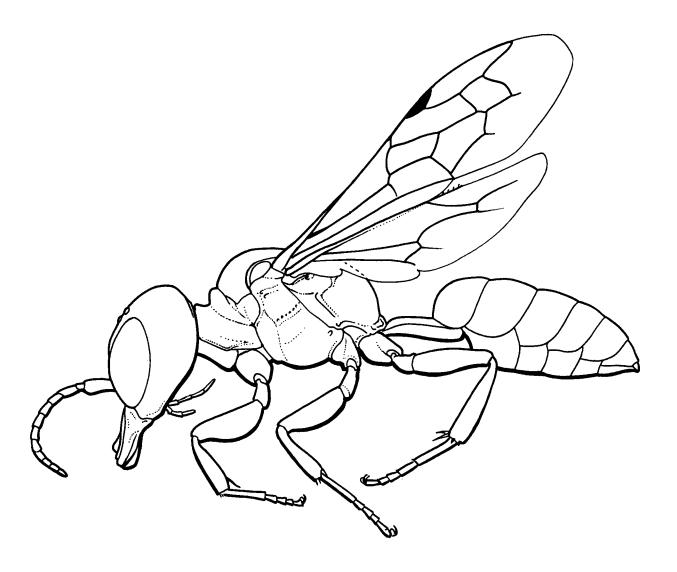


Fig. 100. Pemphredonidae: Pemphredoninae

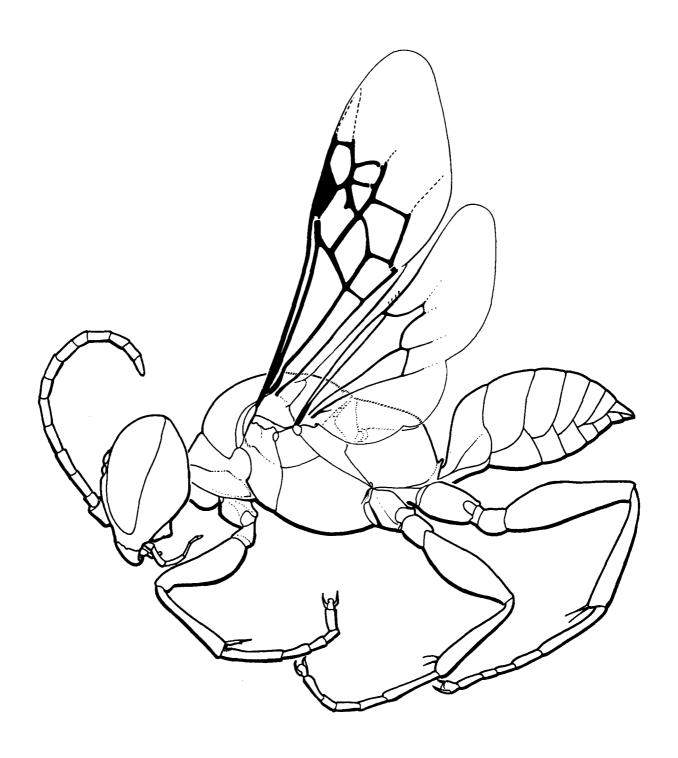


Fig. 101. Astatidae: Astatinae

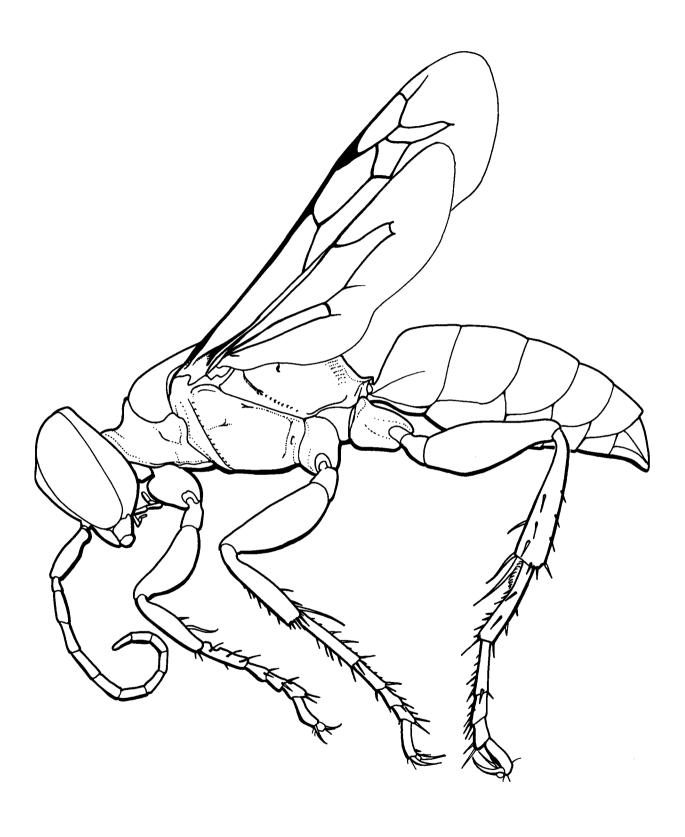


Fig. 102. Crabronidae: Larrinae

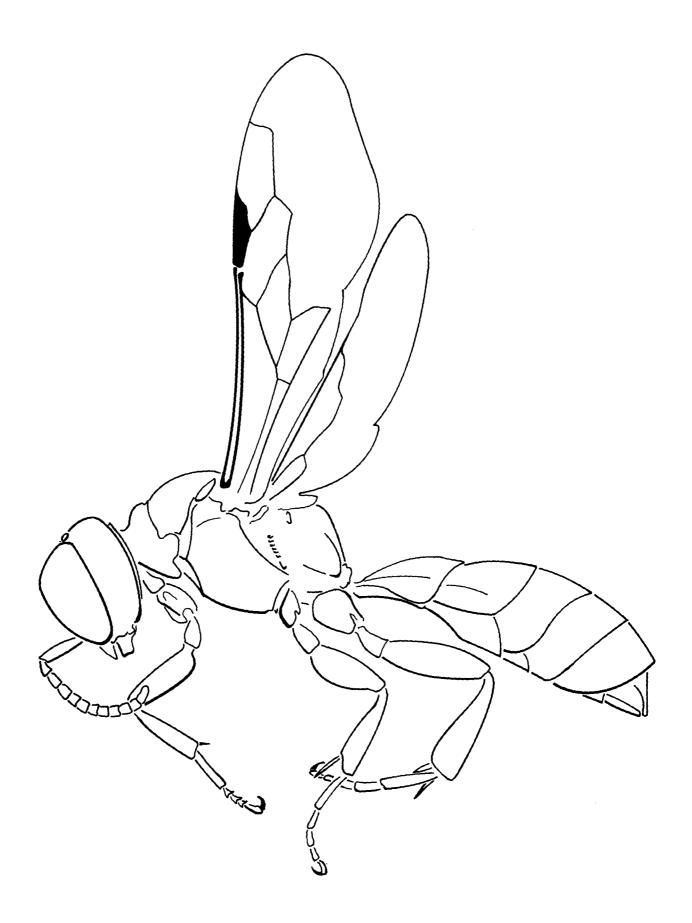


Fig. 103. Crabronidae: Crabroninae

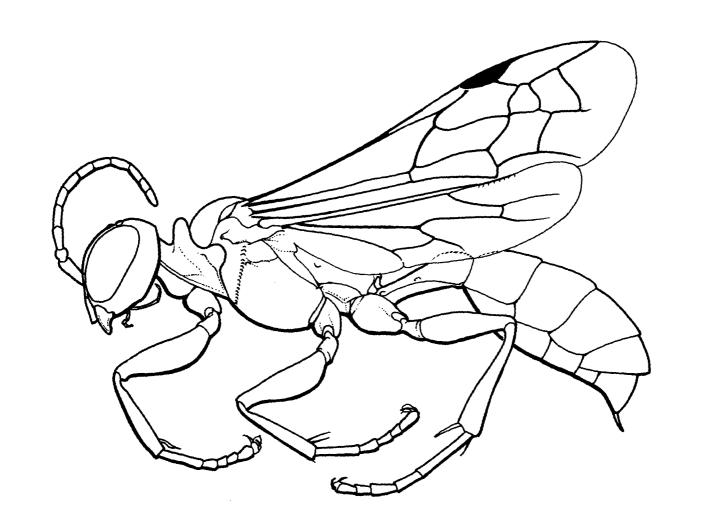


Fig. 104. Mellinidae: Mellininae

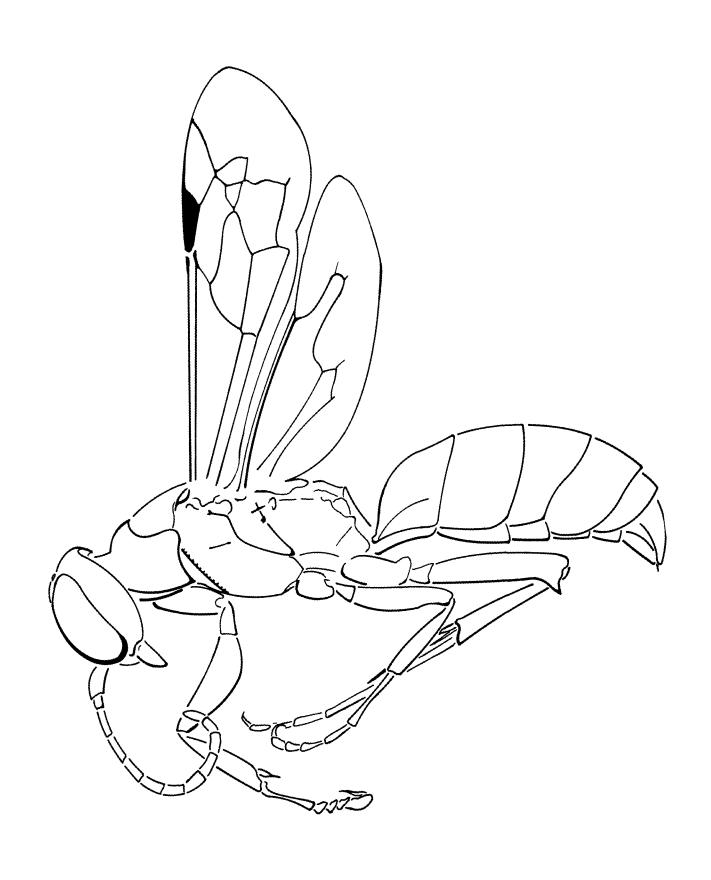


Fig. 105. Nyssonidae: Alyssoninae

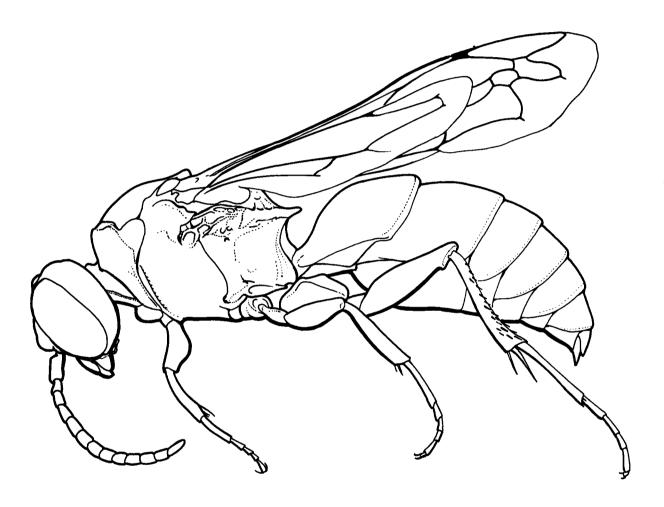


Fig. 106. Nyssonidae: Nyssoninae

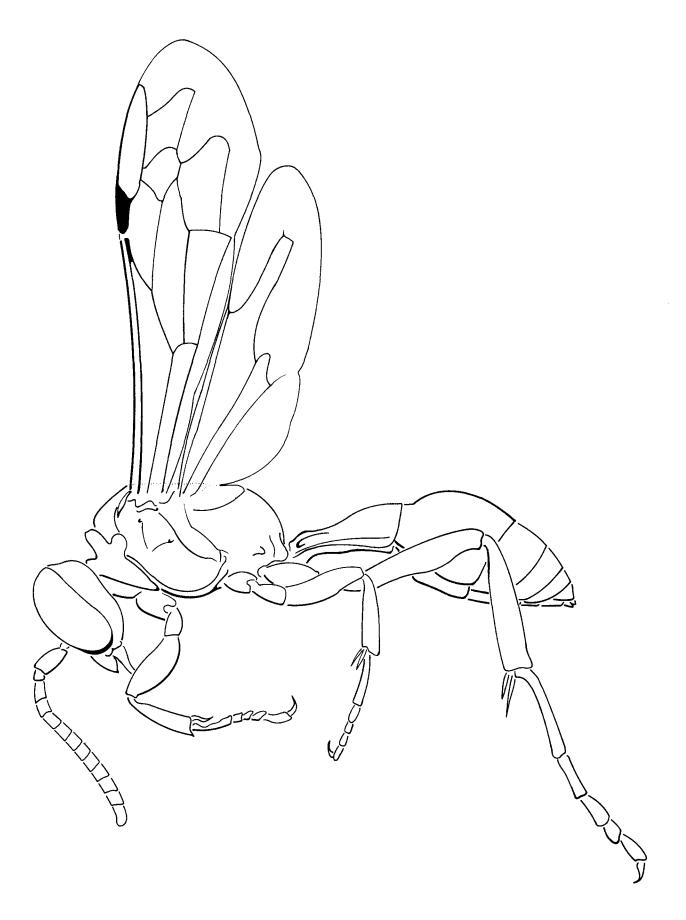


Fig. 107. Nyssonidae: Gorytinae

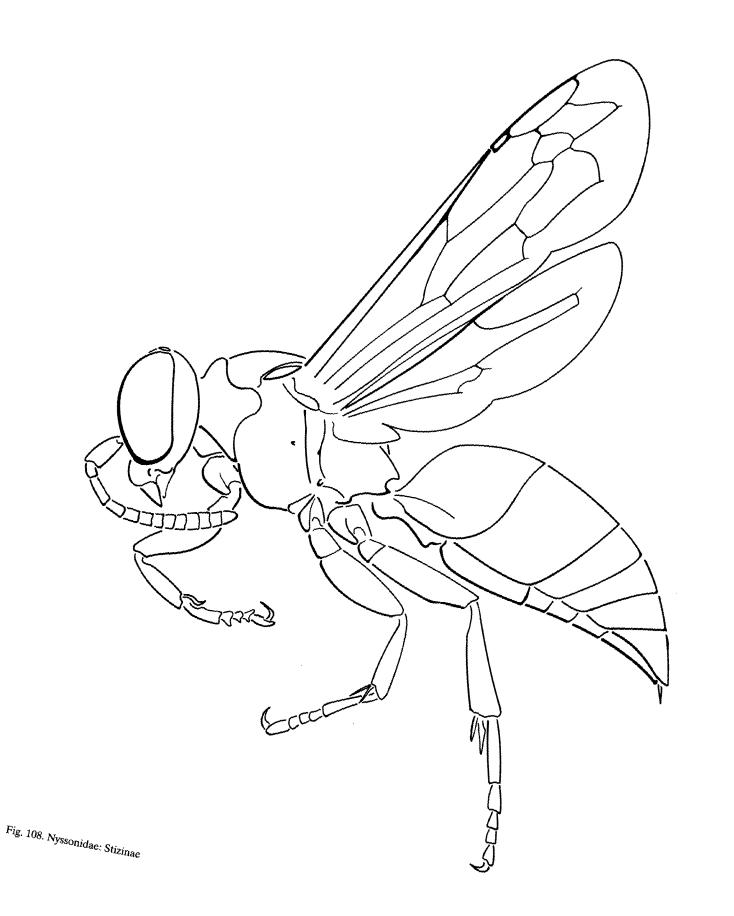




Fig. 109. Nyssonidae: Bembicinae

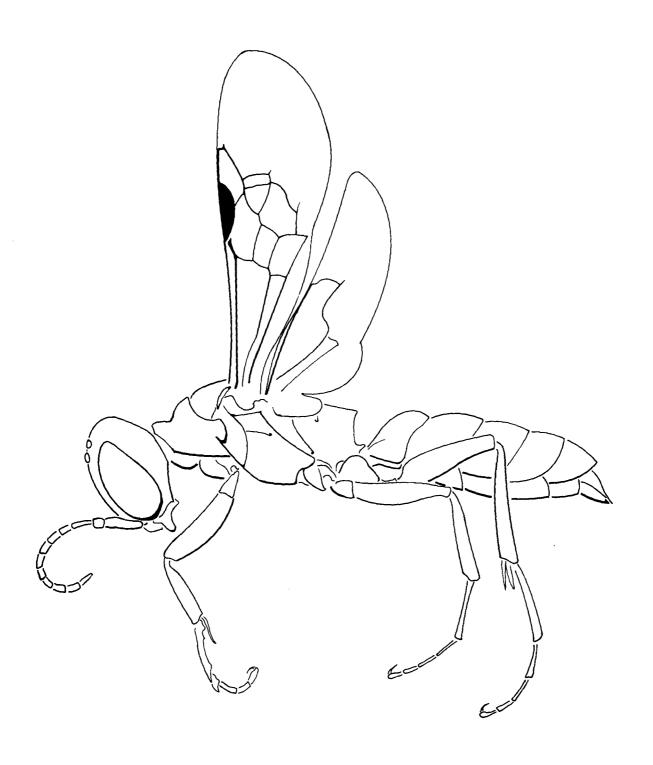


Fig. 110. Philanthidae: Eremiasphecinae

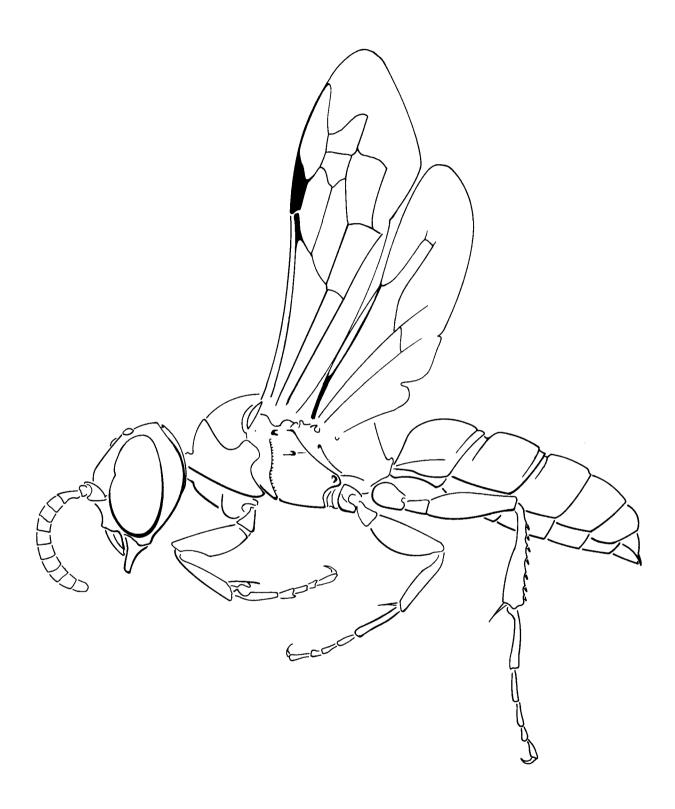


Fig. 111. Philanthidae: Philanthinae

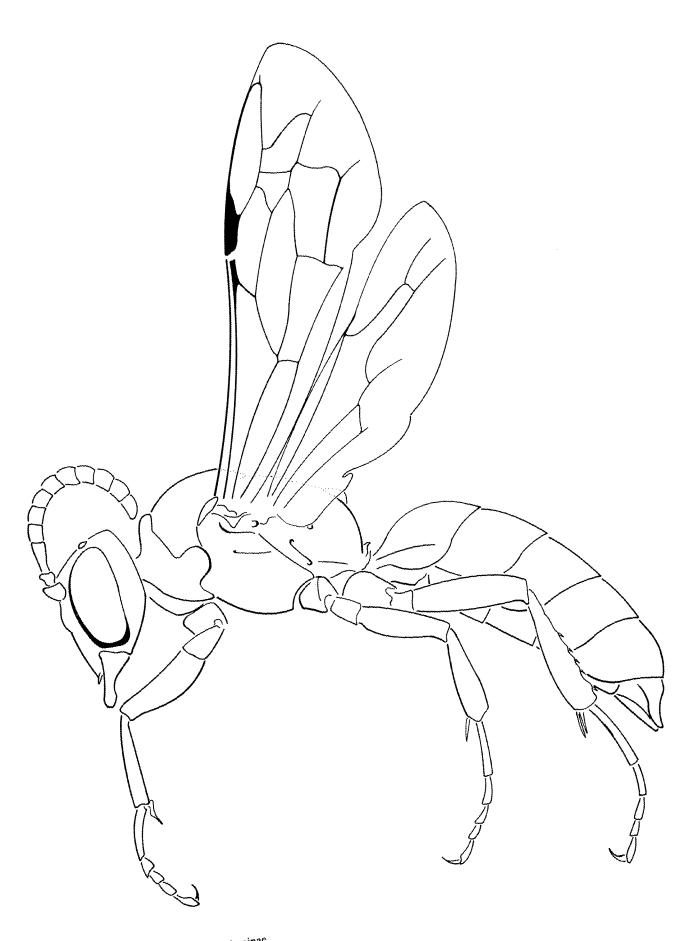


Fig. 112, Philanthidae: Aphilanthopinae

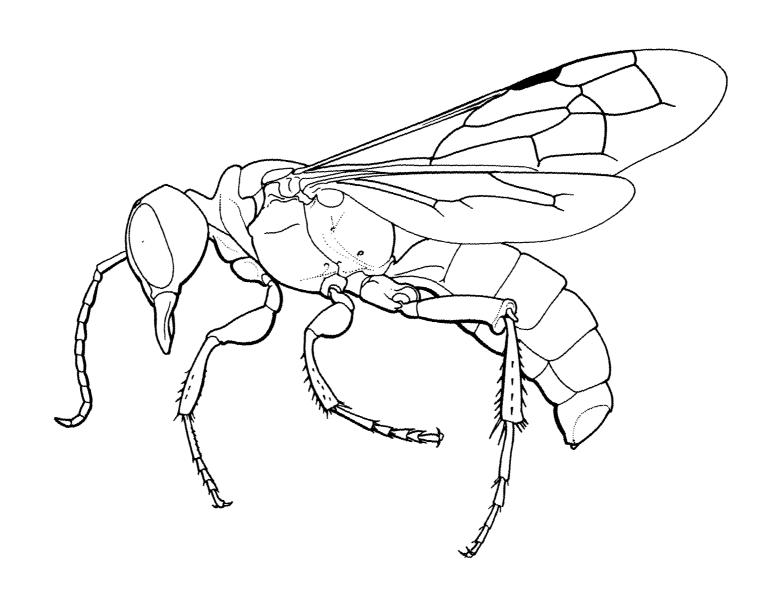


Fig. 113. Philanthidae: Cercerinae

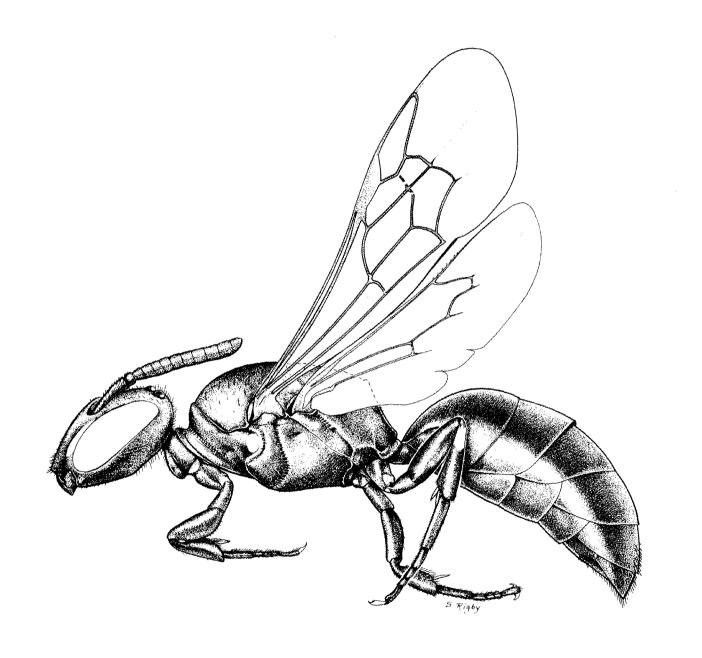


Fig. 114. Colletidae



Fig. 115. Stenotritidae

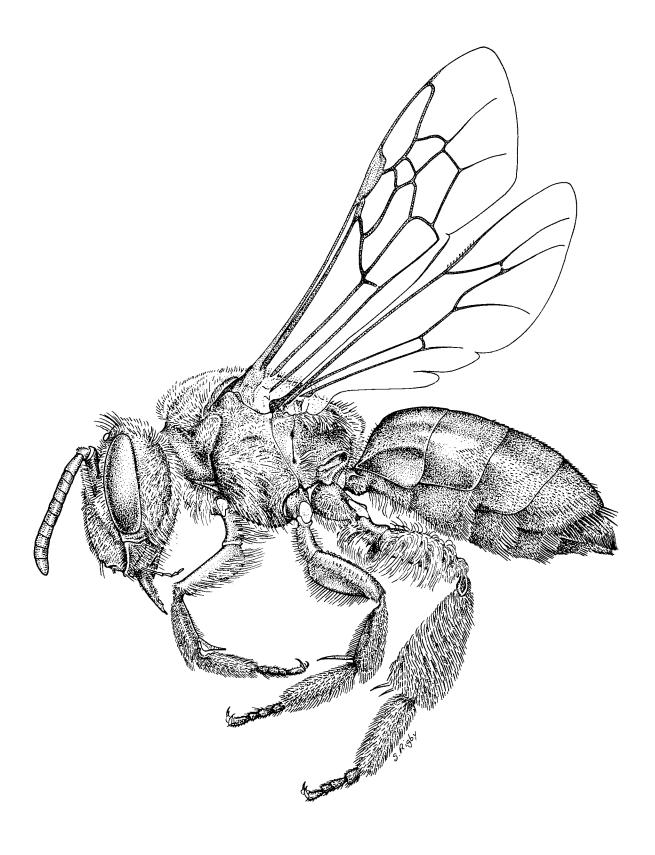


Fig. 116. Andrenidae

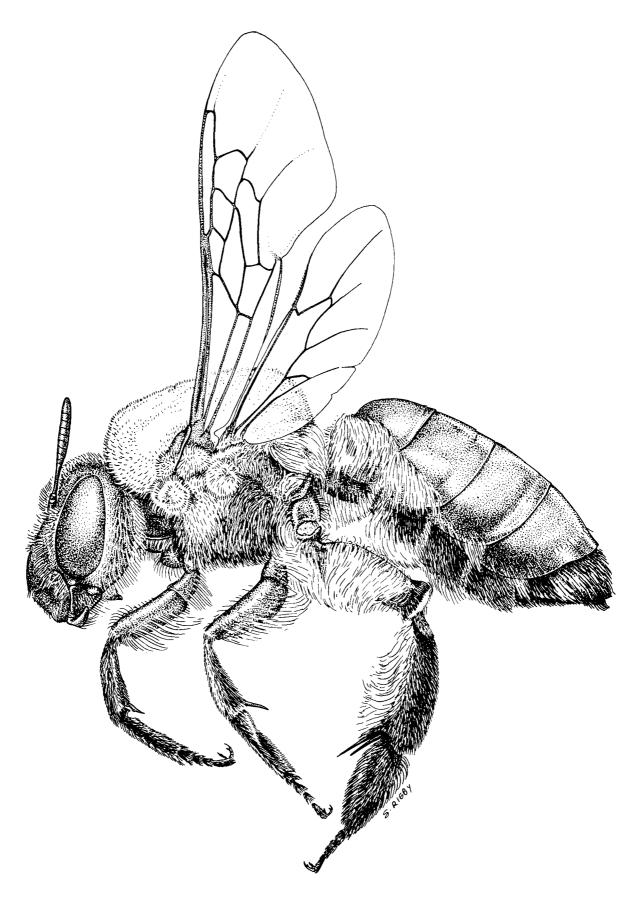


Fig. 117. Oxaeidae

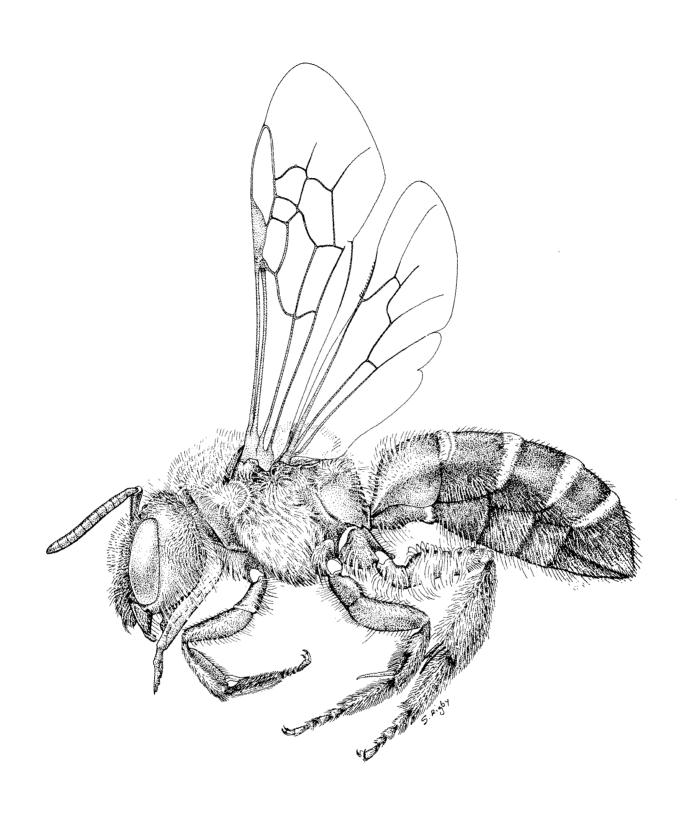


Fig. 118. Halictidae

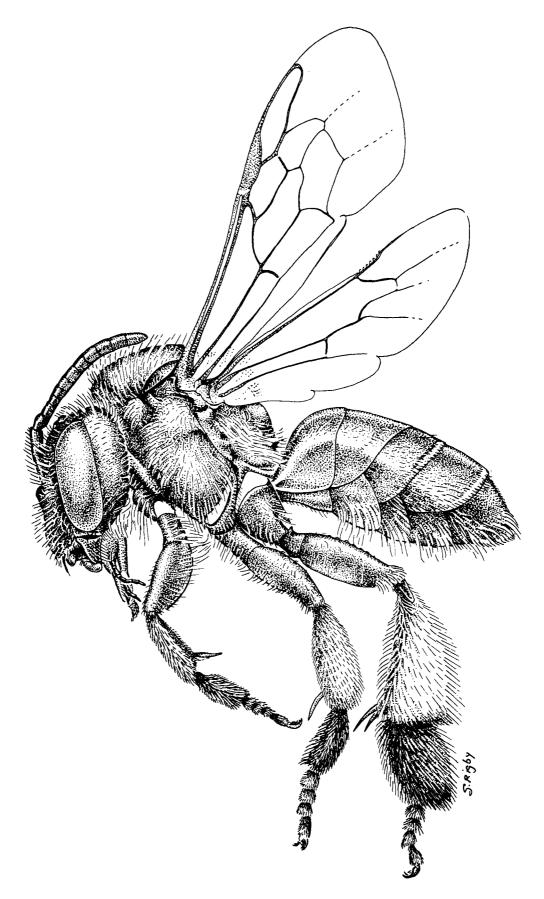


Fig. 119. Melittidae

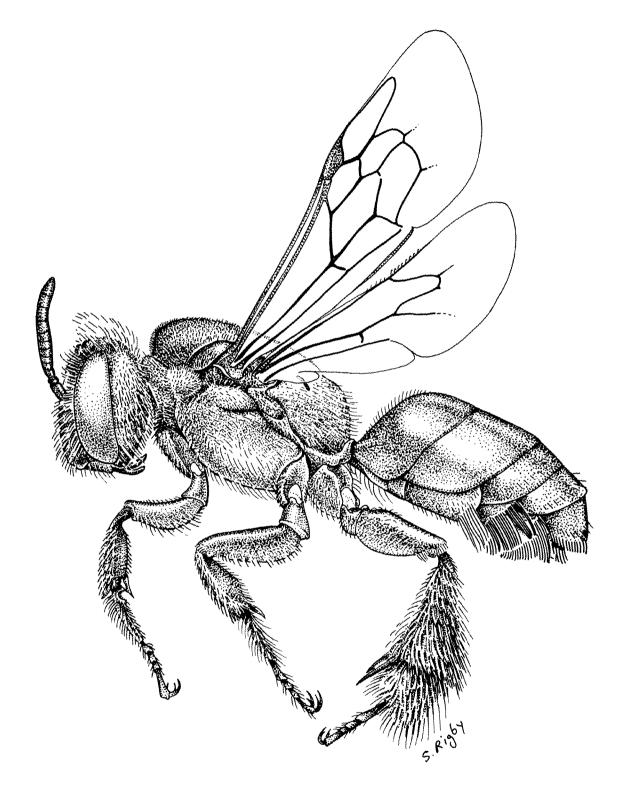


Fig. 120. Ctenoplectridae

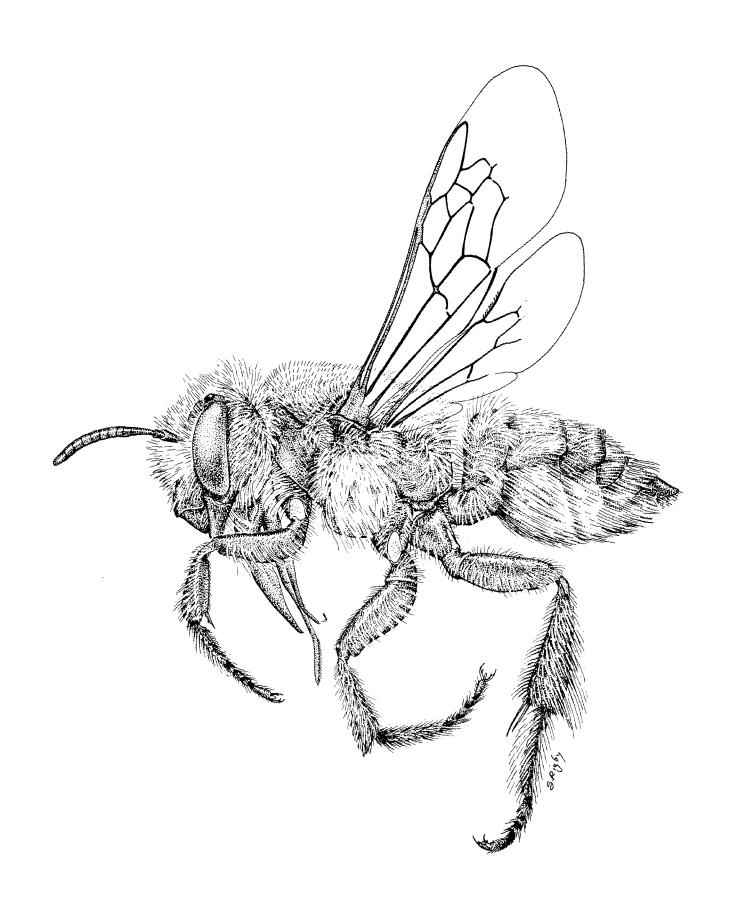


Fig. 121. Fideliidae

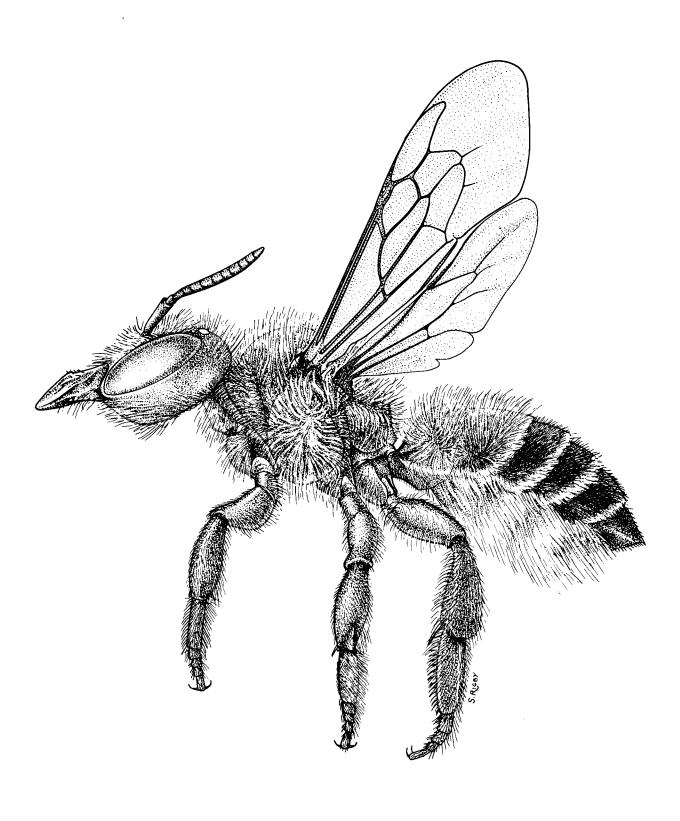


Fig. 122. Megachilidae

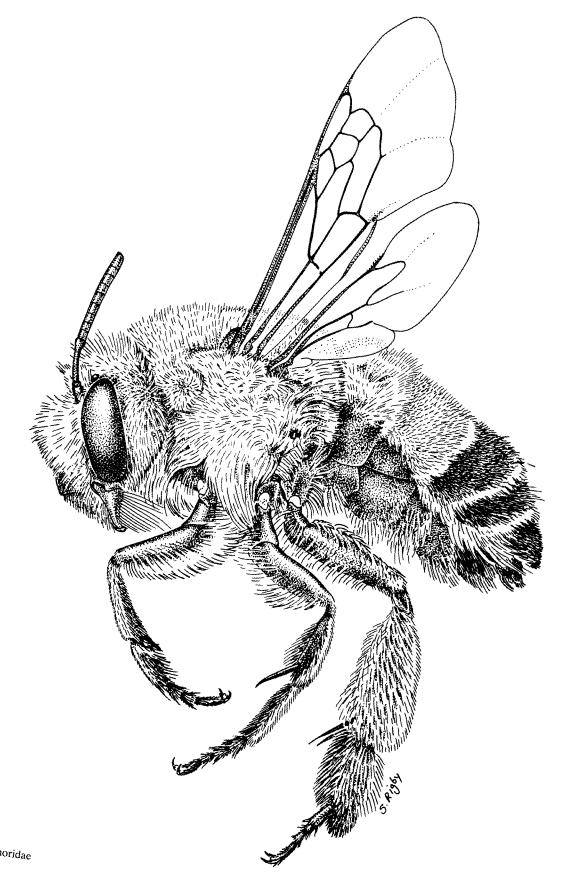


Fig. 123. Anthophoridae

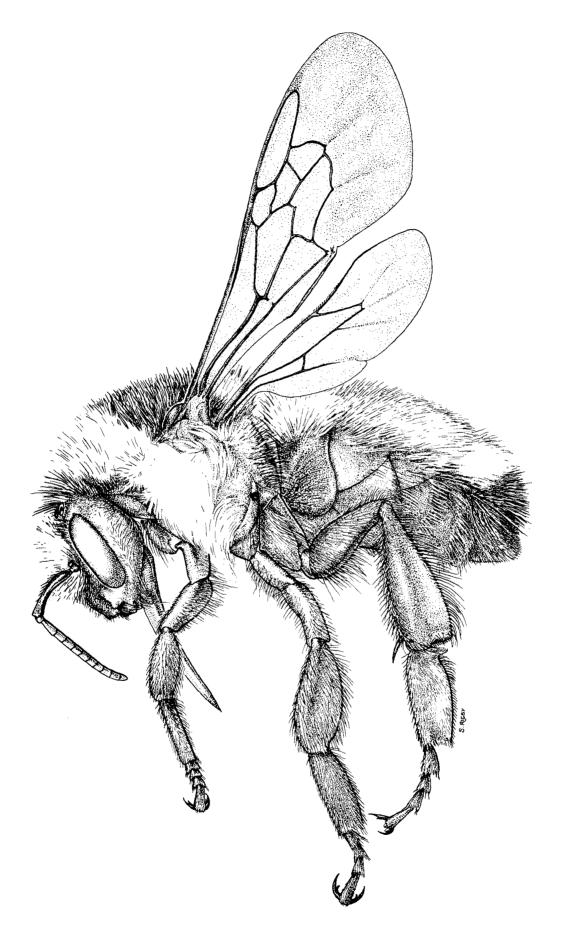


Fig. 124. Apidae

# Chapter 10 Superfamily ICHNEUMONOIDEA

(Figs. 125-185)

David B. Wahl and Michael J. Sharkey

Included families (2): Braconidae, Ichneumonidae.

**Diagnosis** Veins C and R of fore wing adjacent or fused, so that cell C is absent or apically nearly so; antenna not elbowed, almost always with more than 11 flagellomeres; ovipositor often exserted and long; trochantelli present; metasomal sternum 1 divided in half and apical portion weakly sclerotized; metasomal tergum 1 often with lateral pit (glymma) on anterior half; mandible usually with 2 teeth.

**Comments** Ichneumonoidea contains the two largest families in the Hymenoptera: Braconidae, with approximately 40 000 species, and Ichneumonidae, with approximately 60 000 species. Both families are found around the world.

Only two families, Braconidae and Ichneumonidae, are recognized here. Several other families have been placed in the superfamily. The family Stephanidae has often been included (Townes 1969, Carlson 1979), but it possesses none of the autapomorphies that define Ichneumonoidea (Sharkey and Wahl 1992). The ichneumonid subfamily Paxylommatinae has been variously treated as a subfamily of braconids (van Achterberg 1976) or as a separate family (Mason 1981). The paper by Mason showed that it could not be regarded as belonging in the Braconidae; Rasnitsyn (1980) and Gauld (1984a) treat the group as a subfamily of ichneumonids. Some workers, such as Mason (1971), regard the ichneumonid subfamily Agriotypinae as having family status, placing emphasis upon certain specialized attributes. Ichneumonid specialists see no compelling reason to regard them as anything other than a derived group of ichneumonids. Aphidiine braconids are often treated as a family. A major autapomorphy of Braconidae, tergum 2 fused with 3, is present in the aphidiines, although the fusion is weakened and some bending occurs. The braconid subfamily Apozyginae was originally described as a separate family (Mason 1978) but is best considered as belonging to the cyclostome braconids. See Sharkey and Wahl (1992) for a detailed discussion of these taxa as well as fossil ichneumonoids.

The following is only an introduction to the major features of ichneumonoid biology. For a synthesis of the literature, the student should refer to Clausen (1940), Askew (1971), Gauld (1988), Gauld and Bolton (1988), any of several textbooks on biological control (DeBach 1964, Huffaker and Messenger 1976), and Marsh and Carlson (1979). Vinson (1976) and Vinson and Iwantsch (1980)

provided good summaries of the literature on host selection and suitability.

Ichneumonoids parasitize mainly the larvae and pupae of holometabolous insects, excluding the Megaloptera and Siphonaptera. Whereas ichneumonids are almost completely restricted to the immature stages of the Holometabola (a few groups use egg nests of Pseudoscorpionida, egg cocoons of Araneae or adult Araneae), many braconids parasitize nymphal Hemimetabola (Homoptera—Aphididae, Heteroptera, Isoptera, and Psocoptera). No braconids are known to parasitize Araneae or their eggs. A few braconids also parasitize adult Coleoptera and Hymenoptera. Unlike microhymenoptera, ichneumonoids rarely parasitize individual eggs, although many braconids and a few ichneumonids are egg-larval parasitoids, laying an egg in the host egg but consuming the host in its larval stage. Symphyta parasitism is quite common in Ichneumonidae, having arisen on several separate occasions. In braconids, only Ichneutinae and a few scattered species of other groups are sawfly parasitoids.

Ectoparasitism, that is, living on the surface of the host and feeding through an integumentary wound, is the primitive condition for ichneumonoids (and Apocrita). External parasitoids generally parasitize hosts in concealed locations, such as stem tunnels, pupal cells, leaf rolls, or cocoons. Many species inject venom before the eggs are laid; the resulting paralysis may be temporary or permanent, or even fatal. The egg is sometimes deposited next to the host, especially when paralysis is permanent. If only temporary paralysis is induced, the egg is often deposited on the host but where the host cannot get to it.

Endoparasitism has evolved independently on several occasions within the ichneumonoids, the exact number of times within each family being uncertain. Although certain advantages are gained by developing inside the host, the ichneumonoid is subject to attack by the host's immune system. A variety of strategies are used to overcome this, including the injection of viruses at the time of oviposition. These serve to control the immune reactions of the host (Edson et al. 1981).

In addition to ectoparasitic and endoparasitic lifestyles, ichneumonoid biology can be viewed in another way. Askew and Shaw (1986) distinguished between idiobionts, which do not allow the host to develop after oviposition, and koinobionts, which allow host development after oviposition and do

not kill it until a later stage. Mature larvae, prepupae, or pupae are the hosts of idiobionts, which are often ectoparasitoids. A venom that paralyzes or kills the host is usually injected at oviposition. To quote Gauld (1987), the host is an "immobile piece of meat." Idiobiont endoparasitic taxa are known, some of which are quite speciose, such as Pimplini and most Ichneumoninae in Ichneumonidae, and most Euphorinae in Braconidae. Koinobionts are usually endoparasitoids, parasitizing the eggs or early larval stages of the host. Parasitoid development is delayed or protracted, allowing the host to reach the later larval instars or pupal stage before it is consumed. Gauld (1987) discussed the subject further with respect to patterns of diversity in tropical ichneumonid fauna.

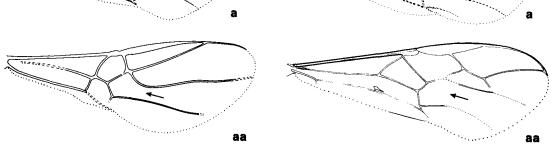
Gregarious parasitism is more common in braconids than ichneumonids. In contrast,

hyperparasitism is only infrequently encountered in braconids, whereas many ichneumonids are hyperparasitoids of other ichneumonoids or Tachinidae (Diptera).

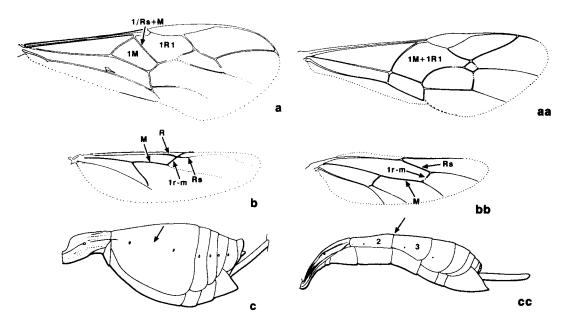
There are three to five larval instars; and the mature larva is grub-like and apodous, resembling the larvae of Aculeata. Several heavily sclerotized rods and bands occur around the mouthparts and are of great taxonomic value. The cast-off skin of the mature larva is retained in the parasitoid's cocoon, or in the host remains if no parasitoid cocoon is spun, along with the larval meconium and the cast-off pupal skin. The larval skins can be mounted on slides for study (Wahl 1984, 1989), and head structures can then be examined. The cocoon and its contents should *always* be preserved with reared specimens, preferably in a gelatin capsule pinned with the reared adult.

## **Key to families of ICHNEUMONOIDEA**

aa. Wings reduced (at most reaching level of metasomal segment 2) or absent 7

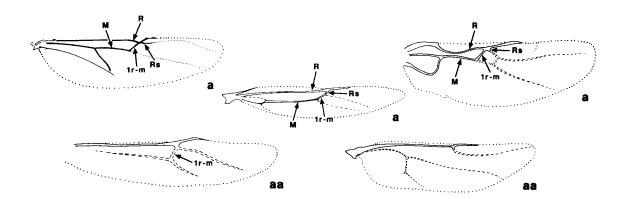


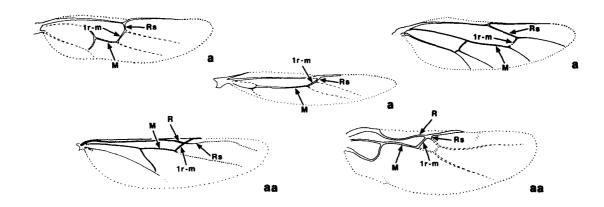
- - aa. Fore wing with vein 2m-cu absent, not even visible as spectral vein .......



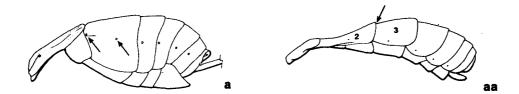
- a. Fore wing with vein 1/Rs+M separating cells 1M and 1R1.
  - b. Hind wing with vein 1r-m basal to separation of veins R1 and Rs.
  - c. Metasomal tergum 2 fused with 3 and junction between them inflexible.

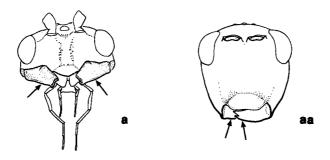
  - aa. Fore wing without vein 1/Rs+M, with compound cell 1M+1R1 present.
  - bb. Hind wing with vein 1r-m opposite or apical to separation of veins R1 and Rs.
  - cc. Metasomal tergum 2 usually separate from 3, with flexible junction between them.



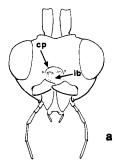


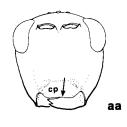
- - aa. Hind wing with vein 1r-m basal to separation of veins R1 and Rs. . . . . . . . . . . . . . . . . . (most genera) BRACONIDAE (p. 363)





- - aa. Mandibles with tips touching when closed, or overlapping and teeth pointing inward . . . . . 8





### **Family BRACONIDAE**

(Figs. 125-153)

Michael J. Sharkey

**Diagnosis** Vein 2m-cu of fore wing absent, except in specimens of *Apozyx penyai* Mason from Chile (present in 95% of Ichneumonidae); vein 1/Rs+M of fore wing often (85%) present (absent in all Ichneumonidae); vein 1r-m of hind wing usually (95%) basal to separation of R1 and Rs (opposite or apical in Ichneumonidae); metasomal tergum 2 fused with 3, though secondarily flexible in Aphidiinae (90% of Ichneumonidae with flexible suture).

Comments Braconidae is the second largest family of Hymenoptera, with at least 40 000 species. The family occurs around the world and is diverse in all areas, with no striking preference for tropical or temperate regions or for wet or dry habitats. Van Achterberg (1976) provided a summary of the taxonomic history of the family; Shaw and Huddleston (1991) discussed the family's classification and biology.

Members of Braconidae have a variety of biologies that are summarized under the appropriate subfamilies. Hosts are usually the larvae of Holometabola, although nymphs of Hemimetabola and adults of both Holometabola and Hemimetabola are also parasitized. Two major lineages occur within the Braconidae, the cyclostome and non-cyclostome braconids. Most species of Braconidae are endoparasitic koinobionts, although a large number are idiobiont ectoparasitoids. Idiobionts generally paralyze their hosts, lay an egg on or near the host, and begin consuming the host immediately after the egg hatches. Most idiobionts are ectoparasitoids. Koinobionts usually do not paralyze their prey, and

typically an egg is laid inside the host; the egg hatches immediately but undergoes a quiescent period while the host grows to an appropriate size and stage. Koinobionts usually exercise some control over the development of their hosts (Vinson and Iwantsch 1980), and because they are closely associated with the life cycles of their hosts they have limited host ranges. Conversely, idiobionts are usually not closely synchronized with their hosts, and host ranges are generally quite large (Askew and Shaw 1986). Ectoparasitism and the idiobiont way of life are ground-plan attributes of Braconidae. However, both endoparasitism and koinobiosis appear to have developed several times within the family.

No consensus has yet been reached on the number of subfamilies in Braconidae which, in part, reflects the lack of knowledge concerning the phylogeny of the group. This problem is rapidly being rectified by several researchers, including the author, who are investigating the phylogenetic relationships of the family. No doubt this work will result in further instability in subfamily classification in the short term, but it should produce stability in the end. The most recent subfamily analyses of Braconidae were by van Achterberg (1976, 1984a) and Quicke and van Achterberg (1990). I follow some of their modifications here and reject others in an attempt to produce a classification based, to a greater extent, on monophyletic taxa. The greatest difference from their classifications is that I treat many of the smaller subfamilies as tribes within larger subfamilies. Where I have presented new groupings, I have discussed the rationale under the

appropriate subfamily. Several of the subfamilies recognized in this treatment are probably polyphyletic, whereas a few others are undoubtedly paraphyletic. This is not a desirable situation, but I have nothing better to present at the moment. Twenty-nine subfamilies are recognized in this work. The discussions of the various subfamilies are divided into two sections, which represent natural (monophyletic) groupings. I refer to these as the cyclostome and non-cyclostome braconids. The 29 subfamilies recognized here are included in the following key.

**References** Shenefelt (1965) published a bibliography of articles on Braconidae. Shenefelt (1969, 1970a, 1970b, 1972, 1973a, 1973b, 1974, 1975, 1978), Shenefelt and Marsh (1976), Fischer (1971), Mackauer and Starý (1967) and Mackauer (1968) cataloged the described species of Braconidae. Shenefelt (1980) indexed his catalogs. Tobias,

Belokobylskij, and Kotenko (1986) and Tobias, Yakimavichus, and Kirijak (1986), building on the historic works of Telenga (1936, 1941, 1955) and Tobias (1975), keyed all the described species of Braconidae of European USSR. Marsh (1979) cataloged the described species of Braconidae of North America. Marsh et al. (1987) keyed the genera of Braconidae occurring in North America. Van Achterberg (1990) provided a key to the Holarctic subfamilies and (1984a) discussed their phylogenetic relationships. Capek (1970) investigated larval braconids and discussed the phylogeny of Braconidae in light of larval morphology. Capek (1973) provided a key to the larvae of braconid subfamilies. Huddleston (1988) discussed the Braconidae of Britain at the subfamily level. Shaw and Huddleston (1991) provided a key to the subfamilies of Britain and discussed in considerable detail the biological attributes of each.

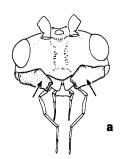
#### List of subfamilies of Braconidae

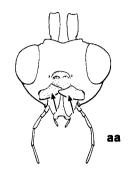
Adeliinae Ichneutinae Agathidinae Khoikhoiinae Alysiinae1 Macrocentrinae Amicrocentrinae Meteoridiinae Aphidiinae1 Meteorinae Apozyginae<sup>1</sup> Microgastrinae Braconinae<sup>1</sup> Miracinae Cardiochilinae Neoneurinae Cheloninae Opiinae1 Dorvctinae1 Orgilinae Dirrhopinae Rogadinae1 Euphorinae Sigalphinae Gnamptodontinae1 Trachypetinae Helconinae Xiphozelinae Homolobinae

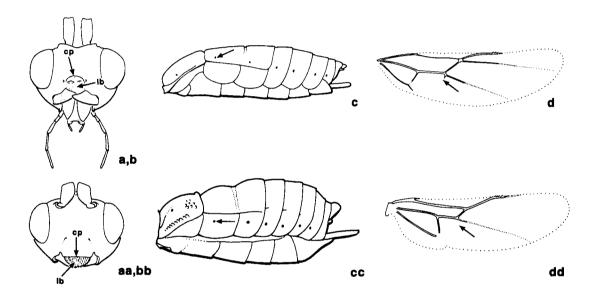
## Key to subfamilies of BRACONIDAE

1	a.	Wingless or with wings reduced, not extending past tergum 1		
	aa.	Wings present and extending past tergum 1	2	

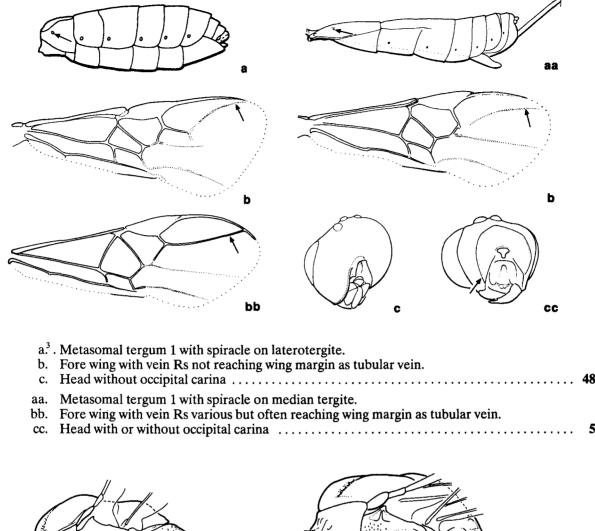
<sup>&</sup>lt;sup>1</sup> Member of the cyclostome group of Braconidae.

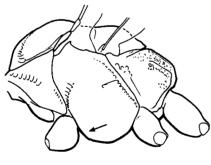




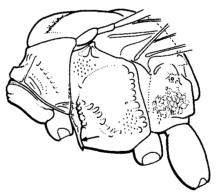


<sup>&</sup>lt;sup>2</sup> Percentage refers to proportion of fauna with attribute in question.





4(3)

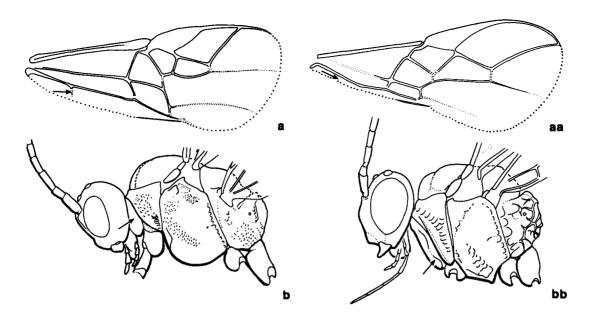


5(4)	a.	Mesopleuron without epicnemial carina	6
	aa.	Mesopleuron with epicnemial carina	11

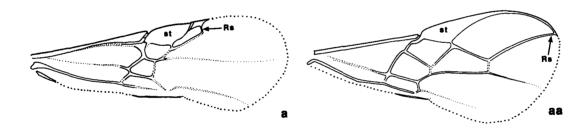
<sup>3</sup> If the spiracle is on the laterotergite then it is often hidden under the metasoma and obscured by folds in the laterotergite and by the metacoxa. It is best to look for a spiracle on the median tergite, and if one is not visible there, it can be assumed to be on the laterotergite.





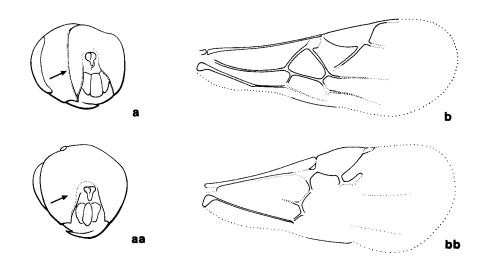


- 8(7) a. Fore wing with anal crossvein.
  - b. Propleuron usually (95%) with dorsolateral margin smooth, usually (95%) without longitudinal carina that couples with pronotum ....... some Ichneutinae (p. 390)
  - aa. Fore wing without anal crossvein.



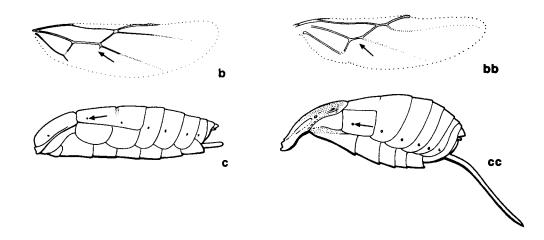
- 9(8) a. Fore wing with vein Rs ending near stigma (st) ...... (Neoneurus) Neoneurinae (p. 391)

<sup>4</sup> This carina is often difficult to see if the propleuron is closely appressed to the pronotum, but it is usually visible on the extreme anterior and posterior ends of the pronotum.



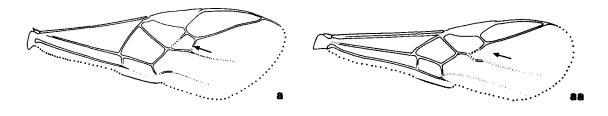
- 10(7) a. Head with occipital carina.

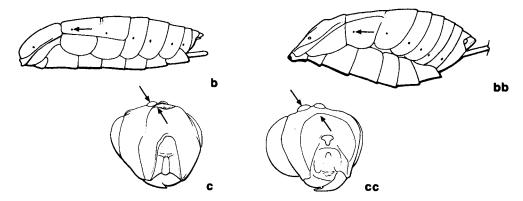
  - aa. Head without occipital carina.
  - bb. Fore wing with venation as figured ...... (Elasmosoma) Neoneurinae (p. 391)



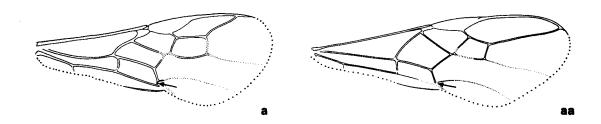
- a. With the following combination of attributes:
  - b. Hind wing with vein 2m-cu'.

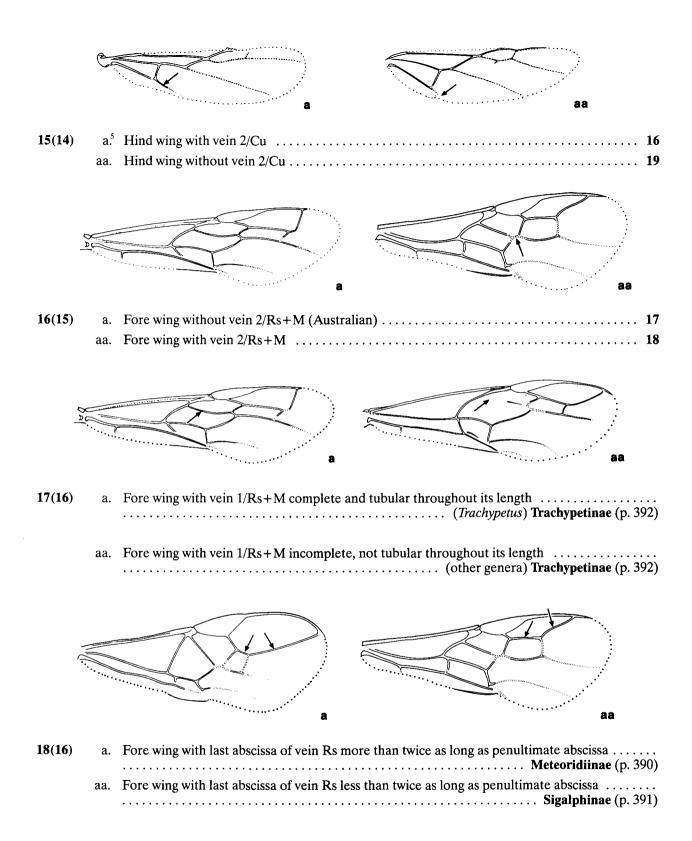
  - aa. Without the preceding combination of attributes:
  - bb. Hind wing usually (99%) without vein 2m-cu'.



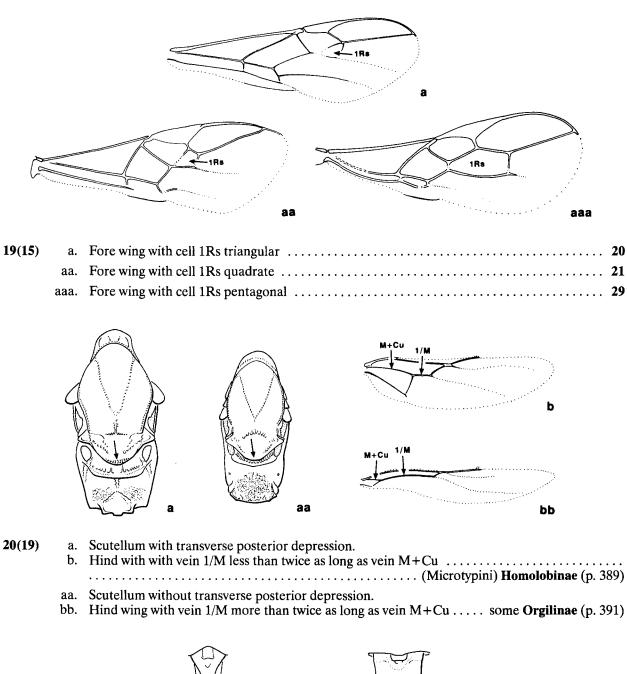


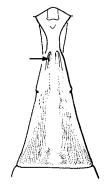
- 13(12) a. With the following combination of attributes:
  - b. Metasomal tergum 2 with spiracle on median tergite.
  - c. Head with occipital carina almost meeting lateral ocellus . . . . . . (Ademon) Opiinae (p. 394)
  - aa. Without the preceding combination of attributes:
  - bb. Metasomal tergum 2 usually (95%) with spiracle on laterotergite.
  - cc. Head with occipital carina, if present, usually (98%) not approaching lateral ocellus ..... 14





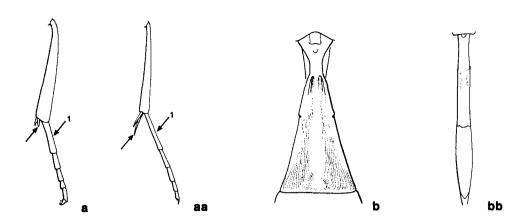
<sup>&</sup>lt;sup>5</sup> This attribute is sometimes difficult to interpret because vein 2/Cu may be in a very posterior position, as in Fig. 15a, and therefore appears to be vein 2/1A, which is present, though weakly so, in Fig. 15aa. The best way to distinguish the two is to note the position of the bulla: if the bulla is on vein 1A, the vein is 2/Cu; if the bulla is on vein Cu and cu-a, the vein is 2/1A.

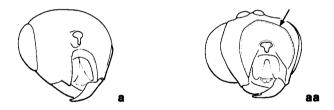






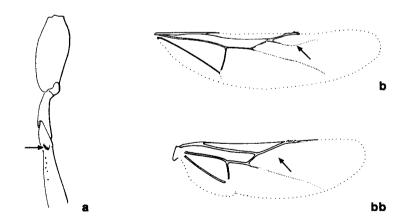
aa





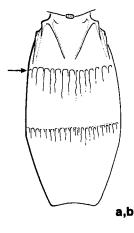
 23(21)
 a. Head without occipital carina
 24

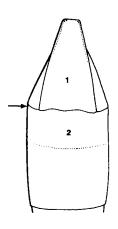
 aa. Head with occipital carina
 25







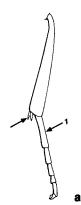




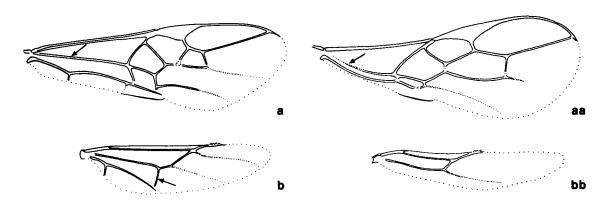
aa,bb

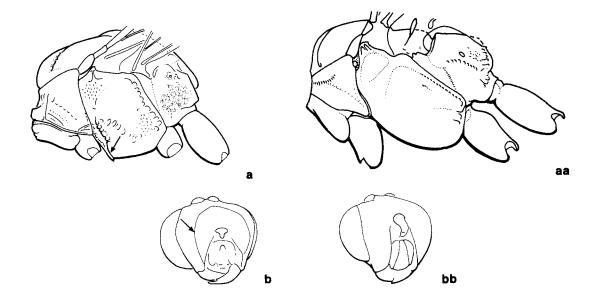
a. Metasomal tergum 1 fused with tergum 2.
b. Metasomal terga 1-3 forming carapace covering remaining terga . . . . some Cheloninae (p. 388)
aa. Metasomal tergum 1 articulating with tergum 2.

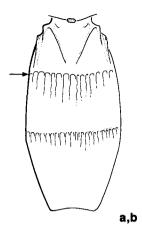
bb. Metasomal terga 1–3 not forming carapace ..................... some **Helconinae** (p. 389)



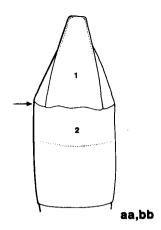


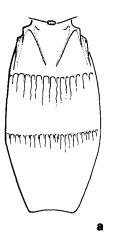






32(14)

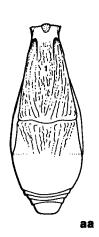


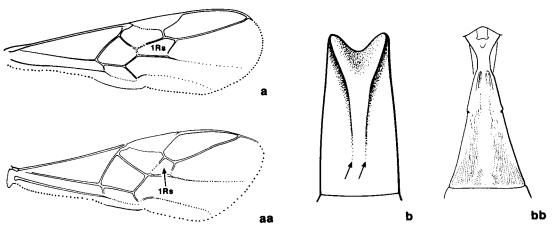


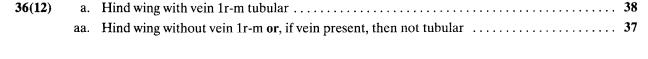


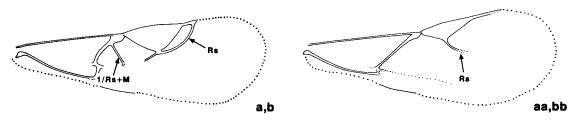


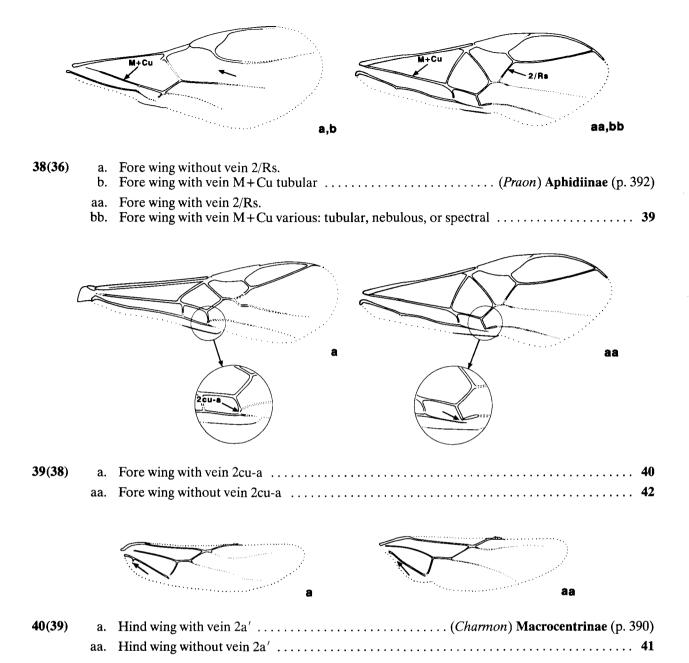


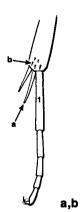




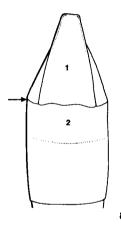


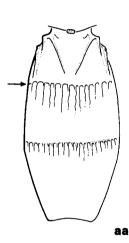










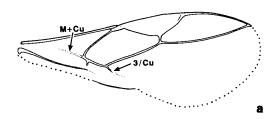


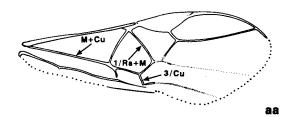


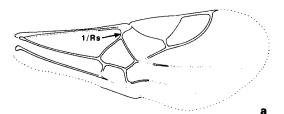


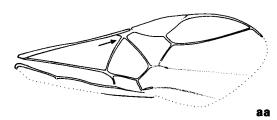
 43(42)
 a. Head with occipital carina, at least laterally
 44

 aa. Head without occipital carina
 46



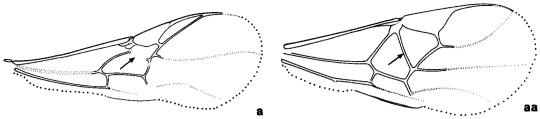




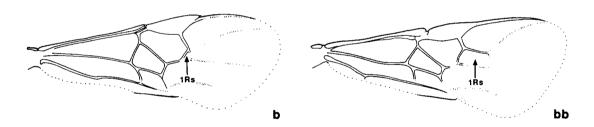




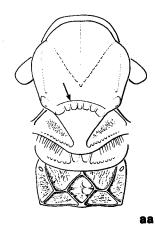


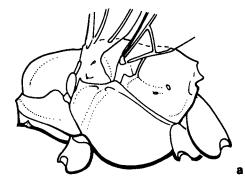


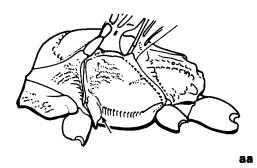
			a			aa		
47(46)	a.	Fore wing with vein 1	/Rs+M incomple	ete or not tubular th	roughout its length some <b>Agath</b>			
á	aa.	Fore wing with vein 1/Rs+M complete and tubular throughout its length						
						bb		











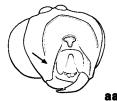
51(3)a. Mesopleuron without epicnemial carina52aa. Mesopleuron with epicnemial carina61



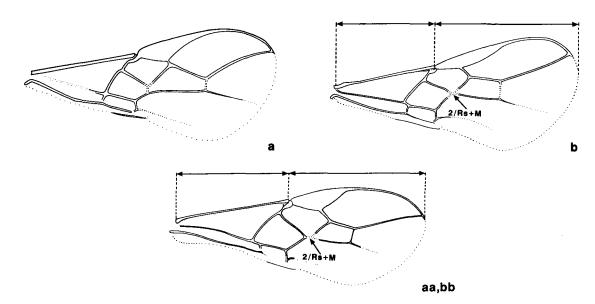




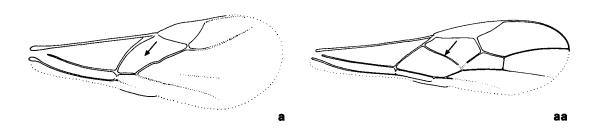




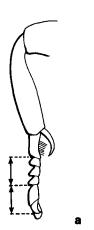


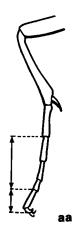


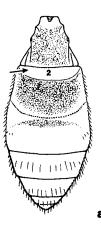
- 54(53) a. Fore wing usually (80%) without vein 2/Rs+M; if vein 2/Rs+M present, then b always applies.
  - b. Fore wing length from base of stigma to wing apex usually (80%) more than 1.4 times as long as length from base of stigma to tegula ........................ some Opiinae (p. 394)
  - aa. Fore wing usually (90%) with vein 2/Rs+M; if vein 2/Rs+M absent, then:



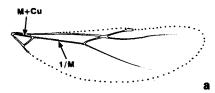
- a. Fore wing with vein 1/Rs+M absent or, if present, then not tubular throughout its length ...... (Cosmophorus) Euphorinae (p. 389)

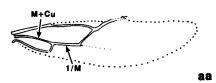




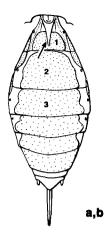


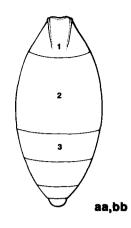




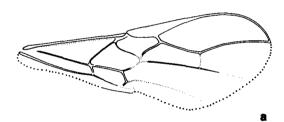


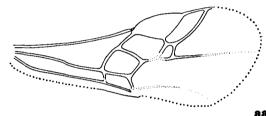
a. Hind wing with vein M+Cu less than half as long as vein 1/M ...... Braconinae (p. 393) aa. Hind wing with vein M+Cu more than half as long as vein 1/M ..... 59



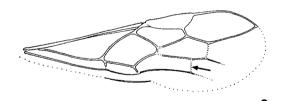


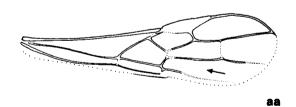
- 59(58) a. Posterior portion of metasomal tergum 1 and most of terga 2 and 3 membranous.
  - b. Metasomal tergum 1 with median longitudinal carina ...... (Leurinion) Rogadinae (p. 394)
  - aa. Posterior portion of metasomal tergum 1 and most of terga 2 and 3 well sclerotized.



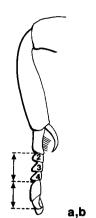


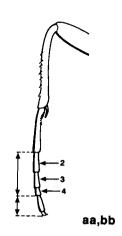
- 60(59) a. Venation similar to that figured (New World) ...... some Opiinae (p. 394)
  - aa. Venation as figured (Palaearctic) ...... (Telengaia) Gnamptodontinae (p. 393)





- - aa. Fore wing without vein 2m-cu 62

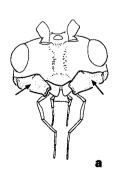


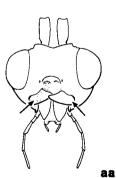


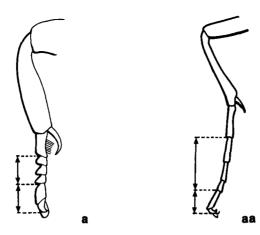


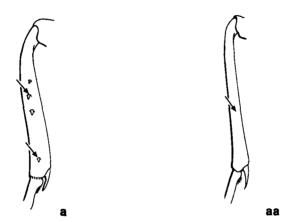


a. Protibia with pegs or spines on anterior surface ....... some **Doryctinae** (p. 393) aa. Protibia without pegs or spines on anterior surface ....... (various tribes) **Rogadinae** (p. 394)









a. Protibia with spines or pegs on anterior surface ...... some **Doryctinae** (p. 393) aa. Protibia without spines or pegs on anterior surface ..... (some Hormiini) **Rogadinae** (p. 394)

## Non-cyclostome Braconidae

**Diagnosis** Labrum not concave, usually sculptured, and often concealed beneath mandibles; vein m-cu of hind wing absent, except for a very small stub in specimens of *Dirrhope* and *Acampsis*; spiracle of metasomal tergum 2 usually (99%) on laterotergite; metasoma not bent between segments 2 and 3; species not parasitic on Aphidae (Homoptera).

**Biology** All are endoparasitoids, most are koinobionts, though secondarily some have reverted to the idiobiont mode of parasitism. Female venom glands usually have the musculature reduced, suggesting little venom is used. This seems probable in light of the fact that most hosts are parasitized when they are small compared with the parasitoid.

Interestingly, members of Ichneutinae have heavily muscled venom glands, and they parasitize the egg stage of their host. When this occurs, the muscles may be necessary to counter the pressure in the egg.

The most common hosts are Lepidoptera larvae, followed by Coleoptera larvae. Other hosts include Hemiptera nymphs and adults; Orthoptera and Psocoptera nymphs; adult Hymenoptera, Coleoptera, and Chrysopidae (Neuroptera); and Symphyta larvae. Typically, an early instar of the host is parasitized, the parasitoid egg hatches, and its development is arrested until the host is nearly full grown, at which time the parasitoid rapidly develops and consumes the host. The parasitoid often oviposits into a host egg and delays

development as described above. The development of the host is often regulated so that the parasitoid emerges in synchrony with the next generation of hosts. Members of Euphorinae and several other smaller groups oviposit into adult or nymphal insects, and some are idiobionts.

## **Subfamily Adeliinae**

(Fig. 125)

**Diagnosis** Vein Rs of fore wing not tubular to wing margin; fore wing without vein r; hind wing with vein A not tubular; transscutal suture present; metasomal terga 1-3 fused but not forming carapace over remaining terga.

**Biology** Solitary endoparasitoids of leaf-mining Lepidoptera larvae. Because of their close phylogenetic relationship with Cheloninae, members are possibly egg-larval koinobiont parasitoids.

**Distribution** Worldwide, although not recorded in the Neotropical or Oriental regions. However, several species are in the Canadian National Collection from South America (Bolivia, Ecuador), and undoubtedly members will be found in the Oriental region as well; two genera.

**Reference** Whitfield (1988) differentiated the two included genera and commented on the biology of the subfamily.

## Subfamily Agathidinae (including Mesocoelus)

(Fig. 126)

**Diagnosis** Fore wing with cell 1Rs small or absent, with last abscissa of vein Rs close to stigma such that cell 2R1 narrow, and with wing fold between prestigma and vein 1/Rs; gena and mouthparts sometimes (25%) elongate; occipital carina absent.

**Biology** Solitary koinobiont endoparasitoids of Lepidoptera larvae. Most are diurnal, but about 10% to 20% are nocturnal. The last instar parasitoid larva leaves the body of the host and consumes the remains externally, except for the head capsule. Agathidines spin a cocoon, which is often inside the cocoon spun by the final instar of the host.

**Distribution** Worldwide; 54 genera.

**Comments** Sharkey (1986) discussed the rationale for including *Mesocoelus* in Agathidinae.

**References** Shenefelt (1970b) cataloged the world species. Nixon (1986) revised the Western European species. Sharkey (1992) discussed the

phylogeny of the subfamily and proposed a tribal classification, with a key to tribes.

### **Subfamily Amicrocentrinae**

(Fig. 127)

**Diagnosis** Body length more than 8 mm; occipital carina absent; epicnemial carina absent; fore wing with cell 1Rs with five bordering veins; ovipositor about as long as fore wing.

**Biology** Parasitoids of large, stem-boring Lepidoptera larvae. The pale yellowish brown color of adults suggests that they are nocturnal.

**Distribution** Madagascar and continental Africa; one genus (*Amicrocentrum*).

**Reference** Van Achterberg (1979a) first recognized the subfamily and revised the species.

#### **Subfamily Cardiochilinae**

(Fig. 128)

**Diagnosis** Fore wing with last abscissa of vein Rs weakly sclerotized and decurved, and with cell 1Rs present and distinctly wider than long; antenna with more than 16 flagellomeres; metasomal tergum 1 with spiracle on laterotergite; occipital carina absent; transscutal suture inflexible, superficial.

**Biology** Solitary koinobiont endoparasitoids of Lepidoptera larvae.

**Distribution** Worldwide; five genera.

**References** Huddleston and Walker (1988) reviewed the biology of *Cardiochiles*. Mason (1983) discussed the relationships of Cardiochilinae with other subfamilies. Shenefelt (1973a) cataloged the world species.

#### **Subfamily Cheloninae**

(Fig. 129)

**Diagnosis** Metasomal terga 1-3 fused, forming a carapace covering remaining terga; fore wing with vein r-s present though not always tubular; postpectal carina present anterior to mesocoxa; epicnemial carina absent.

**Biology** Solitary egg-larval koinobiont endoparasitoids of Lepidoptera. The egg is laid in the host egg, and development of the parasitoid is arrested at the first-instar larval stage until the host larva has prepared a pupation retreat (Shaw and Huddleston 1991).

**Distribution** Worldwide; seven genera.

**References** Shenefelt (1973b) cataloged the world species. Vance (1932a) described the life history of *Chelonus annulipes* Wesmael.

#### **Subfamily Dirrhopinae**

(Fig. 130)

**Diagnosis** Fore wing with vein Rs not tubular to wing margin, and with vein r present; metatarsomere 1 with longitudinal comb of closely appressed setae; transscutal articulation groove-like; metasoma not greatly constricted anteriorly, not petiolate; metasomal terga 1-3 not forming carapace.

**Biology** Solitary endoparasitoids of leaf-mining Lepidoptera larvae. Because of their close phylogenetic relationship with Cheloninae they may be egg-larval koinobionts.

**Distribution** Described species are from the Palaearctic and Nearctic regions; undescribed specimens from South Africa and the Solomon Islands (Australian region) are in the Canadian National Collection; more collecting will likely extend the distribution to other regions; one genus (*Dirrhope*).

**Reference** Shenefelt (1973a) cataloged the world species.

**Subfamily Euphorinae** (including Centistini, and *Ecnomios*)

(Fig. 131)

**Diagnosis** This is a rather diverse and likely polyphyletic assemblage that is difficult to diagnose; metasoma usually (85%) petiolate; fore wing with cell 2Cu open apically and with vein r-m usually (85%) absent; maxillary palpus usually (85%) 5-segmented.

**Biology** Solitary, rarely gregarious, usually koinobiont endoparasitoids of several different orders of insects including the following, in order of frequency: Coleoptera, Hemiptera, Neuroptera, Psocoptera, Orthoptera, and Hymenoptera. Adult and nymphal stages are usually parasitized, although the larvae of Coleoptera are parasitized by a few members.

**Distribution** Worldwide; 63 genera.

**References** Shaw (1985) revised the world genera and presented a phylogenetic analysis. Shenefelt (1969) cataloged the world species. Van Achterberg (1985) revised the genera of Centistini. Shaw and

Huddleston (1991) detailed the biology of the subfamily.

**Subfamily Helconinae** (comprising Blacini (including *Dyscoletes*), Brachistini, Brulleiini, Cenocoeliini, Diospilini, and Helconini)

(Fig. 132)

**Diagnosis** Brulleiini, Cenocoeliini, Diospilini, and Helconini: occipital carina present; fore wing with vein r-m present and with cell 1Rs quadrate or pentagonal; metasomal tergum 1 usually (95%) rugose and remaining terga smooth; metasomal tergum 1 not greatly narrowed anteriorly.

Blacini: occipital carina present; fore wing with vein r-m usually (99%) absent (except *Dyscoletes*), and with vein 2cu-a usually (99%) absent (except members of *Blacozona* and *Stegnocella*); metasomal tergum 1 with dorsolateral pits.

Brachistini: occipital carina present; fore wing without vein r-m and with vein 2cu-a usually (95%) present; metasomal tergum 1 with dorsolateral pits very weak or absent.

**Biology** Mostly koinobiont endoparasitoids of Coleoptera larvae. Male mating swarms have been observed in several species of *Blacus* (Southwood 1957, Haeselbarth 1973). Members of *Dyscoletes* (Blacini) are parasitic on *Boreus* larvae (Mecoptera) (Mason 1976).

**Distribution** Worldwide; about 50 genera.

**References** Shenefelt (1969, 1970a) cataloged the world species. Van Achterberg (1983a) revised the species of Brulleiini and discussed its phylogenetic relationships within Helconinae. Mason (1974) revised the generic concepts of Brachistini and provided a key to genera. Van Achterberg (1975a, 1988) revised the world genera of Blacini, described many new species, and commented on the phylogeny, biology, and distribution of the tribe. Haeselbarth (1973) revised the European species of *Blacus*.

**Subfamily Homolobinae** (comprising Homolobini and Microtypini)

(Fig. 133)

**Diagnosis** Homolobini: fore wing with vein r-m present but not tubular; body usually (98%) yellowish brown; metasomal tergum 1 long, almost parallel-sided, and usually widest at the spiracles.

Microtypini: fore wing and cell 1Rs triangular, vein A with an a' cross vein; occipital carinae and subpronope present.

**Biology** Solitary koinobiont endoparasitoids of Lepidoptera larvae. Most (90%) species are nocturnal.

**Distribution** Worldwide; four genera.

**Reference** Van Achterberg (1979c) revised the world genera of Homolobini (as Zethinae) and discussed their distribution, biology, and phylogeny.

#### Subfamily Ichneutinae

(Fig. 134)

**Diagnosis** Dorsal longitudinal carina of propleuron usually (95%) absent; occipital carina absent; epicnemial carina often (50%) absent; metasomal terga 1–3 not forming carapace.

**Biology** Members of the tribe Ichneutini and Proteropini are solitary koinobiont larval parasitoids of larval Symphyta; those of Muesebeckiini parasitize leaf-mining Lepidoptera. The egg or first-instar larva of the host is parasitized, and development is delayed until the host larva has spun its cocoon.

**Distribution** Worldwide; nine genera.

**References** Mason (1969) proposed the tribe Muesebeckiini and revised the included genera. Shenefelt (1973a) cataloged the world species.

#### Subfamily Khoikhoiinae

(Fig. 135)

**Diagnosis** Metasomal tergum 1 with spiracle on laterotergite; transscutal articulation functional, groove-like, not superficially impressed; fore wing with apical abscissa of vein Rs spectral or nebulous; epicnemial carina absent.

**Biology** Unknown, but based on their close relationship to Cardiochilinae, members of Khoikhoiinae are likely solitary koinobiont endoparasitoids of Lepidoptera larvae.

**Distribution** South Africa; two genera.

**Reference** Mason (1983) first recognized the subfamily and described two genera.

## Subfamily Macrocentrinae (including Charmon)

(Fig. 136)

**Diagnosis** Charmonini: fore wing without vein r-m; occipital carina reduced dorsally; hind wing with vein 2a'.

Macrocentrini: metatrochantellus with spines; occipital carina absent; body usually (95%)

yellowish brown; sclerotized bridge present between metacoxal cavities and propodeal foramen.

**Biology** Solitary or gregarious endoparasitoids of early-to late-instar Lepidoptera larvae. Some gregarious species of *Macrocentrus* are known to be polyembryonic; many species are nocturnal.

Distribution Worldwide; eight genera.

References Parker (1931) gave a detailed account of the biology of *Macrocentrus grandii* Goidanich (as *M. gifuensis* Ashmead). Daniel (1932) gave a thorough description of the biology and morphology of all life stages of *Macrocentrus ancylivorus* Rowher. Quicke and van Achterberg (1990) suggested the sister group relationship between *Charmon* and Macrocentrini.

#### **Subfamily Meteoridiinae**

(Fig. 137)

**Diagnosis** Hind wing with vein 2/Cu; fore wing with cell 1Rs quadrate and with vein 2cu-a present.

**Biology** Larval-pupal endoparasitoids of Lepidoptera. Eggs are laid into the host larvae, but adults emerge from the host pupae.

**Distribution** Worldwide; two genera.

**Reference** Shenefelt (1970a) cataloged the world species.

#### Subfamily Meteorinae (including Zele)

(Fig. 138)

Diagnosis Metasomal tergum 1 usually (95%) much narrower anteriorly than posteriorly; fore wing with vein r-m present and with cell 1Rs quadrate; metacoxal cavities not separated from propodeal foramen by sclerotized bridge; metasomal tergum 1 often (80%) with deep dorsal pits.

**Biology** Solitary or gregarious koinobiont endoparasitoids of Coleoptera or Lepidoptera larvae. Some species of *Meteorus* that parasitize Lepidoptera larvae suspend their cocoons from a line of silk resembling a meteor, hence the generic name. Many species of *Meteorus* and *Zele* are nocturnal. Some species are idiobionts.

Distribution Worldwide; two genera.

**Comments** Some researchers consider the two included genera to be members of Euphorinae and others treat them as separate monotypic subfamilies.

**References** Huddleston (1980) revised the western Palaearctic species of *Meteorus* and discussed taxonomic history, biology, and host records. Shenefelt (1969) cataloged the world species. Madel (1963) reported in detail the biology of *M. colon* Haliday (as *M. fragilis* Wesmael). Van Achterberg (1979c) revised the world fauna of *Zele*. Maetô (1990) discussed the phylogenetic relationships and host associations of the subfamily.

#### **Subfamily Microgastrinae**

(Fig. 139)

**Diagnosis** Fore wing with last abscissa of vein Rs not tubular; metasomal tergum 1 with spiracle on laterotergite; occipital carina absent; antenna with 16 flagellomeres (because of a median constriction in each flagellomere, the flagellum may appear to have 32 articles); apical (ventral) margin of clypeus concave.

**Biology** Solitary or gregarious koinobiont endoparasitoids of Lepidoptera larvae (see Shaw and Huddleston, 1990, for a detailed summary). Usually koinobionts, sometimes egg-larval parasitoids.

**Distribution** Worldwide; 52 genera (largest braconid subfamily in terms of number of species).

**References** Mason revised the world genera and discussed phylogenetic relationships. Shenefelt (1972, 1973a) cataloged the world species. Austin and Dangerfield (1992) reviewed the Australian fauna.

#### **Subfamily Miracinae**

(Fig. 140)

**Diagnosis** Fore wing with last abscissa of vein Rs not sclerotized and without vein r-m; metasomal tergum 1 with spiracle on membranous laterotergite; antenna with 12 flagellomeres.

**Biology** Solitary endoparasitoids of leaf-mining Lepidoptera larvae.

**Distribution** Worldwide; two genera.

**Reference** Shenefelt (1973a) cataloged the world species.

#### **Subfamily Neoneurinae**

(Fig. 141)

**Diagnosis** Epicnemial carina absent; occipital carina absent; maxillary palpus with 3 segments; labial palpus with 2 segments; metasomal terga with

setae scattered over surface and not restricted to posterior transverse row.

**Biology** Internal parasitoids of adult Formicidae. The ovipositor is greatly curved and is thrust directly into the gaster of the adult ant.

**Distribution** Holarctic, including northern Africa; two genera.

Comments This subfamily may be a derived lineage of Centistini (Euphorinae). Some attributes that suggest this supposition are parasitization of adult insects, laterally compressed ovipositor, and specialized pit-like antennal sensilla.

**Reference** Huddleston (1976) revised the world species of *Elasmosoma* and discussed the biology of the subfamily.

#### **Subfamily Orgilinae**

(Fig. 142)

**Diagnosis** Fore wing with vein r-m usually absent but, if present, then cell 1-Rs triangular, and vein A lacking anal crossveins; occipital carina usually (90%) present; no wing fold between vein 1/Rs and stigma; dorsal pit absent; vein 2cu-a of fore wing present. *Antestrix*, known only from two Chilean species, is not included in this diagnosis.

**Biology** Solitary koinobiont endoparasitoids of Lepidoptera larvae.

Distribution Worldwide; seven genera.

**References** Van Achterberg (1987) partly revised the subfamily. Shenefelt (1970a) cataloged the world species. Oatman et al. (1969) described the biology of *Orgilus lepidus* Muesebeck.

**Subfamily Sigalphinae** (including *Acampsis*, *Minanga*, *Neoacampsis*, *Pselaphanus*, and *Sigalphus*)

(Fig. 143)

**Diagnosis** Occipital carina absent dorsally; fore wing with free apical abscissa of vein Cu present and with vein r-m present; metacoxal cavities open to propodeal foramen and not separated by sclerotized bridge; metasomal tergum 1 usually (95%) with pair of percurrent longitudinal carinae.

**Biology** Solitary endoparasitoids of Lepidoptera larvae.

**Distribution** Worldwide; five genera.

**References** Shenefelt (1970a, 1973b) cataloged the world species.

#### **Subfamily Trachypetinae**

(Fig. 144)

**Diagnosis** Fore wing with cell 1Rs pentagonal; ovipositor barely exerted; antennal flagellomere with more than 50 articles.

**Biology** Unknown. I suspect, based on presumed phylogenetic affinites, that members are endoparasitoids of Lepidoptera larvae. More than half of the known specimens have been collected at light in desert habitats (A.D. Austin, personal communication).

**Distribution** Australian region; three genera.

**Reference** Tobias (1979) proposed the subfamily and revised the genera. Austin et al. (in press) revised the genera and species.

#### **Subfamily Xiphozelinae**

(Fig. 145)

Diagnosis Occipital carina absent; sclerotized bridge between metacoxal cavities and propodeal foramen; hind wing with cell 1Cu much longer on posterior margin than on anterior margin (vein 1A much longer than vein M+Cu); metasomal segment 1 with median tergite more than five times as long as apical width.

**Biology** Solitary nocturnal endoparasitoids of Noctuidae (Lepidoptera) larvae.

**Distribution** Palaearctic, Oriental, and Australian regions; two genera.

**Reference** Van Achterberg (1979b) revised the subfamily.

## **Cyclostome Braconidae**

**Diagnosis** Labrum usually (70%) concave, smooth, and often (80%) mostly glabrous (many Doryctinae have microsculpture and many setae on the labrum, but in those forms the labrum is distinctly concave); many members without these attributes have exodont mandibles; hind wing with vein m-cu often (50%) present; metasomal tergum 2 with spiracle usually (90%) on median tergite. Members of Aphidiinae, which are here associated with the cyclostomes for the first time, do not share some of the more obvious diagnostic attributes of the other cyclostomes. They are best diagnosed by the following: joint between metasomal terga 2 and 3 flexible; metasoma often (50%) bent ventrally between segments 2 and 3; hind wing with vein 1A and vein cu-a absent or spectral, never sclerotized, and with long sensory setae near junction of veins R and 1r-m; parasitoids of Aphidae (Homoptera).

**Biology** Most are idiobiont ectoparasitoids of Lepidoptera larvae and Coleoptera, although many members are endoparasitoids of Diptera, Aphidae (Homoptera), and Lepidoptera, and many of these are koinobionts. Isoptera and Embioptera are also known hosts and one genus may be phytophagous (Marsh 1991). Most females have well-muscled venom glands and use venom to subdue their prey and paralyze it, at least temporarily. Development of the parasitoid usually begins immediately, with little or no visible effect on the development of the host, which is quickly consumed.

#### Subfamily Alysiinae

(Fig. 146)

**Diagnosis** Mandibles exodont, not touching when closed; epicnemial carina absent; occipital carina

absent; hind wing with vein 2m-cu often (50%) present.

**Biology** Most (90%) are solitary koinobionts and all are endoparasitic on Cyclorrhapha (Diptera) larvae.

**Distribution** Worldwide, but much more speciose in temperate regions; 65 genera.

Comments Alysiinae is a derived lineage of the paraphyletic subfamily Opiinae (Buckingham and Sharkey 1988).

References Wharton (1980) reviewed the taxonomy of Nearctic Alysiini, and Wharton (1984) summarized the biology of Alysiini. Griffiths (1964) discussed the evolution, biology, and taxonomy of Alysiinae, especially of Dacnusini.

#### Subfamily Aphidiinae

(Fig. 147)

**Diagnosis** Antenna usually (80%) curved ventrally in dead specimens; flexible joint between metasomal terga 2 and 3 (in dead specimens the metasoma is often (50%) bent at this point); hind wing with veins 1A and cu-a absent or not tubular; parasitic on Aphidae (Homoptera).

**Biology** Solitary koinobiont endoparasitoids of Aphidae (Homoptera) nymphs and adults.

**Distribution** Worldwide, but more speciose in temperate regions; about 51 genera (P. Starý, personal communication).

Comments Aphidiinae is placed with the idiobiont (cyclostome) Braconidae because of the presence of the following apomorphies: hind wing with anterior margin excavated basally and with long sensory setae present near junction of veins R and r-m; metasomal terga weakly sclerotized, labrum smooth, triangular, and mostly glabrous; and host mummified (as in most Rogadinae).

**References** Starý (1970) summarized most information on Aphidiinae, including morphology, key to world genera, and phylogeny. Mackauer (1968) cataloged the world species.

#### Subfamily Apozyginae

(Fig. 148)

**Diagnosis** Fore wing with vein 2m-cu; labrum glabrous and concave; hind wing with vein 2/Cu.

**Biology** Unknown, but judging from a general similarity to some Doryctinae members are possibly idiobiont ectoparasitoids of xylophagous Coleoptera larvae.

**Distribution** Chile; one genus with one species, *Apozyx penai* Mason.

**Comments** Apozyginae is treated here as a subfamily of Braconidae rather than as a distinct family as originally proposed by Mason (1978, 1987). Sharkey and Wahl (1992) justified this placement.

**References** Mason (1978) described *Apozyx* and proposed a new family for it. Mason (1987) also described the previously unknown female and discussed phylogenetic relationships.

#### Subfamily Braconinae (including Vapellina)

(Fig. 149)

**Diagnosis** Labrum concave; occipital carina absent; epicnemial carina absent; hind wing with vein 1/M at least twice as long as M+Cu.

**Biology** Most members are idiobiont ectoparasitoids of concealed larvae of xylophagous and stem-boring Coleoptera and Lepidoptera larvae, and rarely of Diptera and Symphyta. Several genera are gregarious endoparasitoids of Lepidoptera pupae (van Achterberg 1984b, Quicke 1987a).

**Distribution** Worldwide; 151 genera.

**Comments** Vapellini, proposed by Quicke (1987b) as a new subfamily, is included here as a tribe of Braconinae.

**References** Quicke (1987a) revised the genera of the Old World and presented notes on the subfamily. Quicke (1988) also discussed the higher classification, biology, and biogeography of the group. Quicke and Sharkey (1989) revised the genera of North America.

#### Subfamily Doryctinae (including Histeromerus)

(Fig. 150)

**Diagnosis** Labrum concave; protarsus usually (99%) with spines along anterior margin; occipital carina present but usually (80%) absent ventrally; epicnemial carina present.

**Biology** Mostly solitary idiobiont ectoparasitoids of xylophagous and stem-boring Coleoptera larvae, though one genus is known to parasitize Embioptera (Shaw and Edgerly 1985) and another may be phytophagous (Marsh 1991).

**Distribution** Worldwide; 75 genera.

**References** Shenefelt and Marsh (1976) cataloged the world species. Marsh (1965) reviewed the genera of North America.

# **Subfamily Gnamptodontinae** (including *Telengaia*)

(Fig. 151)

**Diagnosis** Labrum concave to flat; fore wing with cell 2Cu open (vein 1A incomplete); metasomal tergum 2 with smooth, anterior, transverse elevation; propodeum without sculpture.

**Biology** Parasitoids of leaf-mining larvae of Nepticulidae (Lepidoptera). It is not known if they are endoparasitoids or ectoparasitoids, but based on their possible sister group relationship with Opiinae plus Alysiinae (Buckingham and Sharkey 1988), I suspect that they are endoparasitoids.

**Distribution** Worldwide; four genera.

Comments Telengaia is similar to most gnamptodontines. Members have a modified metasoma, but wing venation and head and mesosomal structures lead me to believe that Gnamptodontinae, including Telengaia, is monophyletic.

**References** Van Achterberg (1983b) provided revisionary notes on the subfamily. Shenefelt (1975) cataloged the world species.

## Subfamily Opiinae (including Mesostoa)

(Fig. 152)

**Diagnosis** Epicnemial carina absent (except *Ademon*); occipital carina often (85%) absent dorsally but usually (98%) present laterally; occipital carina, when present, usually (98%) meeting subgenal carina, not hypostomal carina; hind wing with vein 2m-cu often (50%) present; clypeus with ventral margin usually (90%) not concave.

**Biology** Solitary endoparasitoids of Cyclorrhapha (Diptera) larvae. As with members of Alysiinae, they often parasitize a late larval instar, but they are also known to parasitize eggs and early instar larvae.

**Distribution** Worldwide; 17 genera; most species are in the large genus *Opius*, which is divided into about 50 subgenera.

Comments Van Achterberg (1975) proposed *Mesostoa* as a separate monotypic subfamily. It is included here in the Opiinae based on the shared possession of the following: labrum not greatly concave; clypeus straight ventrally; epicnemial carina absent; ovipositor bent dorsally. Opiinae is paraphyletic in that Alysiinae is a derived lineage of this assemblage (Buckingham and Sharkey 1988).

**References** Fischer (1971) cataloged the world species and Fischer (1972, 1977, 1987) revised the world fauna of Opiinae. Wharton (1987, 1988) made some changes in the generic classification.

**Subfamily Rogadinae** (including Exothecini, Hormiini, Lysterimini, Pambolini, Rhyssalini, Rhysipolini, Hydrangiacolini, Rogadini, and Ypsistoceratini)

(Fig. 153)

Note: This subfamily is certainly not monophyletic. Many of the constituent tribes have been placed in other subfamilies (Doryctinae) or have been treated as independent subfamilies. Because the relationships of these taxa are poorly understood, I have adopted a very broad definition of Rogadinae. Most of the tribes comprising the Rogadinae are discussed and diagnosed separately below. I hope this approach will make this section more useful as the subfamily concepts of Braconidae evolve.

#### Tribe Exothecini

**Diagnosis** Labrum concave; occipital carina ending ventrally on subgenal carina or absent ventrally but present at least laterally; epicnemial carina absent.

**Biology** Idiobiont ectoparasitoids of concealed (usually leaf-mining) Lepidoptera, Diptera, Coleoptera, and Symphyta larvae.

**Distribution** Worldwide (?); five genera.

**References** Shenefelt (1975) cataloged the world species. Shaw (1983) described the biology of several genera.

#### Tribes Hormiini, Lysterimini, and Pambolini

Diagnosis Labrum concave; metasomal tergum 2 with spiracle on median tergite or near margin of median and lateral tergites; occipital carina absent ventrally or meeting hypostomal carina; metasomal tergum 1 without median longitudinal carina, often (80%) with 2 percurrent longitudinal carinae; protibia without pegs or spines; epicnemial carina present. Hormiini: metasomal terga, except first, membranous. Lysterimini: metasomal segments 1–3 with median tergites heavily sclerotized and sculptured and usually covering following terga. Pambolini: propodeum often with posterolateral spine or bump; metasomal terga 2 and 3 not membranous, usually smooth, but if sculptured then not covering following terga.

**Biology** Members of Hormiini and Lysterimini are usually gregarious ectoparasitoids of concealed Lepidoptera larvae. Members of Pambolini are solitary ectoparasitoids of Coleoptera and Lepidoptera larvae.

Distribution Worldwide; about 15 genera.

**References** Shenefelt (1975) cataloged the world species. Hedqvist (1963) revised the world genera of Hormiinae s.l. Mason (1948) presented a detailed account of the biology of *Chremylus rubiginosus* (Nees) (Pambolini).

#### Tribe Rhyssalini

**Diagnosis** Labrum concave; metasomal tergum 2 with spiracle on laterotergite, well below margin of median tergite; occipital carina ending ventrally on hypostomal carina; metasomal tergum 1 without median longitudinal carina, or metasoma not coarsely sculptured beyond tergum 1, or both; protibia without spines or pegs on anterior surface.

**Biology** Usually gregarious, sometimes solitary, idiobiont ectoparasitoids of Coleoptera and Lepidoptera larvae.

**Distribution** Worldwide (Australian?); five genera.

**References** Shenefelt (1975) cataloged the world species.

Tribe Rhysipolini (including Hydrangiacolini)

**Diagnosis** Labrum concave; occipital carina ending ventrally on subgenal carina; metasomal tergum 1 without median longitudinal carina, or metasoma not coarsely sculptured beyond tergum 1, or both; anterior surface of protibia without pegs and spines.

**Biology** Koinobiont ectoparasitoids of Lepidoptera larvae.

Distribution Worldwide; seven genera.

**References** Shenefelt (1975) cataloged the world species. Shaw (1983) described the biology of several species of *Rhysipolis*.

**Tribe Rogadini** (including *Betylobracon*, *Leurinion* and Ypsistoceratini)

**Diagnosis** Occipital carina present; labrum usually (95%) concave; metasomal tergum 1 usually (95%) with sharp median longitudinal carina; metasomal terga 3 and 4 also often (75%) have median longitudinal carina; protibia without pegs and spines on anterior surface.

**Biology** Koinobiont endoparasitoids of Lepidoptera larvae; pupation takes place inside the mummified remains of the host, except for members of *Leurinion*, which do not mummify their hosts. The biology of members of Ypsistoceratini is unknown, but they have been associated with termite nests (Isoptera).

**Distribution** Worldwide; about 45 genera.

Comments Leurinion is usually placed in Hormiinae because, as in members of Hormiinae, the median tergites of some metasomal segments are membranous. However, this attribute occurs in several other cyclostome subfamilies including members of Rogadinae, e.g., Aeliodes excavatus (Telenga). Furthermore, the membranous portions of the metasomal terga of Leurinion species are more widespread than the membranous proportions

of Hormiinae species and include the posterior part of tergum 1. Members of *Leurinion* have a sharp median longitudinal carina on the propodeum and metasomal terga 2 and 3. This combination of derived characters is unknown to me outside Rogadinae s.s.

Ypsistoceratini, composed of *Ypsistocerus*, *Termitobracon*, and an undescribed genus from the southeastern USA, are sometimes placed in their own subfamily. They are a derived group morphologically and have lost many attributes that allow for their easy placement in any cyclostome subfamily. They share several derived characters with the rogadine genus *Yelicones*: expanded apical tarsomeres of all legs and the presence of spines on the anterior surface of the protibia.

Tobias (1979) placed Betylobracon in its own subfamily. However, based on the presence of a strong m-cu' vein in the fore wing (a derived character within the idiobiont Braconidae) and metasomal spiracles located on the median tergites (a primitive character that excludes it from the koinobiont Braconidae) it appears to belong to the idiobiont lineage. Of the subfamilies in this lineage it appears to be closely related to Yelicones and allies. This is shown by the following: femora swollen, apical tarsomeres swollen and elongate, and ovipositor short (shared by all Rogadini). Betylobracon waterhousei Tobias, the only species described to date, bears a striking resemblance to Yelicones delicatus (Cresson). The principal difference between the two species is that the clypeus of the former is not concave ventrally, but this character state reversal is not uncommon within the idiobiont clade.

References Shenefelt (1975) cataloged the world species. Shaw (1983) described the biology of several species. Tobias (1979) discussed the phylogenetic placement of *Betylobracon*. After this publication was in proof, van Achterberg (1992) revised the West Palaearctic and Afrotropical genera and proposed two new tribes, Clinocentrini for *Clinocentrus*, and allies and Yeliconini for *Yelicones*, *Betylobracon*, and allies.

## Family ICHNEUMONIDAE

(Fig. 154-185)

David B. Wahl

**Diagnosis** Fore wing with vein 2m-cu present (lost in a few Ichneumonidae, absent in all Braconidae except Apozyginae) and with vein 1/Rs+M absent, forming the compound cell 1M+1R1 (vein present in about 85% of the Braconidae); hind wing with vein 1r-m opposite or apical to the separation of veins R1 and Rs (basal in Braconidae); metasomal tergum 2 usually separated from 3 and their

junction flexible (tergum 2 fused with 3 in the Braconidae).

Comments Ichneumonidae is the largest family in the Hymenoptera (and one of the largest in the Insecta) with at least 60 000 species. The family occurs around the world, with more species in cool moist climates than in warm dry ones. The eastern

Palaearctic and eastern Nearctic regions are particularly rich in species.

Townes (1969) gives an account of the taxonomic history of the family. Briefly, five subfamilies were used by most workers from 1855 until about 1940, when the trend toward splitting up the subfamilies began. Perkins (in Beirne 1941) recognized 14 subfamilies. Townes's classification is the dominant system today. He began his research in 1945, culminating in 1969–1971 with a series of four monographs treating the genera of all subfamilies except Ichneumoninae. He recognized 25 subfamilies. Since then, additional subfamilies have been proposed for various taxa that are misfits in Townes's classification. Much of this recent work has been based on the morphology of the mature larva. I recognize 35 subfamilies.

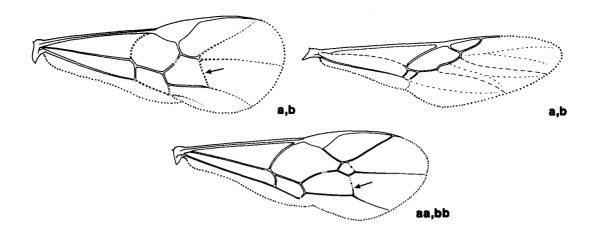
The novice trying to learn ichneumonid systematics is confronted by a bewildering array of family-group (subfamily, tribe, subtribe) names. This problem was caused by Townes, who refused to follow the *International Code of Zoological Nomenclature* or to recognize the validity of certain Opinions of the International Commission on Zoological Nomenclature (see Townes (1969) for a discussion of his position). Thus, many of Townes's family-group names are invalid if one chooses to follow the *International Code of Zoological Nomenclature*. Fitton and Gauld (1976, 1978) have discussed the subject of family-group names, and I have followed their recommendations.

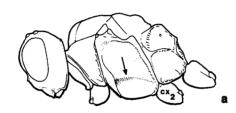
The major biological aspects (ectoparasitism and endoparasitism, idiobioncy, and koinobioncy), including the most striking differences in the biology of ichneumonids and braconids, were discussed in the introduction to Ichneumonoidea. Host preferences for the various subfamilies are given in the appropriate subfamily. Ichneumonids are parasitoids of immature holometabolous insects (Coleoptera, Diptera, Hymenoptera, Lepidoptera, Raphidioptera, Trichoptera) or Chelicerata (Araneae and Pseudoscorpionida eggs, adult Araneae). Symphyta and Lepidoptera are the most common hosts. Perhaps Gauld (1984a) provided the best overview of the biology of the various groups.

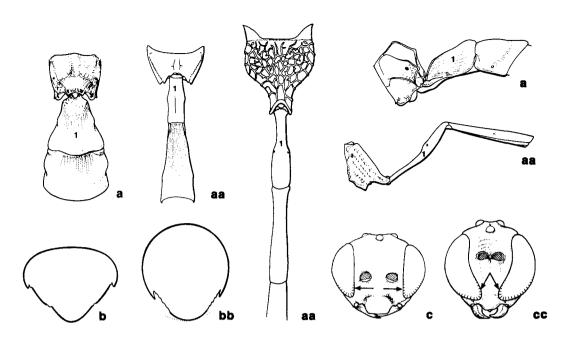
References Keys and descriptions for all genera were published in Townes (1969, 1970a, 1970b, 1971), except for Ichneumoninae (regional generic keys are listed under this subfamily). Revisionary work published since then is cited under each subfamily. Short (1978) gave a comprehensive treatment of ichneumonid larvae. Catalogs of species for various biogeographical regions are as follows: Nearctic, Carlson (1979); Indo-Australian, Townes, Townes, and Gupta (1961), Gupta (1987); eastern Palaearctic, Townes, Momoi, and Townes (1965); Neotropical, Townes and Townes (1966); Ethiopian, Townes and Townes (1973). Gauld (1984a) provided updated generic keys for Australia.

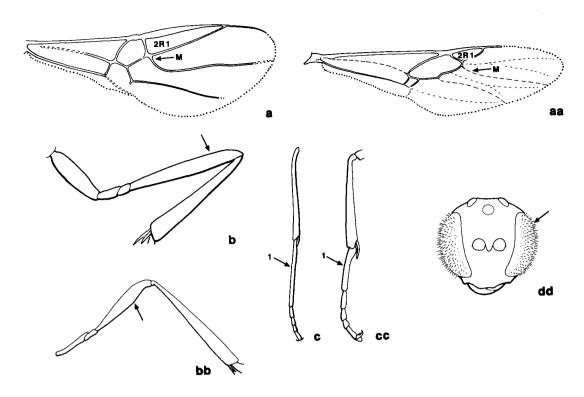
## Key to subfamilies of Holarctic and Neotropical ICHNEUMONIDAE

1	a.	Wings vestigial or absent
		(wing reduction or absence occurs in members of several subfamilies (Ichneumoninae,
		Orthocentrinae, Phygadeuontinae, Xoridinae), but the majority of such species belong to Gelis
		(Phygadeuontini); they are not keyed further).
	aa.	Wings normal



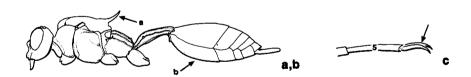




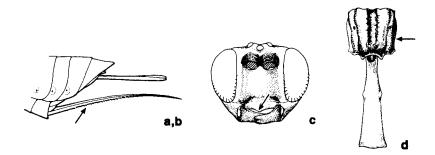


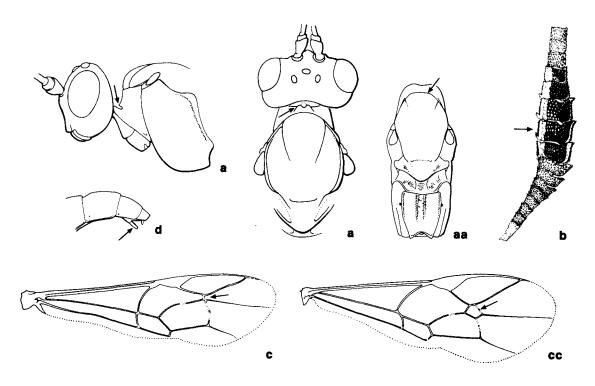
- 5(4) a. Fore wing with vein M tubular and pigmented, appearing to originate from cell 2R1.
  - b. Metafemur not expanded apically.
  - c. Fore leg with tarsomere 1 longer than total length of remaining tarsomeres.
  - d. Eye without distinct setae.

  - aa. Fore wing with vein M spectral, not originating from cell 2R1.
  - bb. Metafemur expanded subapically.
  - cc. Fore leg with tarsomere 1 about as long as total length of remaining tarsomeres.
  - dd. Eye with dense setae.
  - ee. Antenna with about 22 flagellomeres ..................... (Ophionellus) Anomaloninae (p. 433)

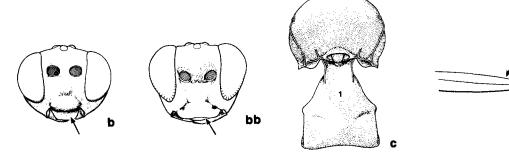


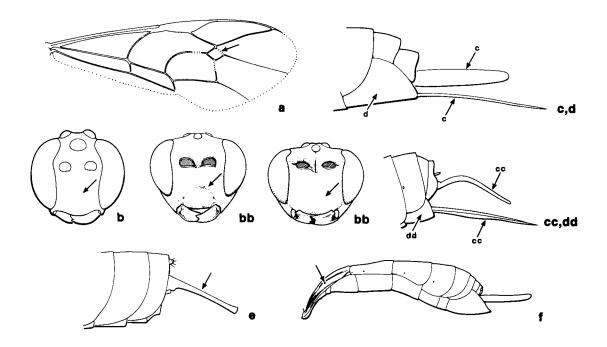
- a. Apex of scutellum with median spine about as long as scutellum.
  - b. Metasomal sterna 2-4 completely sclerotized and convex.
  - c. Metatarsal claws about half as long as tarsomere 5 ...... Agriotypinae (p. 432)
  - aa. Apex of scutellum without median spine or spine shorter than scutellum.
  - bb. Sterna 2–4 partly membranous or, if completely sclerotized, then flat.





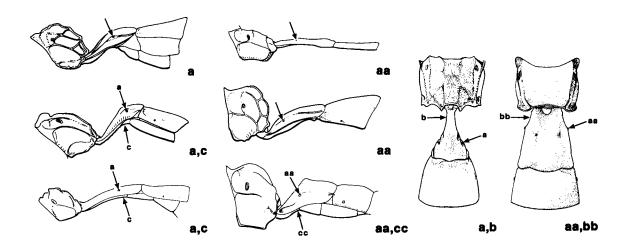
- - dd. Ovipositor sheath usually visible .....



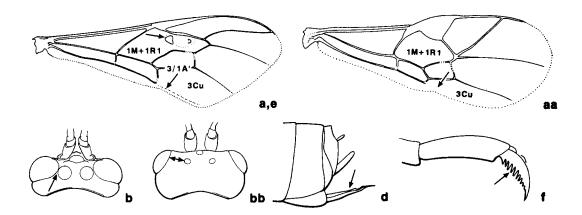


- a. Fore wing with areolet large and rhombic (diamond-shaped) (except in *Cidaphus*, which has eye swollen and ocelli enlarged).
  - b. Clypeus not separated from face by distinct groove, clypeus plus face forming wide and weakly convex surface.
  - c. Ovipositor long and needle-like, ovipositor sheath long and rigid.
  - d. Female hypopygium in lateral view large and triangular, not extending beyond metasomal apex.
  - e. Male genitalia with outer lobe (gonoforceps) produced into elongate process.

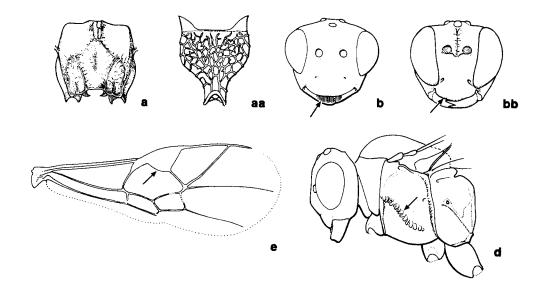
  - aa. Fore wing with areolet various but usually not rhombic.
  - bb. Clypeus usually separated from face by distinct groove; if groove absent then clypeus plus face usually forming strongly convex surface.
  - cc. Ovipositor almost always stouter, ovipositor sheath often curved.
  - dd. Female hypopygium various; if large and triangular then usually extending beyond metasomal apex.
  - ee. Male genitalia with outer lobe (gonoforceps) very rarely produced into elongate processes.



11(10)		Metasomal segment 1 with spiracle posterior to middle.  Metasomal segment 1 in dorsal view with anterior part usually slender, often cylindrical and widened apically.  Metasomal sternum 1 usually extending to or posterior to spiracle
,	<u> </u>	b d cc
12(11)	a. b. c. d. aa. bb. cc. dd.	Metasoma laterally compressed, segments 3 and 4 higher than wide, if indistinctly so either: Tarsal claws conspicuously comb-like or: Fore wing with areolet often petiolate when closed. Ovipositor almost always with dorsal subapical notch
• 17/	2m	2m-cu 2m-cu 2m-cu 2aa
13(12)	a. aa.	Fore wing with areolet open, the remaining vein apical to vein 2m-cu by more than two-fifths length of remaining vein



- 14(13) a. Fore wing cell 3Cu with adventitious vein 3/1A' present and parallel to wing margin.
  - b. Ocelli usually large, the lateral ocellus close to or contiguous with eye.
  - c. Body usually pale brownish-orange, rarely black.
  - d. Ovipositor short, barely extending beyond metasomal apex (with rare exceptions).
  - e. Fore wing with cell 1M+1R1 often with hairless area and sclerotized inclusions.
  - f. Tarsal claws usually densely comb-like ...... Ophioninae (p. 437)
  - aa. Fore wing cell 3Cu without adventitious vein 3/1A' or with only short one.
  - bb. Ocelli not enlarged, with lateral ocellus (oc) seperated from eye by at least half its diameter or more.



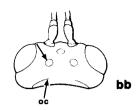
- 15(14) a. Propodeum with transverse and longitudinal carinae; propodeal sculpture not coarse and reticulate.
  - b. Apical margin of clypeus with fringe of long parallel setae.
  - c. Maxillary palpus with 4 segments; labial palpus with 3 segments.
  - d. Mesopleuron usually with long foveate groove.
  - e. Fore wing with stigma enlarged ...... some Tersilochinae (p. 441)
  - aa. Propodeum usually without carinae, at most with basal transverse carina; propodeal sculpture usually coarse and reticulate.
  - bb. Apical margin of clypeus without fringe of setae.
  - cc-ee. Not as above ...... (Anomalonini and Ophiopterus) Anomaloninae (p. 433)

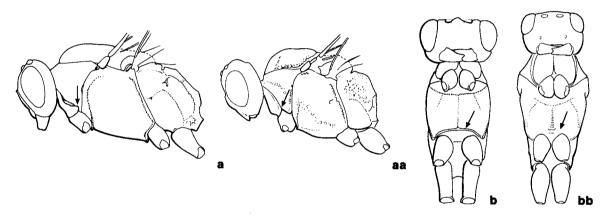
Names of specific carinae on propodeum are according to Townes (1969: 46).





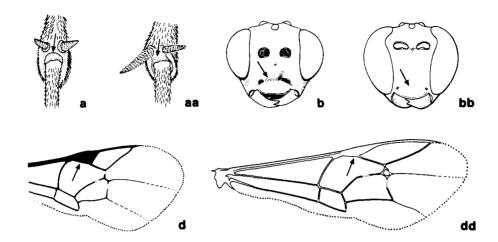




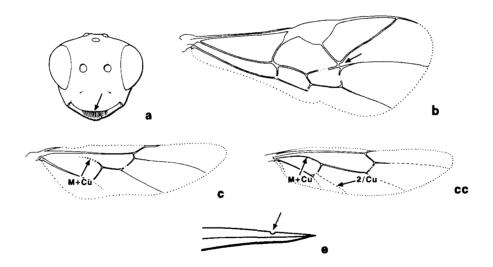


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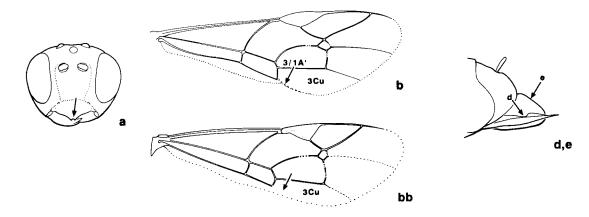
<sup>&</sup>lt;sup>1</sup> See note under couplet 15.



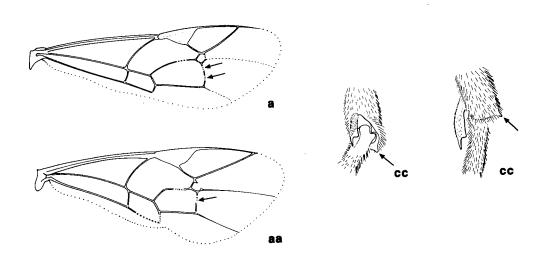
- a. Mesotibial and metatibial spurs separated by sclerotized bridge from respective tarsomere 1, the tibial apices thus with 2 membranous insertions.
  - b. Clypeus separated from face by groove.
  - c. Face usually more or less pale.
  - d. Fore wing with stigma often quite short and widely triangular ...... Cremastinae (p. 434)
  - aa. Mesotibia and metatibial spurs not separated by bridge from respective tarsomere 1, the tibial apices thus with 1 membranous insertion.
  - bb. Clypeus weakly or not separated from face (except some Chriodes).
  - cc. Face usually entirely black.

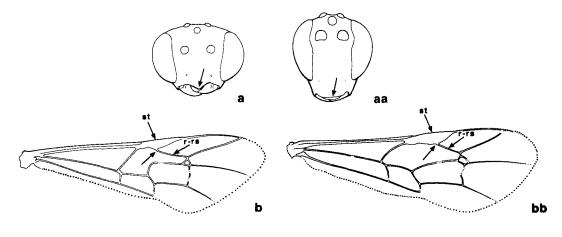


- 19(17) a. Apical margin of clypeus with fringe of long parallel setae.
  - b. Fore wing with areolet open.
  - c. Hind wing with basal three-fifths of vein M+Cu nebulous or absent; vein 2/Cu absent.
  - d. Maxillary palpus with 4 segments; labial palpus with 3 segments.
  - e. Ovipositor with dorsal subapical notch ..... most **Tersilochinae** (p. 441)
  - aa. Apical margin of clypeus with or without fringe of long parallel setae.
  - bb. Fore wing usually with areolet closed.
  - cc. Hind wing with vein M+Cu complete; vein 2/Cu present, at least as spectral vein.
  - dd. Maxillary palpus with 5 segments; labial palpus with 4 segments.

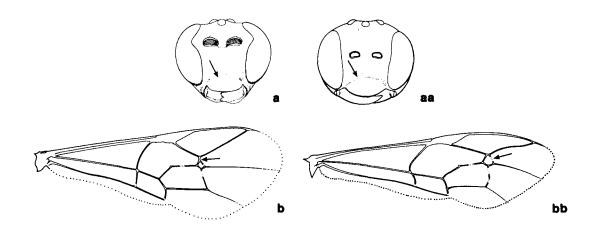


- 20(19) a. Apical margin of clypeus with 2 blunt median teeth.
  - b. Fore wing cell 3Cu with adventitious vein 3/A1' present parallel to wing margin (vein is nebulous and surrounded by brown pigmentation).
  - c. Propodeum with anterolateral corner overhanging propodeal spiracle.
  - d. Ovipositor with dorsal subapical notch.
  - e. Ovipositor sheath wide, flat, polished, and smooth ...... (Tatogaster) Tatogastrinae (p. 441)
  - aa. Apical margin of clypeus simple.
  - bb. Fore wing cell 3Cu without adventitious vein.
  - cc. Propodeum with anterolateral corner not developed.
  - dd. Ovipositor without dorsal subapical notch.

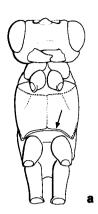


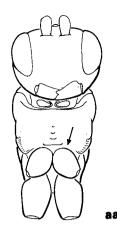


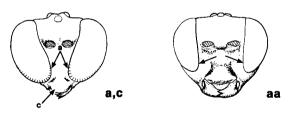
23(22)		Apical margin of clypeus with large median tooth.
	υ.	Fore wing with vein r-rs originating from base of stigma (st)
		Apical margin of clypeus without tooth.  Fore wing with vein r-rs originating from middle of stigma (st)
	00.	

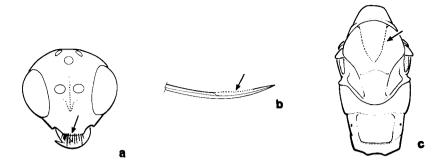


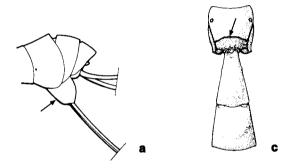
24(22)		Clypeus not separated from face by distinct groove and/or: Fore wing with areolet petiolate	25
	aa.	Clypeus separated from face by groove or: Fore wing with areolet closed or open, not petiolate	



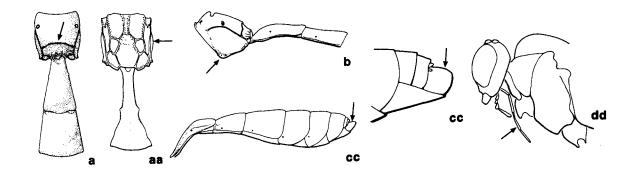








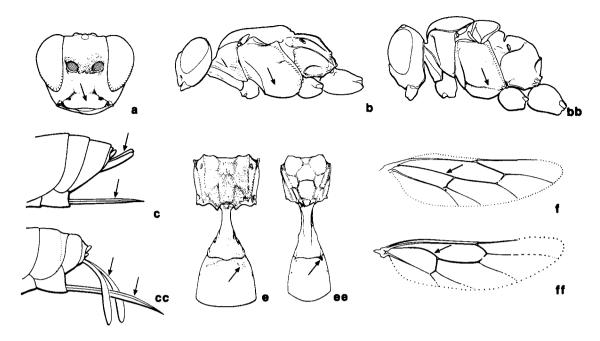
<sup>1</sup> See note under couplet 15.



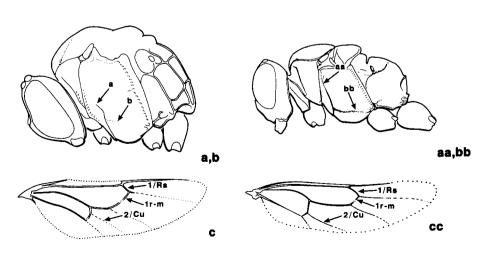
**30(29)** a. Propodeum without carinae or with only apical transverse carina.<sup>1</sup>

- b. Metapleuron with submetapleural carina widened anteriorly into flange.
- c. Ovipositor sheath narrow, tightly covering ovipositor.
- d. Maxillary palpus short, not reaching middle of mesopleuron ...... a few Banchinae (p. 433)
- aa. Propodeum with normal complement of carinae.
- bb. Metapleuron with submetapleural carina not widened anteriorly.
- cc. Ovipositor sheath much wider than ovipositor (similar to couplet Figs. 20d,e).

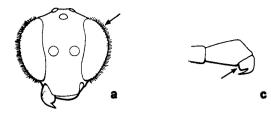
<sup>&</sup>lt;sup>1</sup> See note under couplet 15.

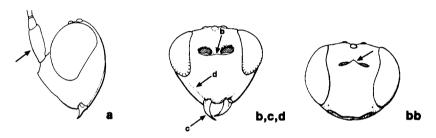


- a. Clypeus usually wide and flattened, the apical margin widely truncate or almost truncate and not or only weakly impressed.
  - b. Mesopleuron with sternaulus almost always short, less than half as long as mesopleuron, or absent.
  - c. Ovipositor almost never extending conspicuously beyond metasomal apex; sheath rigid.
  - d. Fore wing with areolet closed (except in Lusius and Epitomus).
  - e. Metasomal tergum 2 with thyridium usually well developed and usually with transverse gastrocoelus.
  - f. Hind wing with vein M+Cu almost always straight ...... Ichneumoninae (p. 435)
  - aa. Clypeus various, usually moderately to strongly convex, the apical margin usually convex and impressed.
  - bb. Mesopleuron usually with sternaulus at least half as long as mesopleuron and usually extending to mesocoxa.
  - cc. Ovipositor usually extending conspicuously posterior to metasomal apex; sheath flexible except when very short.
  - dd. Fore wing with areolet closed or open.
  - ee. Metasomal tergum 2 without gastrocoelus, the thyridium usually small or absent.



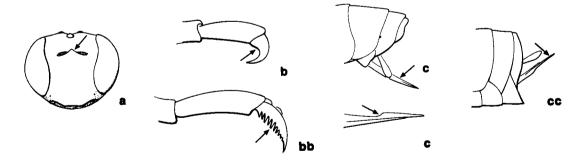
32(31)	a.	Mesopleuron with epicnemial carina far from anterior margin of mesopleuron; dorsal apex of
	b.	carina ventral to midpoint of posterior margin of pronotum and: Mesopleuron with sternaulus $0.2-0.5$ times as long as mesopleuron.
	c.	Hind wing with vein 2/Cu spectral and with vein 1/Rs often shorter than vein 1r-m
		(Brachycyrtini) Labeninae (p. 436)
		Mesopleuron with epicnemial carina at, or close to, anterior margin of mesopleuron; dorsal apex of carina dorsal to midpoint of posterior margin of pronotum or:
		Mesopleuron with sternaulus at least half as long as mesopleuron (usually extending to mesocoxa).
	cc.	Hind wing with vein 2/Cu usually pigmented (tubular or nebulous), rarely spectral or absent, and with vein 1/Rs as long as, or longer than, vein 1r-m
		most Phygadeuontinae (p. 439)
33(11)	) a.	Mesotibia with 1 apical spur
	aa.	Mesotibia with 2 apical spurs
34(33)	b.	Face with large, flat or concave shield-shaped area bordered by ridges. Face dorsally with projection between toruli
35(33)	a.	Clypeus not separated from face by groove and in lateral view forming almost continuous strongly to weakly convex bulge
	aa.	Clypeus separated from face by more or less distinct groove (groove may be weak medially but is present laterally) or, if groove rarely absent, then face rather flat





- 37(36) a. Scape in dorsal view 1.8-2.4 times as long as wide.
  - b. Face with dorsal margin simple, not produced as triangular process above or between toruli.
  - c. Mandible very slender and twisted apically.

  - aa. Scape in dorsal view 1.2-1.7 times as long as wide.
  - bb. Face usually with dorsal margin produced into triangular process extending between toruli or over ventral margins of toruli.



- a. Face with dorsal margin produced into triangular process, the process extending between toruli or over ventral margins of toruli (except *Apolophus* and *Macromalon* in which tarsal claws are simple).
  - b. Tarsal claws simple or comb-like.

aa. Face with dorsal margin simple, the margin not produced as triangular process between toruli. bb. Tarsal claws comb-like to apex. cc. Ovipositor tapering to needle-like point and without dorsal notch ...... ......(Rhorus) Ctenopelmatinae (p. 434) bb b CC a. Mandible with dorsal tooth wide, more or less distinctly divided into upper and lower points by weak notch or impression, and mandible thus apparently three-toothed. b. Tergum 1 rectangular in dorsal view and not distinctly narrowed anteriorly. c. Hind wing with vein 1/Cu about as long as vein cu-a. d. Ovipositor not extending beyond metasomal apex. e. Small species (fore wing about 3-8 mm long) with transverse head ..... ...... Diplazontinae (p. 435) aa. Mandible with dorsal tooth not divided, and thus with 1 or 2 teeth or, if dorsal tooth rarely more or less divided, then: Tergum 1 in dorsal view narrowed anteriorly and: cc. Hind wing with vein 1/Cu two-fifths as long as or less than vein cu-a (usually much less). a. Metasoma joined to propodeum distinctly above metacoxal cavity. b. Flagellum often slightly enlarged apically, circular in cross section ......

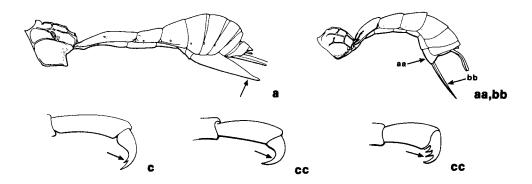
..... some Labeninae (p. 436)

bb. Flagellum not enlarged apically, sometimes tapering apically ....... 41

aa. Metasoma joined to propodeum between or just dorsal to metacoxal cavities.

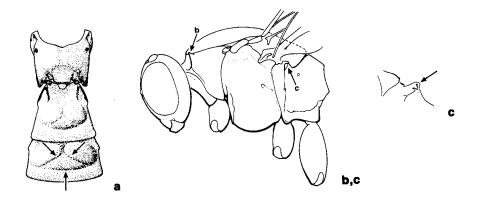
39(35)

40(39)



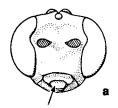
- a. Female hypopygium in lateral view very large and triangular, folded along midline, usually elongated and projecting beyond metasomal apex.
  - b. Ovipositor long and without dorsal subapical notch.

  - aa. Female hypopygium smaller and shorter, not conspicuously projecting beyond metasomal apex.
  - bb. Ovipositor various, sometimes with dorsal subapical notch.

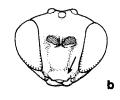


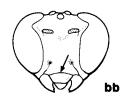
- a. Metasomal terga 2-5 in dorsal view with sharp grooves delimiting median triangular area; triangle apex pointing to anterior margin of tergum and:
  - b. Pronotum with epomia strong; dorsal apex of epomia projecting as tooth and:

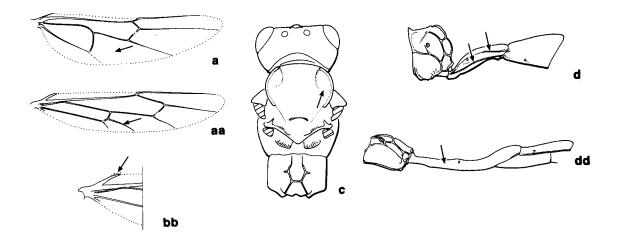
  - aa. Metasomal terga 2-5 in dorsal view smooth or with various impressions, sometimes with median pair of deep oblique grooves, or having a triangle with apex pointing to posterior margin of tergum.
  - bb. Pronotum with or without epomia, rarely with dorsal apex of epomia projecting as tooth.



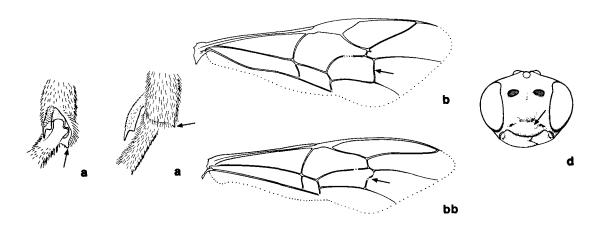


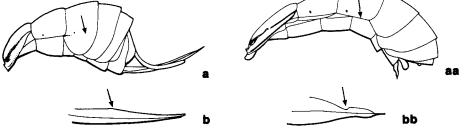






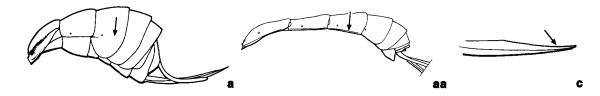
- 44(43) a. Hind wing without vein 2/Cu.
  - b. Hind wing with only 1 basal hamulus.
  - c. Mesoscutum with notaulus as figured.
  - d. Metasomal segment 1 in lateral view as figured; tergum and sternum separated by suture, the tergum with prominent longitudinal ridges.
  - e. Small species of normal habitus, fore wing 3-4 mm long ...... Orthopelmatinae (p. 438)
  - aa. Hind wing with vein 2/Cu.
  - bb. Hind wing with 5-6 basal hamuli.
  - cc. Mesoscutum without notaulus.
  - dd. Metasomal segment 1 in lateral view as figured; tergum and sternum fused with no trace of suture, the tergum without longitudinal ridges.
  - ee. Larger species of elongate habitus, fore wing 4-12 mm long .... (Grotea) Labeninae (p. 436)





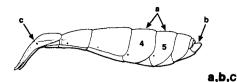
- **46(45)** a. Metasomal tergum 3 with laterotergite large and not separated by crease.

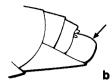
  - aa. Metasomal tergum 3 with laterotergite not especially large, separated by crease.
  - bb. Ovipositor barely or not extending beyond metasomal apex and with dorsal subapical notch (except species with needle-like ovipositor) ...................... most Ctenopelmatinae (p. 434)



- 47(45) a. Metasomal tergum 3 (and sometimes 2) with laterotergite large and not separated by crease and:
  - b. Fore wing vein 2m-cu with 1 bulla.
  - c. Ovipositor tapered to slender point and without dorsal subapical notch or ventral ridges.

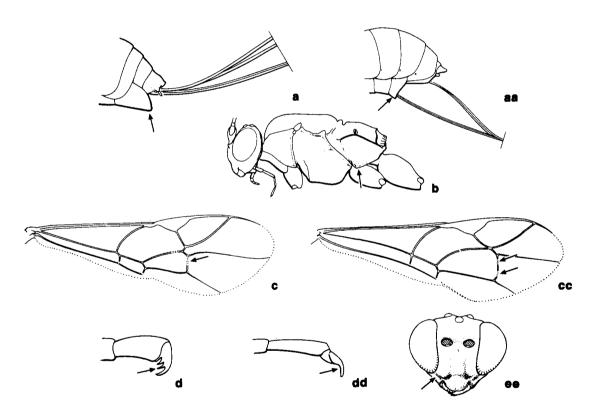
	bb. cc.	Metasomal tergum 3 with laterotergite large to vestigial, nearly always separated by crease.  Fore wing vein 2m-cu with 1 or 2 bullae.  Ovipositor often with dorsal subapical notch or ventral ridges.  Fore wing length various
48(47)	a.	Female
	aa.	Male (correct placement of males to subfamily for the following groups is difficult for the beginner; most males will key out to the correct subfamily, but using the subfamily diagnoses and cross-checking with the female key is recommended)
		а прина ва
		a aa
49(48)	a.	Ovipositor with dorsal subapical notch; ventral apical margin smooth or with very inconspicuous ridges (NOTE: ovipositor sheaths may have to be separated from ovipositor to see notch)
	aa.	Ovipositor without dorsal subapical notch or with weak notch surmounting raised dorsal apical node; ventral apical margin of ovipositor usually with conspicuous ridges or teeth
50(49)	a.	Metasomal terga 2-4 with submedian pair of deep oblique grooves
	aa.	





51(50) a. Metasomal sterna 4-5 completely sclerotized, forming evenly convex and shining surface.

- b. Metasomal apex as figured: hypopygium large, ovipositor sheath partly concealed and flattened; general appearance of metasomal apex compact and pointed in dorsal view.
- c. Metasomal segment 1 elongate; glymma absent; spiracle at or near middle of segment; sternum 1 long and extending beyond spiracle.
- d. Propodeum with basal transverse carina<sup>1</sup> complete ...... Oxytorinae (p. 438)
- aa. Metasomal sterna 4-5 partly membranous or folded along midline, or both.
- bb. Metasomal apex not as above: ovipositor sheath not as enlarged or concealed and general appearance less compact, with segments not as closely adhering.
- cc. Metasomal segment 1 not as above: glymma often present; spiracle usually near anterior of segment; sternum 1 shorter.



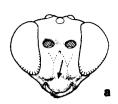
52(51) a. Female hypopygium enlarged and with median apical notch.

- b. Metapleuron with submetapleural carina widened anteriorly into flange.
- c. Fore wing vein 2m-cu usually with 1 bulla.
- d. Tarsal claws usually comb-like.
- e. Malar space without distinct subocular groove ...... 53

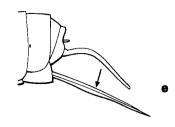
<sup>&</sup>lt;sup>1</sup> See note under couplet 15.

	aa. bb. cc. dd. ee.	Female hypopygium not enlarged and/or without median apical notch.  Metapleuron with submetapleural carina not widened anteriorly into flange.  Fore wing vein 2m-cu usually with 2 bullae.  Tarsal claws simple.  Malar space usually with distinct subocular groove
		a
53(52)	a.	Propodeum with median longitudinal carina¹ indistinct or absent
	aa.	Propodeum with median longitudinal carinae <sup>1</sup> sharp and distinct
	0	a a,b,d aa bb
54(52)		Clypeus convex basally, with remainder weakly concave, and with apical margin truncate. Face never strongly produced forward at level of toruli <b>and</b> :
	c.	Head with occipital carina complete.  Malar space length less than mandibular width at base and without distinct subocular groove.
	e. aa.	Body robust; metasoma well sclerotized
	bb. cc.	Face strongly produced forward at level of toruli and: Head with occipital carina incomplete medially. Malar space usually as long as or longer than mandibular width at base and usually with distinct subocular groove.
	ee.	Body delicate; metasoma weakly sclerotized and often collapsed in air-dried specimens some Orthocentrinae (p. 438)

<sup>&</sup>lt;sup>1</sup> See note under couplet 15.



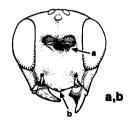


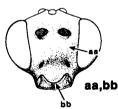


- **55(49)** a. Clypeus usually small and strongly convex, with apical margin usually convex.
  - b. Malar space usually as long as or longer than mandibular width at base and usually with distinct subocular groove.
  - c. Mandible small, thin, and blade-like.
  - d. Head in anterior view strongly tapering ventrally; eve prominent.
  - e. Ovipositor not as in Fig. 55e.
  - f. Body delicate; metasoma weakly sclerotized and often collapsed in air-dried specimens ..... some **Orthocentrinae** (p. 438)

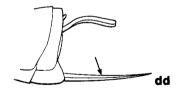


- **56(55)** a. Female hypopygium large and conspicuous in lateral view.
  - b. Ovipositor without ventral apical teeth ...... 57
  - aa. Female hypopygium smaller and inconspicuous.

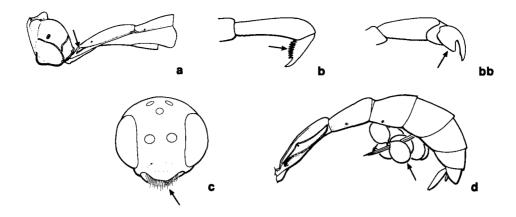




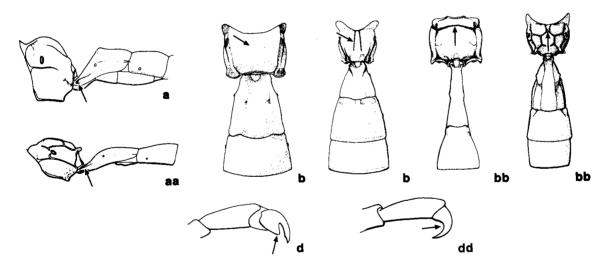




- 57(56) a. Clypeus and face forming wide and flat area, the face with prominent ridge ventral to toruli; head quadrate in anterior view.
  - b. Clypeus with median tooth on apical margin.
  - c. Malar space shorter than mandibular width at base and with distinct subocular groove.
  - d. Ovipositor less than half as long as metatibia ...... Microleptinae (p. 437)
  - aa. Clypeus and face not as above; head triangular in anterior view.
  - bb. Clypeus without median tooth on apical margin.
  - cc. Malar space shorter than mandibular width at base and without subocular groove.



- 58(56) a. Metasomal segment 1 with glymma, the glymmae sometimes deep and almost meeting at midline.
  - b. Tarsal claws usually comb-like (sometimes simple), without large basal tooth.
  - c. Clypeus often wide, the apical margin with fringe of long parallel setae and without median notch.
  - d. Eggs often found attached to ovipositor by stalk ...... most **Tryphoninae** (p. 442)
  - aa. Metasomal segment 1 often without glymma or, if glymmae present (many Pimplinae), then:
  - bb. Tarsal claws not comb-like but often with large basal tooth or lobe and:
  - cc. Clypeal margin without apical setae and usually with median notch.
  - dd. Eggs not found attached to ovipositor ...... 59

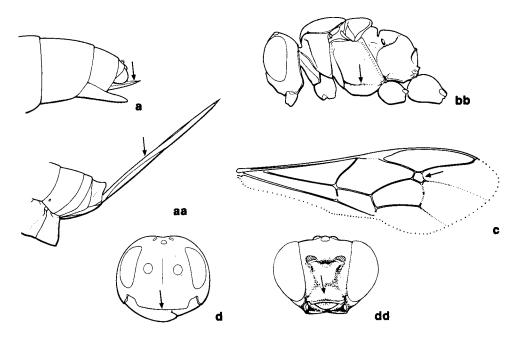


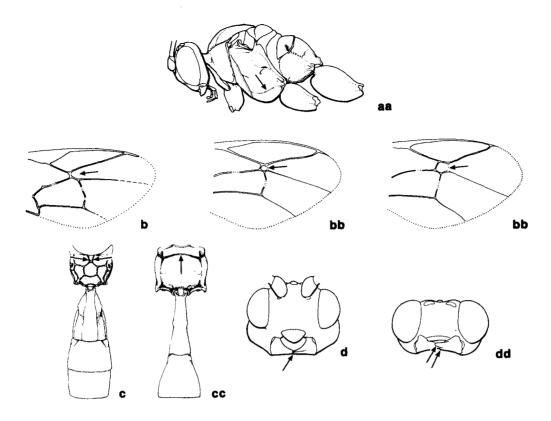
59(58) a. Metasomal segment 1 with glymma and/or:

- b. Propodeum without basal transverse carina, often with only trace of median longitudinal carinae.
- c. Clypeus with apical half often thin and apical margin with median notch (appearing bilobed).
- aa. Metasomal segment 1 without glymma and:
- bb. Propodeum with at least trace of basal transverse carina.1
- cc. Clypeus not as above.
- dd. Tarsal claws simple ...... **60**

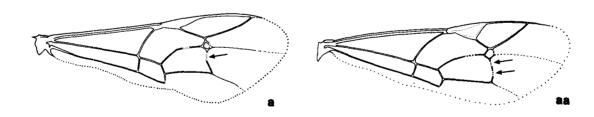
See note under couplet 15.

<sup>&</sup>lt;sup>2</sup> See comments under Pimplinae (p. 440) concerning division of this group.



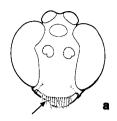


- 61(60) a. Mesopleuron with sternaulus indistinct or less than half as long as mesopleuron, or absent.
  - b. Fore wing with areolet open.
  - c. Propodeum with median longitudinal carinae; transverse carinae also usually present.
  - d. Mandible with 1 or 2 teeth ...... some **Xoridinae** (p. 442)
  - aa. Mesopleuron with sternaulus usually distinct and more than half as long as mesopleuron.
  - bb. Fore wing with areolet closed or open.
  - cc. Propodeal carinae various, often only with transverse carinae.
  - dd. Mandible with 2 teeth ...... some **Phygadeuontinae** (p. 439)



62(48)	a.	Fore wing with vein 2m-cu with 1 bulla	63
	aa.	Fore wing with vein 2m-cu with 2 bullae	70
63(62)	a.	Metasomal segment 1 with glymma	64
	aa.	Metasomal segment 1 without glymma	66

<sup>&</sup>lt;sup>1</sup> See note under couplet 15.



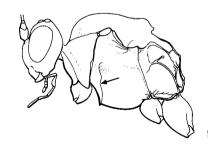
64(63)	b. с.	Clypeus with fringe of long parallel setae on apical margin.  Metapleuron with submetapleural carina not widened anteriorly into flange.  Propodeal carinae various.  Metasomal terga 2-4 without submedian pair of deep oblique grooves
		Clypeus without fringe of setae on apical margin.
		Metapleuron with submetapleural carina widened anteriorly into flange.
		Propodeal carinae various but often with only apical transverse carina. <sup>1</sup>
	aa.	Metasomal terga with or without submedian pair of deep grooves

a. Propodeum usually without median longitudinal carinae; if median longitudinal carinae present then:

aa. Propodeum with median longitudinal carinae<sup>1</sup> and:

bb. Metasomal terga 2-4 without grooves ..... (Notostilbops and Panteles) Stilbopinae (p. 441)





bD

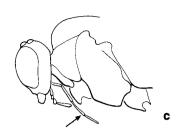
a. Gena with dorsal half having weak to strong minute denticles.

b. Mesopleuron without epicnemial carina.

See note under couplet 15.

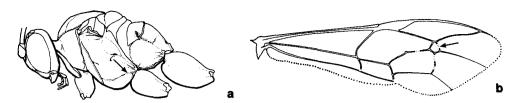
<sup>&</sup>lt;sup>2</sup> See comments under Pimplinae (p. 440).

	aa. bb.	Gena with dorsal half smooth.  Mesopleuron with epicnemial carina.
	cc.	Clypeus various
		a,b,c
67(66)		Clypeus and face forming wide and flat area, the face with prominent carina ventral to toruli.
		Clypeal margin with median tooth.  Malar space with subocular groove.
	d.	Fore wing with vein 1cu-a apical to vein 1/M by seven-tenths the latter's length.
		Fore wing with areolet open
	cc.	Malar space usually without subocular groove.
	dd,ee.	Not as above
		a c
68(67)	a. b. c. aa. bb. cc.	Mesopleuron with sternaulus extending to at least middle and usually reaching mesocoxa. Fore wing with areolet pentagonal when closed.  Propodeum with only transverse carinae

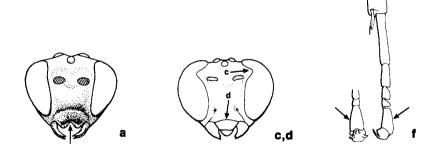


69(68)	a. b. c.	Propodeum with basal transverse carinae. <sup>1</sup> Propodeal spiracle elongate.  Maxillary palpus elongate, reaching middle of mesopleuron Oxytorinae (p. 438)
	aa. bb. cc.	Propodeum without basal transverse carina. <sup>1</sup> Propodeal spiracle round. Maxillary palpus shorter some <b>Orthocentrinae</b> (p. 438)
		aa
70(62)	a. b.	Tarsal claws comb-like, at least basally. Clypeus with apical margin simple and without median notch (not bilobed) or tooth 71
	aa. bb.	Tarsal claws simple. Clypeus with apical margin various, sometimes with median notch or tooth
71(70)		Clypeus with fringe of long parallel setae on apical margin or:  Propodeum without carinae and surface transversely striate.  Metasomal segment 1 with glymmae sometimes deep and meeting almost at midline most Tryphoninae (p. 442)
	aa. bb. cc.	Clypeus without fringe of setae on apical margin.  Propodeum with carinae reduced and usually with only apical transverse carina.  Metasomal segment 1 with glymmae but glymmae not deep and not meeting almost at midline

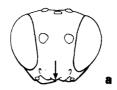
<sup>&</sup>lt;sup>1</sup> See note under couplet 15.



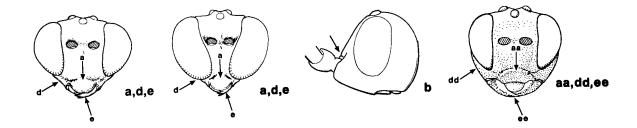
72(70)	b.	Mesopleuron with sternaulus long, the sternaulus usually extending to mesocoxa. Fore wing with areolet pentagonal if closed; vein 3r-m sometimes nebulous.  Metasomal segment 1 without glymma
		Mesopleuron with sternaulus short, less than one-third as long as mesopleuron, or sternaulus absent.
	bb. cc.	Fore wing with areolet closed or open, when closed pentagonal only in Ichneumoninae.  Metasomal segment 1 with or without glymma



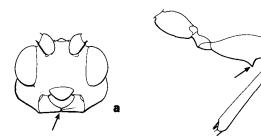
<sup>&</sup>lt;sup>2</sup> See comments under Pimplinae (p. 440) concerning the division of this group.

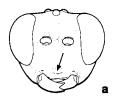


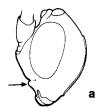
75(74)	a. aa.	Clypeus with median tooth on apical margin
		a,b aa,bb
-	\$	C CC
76(75)	a. b. c. aa. bb. cc.	Mesosoma strongly flattened. Genal width opposite mid-height of eye about 1.5 times as long as eye width. Fore wing with areolet open
		a,b c
		Tou-s e
77(75)	a. b. c. d. e.	Malar space as long as mandibular width at apex. Clypeus small and basally convex, with apex noticeably flattened. Head with junction of hypostomal and occipital carinae separated from base of mandible by about basal width of mandible; occipital carina obsolescent ventrally. Fore wing with vein 1cu-a apical to vein 1/M by about half length of vein 1cu-a. Propodeum with transverse carinae (Stilbops) Stilbopinae (p. 441)

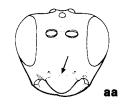


- 78(77) a. Clypeus usually small and strongly convex, with apical margin usually convex; if clypeus flat then:
  - b. Face strongly produced forward at level of toruli and:
  - c. Head with occipital carina medially incomplete.
  - d. Head in anterior view strongly tapering ventrally; eye prominent.
  - e. Mandible small, thin, and blade-like, with 2 teeth.
  - f. Usually small, delicate species (fore wing 2-5 mm long); metasoma weakly sclerotized and often collapsed in air-dried specimens ....................... some **Orthocentrinae** (p. 438)
  - aa. Clypeus flat or weakly convex, and:
  - bb. Face not strongly produced at level of toruli.
  - cc. Head with occipital carina complete.
  - dd. Head in anterior view oblong or only weakly tapering medially.
  - ee. Mandible robust, with 1 or 2 teeth.











80(79)

- a. Clypeus convex basally, with remainder weakly concave and with apical margin truncate.
- b. Flagellomeres 3 and 4 usually with deep semicircular notches.
- c. Hind wing with vein 1/Cu about as long as vein cu-a or longer . . . . . . . Cylloceriinae (p. 434)
- aa. Clypeus uniformly flattened and apical margin convex.
- bb. Flagellomeres 3 and 4 without notches.

## **Subfamily Acaenitinae**

(Fig. 154)

**Diagnosis** Medium to large (fore wing 5-20 mm long). Clypeus separated from face by a groove or not, with apex often appearing thick because of preapical ridge; labrum usually conspicuous and semicircular in appearance; sternaulus of mesopleuron absent; propodeum with variable number of carinae, with areola often present; protarsal and mesotarsal claws usually with accessory tooth near apex; metasomal segment 1 stout to slender, rather straight, usually without glymma, and with spiracle at or before middle; apical 0.3-0.5 of metasoma laterally compressed; female hypopygium very large, triangular in lateral view, the apex surpassing metasomal apex; ovipositor extending beyond metasomal apex and usually as long as metasoma, the dorsal subapical notch absent.

**Biology** Relatively few species have been reared; hosts are larvae in wood or woody tissues (Coleoptera and probably dubious records of Sesiidae (Lepidoptera) and Siricoidea). Speculation that they are endoparasitoids (Gauld 1984b; Wahl, 1986) has been confirmed by rearing one species as a koinobiont endoparasitoid of a weevil (Coleoptera: Curculionidae) (Shaw and Wahl 1989).

**Distribution** Worldwide, except South America; 24 genera.

#### **Subfamily Adelognathinae**

(Fig. 155)

**Diagnosis** Small (fore wing 2–4 mm long). Clypeus convex and separated from face by weak groove, the apical margin truncate; labrum exposed and conspicuous, with apical margin having median notch that varies from weak to strong; antenna with

12–13 flagellomeres; sternaulus of mesopleuron absent; propodeum varying from having at least transverse carina absent to lacking all carinae; fore wing with vein 3r-m weak or absent; metasomal segment 1 without glymma, with spiracle usually barely beyond middle but occasionally near apex; metasoma dorsoventrally compressed; ovipositor about as long as metasomal height at apex, the dorsal subapical notch absent.

**Biology** Solitary and gregarious idiobiont ectoparasitoids of Symphyta larvae.

Distribution Holarctic; one genus (Adelognathus).

#### **Subfamily Agriotypinae**

(Fig. 156)

**Diagnosis** Medium (fore wing about 5 mm long). Clypeus small and produced apically as long median tooth; mandible with upper tooth shorter than lower tooth; scutellum with long apical spine; tarsal claws long, weakly curved, and simple; sternaulus of mesopleuron extending to mesocoxa, though sometimes weak; propodeum without transverse carinae and with strong longitudinal carinae; metasomal segment 1 without glymma and with no trace of separation between tergum and sternum; tergum 2 of male partly fused with 3; tergum 2 and sternum 2 of female fused with tergum 3 and sternum 3, respectively; sterna 2–6 of both sexes completely sclerotized.

**Biology** Idiobiont ectoparasitoids of Trichoptera pupae and prepupae in streams.

**Distribution** Palaearctic; one genus (*Agriotypus*).

**Comments** Mason (1971) argued that *Agriotypus* does not belong in Ichneumonidae but is instead better placed in Proctotrupoidea; most ichneumonid and proctotrupoid workers do not

agree with this. Bill Mason himself (personal communication) later changed his views and agreed that they should be in the Ichneumonoidea, albeit as a separate family.

**References** Chao and Zhang (1981) keyed the six species described up to that time; one has been described since then.

**Subfamily Anomaloninae** (= Anomalinae of Townes; includes Theriinae of Dasch)

(Fig. 157)

**Diagnosis** Small to large (fore wing 2–25 mm long). Clypeus convex and often not separated from face by groove, the apical margin often with median point; lateral ocellus usually positioned close to occipital ridge; ventroposterior corner of propleuron with strongly produced lobe that touches or overlaps pronotum; sternaulus of mesopleuron absent; postpectal carina usually complete; mesosoma usually coarsely punctate; propodeum without regular carinae and usually coarsely reticulate, with apex projecting between metacoxae; fore wing with areolet open, with remaining vein (2/Rs) usually apical to vein 2m-cu but may sometimes be opposite or basal; metasomal segment 1 long and slender, without glymma, with no trace of tergal-sternal suture, and with spiracle near apex; metasoma strongly compressed laterally; ovipositor varying from about as long as height of metasomal apex to as long as metatibia, the dorsal subapical notch present.

**Biology** Koinobiont endoparasitoids of Lepidoptera or Coleoptera; oviposition is into larvae, with emergence always from the pupa; adults often found in drier habitats than usual for the family.

**Distribution** Worldwide; 38 genera.

Comments Townes (1971) subdivided the family into four tribes. Gauld (1976) found one of these was polyphyletic and recognized only two tribes, Anomalonini and Therionini (now known as Gravenhorstiini). These tribes, for no explicit reason, were raised by Dasch (1984) to subfamilies (Dasch's Theriinae should be Gravenhorstiinae). Because the subfamily as recognized by Townes and Gauld is a natural group defined by many autapomorphies, Dasch's division is not sound.

**Reference** Gauld (1976) gave generic diagnoses, with keys to world genera.

## **Subfamily Banchinae**

(Fig. 158)

**Diagnosis** Small to large (fore wing 3–16 mm long). Clypeus convex, nearly always separated from face by groove, the apical margin varying from rounded to sharp, thin, and evenly convex (sometimes with median notch); upper tooth of mandible sometimes subdivided; sternaulus of mesopleuron absent or short; anterior part of submetapleural carina usually produced as strong lobe; propodeum often only with posterior transverse carina present or carinae absent; metasomal segment 1 usually wide with spiracle before middle but sometimes slender, with spiracle near apex; glymma present or absent; terga 2-4 sometimes with conspicuous median pair of deep oblique grooves converging anteriorly and diverging posteriorly; female hypopygium large and triangular in lateral view, not extending beyond metasomal apex, the apex with median notch; ovipositor short to very long, with dorsal subapical notch.

**Biology** Koinobiont endoparasitoids of Lepidoptera larvae; Glyptini and Atrophini parasitize caterpillars in leaf rolls, tunnels, buds, and other concealed situations, whereas Banchini parasitize more exposed hosts (especially Noctuidae).

**Distribution** Worldwide; 53 genera.

**Comments** Lissonotini of Townes (1971) is now replaced by Atrophini (Gauld 1984*a*).

**Subfamily Campopleginae** (= Porizontinae of Townes)

(Fig. 159)

**Diagnosis** Small to large (fore wing 2–14 mm long). Clypeus usually not distinctly separated from face, the apical margin thin or blunt, sometimes with median tooth or angle; mandible often with ventral flange; ventroposterior corner of propleuron with strongly produced lobe touching or overlaping pronotum; mesotibial and metatibial spurs not separated from tarsomere 1 by sclerotized bridge; sternaulus of mesopleuron almost always absent or short, very rarely reaching mesocoxa; postpectal carina usually complete; propodeum usually with fairly complete set of carinae; fore wing with areolet closed or open; hind wing with vein 1/Rs varying from slightly longer to shorter than vein 1r-m; metasomal segment 1 usually long and slender, widened apically, with or without glymma, and with spiracle near apex; metasoma usually weakly to strongly compressed laterally, at least apically in females; ovipositor short to long, often upcurved, dorsal subapical notch almost always

present. Predominant color black or black and red; face rarely pale in Holarctic species.

**Biology** Koinobiont endoparasitoids mainly of Lepidoptera or Symphyta larvae; some parasitize Coleoptera larvae and a few parasitize Raphidiidae (Raphidioptera).

**Distribution** Worldwide; 65 genera.

**Comments** This is one of the most commonly encountered subfamilies, and its members are very abundant. Many of the genera, however, are poorly defined and therefore difficult to identify.

## **Subfamily Collyriinae**

(Fig. 160)

**Diagnosis** Medium (fore wing 5–7 mm long). Apex of clypeus subtruncate, with weak median tooth; sternaulus of mesopleuron absent; propodeum long, with transverse carinae usually missing; protarsal and mesotarsal claws with median tooth; fore wing with areolet open; metasomal segment 1 elongate and narrow, straight, without glymma, and with spiracle a little in front of middle; metasoma subcylindrical, with apical half weakly compressed laterally; ovipositor curved downward, tapered to slender apex, the apical half of ventral margin having row of small weak teeth, the dorsal subapical notch absent.

**Biology** Koinobiont endoparasitoids of *Cephus* (Cephidae); oviposition is into the host egg and emergence is from the mature host larva.

**Distribution** Holarctic (*Collyria coxator* (Villers) introduced to Nearctic); one genus.

#### **Subfamily Cremastinae**

(Fig. 161)

**Diagnosis** Small to medium (fore wing 3-14 mm long). Clypeus usually convex, separated from face by groove, the apical margin usually without projections; ventroposterior corner of propleuron with strongly produced lobe, the lobe touching or overlaping pronotum; sternaulus of mesopleuron short or absent; postpectal carina complete; mesotibial and metatibial spurs separated from tarsomere 1 by sclerotized bridge; propodeal carinae complete or almost so; fore wing with areolet often open, stigma often wide and triangular; vein 1/Rs of hind wing often much shorter than vein 1r-m; metasomal tergum 1 elongate, with glymma (if present) forming an elongate groove, and with spiracle near apex; metasoma strongly compressed laterally; ovipositor long, with apex sometimes slightly decurved or

sinuous, and with dorsal subapical notch; face usually pale.

**Biology** Koinobiont endoparasitoids of Lepidoptera and, less commonly, Coleoptera larvae in tunnels, leaf rolls, buds, galls, and other concealed situations.

Distribution Worldwide; 25 genera.

**Subfamily Ctenopelmatinae** (= Scolobatinae of Townes)

(Fig. 162)

Diagnosis Small to large (fore wing 2.9–22 mm long). Clypeus fairly flat, usually wide and short, usually separated from face by groove, the apical margin often blunt or rounded; mandible long and weakly narrowed; apex of protibia with tooth on dorsal margin; sternaulus of mesopleuron absent or short; metasomal segment 1 slender to very stout, with or without glymma, and with spiracle before or at middle; metasoma usually cylindrical or dorsoventrally depressed, sometimes laterally compressed; ovipositor barely extending beyond metasomal apex, the dorsal subapical notch present except when ovipositor needle-like.

**Biology** Koinobiont endoparasitoids of Symphyta and, rarely, Lepidoptera; oviposition is into the egg or larva, with emergence after the host cocoon is spun.

**Distribution** Worldwide, most species in Holarctic region; 95 genera.

# **Subfamily Cylloceriinae**

(Fig. 163)

**Diagnosis** Small to medium (fore wing 4–8 mm long). Clypeus separated from face by groove and convex basally, the remainder weakly concave and the apical margin simple and almost truncate; mandible stout and with 2 teeth; male flagellomeres 3–4 simple or with deep semicircular notches; sternaulus of mesopleuron absent; postpectal carina completely absent; fore wing with areolet open; metasomal segment 1 with glymma, and with spiracle before middle; ovipositor about twice as long as metatibia and upcurved, and with dorsal subapical notch.

**Biology** Cylloceria has been recorded as a koinobiont endoparasitoid of Tipulidae (Diptera) (Wahl 1986, 1990).

**Distribution** Holarctic and Neotropical; two genera.

**Comments** Townes (1945) placed the two genera *Allomacrus* and *Cylloceria* in his Microleptinae. They were later removed to a separate subfamily (Wahl 1990).

## **Subfamily Diacritinae**

**Diagnosis** Medium (fore wing 5.0-8.5 mm long). Clypeus weakly convex or almost flat, with apical margin narrowly impressed and subtruncate; dorsal half of gena without denticles; ventral part of epomia not sharp and not on raised ridge close to and more or less in parallel with, anterior pronotal margin; epicnemial carina of mesopleuron present; sternaulus of mesopleuron short or absent; mesoscutum smooth, with notauli long and strong; propodeum with carinae absent except for apical transverse carina; metasomal segment 1 elongate and narrow (3-4 times as long as apical width), without glymma; metasoma cylindrical or dorsoventrally compressed; female with metasomal tergum 8 not elongate; ovipositor varying from about 0.7 times as long as metasoma to about twice as long; dorsal subapical notch absent.

Biology Unknown

**Distribution** Holarctic; two genera.

## **Subfamily Diplazontinae**

(Fig. 164)

**Diagnosis** Small to medium (fore wing 2.8–8 mm long). Clypeus small and separated from face by groove, the apical margin usually concave and notched; upper tooth of mandible wide and notched so that mandible appears 3-toothed; male antenna often with tyloids; sternaulus of mesopleuron short or absent; metasomal segment 1 short, wide at base and only slightly to moderately wider at apex, the glymma small and shallow, and the spiracle in front of middle; metasoma dorsoventrally depressed or in some females with apex laterally compressed; ovipositor short, not or barely extending beyond metasomal apex; dorsal notch present at about middle.

**Biology** Koinobiont endoparasitoids of Syrphidae (Diptera); oviposition is into the egg or larva and emergence is from the puparium.

**Distribution** Worldwide; most species in Holarctic region; 19 genera.

**References** Fitton and Rotheray (1982) keyed the European genera and discussed problems with generic definitions.

## **Subfamily Eucerotinae**

(Fig. 165)

Diagnosis Small to medium (fore wing 4–11 mm long). Clypeus usually without distinct groove separating it from face, the apical margin blunt; occipital carina reaching base of mandible without joining hypostomal carina; antenna (especially in males) widened and flattened medially; apex of protibia rarely with tooth on dorsal margin; pronotum mediodorsally with bifurcate raised flange or process; sternaulus of mesopleuron absent; fore wing with areolet open; metasomal segment 1 wide and short, with glymma small and with spiracle before middle; metasoma dorsoventrally depressed; ovipositor short and usually inconspicious, without dorsal subapical notch.

**Biology** Hyperparasitoids of Ichneumonoidea; eggs are laid on leaf surfaces, and the first instar larva attaches itself to a passing Lepidoptera or Symphyta larva and enters the body of an emerging primary endoparasitoid, such as a campoplegine or banchine or an attached ectoparasitoid.

**Distribution** Worldwide; most species in cool temperate areas; one genus (*Euceros*).

Comments Townes has variously placed this genus in Tryphoninae and Ctenopelmatinae. Studies of adult and larval morphology, and the biology, have led most workers to place it in its own subfamily.

**Reference** Barron (1976, 1978) revised the world fauna.

#### Subfamily Ichneumoninae

(Fig. 166)

**Diagnosis** Small to large (fore wing 2.2–21 mm long). Clypeus usually wide and flat and separated from face by weak groove, the apex widely truncate; mandible usually long and slender, with lower tooth (when present) usually much reduced; ventroposterior corner of propleuron without strongly produced lobe; sternaulus of mesopleuron usually short or absent, very rarely reaching mesocoxa; postpectal carina incomplete; propodeal carinae usually complete; fore wing with areolet pentagonal or subtriangular, almost always closed; hind wing with vein M+Cu almost always straight; metasomal segment 1 slender anteriorly, widened posteriorly, without glymma, and with spiracle near apex; tergum 2 usually with deep gastrocoeli; metasoma dorsoventrally depressed; ovipositor short, without dorsal subapical notch and with sheath rigid.

**Biology** Endoparasitoids of Lepidoptera; oviposition is into larvae (koinobionts) or pupae (idiobionts); emergence is always from the pupa. Females search on foot for hosts in shrubs and leaf litter. Many species are sexually dichromatic.

**Distribution** Worldwide; 373 genera.

Comments This is the second largest subfamily and one of the easiest to recognize, although it is sometimes confused with Phygadeuontinae. The distinctive clypeus, short sternaulus, straight M+Cu of hind wing, and deep gastrocoeli are good recognition attributes to separate it from Phygadeuontinae. Perkins and some other European authors have treated the Palaearctic genus Alomya and its relatives as a separate subfamily, Alomyinae. Both larval morphology and consideration of closely related genera such as Pseudalomya and Megalomya unequivocally show Alomya to be related to Phaeogenes and its related genera.

References Heinrich (1961–1962) keyed the Nearctic genera (excluding Alomyini). Heinrich (1977) keyed most of the Nearctic genera described since then. Townes and his collaborators cataloged and keyed the genera of other biogeographic regions. Gauld (1984a) treated the Australian genera. Heinrich (1967–1969) keyed the Ethiopian genera. Perkins's (1959) treatment of western Palaearctic Alomyini (= Phaeogenini) allows identification of most Nearctic genera.

#### **Subfamily Labeninae** (= Labiinae of Townes)

(Fig. 167)

**Diagnosis** Small to large (fore wing 3–25 mm long). Clypeus separated from face by groove, the apical margin without teeth; labrum sometimes prominently exposed; antenna often apically enlarged; apex of protibia sometimes with tooth on dorsal margin; sternaulus of mesopleuron short or absent; propodeal spiracle usually elongate; metasomal insertion on propodeum usually distinctly above metacoxal insertions; metasomal segment 1 short to elongate, sometimes very slender, with spiracle varying in position from before to far behind middle; metasoma usually dorsoventrally depressed; female hypopygium not enlarged; ovipositor short to very long, without dorsal subapical notch.

**Biology** Many species are idiobiont ectoparasitoids of Coleoptera larvae in plant tissue; some may parasitize other hosts in similar situations. Groteini parasitize solitary bees, eating both the larva(e) and pollen stores; Brachycyrtini parasitize cocoons of Chrysopidae (Neuroptera) and Araneae egg sacs. *Poecilocrypus* species are phytophagous, feeding on gall tissues.

**Distribution** Worldwide, with most diversity in the Southern Hemisphere; 14 genera.

**Reference** Gauld (1983) discussed phylogenetic relationships of the genera, tribal classification, biogeography, and other topics.

## **Subfamily Lycorininae**

(Fig. 168)

**Diagnosis** Small to medium (fore wing 3–7 mm long). Clypeus small, separated from face by groove, the apical margin sharp and without teeth; malar space with subocular groove; sternaulus of mesopleuron absent or short; dorsolateral corner of propodeum projecting anteriorly and engaging small hook on metanotum; fore wing with areolet open and with vein 2/Rs longer than sections of vein M between veins 2/Rs and 2m-cu; hind wing with vein 1/Rs longer than vein 1r-m; metasomal segment 1 wide, with glymma, and with spiracle in front of middle; terga 2-4 each with median triangular area surrounded by strongly impressed grooves and with apex of triangular area pointing to tergal base; female hypopygium large and triangular, centrally membranous but without median apical notch; ovipositor long, without dorsal subapical notch, and with apex having strong node.

**Biology** Parasitoids of small Lepidoptera larvae in leaf rolls; probably endoparasitic.

**Distribution** Worldwide; about 30 species in one genus (*Lycorina*—see Gauld 1984a).

## **Subfamily Mesochorinae**

(Fig. 169)

Diagnosis Small to large (fore wing 2–14 mm long). Clypeus usually not separated from face by groove, the apical margin evenly convex and without teeth; sternaulus of mesopleuron short or absent; fore wing with areolet large and usually rhombic (diamond-shaped); metasomal segment 1 slender, with glymma large and deep, and with spiracle near or behind middle; female metasoma usually somewhat laterally compressed; female hypopygium large and triangular in lateral view, not or barely extending beyond metasomal apex, and folded on midline; ovipositor needle-like, without dorsal subapical notch; gonoforceps of male genitalia extended into long and narrow rod.

**Biology** Almost all are koinobiont hyperparasitoids of ectoparasitic or endoparasitic Ichneumonoidea, and, less frequently, of Tachinidae (Diptera). One record exists of a mesochorine reared as a primary endoparasitoid of Lepidoptera.

**Distribution** Worldwide; 10 genera.

**Reference** Dasch (1974) described three new genera in his revision of the Neotropical fauna.

## **Subfamily Metopiinae**

(Fig. 170)

**Diagnosis** Small to large (fore wing 3–11 mm long). Clypeus not separated from face by groove, both forming an evenly convex surface except in *Metopius*, where face has a flat or concave shield-shaped area bounded by ridges; dorsal margin of face produced into triangular process extending between or over toruli (except *Ischyrocnemis*); sternaulus of mesopleuron absent or short; division between trochantellus and femur of front and middle legs often obsolete or absent; metasomal segment 1 short and stout to long and subpetiolate, usually with glymma, and with spiracle before middle (except Bremiella, Ischyrocnemis, and some *Periope*); ovipositor short, not extending beyond metasomal apex, and sometimes with weak dorsal notch some distance from apex.

**Biology** Koinobiont endoparasitoids of Lepidoptera, usually those in leaf rolls or folds; oviposition is into the larva; emergence is from the pupa.

**Distribution** Worldwide; 26 genera.

## **Subfamily Microleptinae**

(Fig. 171)

**Diagnosis** Small (fore wing 4.0–4.8 mm long). Clypeus wide and short, almost flat; face fairly flat, forming transverse ridge below toruli; mandible long and stout, fairly wide at apex; malar space with subocular groove; male antenna with tyloids; sternaulus of mesopleuron short or absent; transverse carina of propodeum medially incomplete; fore wing with areolet open; metasomal tergum 1 without glymma and with spiracle just before middle; apex of metatibia with dense setal fringe on posterior margin; metasoma dorsoventrally depressed; ovipositor not extending beyond metasomal apex, the dorsal subapical notch absent.

**Biology** Endoparasitoids of Stratiomyidae (Diptera) (Wahl 1986); probably koinobionts.

**Distribution** Holarctic; one genus (*Microleptes*).

**Comments** Townes (1945) placed *Microleptes* with genera that are now in Orthocentrinae. On the basis of adult and larval characters, Wahl (1986) removed it to a subfamily of its own. Gauld (1991) placed the subfamily in the Pimpliformes subfamily

group by mistake (I. Gauld, personal communication); see Wahl (1986, 1990) for larval evidence that it does not belong there.

## **Subfamily Neorhacodinae**

(Fig. 172)

**Diagnosis** Small (fore wing about 2 mm long). Clypeus apically convex, margin truncate; mesosoma stout; sternaulus of mesopleuron absent or short; metapleuron without pit below pleural carina; propodeum with transverse carina absent; fore wing without areolet (veins 2/Rs and 3r-m absent), with 2nd-4th abcissae of vein M appearing to begin at cell 2R1, and with vein 2m-cu spectral; metasomal tergum 1 stout but narrowed anteriorly, with glymma present but weak; metasoma dorsoventrally depressed; ovipositor 0.4-1.3 times as long as metatibia, dorsal subapical notch absent.

**Biology** Probably endoparasitic; reared from nests of *Spilomena* (Pemphredonidae).

**Distribution** Ethiopian, Holarctic, and Neotropical; two genera.

**Comments** Townes (1969) originally placed the two genera as a tribe in the Banchinae but later (1970b) put them in a separate subfamily on the basis of adult, larval, and biological characters.

## **Subfamily Ophioninae**

(Fig. 173)

**Diagnosis** Medium to large (fore wing 6-29 mm long). Clypeus separated from face by distinct groove, the apical margin never with teeth; ocelli always large, with lateral ocelli separated from eyes by less than their diameter; antenna long and slender, often with more than 55 flagellomeres; ventroposterior corner of propleuron without strongly produced lobe; postpectal carina complete or interrupted; fore wing with areolet open, with vein 3r-m apical to vein 2m-cu, with cell 3Cu with adventitious vein originating at apical end of vein 2/1A and paralleling wing margin, and with compound cell 1M+1R1 often with hairless area and sclerotized inclusions; metasomal segment 1 long, without glymma, without trace of tergal-sternal suture, and with spiracle near apex; metasoma strongly compressed laterally; ovipositor short, equal to metasomal height at apex, the dorsal subapical notch present. Body usually pale yellowish or brownish.

**Biology** Koinobiont endoparasitoids of Lepidoptera; one species parasitizes Scarabaeidae (Coleoptera).

**Distribution** Worldwide; 32 genera.

**Comments** Ophionines are often confused with other large, pale nocturnal ichneumonids (e.g., *Netelia* of the Tryphoninae). The latter usually have a complete areolet in the fore wing; metasomal tergum 1 has a prominent glymma and the spiracle near or before the middle.

**Reference** Gauld (1985) revised the genera of the world.

**Subfamily Orthocentrinae** (includes part of Microleptinae of Townes and part of Oxytorinae of Fitton and Gauld 1976)

(Fig. 174)

**Diagnosis** Small to medium (fore wing 2-9 mm long). Clypeus usually small and strongly convex, sometimes forming large and strongly convex area with the face (groove between clypeus and face absent in this case); mandible usually slender, thin and blade-like; head in anterior view usually strongly triangular; malar space often long and with subocular groove; male antenna often with concave tyloids; sternaulus of mesopleuron absent or short; hind wing often without vein 2/Cu; metasomal segment 1 stout to slender, with spiracle usually near or in front of middle, and with or without glymma; ovipositor very short to extending beyond metasomal apex by up to 3.5 times length of metatibia, the dorsal subapical notch present or absent.

**Biology** Mycetophilidae and Sciaridae (Diptera) have been recorded as hosts; all are presumably koinobiont endoparasitoids.

**Distribution** Worldwide; 28 genera.

Comments Townes's original concept of Microleptinae (Townes 1971) has been modified considerably. *Microleptes* was placed in its own subfamily on the basis of larval morphology (Wahl 1986). Further study led to the removal of *Tatogaster*, *Oxytorus*, *Allomacrus*, and *Cylloceria*; the remaining genera were combined with Orthocentrinae (Wahl 1990). Explanation of these changes are given in the aforementioned paper.

#### **Subfamily Orthopelmatinae**

(Fig. 175)

**Diagnosis** Small (fore wing 3–4 mm long). Clypeus small and weakly convex, separated from face by groove, the apical margin concave and exposing semicircular labrum; male antenna without tyloids; sternaulus of mesopleuron absent or short; fore wing with areolet open; hind wing without vein 2/Cu; metasomal segment 1 cylindrical and decurved, with tergum 1 as long as sternum 1,

without glymma, and with spiracle near base; metasoma dorsoventrally depressed; laterotergites of terga 2-7 narrow; ovipositor 0.3-1.6 times as long as metatibia, the dorsal subapical notch absent.

**Biology** Endoparasitoids in galls of Cynipidae on *Rubus* and *Rosa*.

**Distribution** Holarctic; one genus (*Orthopelma*).

## **Subfamily Oxytorinae**

(Fig. 176)

**Diagnosis** Small to medium (fore wing 4-7 mm long). Clypeus large, separated from face by groove, apically with pronounced transverse depression; mandible long and stout with 2 apical teeth; maxillary palpus elongate, with apex reaching middle of mesopleuron; sternaulus of mesopleuron absent; fore wing with areolet open or closed; metasomal segment 1 elongate and narrow, with prominent longitudinal carinae, without glymma, and with spiracle at or beyond middle; female hypopygium large and folded on midline, not projecting beyond metasomal apex and partly concealing ovipositor sheaths; metasomal sterna 4−5 completely sclerotized, forming evenly convex and shining surface; apical third of female metasoma laterally compressed; ovipositor about as long as metasomal height at apex, the dorsal subapical notch present; ovipositor sheaths wide and almost flat.

Biology Unknown.

Distribution Holarctic; one genus (Oxytorus).

Comments Townes (1971) placed this genus in his Microleptinae. Wahl (1990) removed it to a separate subfamily. Fitton and Gauld (1976) applied the subfamily name to Microleptinae sensu Townes, as Townes's usage was incorrect according to the *International Code of Zoological Nomenclature*.

#### **Subfamily Paxylommatinae**

(Fig. 177)

Diagnosis Small (fore wing 2-3 mm long). Clypeus small, elongate, and strongly convex; anterior tentorial pits large and prominent; head in anterior view strongly tapered ventrally; mandible small and usually obscured by prominent maxilla; antenna with about 11 flagellomeres; mesosoma short and high; sternaulus of mesopleuron absent; tarsomere 1 of fore leg about twice as long as tarsomeres 2-4; coxae long and slender; propodeum usually with only median longitudinal carina present; fore wing without areolet (veins 2/Rs and 3r-m absent), with second to fourth

abcissae of vein M appearing to originate from cell 2R1; hind wing with vein 1r-m opposite separation of veins R1 and Rs; metasomal segment 1 cylindrical, with tergum 1 and sternum 1 of equal length, without glymma, and with spiracle at middle; ovipositor about as long as metasomal height at apex, without dorsal subapical notch.

**Biology** Observations of flight activity and some rearing records strongly suggest that paxylommatines are endoparasitoids of Formicidae. Donisthorpe and Wilkinson (1930) gave an excellent summary of what is known of the group's biology.

**Distribution** Holarctic; one genus (*Hybrizon*).

## **Subfamily Phrudinae**

(Fig. 178)

**Diagnosis** Small to large (fore wing 2–26 mm long). Clypeus large and transverse, weakly to strongly separated from face by groove, the apical margin thick and usually with fringe of long parallel setae; sternaulus of mesopleuron absent or short; apex of protibia sometimes with tooth on dorsal margin; propodeum with carinae and areola usually complete or sometimes almost absent; fore wing with areolet open or closed; stigma large and triangular; hind wing with vein 1/Rs varying from as long as to shorter than vein 1r-m, and vein 2/Cu present (at least as spectral vein) or absent; metasomal tergum 1 with or without glymma and with spiracle usually at or before middle, the female metasoma slightly compressed laterally; laterotergites of terga 3-6 (and often tergum 2) not separated from median tergites by crease; ovipositor length short to as long as metatibia, without dorsal subapical notch.

**Biology** Very little is known; two genera have been reared as endoparasitoids of Coleoptera larvae.

**Distribution** Worldwide; 12 genera.

**Comments** This is probably not a natural group. Although some are superficially similar to Tersilochinae, phrudines (or the various elements therein) are almost certainly not related to that subfamily. The five-segmented maxillary palpi, anterior position of the spiracle of metasomal segment 1, and lack of a dorsal subapical notch on the ovipositor help to differentiate phrudines from tersilochines. They are rarely encountered.

**Subfamily Phygadeuontinae** (= Gelinae of Townes, Cryptinae of authors)

(Fig. 179)

**Diagnosis** Small to large (fore wing 2-27 mm long). Clypeus usually convex, separated from face by groove, with apical margin usually evenly convex and often with median lobe or teeth; male antenna usually with tyloids; ventroposterior corner of propleuron without strongly produced lobe; sternaulus of mesopleuron usually long and reaching mesocoxa; propodeum with carinae variable, from complete to having only transverse carinae present, and often with posterolateral projections well developed; fore wing with areolet pentagonal when closed; hind wing with vein M+Cu often arched; metasomal segment 1 usually long with some posterior widening, without glymma, and with spiracle usually behind middle; metasoma usually dorsoventrally depressed; ovipositor short to long, without dorsal subapical notch; ovipositor sheaths flexible.

**Biology** Most are idiobiont ectoparasitoids of Holometabola pupae or prepupae; Hedycryptina, Phygadeuontina, and Stilpnina have some endoparasitic species, and a few may be koinobionts. Some species parasitize the egg sacs of Araneae and Pseudoscorpionida. Many can develop as secondary parasitoids.

Distribution Worldwide; 379 genera.

Comments This is the largest subfamily. The characters described in the key distinguish it from Ichneumoninae or brachycyrtine Labeninae, the only subfamilies with which it might normally be mistaken. The traditional name until about 30 years ago was Cryptinae. This name is not available. Townes used Gelinae, based on the oldest generic name, but this practice is not in keeping with the International Code of Zoological Nomenclature.

# **Subfamily Pimplinae** (= Ephialtinae of Townes)

(Fig. 180)

**Diagnosis** Small to large (fore wing 3–28 mm long). Clypeus separated from face by groove, usually with apical half thin and apical margin with median notch (giving a bilobed appearance); dorsal half of gena without denticles; ventral part of epomia not sharp and on raised ridge close to and or more or less parallel with anterior pronotal margin; mesoscutum smooth, with notauli variable; epicnemial carina of mesopleuron present; sternaulus of mesopleuron short or absent; propodeum often with carina reduced, with few or no areas delimited; metasomal segment 1 usually short and wide, usually with glymma, and with spiracle before middle; metasoma cylindrical or

dorsoventrally flattened; metasomal terga 2-4 sometimes with surface impressions and swellings; ovipositor short to very long, without dorsal subapical notch, the apex of ventral valve often with ridges or teeth.

**Biology** Most are idiobiont ectoparasitoids of larvae and pupae of Holometabola. Hosts are generally injected with venom at oviposition and killed or paralyzed. Species of Pimplini are often endoparasitoids of Lepidoptera prepupae and pupae. *Tromatobia* and related genera parasitize egg sacs and adults of Araneae, a trend that culminates in the koinobiont Polysphinctini, which parasitize Araneae exclusively.

**Distribution** Worldwide; 64 genera.

Comments Gauld (1991) divided the Pimplinae sensu Townes into several subfamilies, based upon Eggleton (1989). Rhyssini, Diacritini, and Poemeniini were elevated to subfamily status. In additon, *Pseudorhyssa* was transferred from Delomeristini to Poemeniinae. I was unable to incorporate Gauld's changes into the subfamily key but a key to Pimplinae and related subfamilies that come out at couplets 59, 66, and 74 is provided here:

1	a.	Mesoscutum covered with sharp transverse wrinkles
	aa.	Mesoscutum without transverse wrinkles
2(1)	a.	Metasomal segment 1 with sharp lateral longitudinal carina extending from spiracle to posterior margin.
	b.	Female with posterior apex of tergum 8 not ending in heavily polished rim or truncate horn
	aa.	Metasomal segment 1 without distinct lateral longitudinal carina extending from spiracle to posterior margin.
	bb.	Female with posterior apex of tergum 8 ending in heavily polished rim or truncate horn
3(1)	a.	Epicnemial carina absent and:
,	b.	•
	c.	Epomia with ventral part sharp and on raised ridge close to or more or less in parallel with anterior pronotal margin
	aa.	Epicnemial carina almost always present and:
	bb. cc.	Gena with dorsal half not having minute denticles and:  Epomia not on ridge as described in statement c
4(3)	a.	Metasomal segment 1 long and narrow, 3-4 times as long as wide, and without glymma.
	b. с.	Clypeus weakly convex or almost flat, with apical margin narrowly impressed and subtruncate.  Apical tarsomere of all legs not enlarged
	aa.	Metasomal segment 1 variable in shape, but usually short and rectangular in dorsal view, and
	bb.	with glymma.  Clypeus usually with apical half thin, with apical margin having median notch (appearing bilobed).
	cc.	Apical tarsomere of all legs sometimes enlarged

# **Subfamily Poemeniinae**

**Diagnosis** Small to large (fore wing 4–19 mm long). Clypeus variable, from large and evenly convex to small, quadrate, and flattened; gena with dorsal half usually with weak to strong, minute denticles; epomia with ventral part sharp and on raised ridge close to and or more or less in parallel with, anterior pronotal margin; mesoscutum varying from being covered with sharp transverse wrinkles to smooth, with notauli often prominent; epicnemial carina usually absent; sternaulus of mesopleuron short or absent; propodeum usually without carinae; metasomal segment 1 elongate

(about twice as long as apical width), without glymma, and with spiracle at or before middle; metasoma cylindrical or dorsoventrally flattened; female with metasomal tergum 8 elongate but not ending in polished rim or truncate horn; ovipositor as long as metasoma or longer, without dorsal subapical notch.

**Biology** All are believed to be ectoparasitoids (likely idiobionts) of Holometabola in wood. Although Coleoptera species probably represent the majority of hosts, species of *Poemenia* usually seem to parasitize Aculeata nesting in wood, in abandoned plant galls, and other concealed

locations. One species has also been reared from a species of Tortricidae (Lepidoptera) in pine cones.

**Distribution** Worldwide, except Ethiopian; 10 genera.

## **Subfamily Rhyssinae**

**Diagnosis** Medium to large (fore wing 6-30 mmlong). Clypeus small, subrectangular, its apical margin with median tubercle and/or lateral tubercles; gena without denticles on dorsal half; epomia with ventral part not sharp and on raised ridge close to, and more or less in parallel with, anterior pronotal margin; mesoscutum with irregular sharp transverse wrinkles; epicnemial carina of mesopleuron present except in some species of *Epirhyssa*: sternaulus of mesopleuron short or absent; propodeum without carinae; metasomal segment 1 usually short and wide, with or without glymma, and with spiracle at or before middle; metasoma cylindrical or dorsoventrally flattened; female with tergum 8 elongate and ending in polished rim or truncate horn; ovipositor as long as metasoma or longer, without dorsal subapical notch.

**Biology** Idiobiont ectoparasitoids of wood-boring Symphyta and Coleoptera.

**Distribution** Worldwide; eight genera.

## **Subfamily Stilbopinae**

(Fig. 181)

**Diagnosis** Small (fore wing 4-5 mm long). Clypeus convex (in Stilbops with apical half flattened) and separated from face by groove, the apical margin without teeth; sternaulus of mesopleuron absent or short; metapleuron without pit below pleural ridge; propodeum with carinae usually complete; fore wing with areolet closed or open and with vein cu-a apical to vein 1/M by 0.3-0.5 times length of 1cu-a; metasomal segment 1 short and wide, with glymma, and with spiracle at or before middle; metasoma dorsoventrally flattened; female hypopygium large and triangular in lateral view, not extending beyond metasomal apex; apex of hypopygium without median notch; ovipositor varying from about as long as height of metasoma at apex (sharply tapering and dorsal subapical notch absent) to about as long as metasoma (not tapering and dorsal subapical notch present).

**Biology** Species of *Panteles* and *Stilbops* are endoparasitoids of Incurvariidae (Lepidoptera); oviposition is into the host egg, and adult emergence is from the host cocoon.

**Distribution** Holarctic and Chile; three genera.

Comments Townes (in Townes and Townes 1951) originally placed *Stilbops* and *Panteles* as a tribe in Tryphoninae but later (Townes 1970b) transferred them to the Banchinae and described *Notostilbops* from Chile. *Notostilbops* and *Stilbops* were later placed in a separate subfamily, Stilbopinae (Townes and Townes 1978) leaving *Panteles* in Banchinae. Wahl (1988) transferred *Panteles* to the Stilbopinae.

## **Subfamily Tatogastrinae**

(Fig. 182)

**Diagnosis** Medium (fore wing about 6 mm long). Clypeus large, separated from face by groove, the clypeal apex with median pair of small blunt teeth; sternaulus of mesopleuron short; apex of protibia with tooth on dorsal margin; propodeum long with unbroken profile, with anterolateral corners of propodeum elevated as low crests that overhang spiracles; fore wing with areolet triangular and sessile, and with cell 3Cu with weak adventitious vein originating at apical end of vein 2/1A and paralleling wing margin; metasomal segment 1 long, without glymma, without trace of tergal-sternal suture, and with spiracle at anterior 0.6 of segment; metasoma strongly compressed laterally; ovipositor about as long as metasomal height at apex, with dorsal subapical notch; ovipositor sheath wide and flat.

Biology Unknown.

**Distribution** Argentina and Chile; one species, *Tatogaster nigra* (Townes).

**Comments** Townes (1971) placed the genus in his Microleptinae. It was later removed to its own subfamily (Wahl 1990).

### **Subfamily Tersilochinae**

(Fig. 183)

**Diagnosis** Small to medium (fore wing 2–10 mm long). Clypeus wide, separated from face by groove, the apical margin with fringe of long parallel setae; section of hypostomal carina between foramen and intersection with occipital carina usually absent; ventroposterior corner of propleuron without strongly produced lobe; sternaulus of mesopleuron absent but foveate groove superficially like sternaulus usually present, extending from about midheight of mesopleuron to metacoxa; postpectal carina incomplete; fore wing with areolet open and 2/Rs very short; stigma large and triangular; hind wing with 0.6 of vein M+Cu often spectral or absent, with vein 1/Rs shorter than vein 1r-m, and with vein 2/Cu absent; metasomal segment 1 slender, with or without glymma, and with spiracle near apex; metasoma laterally compressed;

laterotergites of terga 2-4 wide and not separated from median tergites by crease; ovipositor slightly to strongly upcurved, short to very long, with dorsal subapical notch.

**Biology** Most are endoparasitoids of Coleoptera larvae, although Symphyta larvae are recorded as hosts of one genus. Because Curculionidae and Chrysomelidae (Coleoptera) often serve as hosts, the subfamily is of interest for biological control purposes. All are koinobionts.

**Distribution** Worldwide; 18 genera.

## **Subfamily Tryphoninae**

(Fig. 184)

**Diagnosis** Small to large (fore wing 3–23 mm long). Clypeus convex and often large, separated from face by groove, the apical margin with fringe of long parallel setae and often blunt; sternaulus of mesopleuron absent or short; tarsal claws usually pectinate; propodeum sometimes with carinae reduced or absent and with transverse striations; fore wing with areolet usually closed; metasomal segment 1 stout to slender, with glymma usually present and large, and with spiracle usually at or before middle; metasoma usually dorsoventrally flattened (laterally compressed in *Netelia*); ovipositor usually short, not longer than metasomal height at apex, without dorsal subapical notch; ovipositor often with attached eggs.

**Biology** Most species are ectoparasitoids of Symphyta larvae, but members of some genera

(including the very speciose *Netelia*) are ectoparasitoids of Lepidoptera larvae. The egg is attached to the host's cuticle by means of a plug or anchor. All are koinobionts.

**Distribution** Worldwide, but most species Holarctic; 51 genera.

## **Subfamily Xoridinae**

(Fig. 185)

Diagnosis Small to large (fore wing 3–25 mm long). Clypeus separated from face by groove and usually with strong transverse ridge and flattened apical area; mandible short, with 1 or 2 teeth; frons sometimes with crest between toruli; sternaulus of mesopleuron absent or short; ventral margin of metatibia sometimes with prominent tooth; fore wing with areolet open and with vein 2/Rs shorter than sections of vein M between veins 2/Rs and 2m-cu; metasomal segment 1 large and stout, without glymma, and with spiracle at or before middle; metasoma cylindrical or dorsoventrally flattened; ovipositor at least as long as metatibia and frequently longer, and without dorsal subapical notch.

**Biology** Idiobiont ectoparasitoids of wood-boring Coleoptera and Symphyta. Most parasitize larvae, but pupae and pre-eclosion adults may be used.

**Distribution** Worldwide; four genera.

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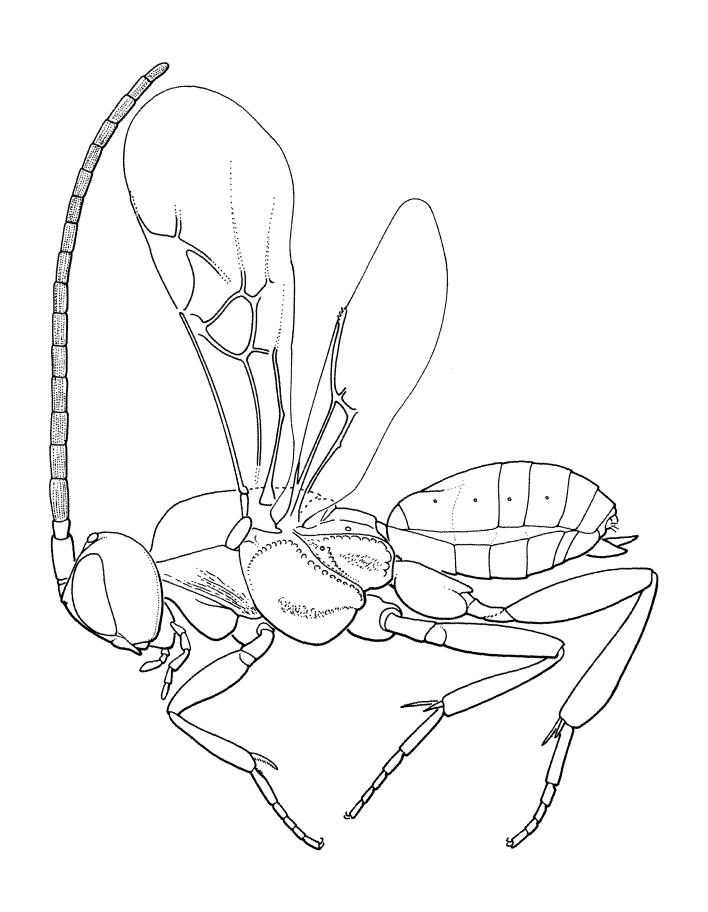


Fig. 125. Braconidae: Adeliinae

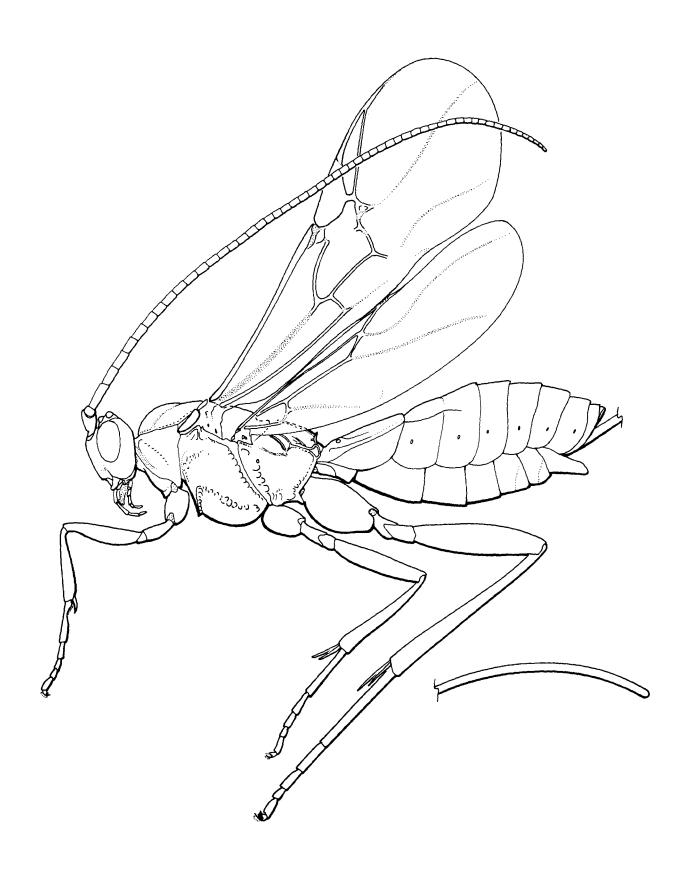


Fig. 126. Braconidae: Agathidinae

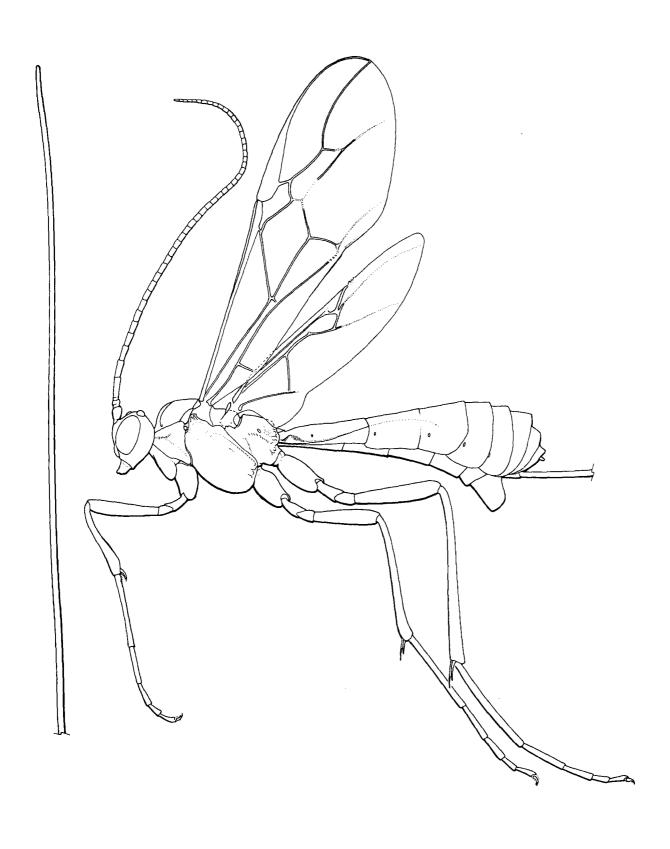


Fig. 127. Braconidae: Amicrocentrinae

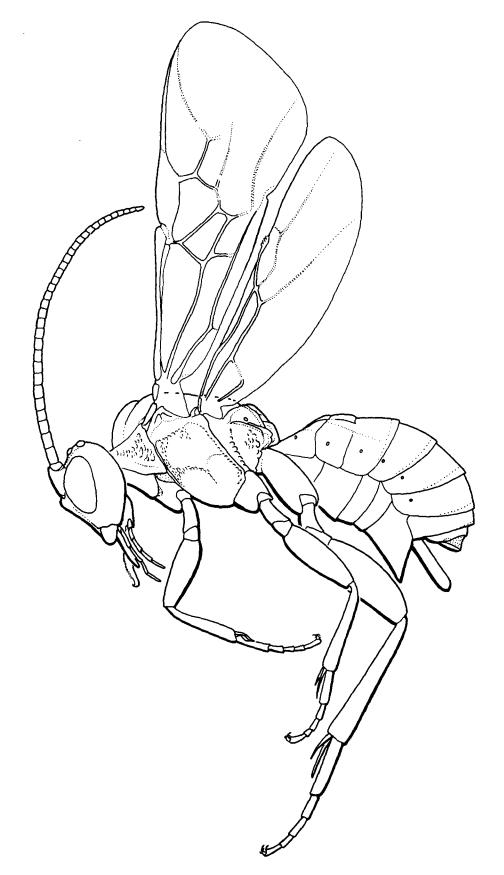


Fig. 128. Braconidae: Cardiochilinae

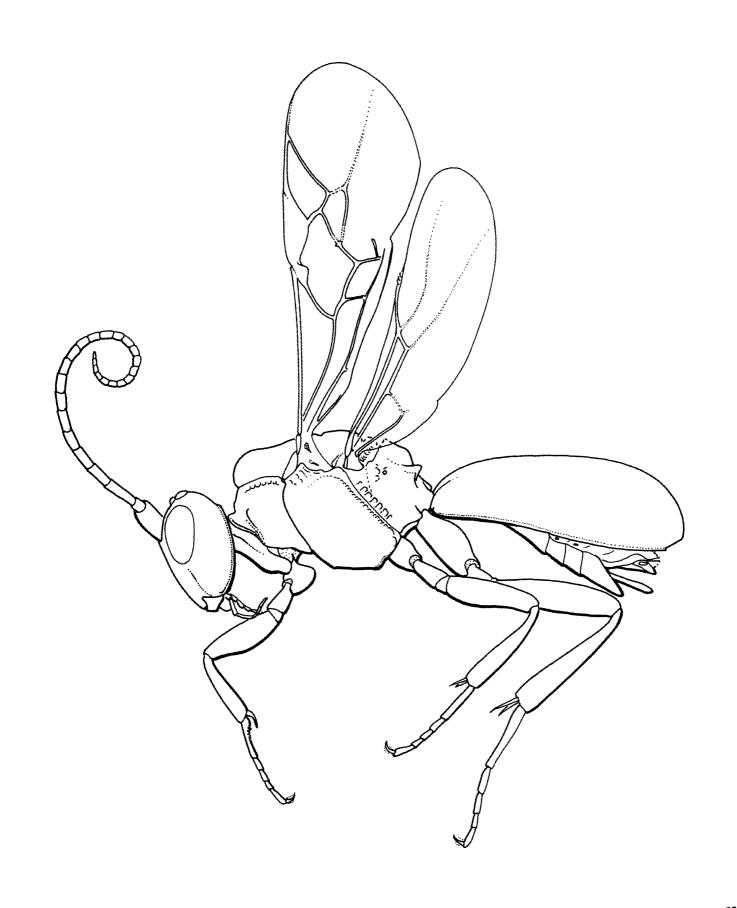


Fig. 129. Braconidae: Cheloninae

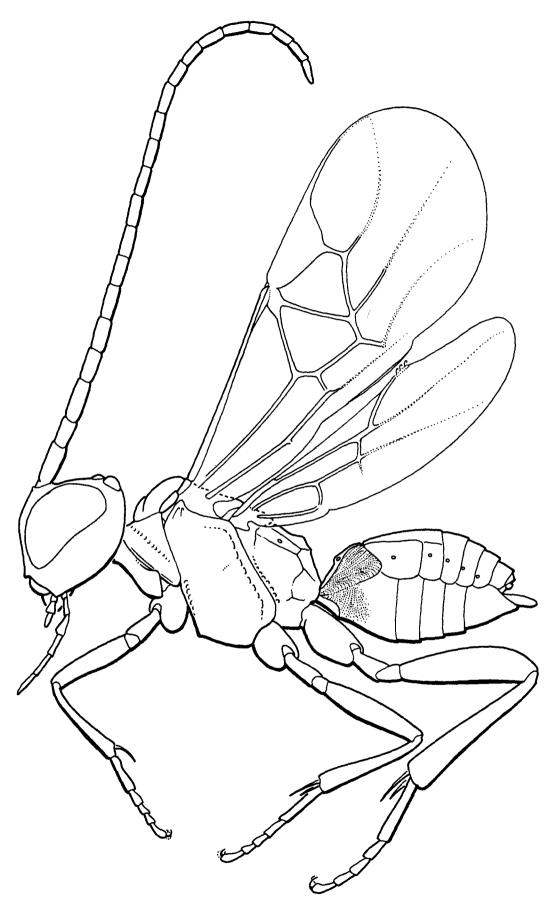


Fig. 130. Braconidae: Dirrhopinae

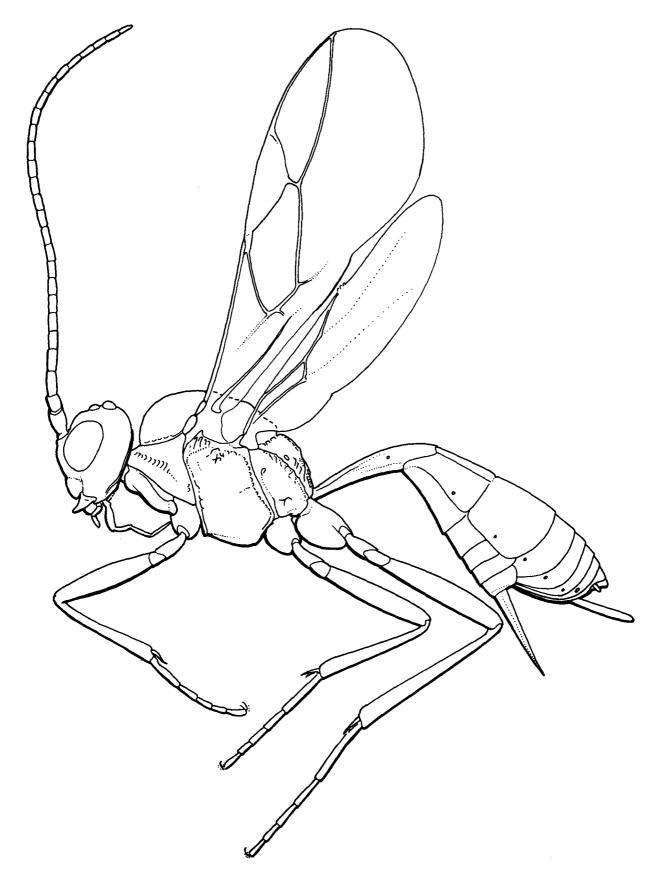


Fig. 131. Braconidae: Euphorinae

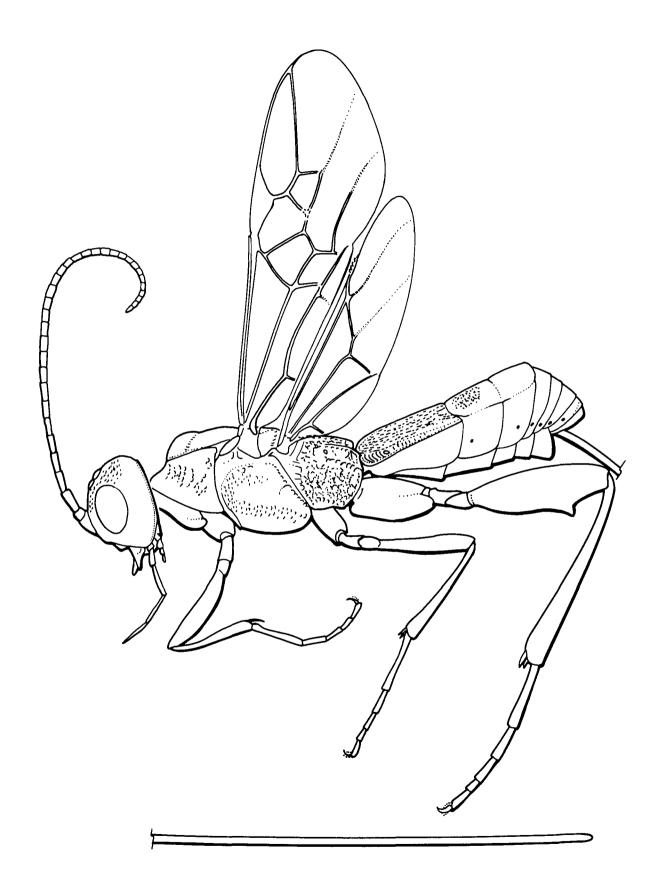


Fig. 132. Braconidae: Helconinae

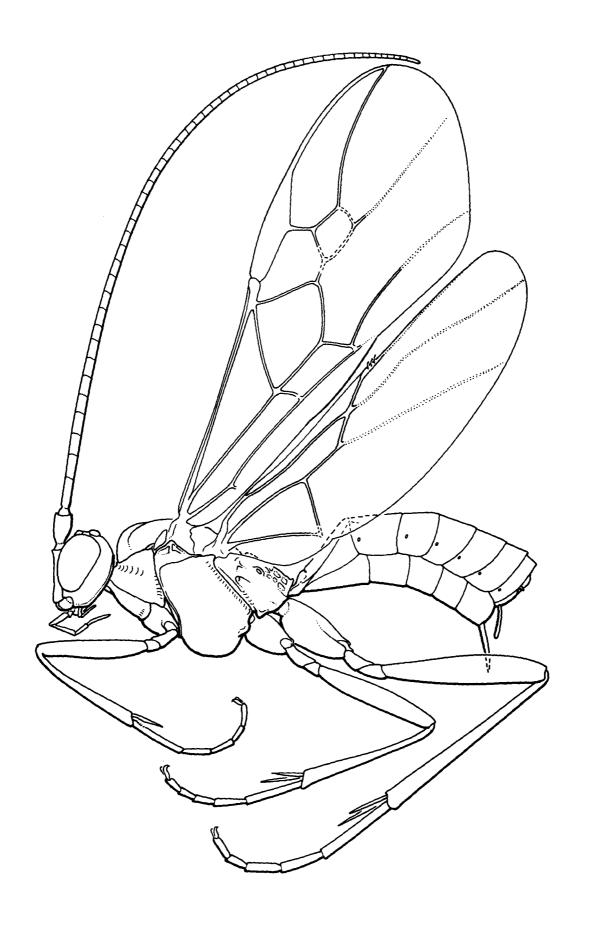


Fig. 133. Braconidae: Homolobinae

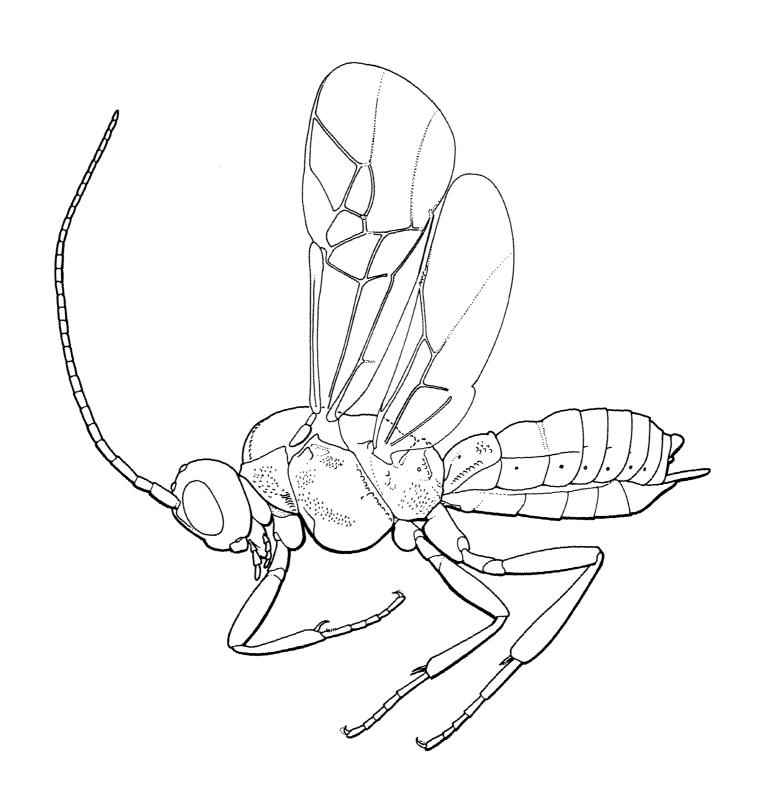


Fig. 134. Braconidae: Ichneutinae

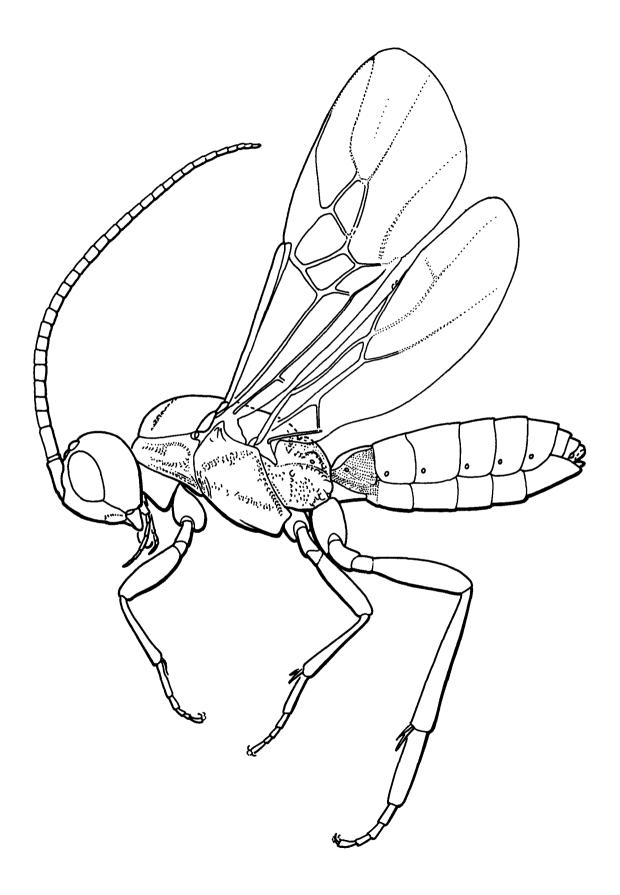


Fig. 135. Braconidae: Khoikhoiinae

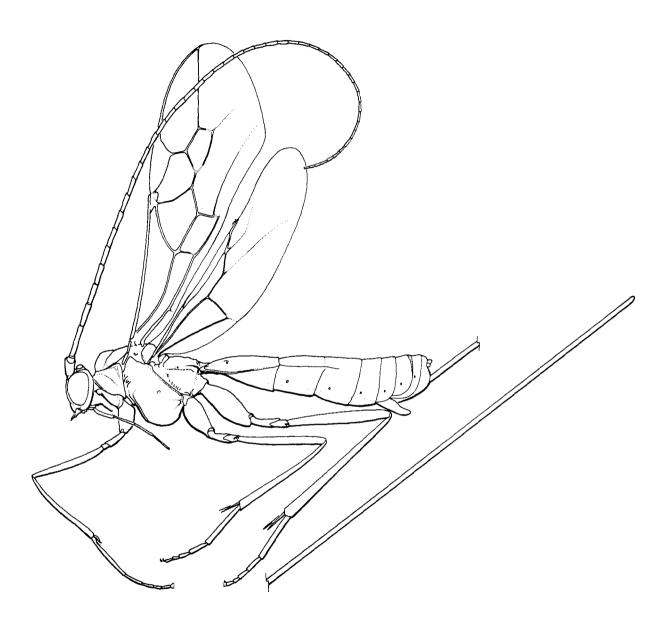


Fig. 136. Braconidae: Macrocentrinae

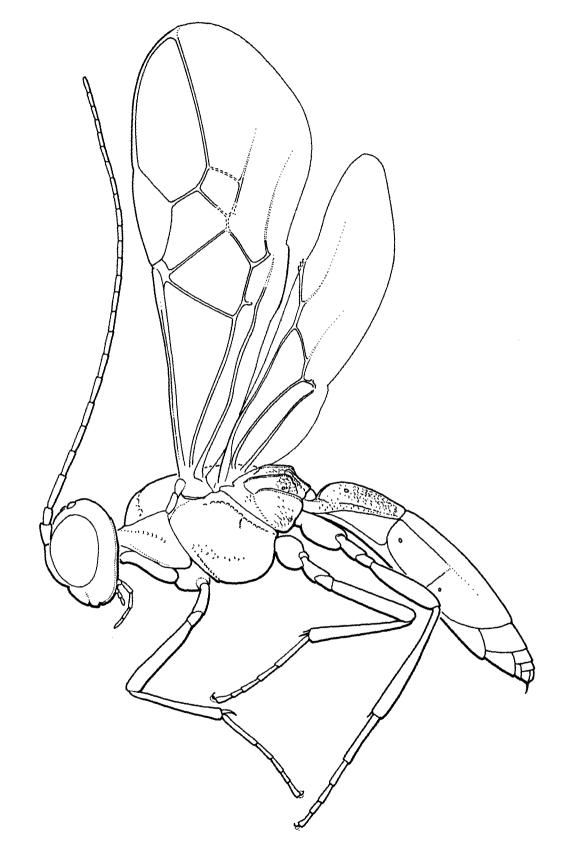


Fig. 137. Braconidae: Meteoridiinae

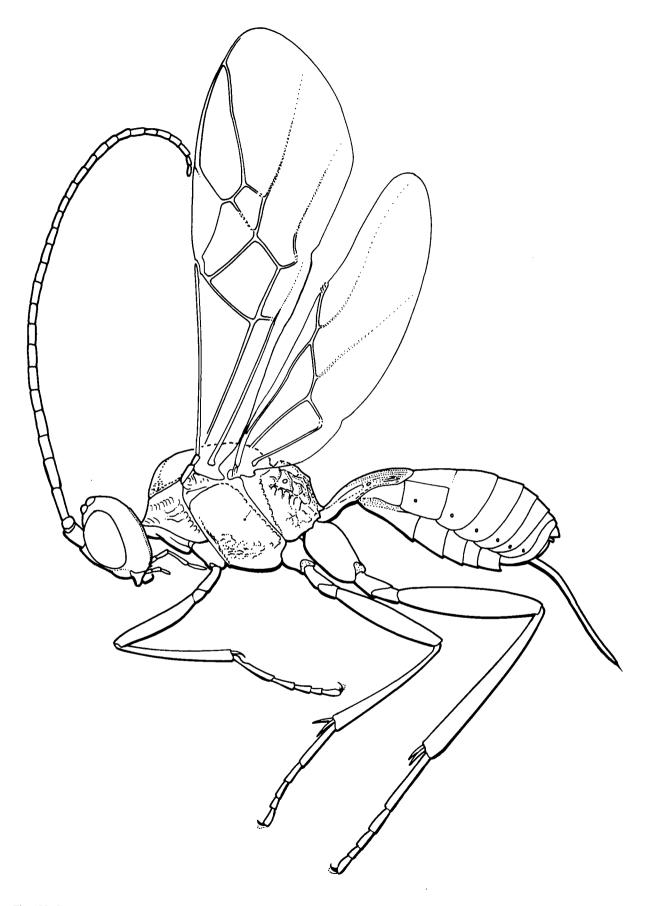


Fig. 138. Braconidae: Meteorinae

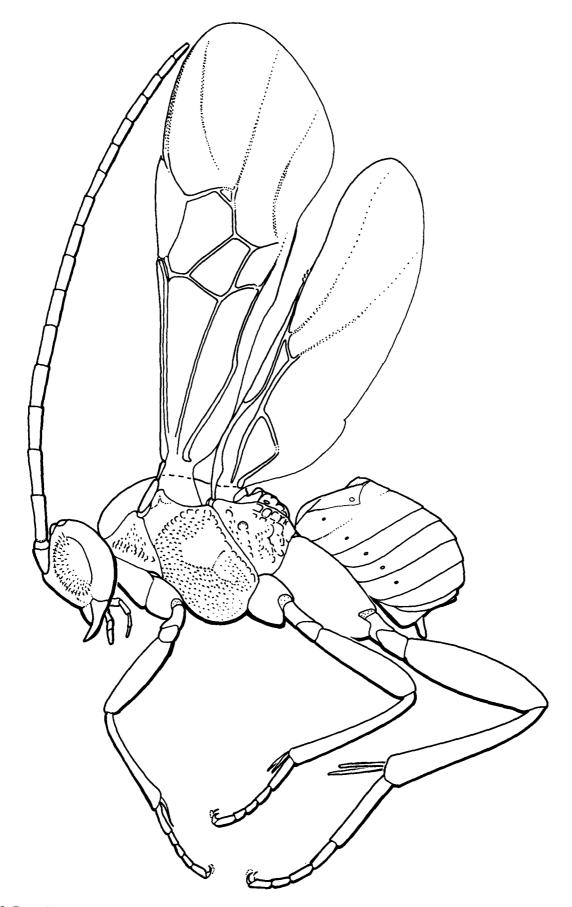


Fig. 139. Braconidae: Microgastrinae

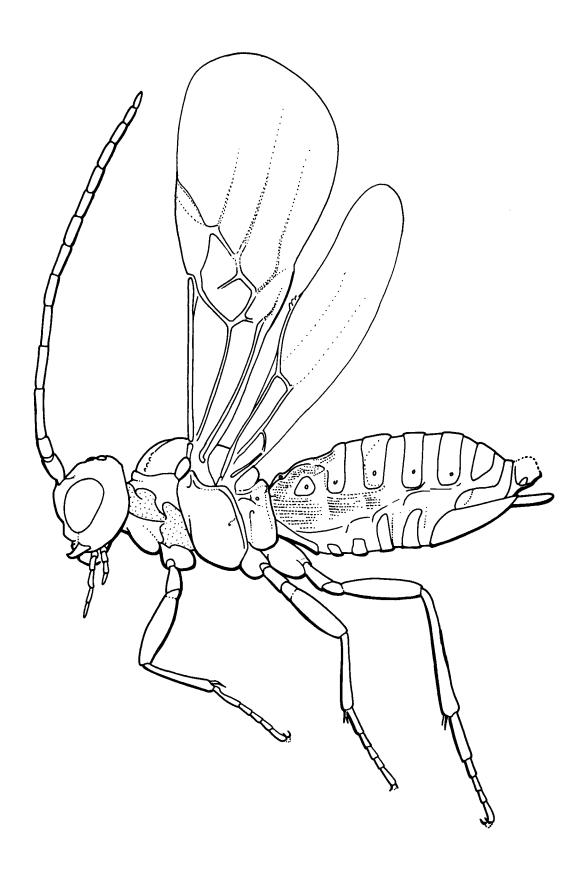


Fig. 140. Braconidae: Miracinae

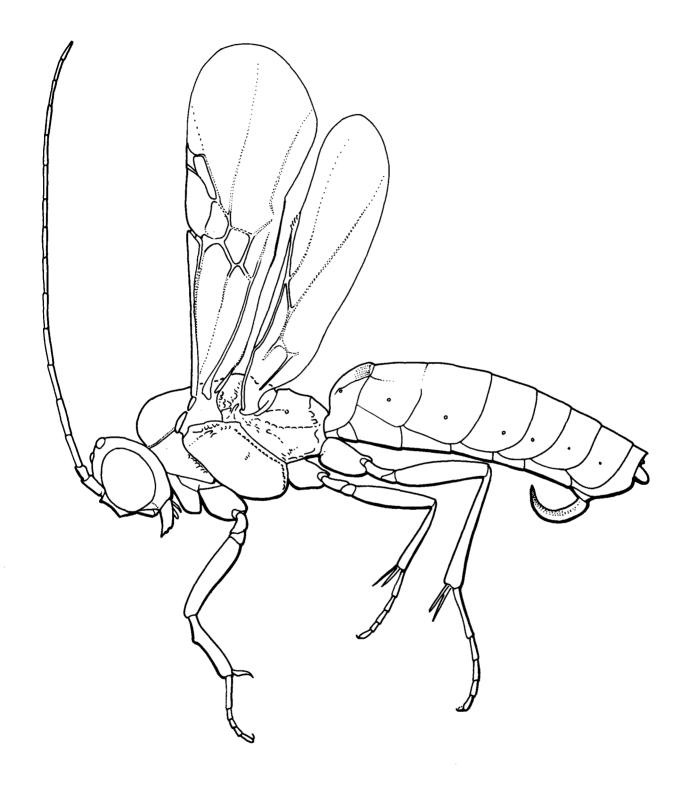


Fig. 141. Braconidae: Neoneurinae

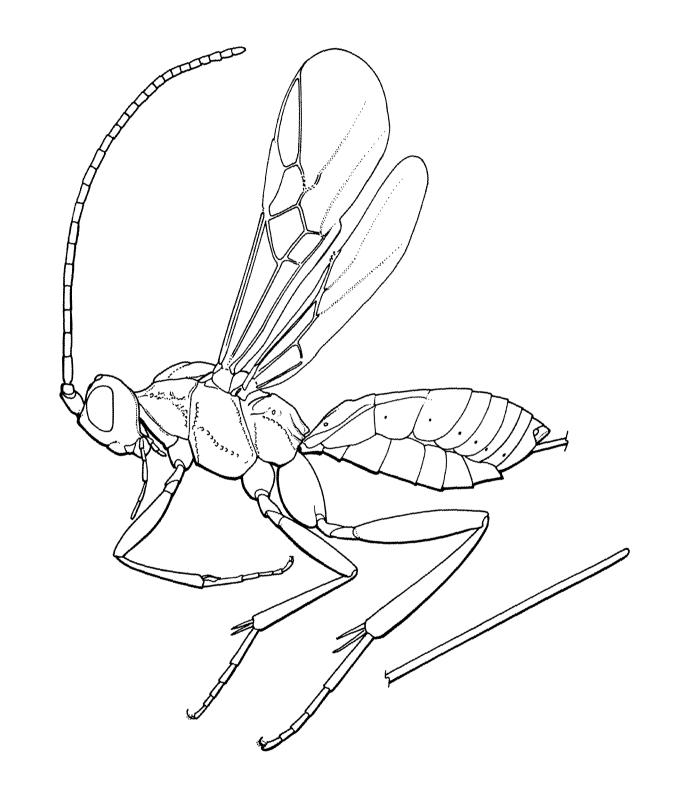


Fig. 142. Braconidae: Orgilinae

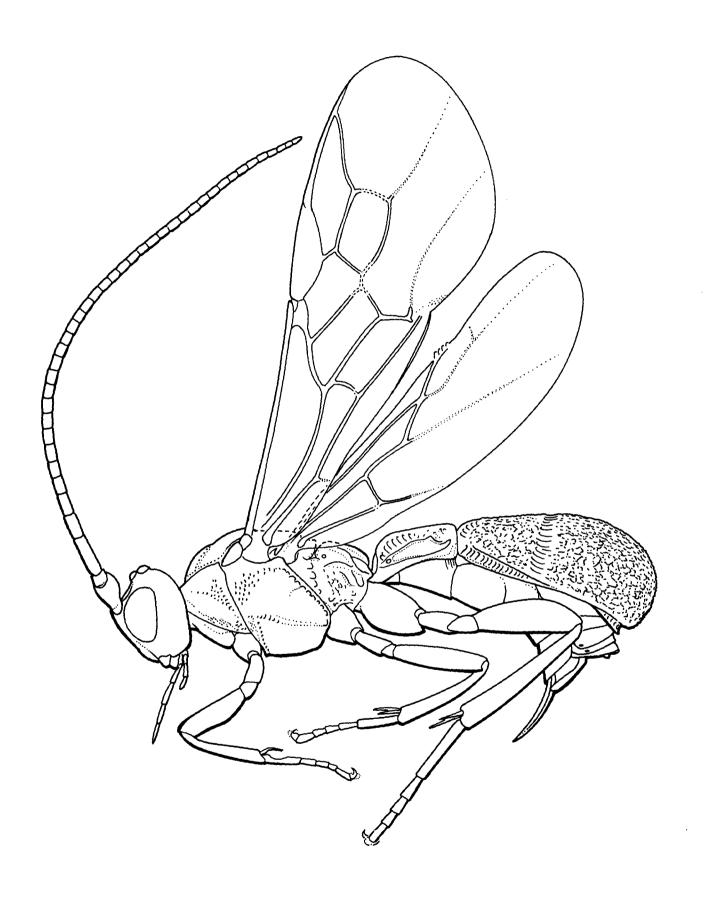


Fig. 143. Braconidae: Sigalphinae

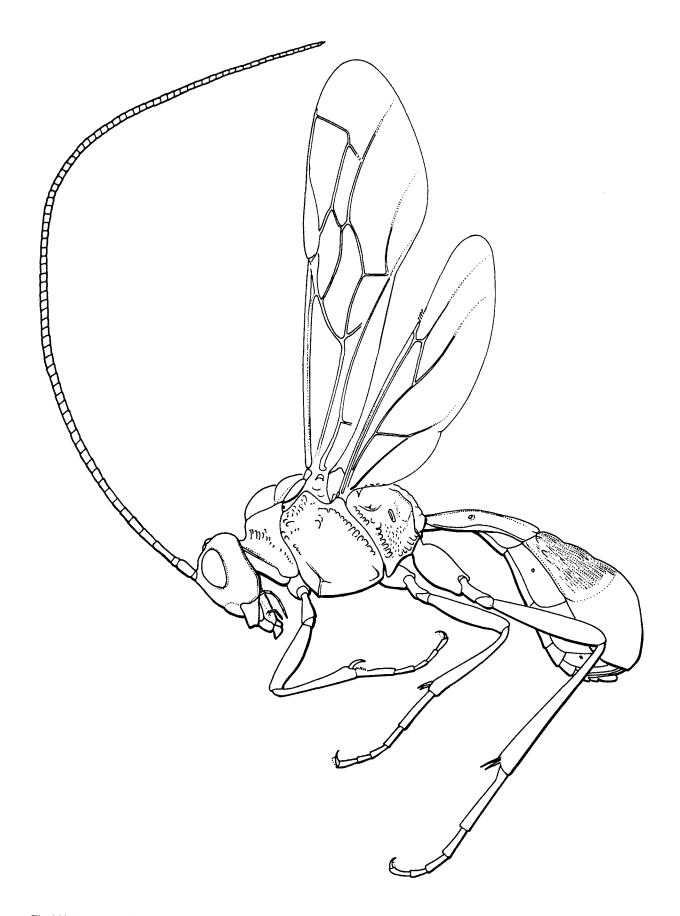


Fig. 144. Braconidae: Trachypetinae

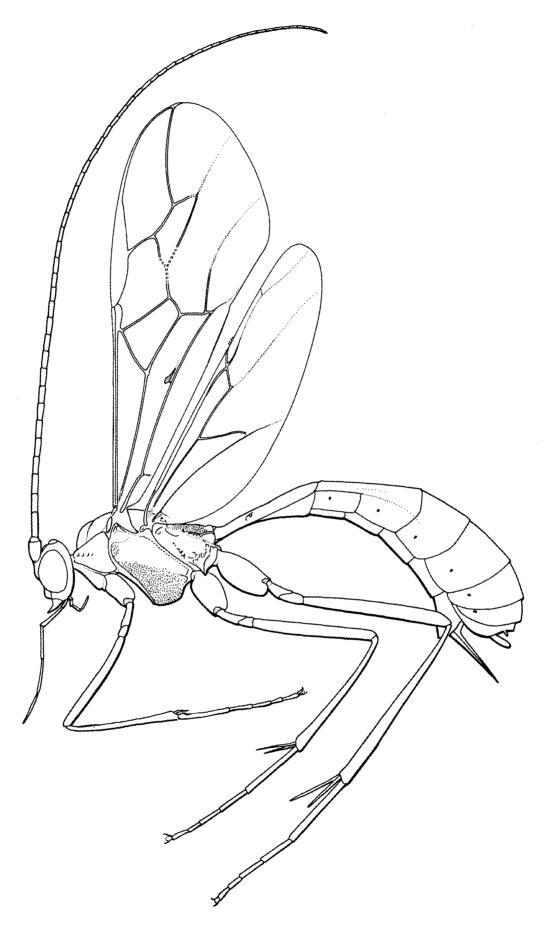


Fig. 145. Braconidae: Xiphozelinae

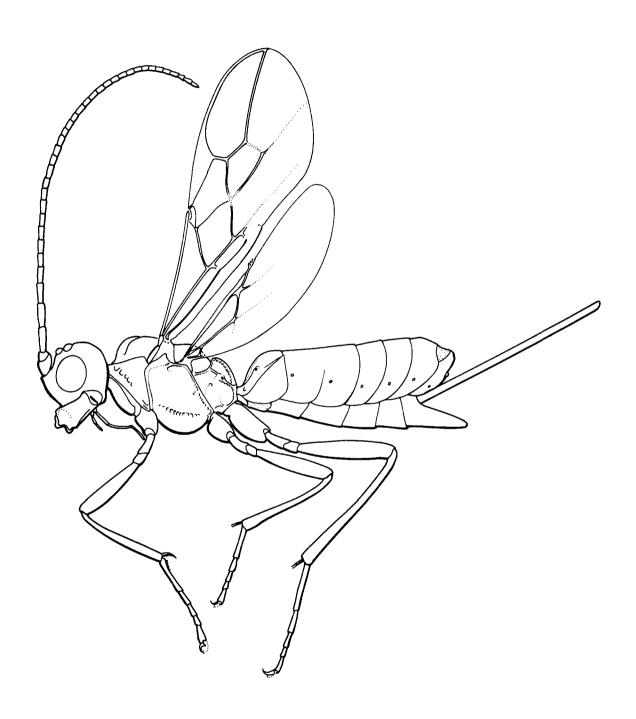


Fig. 146. Braconidae: Alysiinae

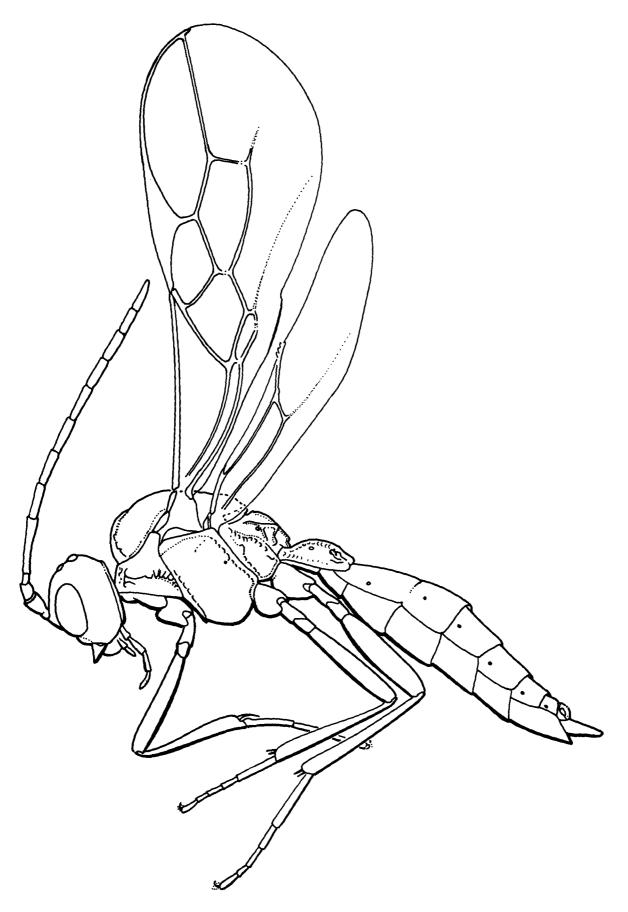


Fig. 147. Braconidae: Aphidiinae

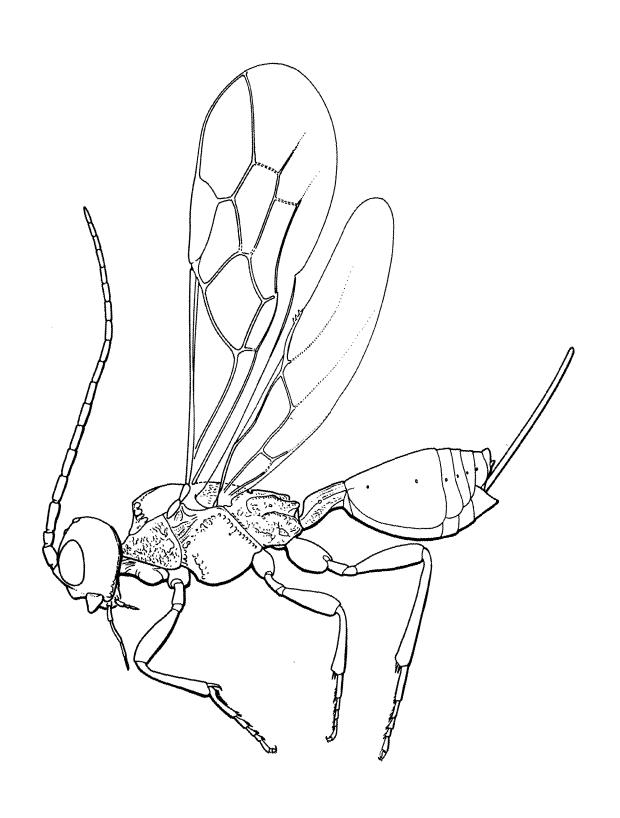


Fig. 148. Braconidae: Apozyginae

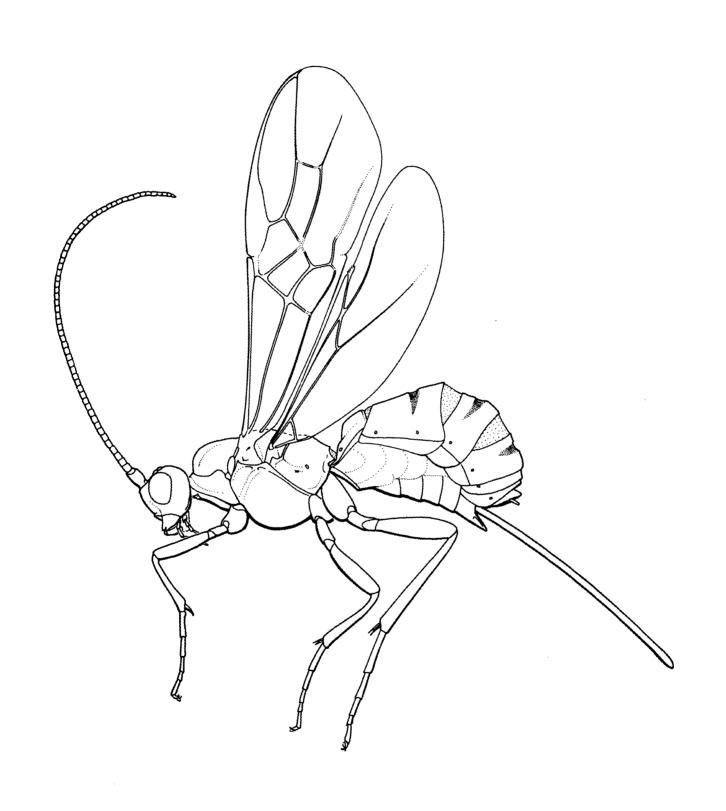


Fig. 149. Braconidae: Braconinae

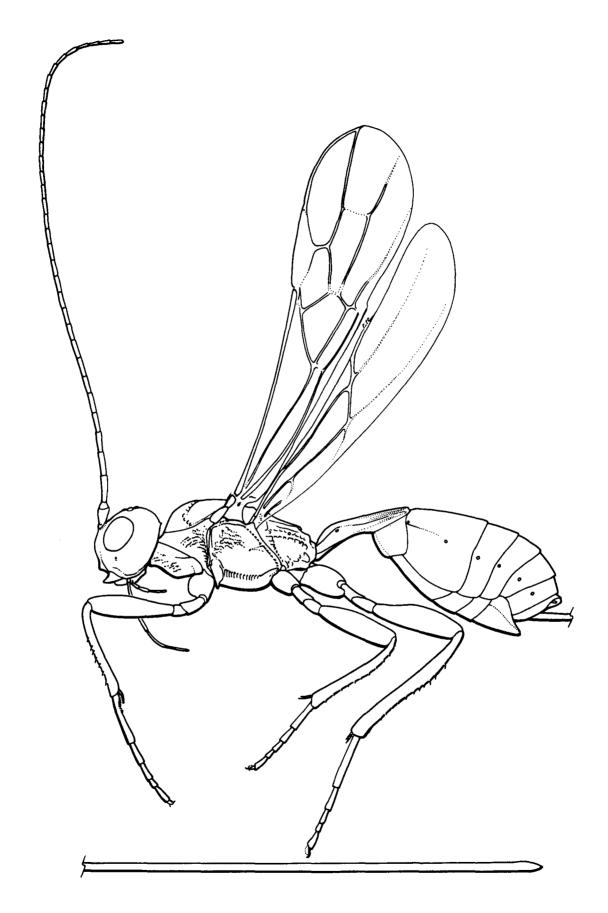


Fig. 150. Braconidae: Doryctinae

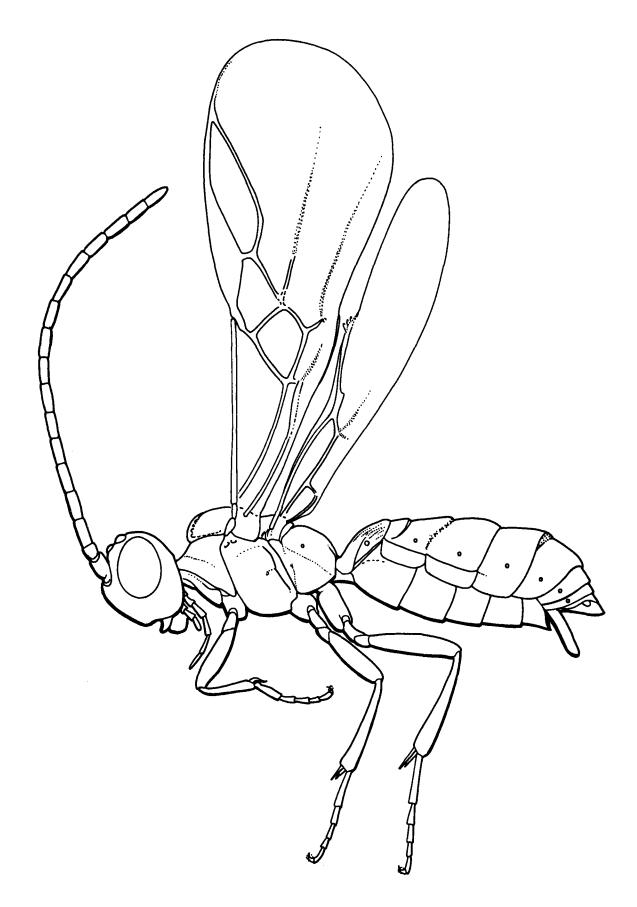


Fig. 151. Braconidae: Gnamptodontinae

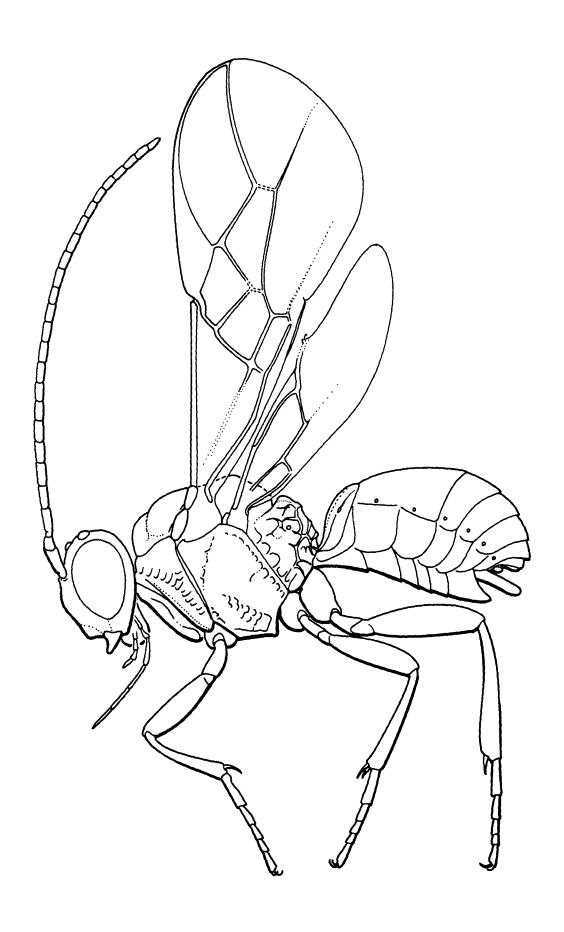


Fig. 152. Braconidae: Opiinae

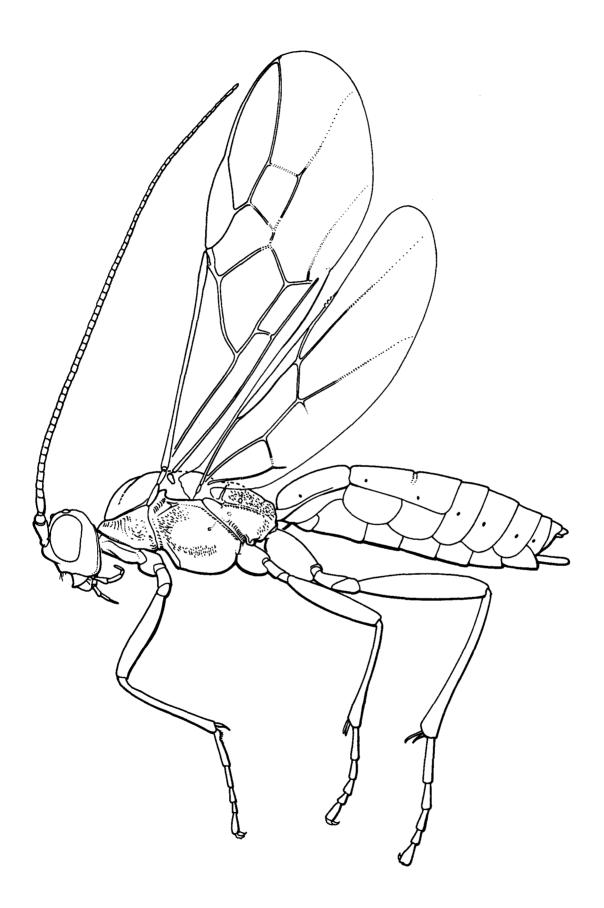


Fig. 153. Braconidae: Rogadinae

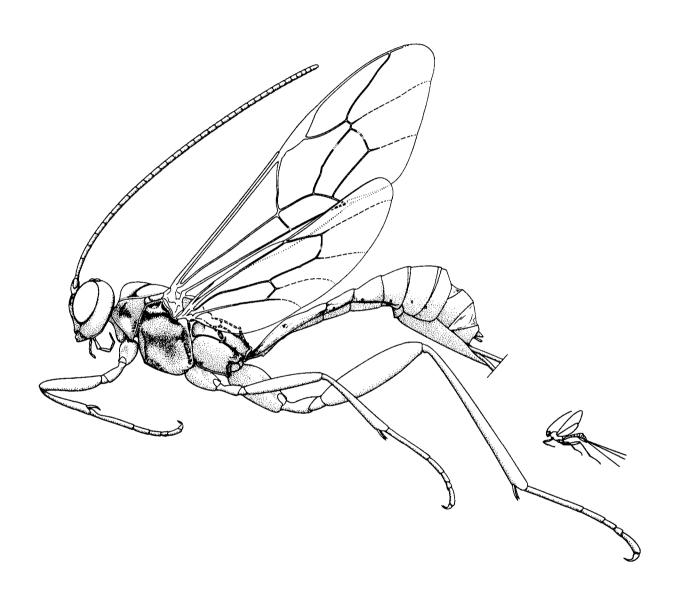


Fig. 154. Ichneumonidae: Acaenitinae

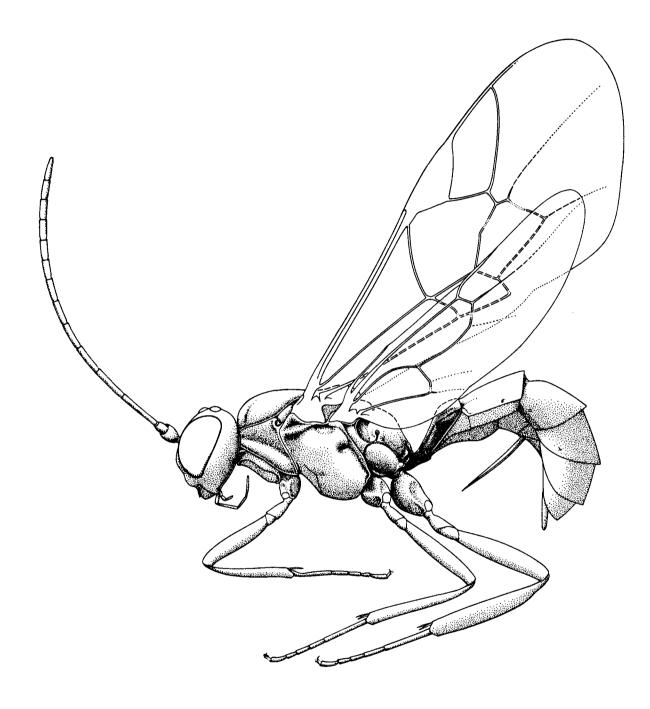


Fig. 155. Ichneumonidae: Adelognathinae

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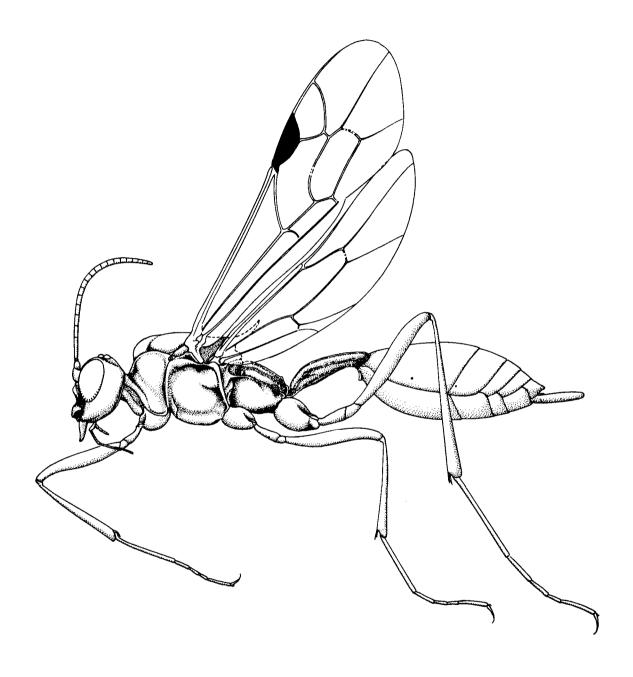


Fig. 156. Ichneumonidae: Agriotypinae

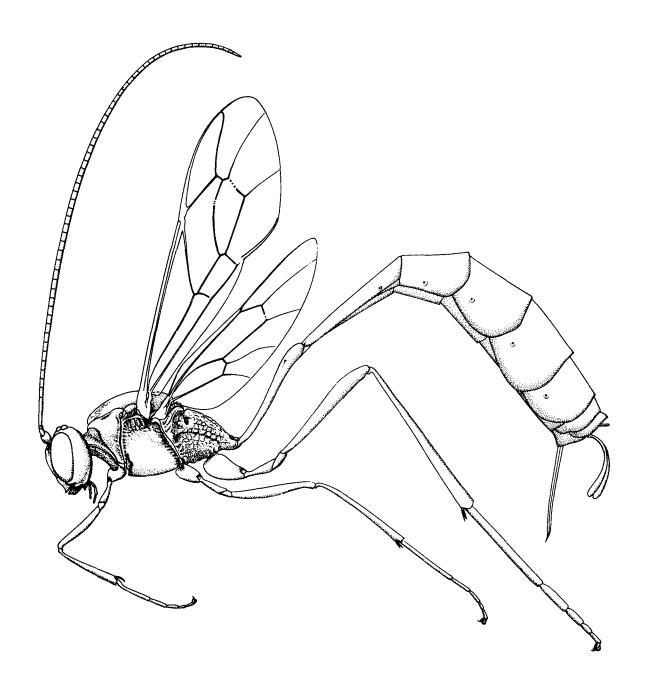


Fig. 157. Ichneumonidae: Anomaloninae

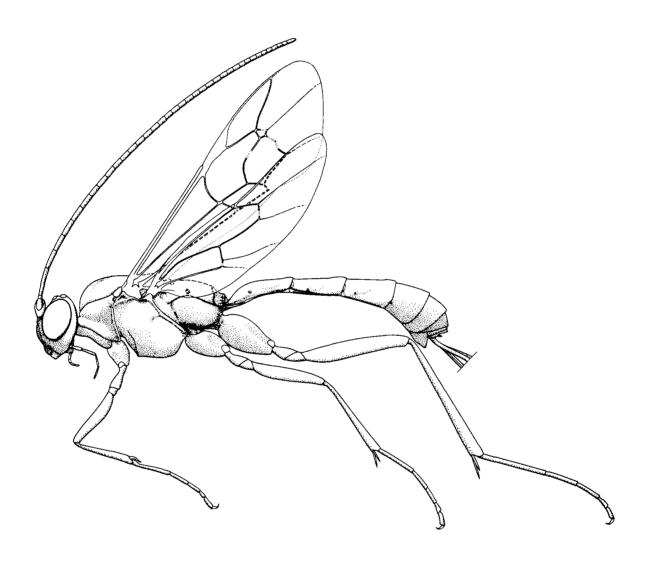


Fig. 158. Ichneumonidae: Banchinae

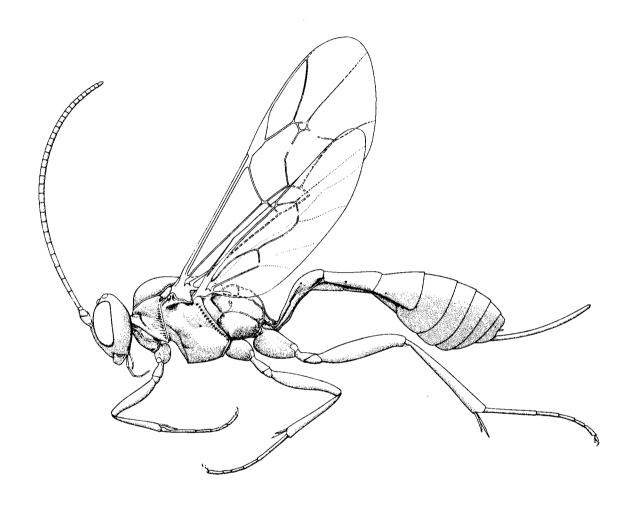


Fig. 159. Ichneumonidae: Campopleginae

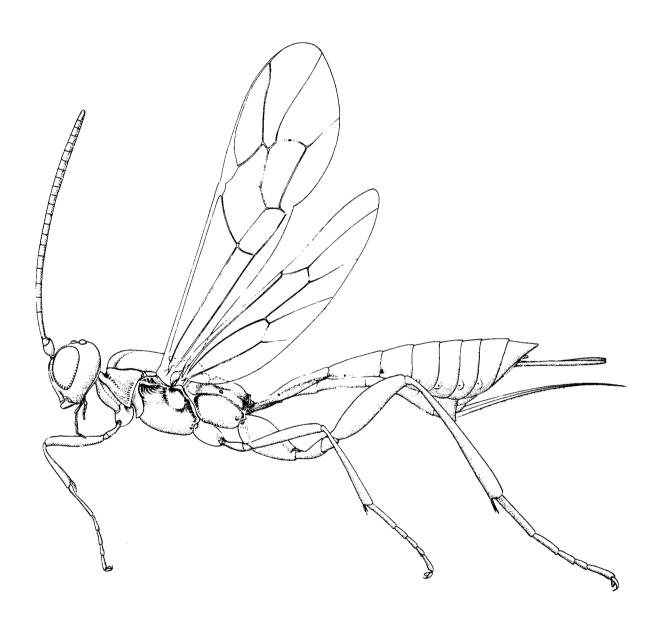


Fig. 160. Ichneumonidae: Collyrinae

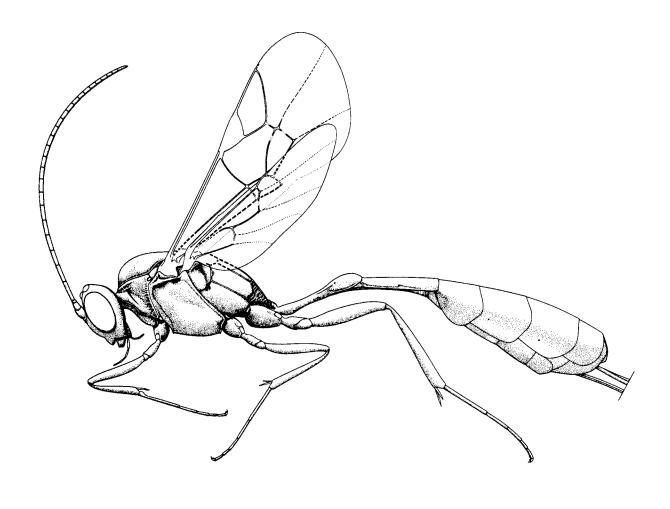


Fig. 161. Ichneumonidae: Cremastinae

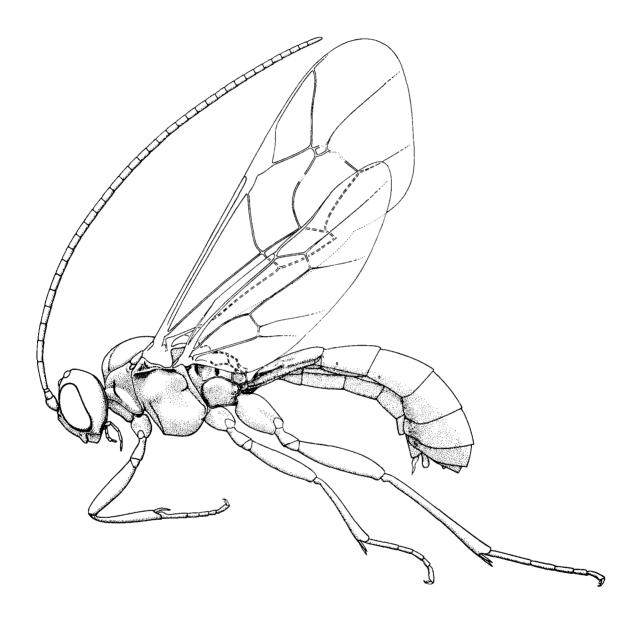


Fig. 162. Ichneumonidae: Ctenopelmatinae

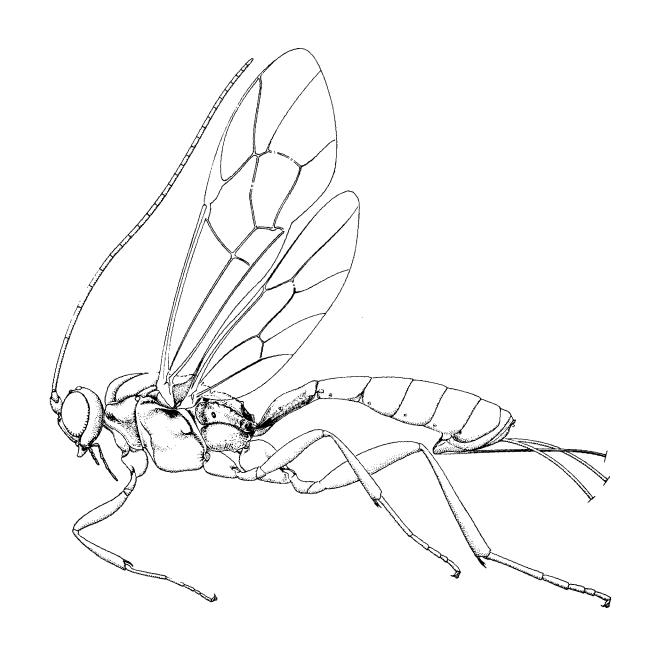


Fig. 163. Ichneumonidae: Cylloceriinae

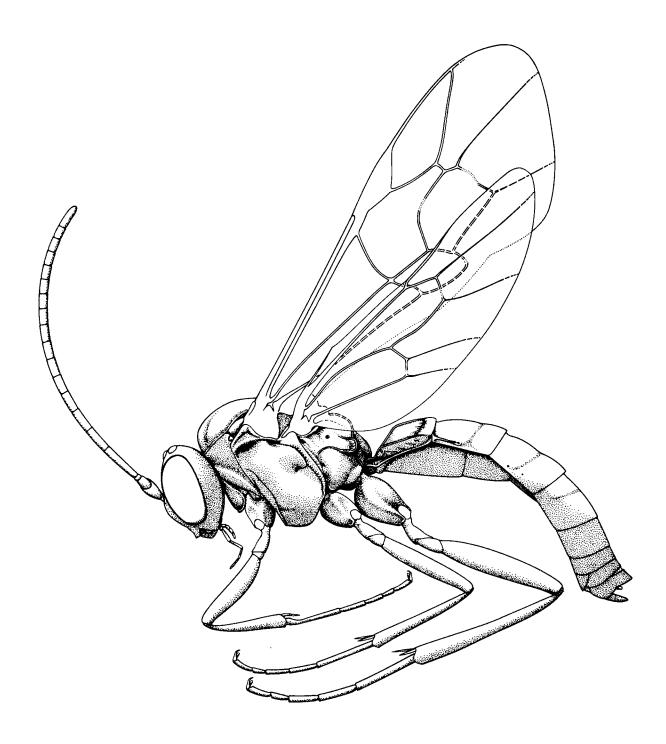


Fig. 164. Ichneumonidae: Diplazontinae

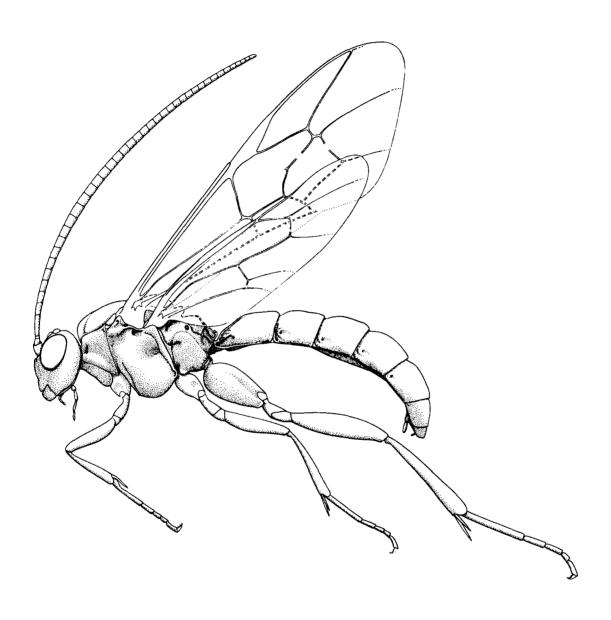


Fig. 165. Ichneumonidae: Eucerotinae



Fig. 166. Ichneumonidae: Ichneumoninae



Fig. 167. Ichneumonidae: Labeninae

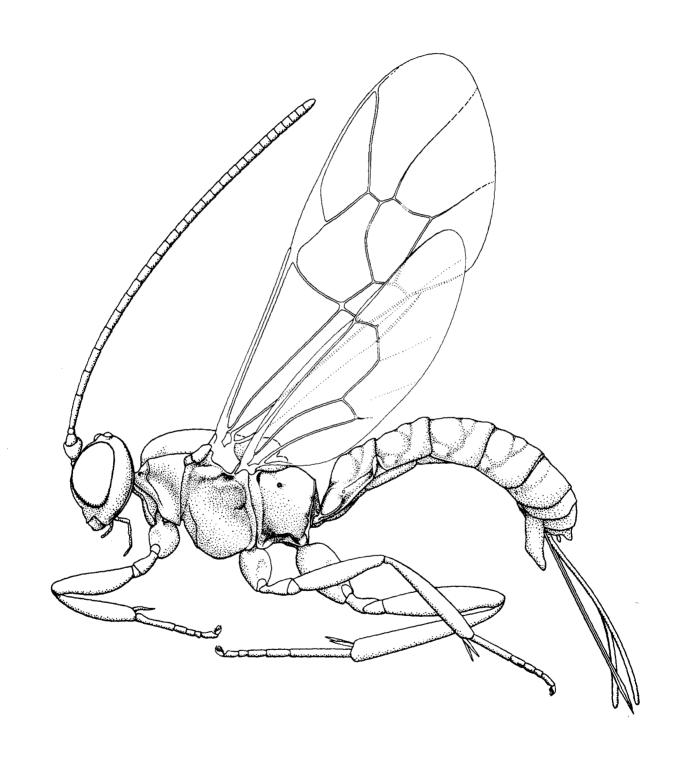


Fig. 168. Ichneumonidae: Lycorininae

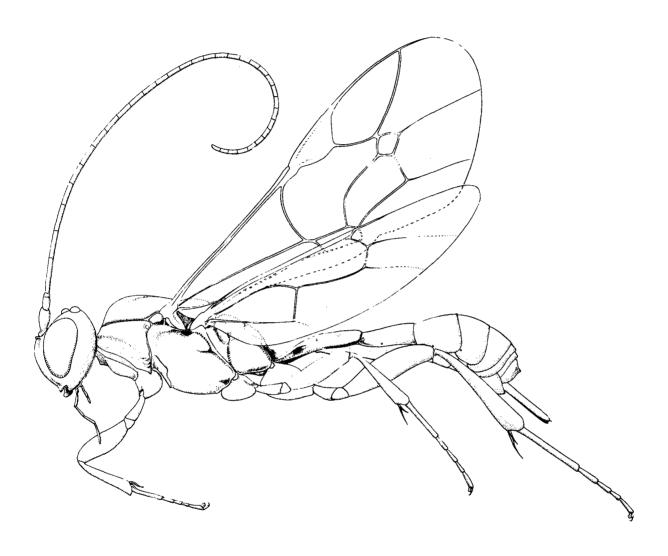


Fig. 169. Ichneumonidae: Mesochorinae

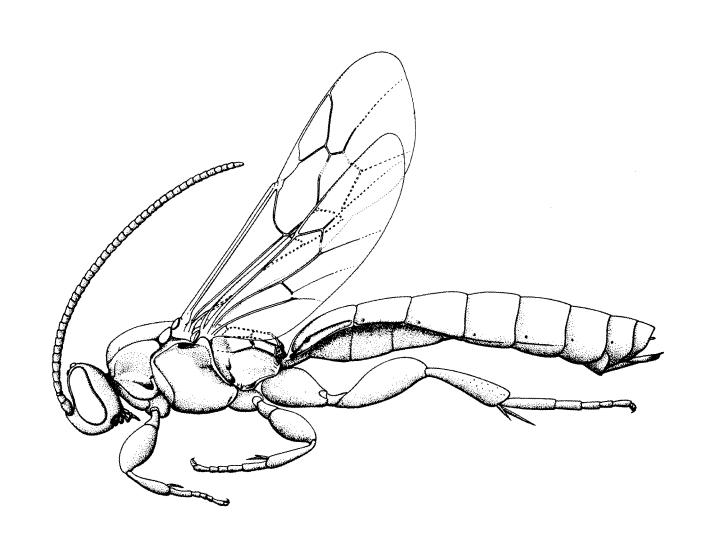


Fig. 170. Ichneumonidae: Metopiinae

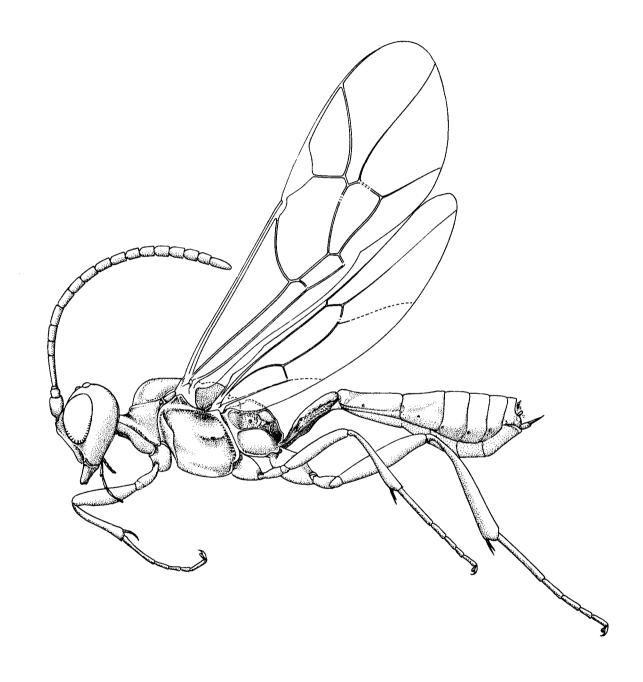


Fig. 171. Ichneumonidae: Microleptinae

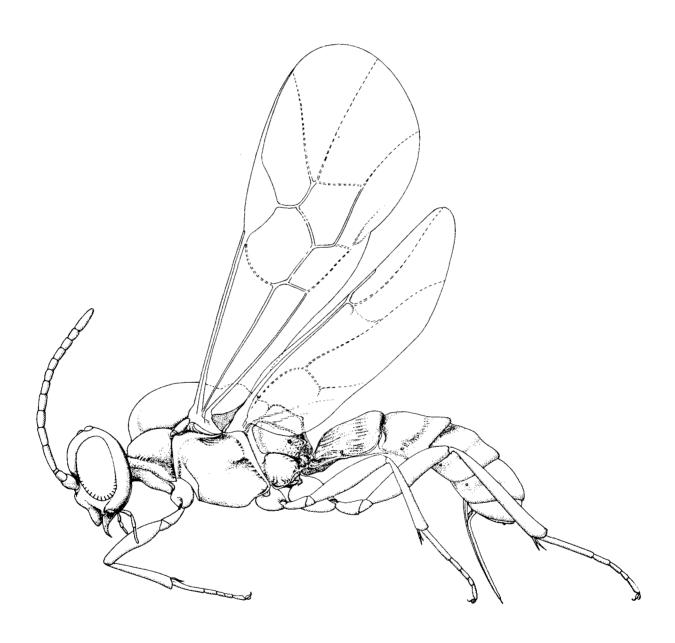


Fig. 172. Ichneumonidae: Neorhacodinae

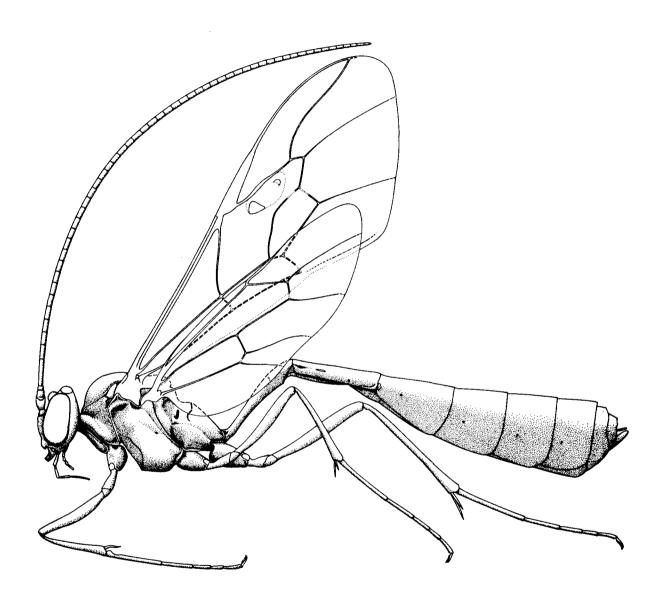


Fig. 173. Ichneumonidae: Ophioninae

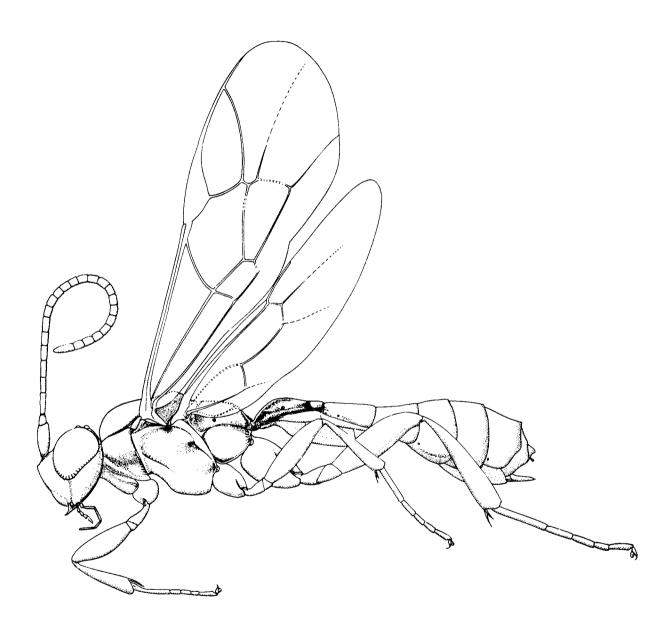


Fig. 174. Ichneumonidae: Orthocentrinae

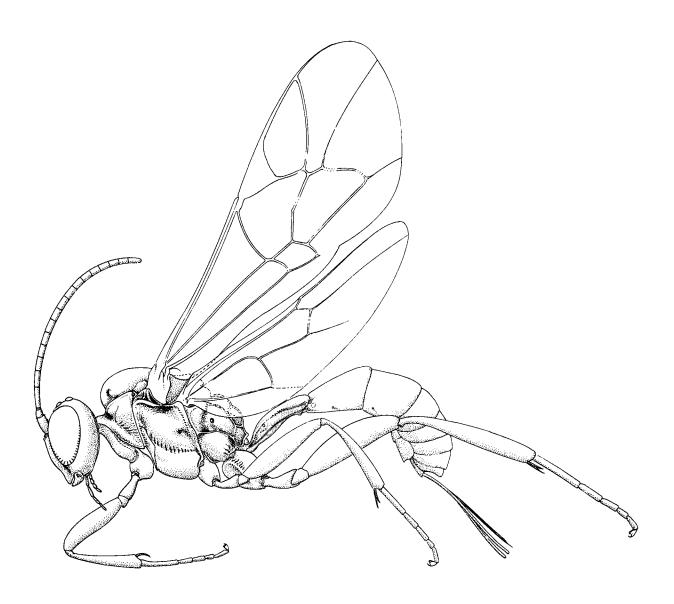


Fig. 175. Ichneumonidae: Orthopelmatinae



Fig. 176. Ichneumonidae: Oxytorinae

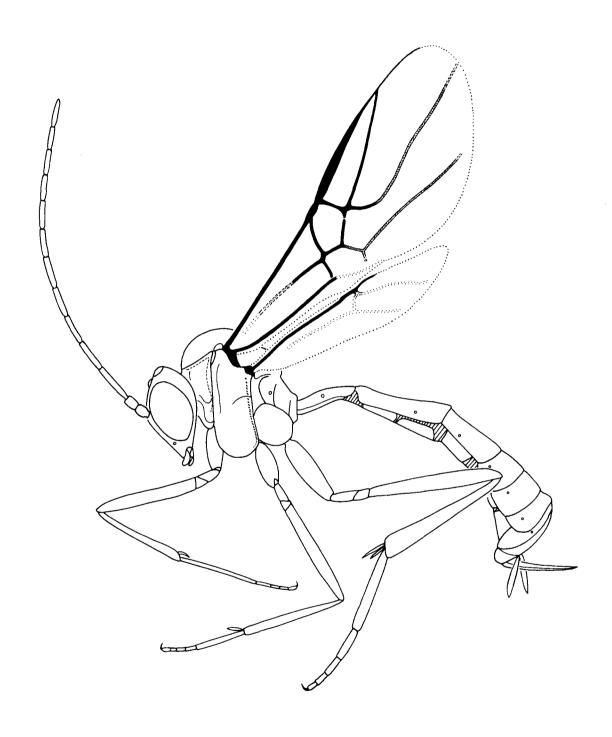


Fig. 177. Ichneumonidae: Paxylommatinae

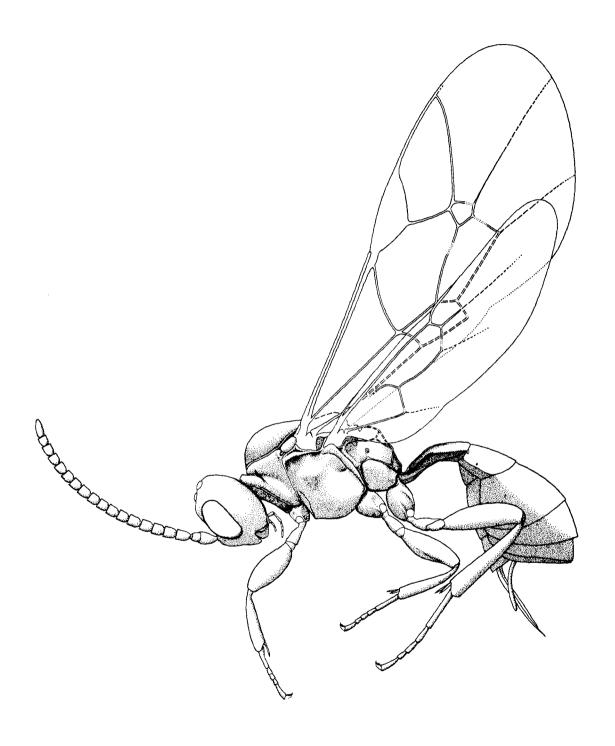


Fig. 178. Ichneumonidae: Phrudinae

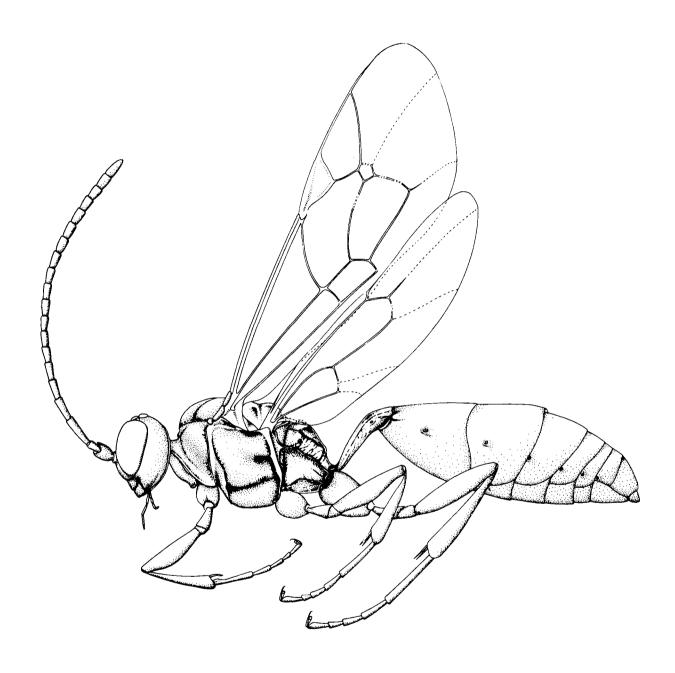


Fig. 179. Ichneumonidae: Phygadeuontinae

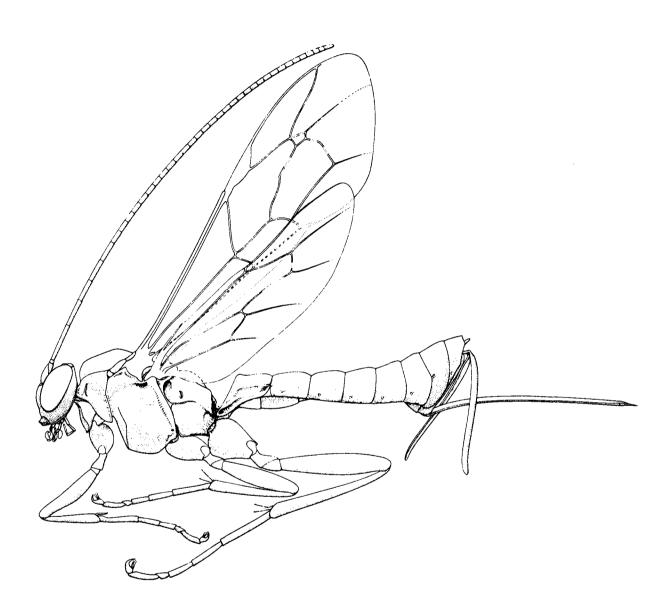


Fig. 180. Ichneumonidae: Pimplinae

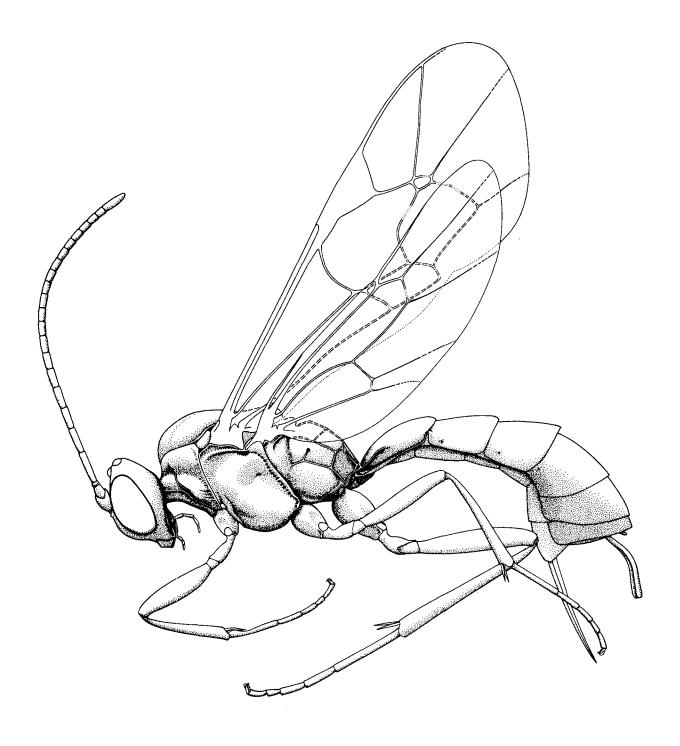


Fig. 181. Ichneumonidae: Stilbopinae

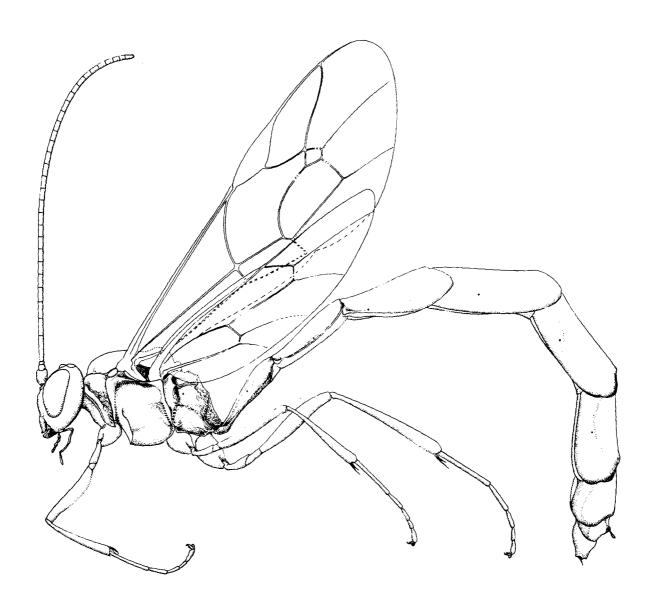


Fig. 182. Ichneumonidae: Tatogastrinae



Fig. 183. Ichneumonidae: Tersilochinae

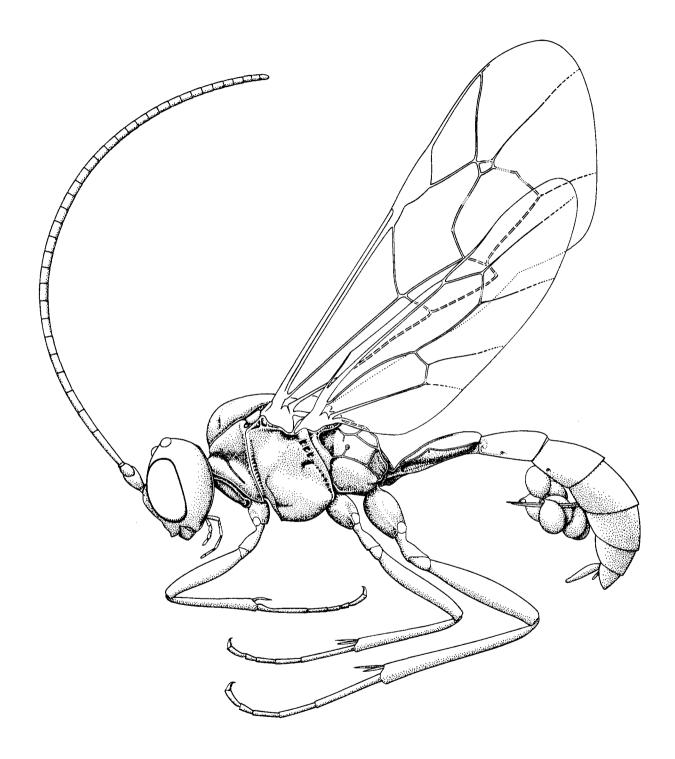


Fig. 184. Ichneumonidae: Tryphoninae

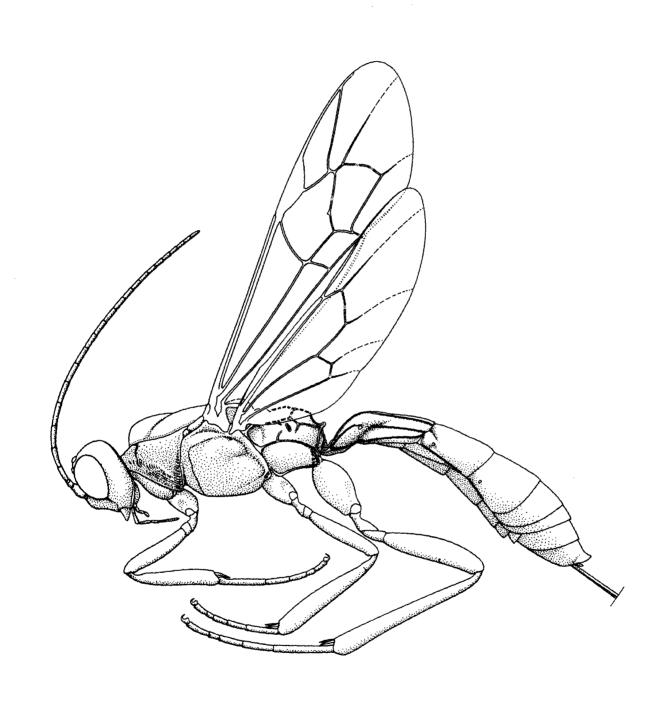


Fig. 185. Ichneumonidae: Xoridinae

# Chapter 11 Superfamilies Evanioidea, Stephanoidea, Megalyroidea, and Trigonalyoidea

(Figs. 186-191)

William R.M. Mason

These four superfamilies are grouped together only for convenience and because their numbers

are comparatively small, totalling just over 1300 species.

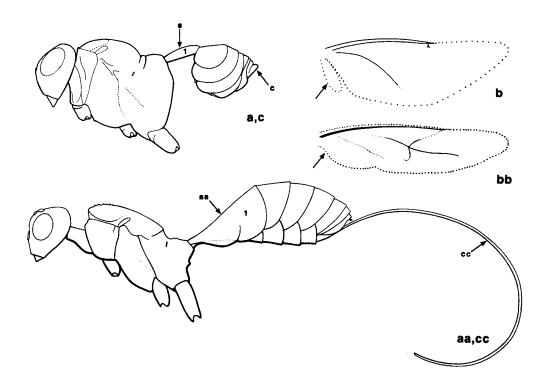
#### Superfamily EVANIOIDEA

(Figs. 186-188)

Included families (3): Aulacidae, Evaniidae, Gasteruptiidae

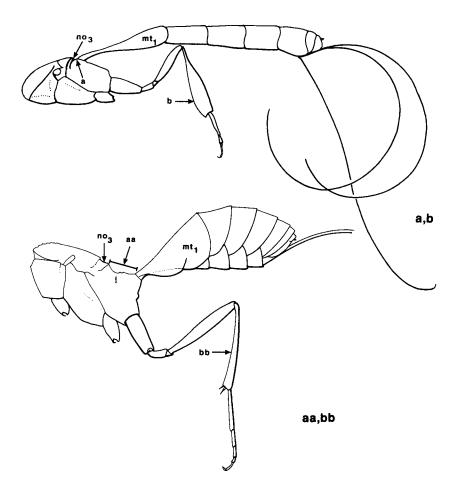
Members of the superfamily fall in two groups: Aulacidae and Gasteruptiidae, which are so similar that they are often placed in one family (Townes 1950); and Evaniidae, which is different enough to be placed in a separate superfamily by some workers (Townes 1949). The three families are united mainly by the peculiar structure of the high attachment of the metasoma on the propodeum, but the rich fossil record suggests that intermediate groups once existed. Aulacidae and Gasteruptiidae share several attributes not found in Evaniidae: metasomal terga 1 and 2 (but not the sterna) fused into a long, gently tapering double segment; propleura extending forward beyond pronotum and, in this neck-like extention, curving upward and inward to meet dorsally; male antenna with 11 flagellomeres, female with 12.

## Key to families of EVANIOIDEA



- a. Metasomal segment 1 petiolate; rest of metasoma disc-shaped.
  - b. Hind wing with jugal lobe.
  - c. Ovipositor sheath very short ...... **EVANIIDAE** (p. 512)

- aa. Metasomal segment 1 usually conical; rest of metasoma elongate.
- bb. Hind wing without jugal lobe.



- 2(1) a. Metasomal segment 1 (mt<sub>1</sub>) with anterior margin almost touching metanotum (no<sub>3</sub>).

  - aa. Anterior margin of metasomal segment 1 (mt<sub>1</sub>) distinctly separated from metanotum (no<sub>3</sub>) (height of metasomal tergum 1 anteriorly equal to, or less than, medial length of propodeum).

#### Family AULACIDAE

(Fig. 186)

**Diagnosis** Body relatively slender; antenna with 12 flagellomeres in female, 11 in male; propleura long and neck-like; mesoscutum often humped anteriorly; metasoma attached high on propodeum but distinctly separated from metanotum by a wide dorsal band of the propodeum; medial (inner) side of female metacoxa usually with a vertical or oblique groove; metatibia not thickened; ovipositor long.

**Comments** This is a worldwide family of ancient lineage containing about 13 genera and 150 known species, as well as many that are not described.

Although there are relatively few extant species, extinct species are abundant in the fossil record and must have formed a major part of Hymenoptera in the Mesozoic era. Adults parasitize larvae of wood-boring Coleoptera; some parasitize wood-boring sawfly larvae of the family Xiphydriidae. They can sometimes be found in relative abundance following lumbering operations or forest fires but are otherwise scarce. Twenty-eight species occur in North America, including about 10 in Canada, some of which are common in the boreal forest.

**References** Kieffer (1912) revised and Hedicke (1939b) cataloged the world species. Townes (1950) reviewed the North American genera and species.

Crosskey (1951) revised the British species. Oehlke (1984) revised the German species. Pagliano (1986) revised the Italian species.

#### Family GASTERUPTIIDAE

(Fig. 187)

**Diagnosis** Body slender; antenna with 12 flagellomeres in female, 11 in male; propleura long and neck-like, clearly separating head from pronotum; metasoma attached so high on propodeum that it appears to touch metanotum; metatibia strongly clavate in both sexes; ovipositor moderately to very long (except in *Hyptiogaster*).

Comments Members of this family have a characteristic hovering flight with the swollen metatibiae hanging down so that the insect resembles a helicopter carrying a large load on a cable. The biology of Nearctic species is not known, but some European species have been reared from nests of solitary bees or wasps in holes in wood

where they are predators, feeding upon one or more of the eggs and larvae found in the nests. The family contains about nine genera and 500 species around the world, with more species in tropical than in temperate areas. Fifteen species occur in North America, including nine in Canada.

**References** Kieffer (1912) revised and Hedicke (1939c) cataloged the world species. Crosskey (1951, 1962) revised the British species and reviewed the world genera. Pasteels (1958 and earlier papers) revised species of *Gasteruption*. Townes (1950) reviewed the North American genera and species. Oehlke (1984) revised the German species.

#### Family EVANIIDAE

(Fig. 188)

**Diagnosis** Body short and stout, with a characteristic appearance; antenna elbowed, with 11 (rarely 8) flagellomeres in both sexes; legs relatively long; hind wing with jugal lobe separated from claval lobe by deep incision; metasoma relatively small and compressed, attached high on propodeum by a curved, tubular petiole; ovipositor short and mostly hidden.

Comments Evaniidae contains about 14 genera and 400 species and is abundant in tropical regions. In Europe one species occurs as far north as the Lapland tundra. A few species are cosmopolitan, living inside warehouses and other buildings with a

cockroach population. Adults seek out and oviposit in the concealed egg-cases of cockroaches (Dictuoptera: Blattodea); the larvae feed on the cockroach eggs and pupate inside the ootheca. By most definitions, evaniids are predators. Eleven species occur in North America, including four in the extreme south of Canada.

**References** Kieffer (1912) revised and Hedicke (1939a) cataloged the world species. Townes (1949) reviewed the genera and species of North America. Crosskey (1951) revised the British species. Oehlke (1984) revised the German species. Pagliano (1986) revised the Italian species.

### Superfamily STEPHANOIDEA

(Fig. 189)

Included family (1): Stephanidae.

#### Family STEPHANIDAE

(Fig. 189)

**Diagnosis** Body long and slender; head globular with a few tooth-like spines around median ocellus; antenna with a variable, high number of flagellomeres, usually over 20; pronotum neck-like; fore wing without vein C between tegula and

stigma; metafemur enlarged and toothed ventrally; ovipositor long.

**Comments** Most species of this family are believed to be parasites of large wood-boring

Coleoptera. Schlettererius cinctipes (Cresson) from western North America was introduced to Tasmania, where it parasitizes an imported siricid in pine plantations. The family contains about nine genera and 100 species, mostly in the tropics. Six species occur in North America, including two in Canada.

**References** Eliot (1922) revised the world species. Townes (1945) reviewed the North American species. Oehlke (1984) revised the German species. Benoit (1984) revised the Central and West African species.

Pagliano (1986) redescribed the single Italian species and a new one from Morocco.

#### Superfamily MEGALYROIDEA

(Fig. 190)

Included family (1): Megalyridae.

#### Family MEGALYRIDAE

(Fig. 190)

**Diagnosis** Body stocky and cylindrical; gena with very large, deep, oval pit in which the antennal scape can be housed. Characteristically, the mesoscutum is relatively flat, has large triangular axillae, and in all but one rare genus has a strong median groove bisecting the mesoscutum.

**Comments** Members of this family are parasitoids mostly of Coleoptera larvae found under tree bark,

but one is known to parasitize a species of Pemphredonidae. The family contains 10 genera and 45 usually rare species that occur in South America, Africa, southeast Asia, and Australia.

**References** Shaw (1987, 1988, 1990a, 1990b) discussed the family and described several genera. Naumann (1987) described a *Megalyra* parasitic on Pemphredonidae.

## **Superfamily TRIGONALYOIDEA**

(Fig. 191)

Included family (1): Trigonalyidae.

#### Family TRIGONALYIDAE

(Fig. 191)

**Diagnosis** Antenna inserted on frons under small lobe; antenna with more than 20 flagellomeres; fore wing with 10 closed cells, the costal cell wide; hind wing with 2 closed cells; tarsomeres 1–4 with apicoventral plantar lobes; metasoma pedunculate; ovipositor reduced.

Comments The life history is complex, and many important details are unknown. Trigonalyids lay thousands of minute (0.1 mm) but thick-shelled eggs on the underside of leaves near the margin. The eggs remain unhatched until they are eaten by a caterpillar (either of Symphyta or of Lepidoptera), when cracks made by the jaws of the caterpillar and its digestive juices cause hatching. The newly hatched trigonalyid larva makes its way into the body cavity of the caterpillar. If the host already carries a parasitoid larva, that parasitoid is attacked; otherwise the trigonalyid larva apparently

waits until the caterpillar is parasitized when it attacks only the parasitoid, not the primary host. Some trigonalyids have been reared from larvae of *Vespula*. They are believed to reach their host by way of infested caterpillars that are fed to the wasp larvae by the worker wasps. The family contains about 75 usually rare species (22 genera) around the world. Four rare species occur in North America; all occur in Canada.

References Schulz (1907) revised the world genera. Bischoff (1938) and Weinstein and Austin (1991) cataloged the world species. Clausen (1940) and Weinstein and Austin (1991) reviewed the biology. Townes (1956) reviewed the North American genera and species, Oehlke (1984) revised the German species, and Tsuneki (1991) revised the species from Japan and adjacent areas.

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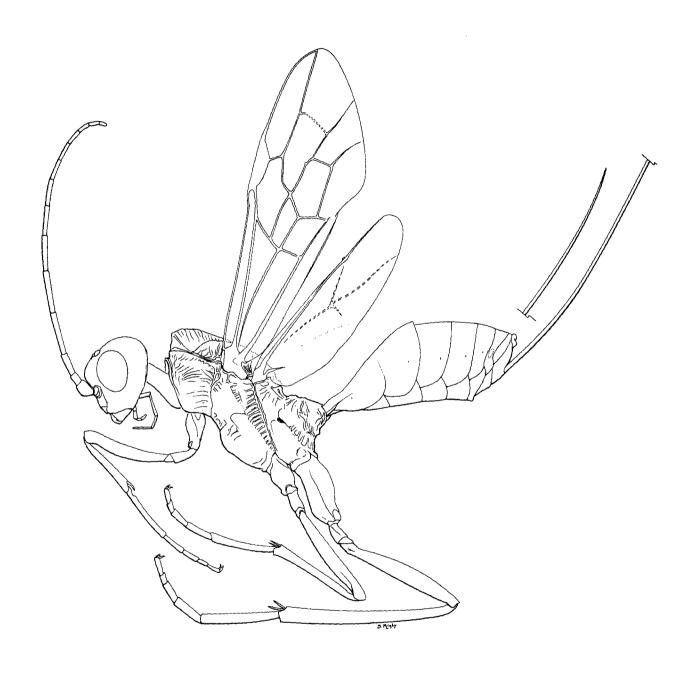


Fig. 186. Aulacidae

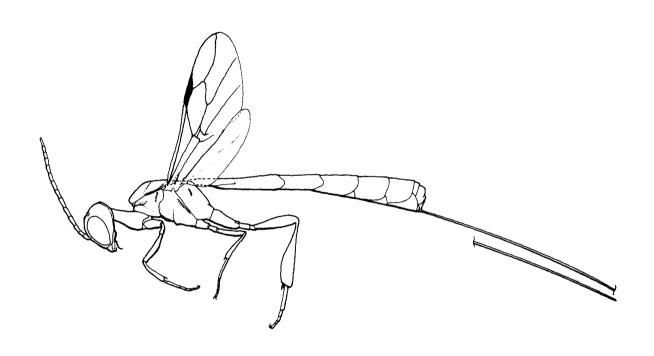


Fig. 187. Gasteruptiidae

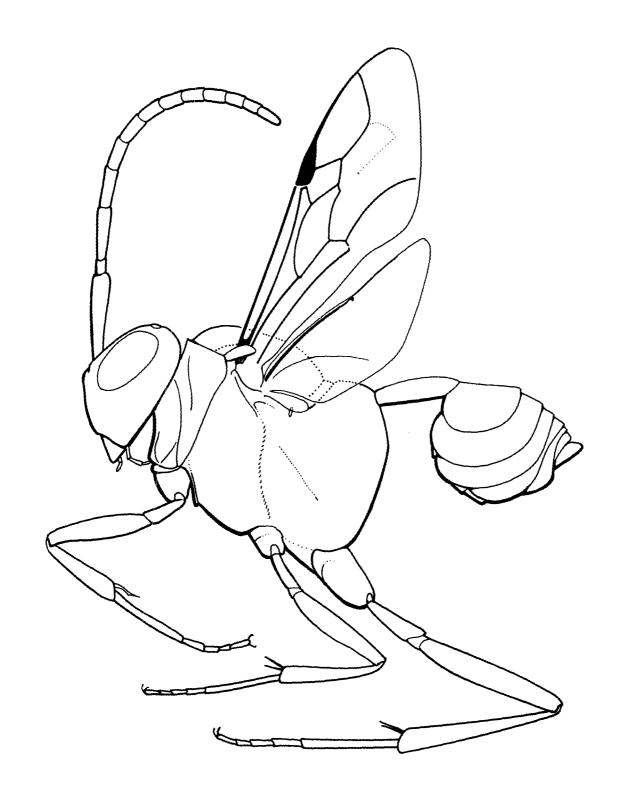


Fig. 188. Evaniidae

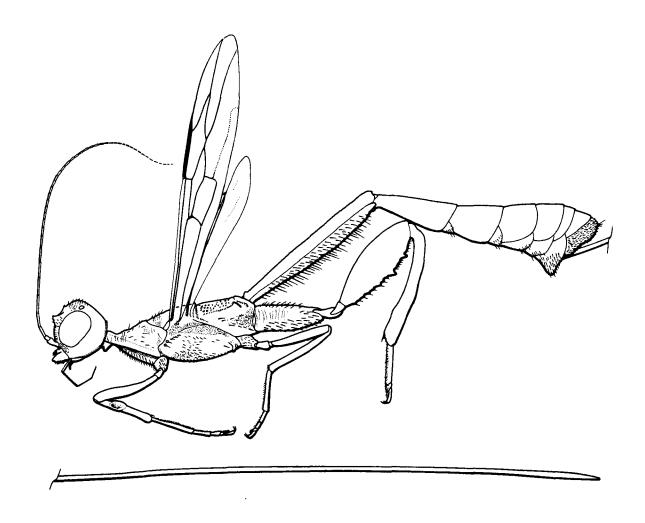


Fig. 189. Stephanidae

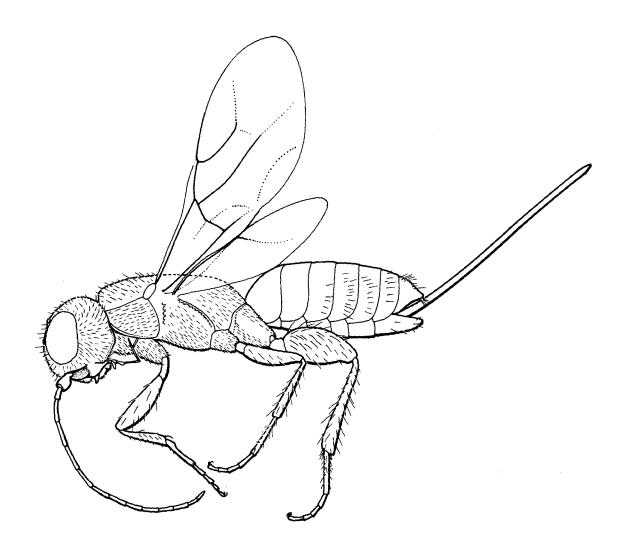


Fig. 190. Megalyridae

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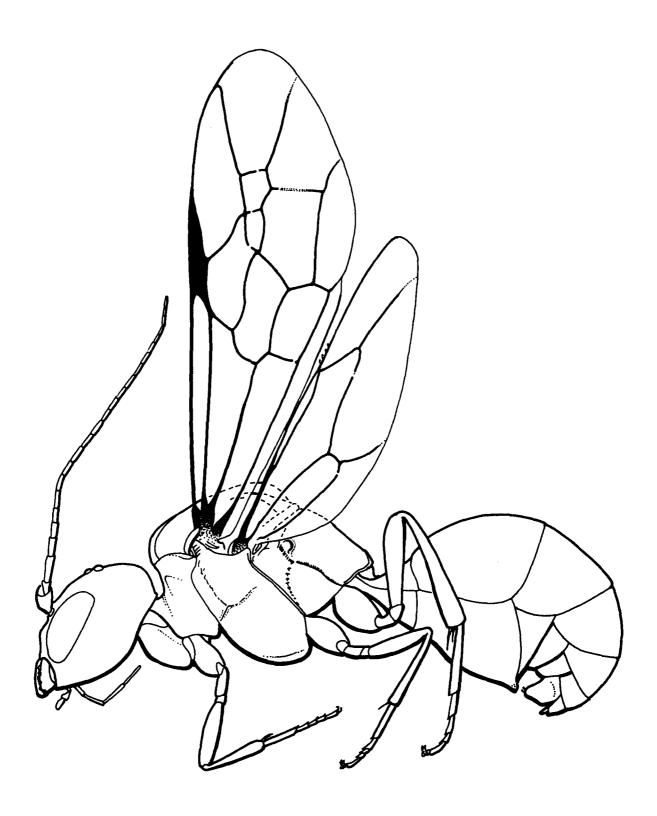


Fig. 191. Trigonalyidae

# Chapter 12 Superfamily CYNIPOIDEA

(Figs. 192-197)

Alasdair J. Ritchie

Included families (6): Charipidae, Cynipidae, Eucoilidae, Figitidae, Ibaliidae, Liopteridae.

**Diagnosis** Body mostly small to medium (rarely up to 30 mm), never with metallic luster; antenna not elbowed, that of female usually with 11 flagellomeres, that of male almost always with 12 or 13 flagellomeres; pronotum reaching tegula; fore wing when present, with distinctive triangular radial cell with the anterior margin either open or closed, and without a true stigma; tarsi 5-segmented; metasoma almost always laterally compressed.

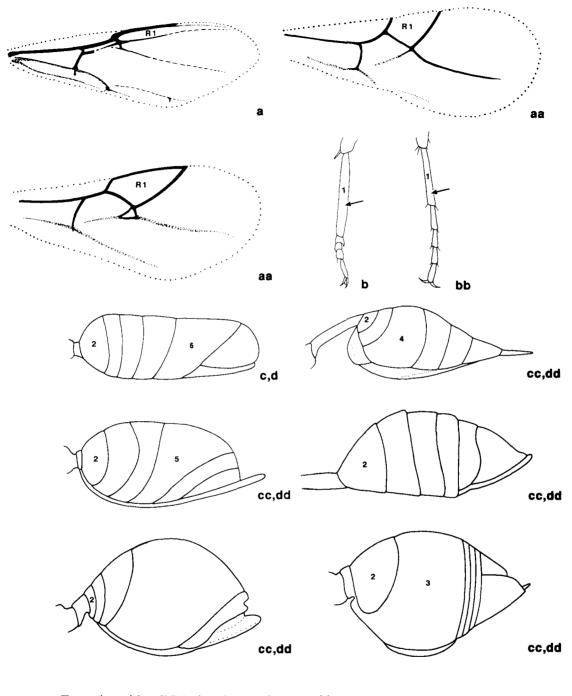
Comments This small superfamily contains both parasitic and phytophagous species. The phytophagous species, including gall formers and inquilines (Cynipidae), are the best known members, but most species are parasitic. The higher classification within Cynipoidea has not been satisfactorily resolved. The current classification is based primarily on biological characteristics and secondarily on morphological evidence.

Approximately 13 natural groups appear to exist but the relationships among them have not been determined. Most authors treat each of the 13

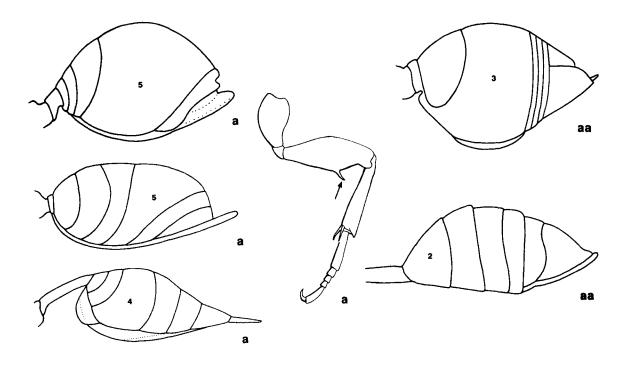
groups as a subfamily; however, there is little agreement on the number and composition of families within the superfamily. Males are typically more difficult to identify because most taxonomic work has been done on females. The following key is for practical identification and is artificial.

**References** Weld's (1952) work is the most recent on the world fauna of Cynipoidea and provides keys to genera for all subfamilies. The only other treatment of the world fauna is the monograph by Dalla Torre and Kieffer (1910). More recently, Riek (1971) and Quinlan (1979) prepared new keys to the families and subfamilies of the Cynipoidea. Riek's key does not work for many males and will not accurately place the inquiline gall formers (Cynipinae). Quinlan's key attempts to place males, but uses many characters that are not present for all taxa. Thus, a new key is presented here. The classification proposed by Quinlan (1979) is followed, but with reservations. The number of genera and species for the world was estimated from a survey of the world literature; the number of Nearctic species is taken from Burks (1979).

# Key to families of CYNIPOIDEA

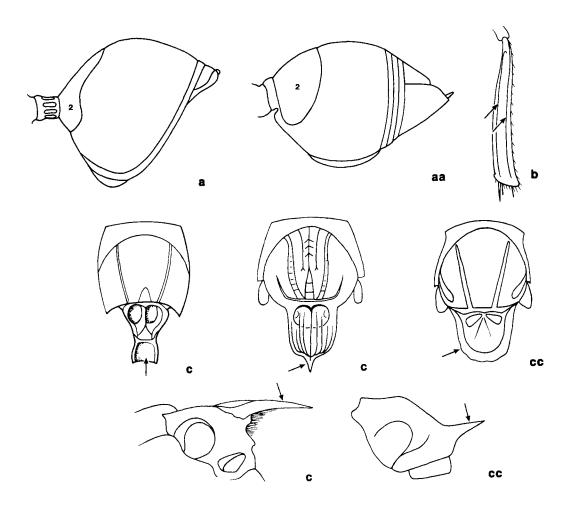


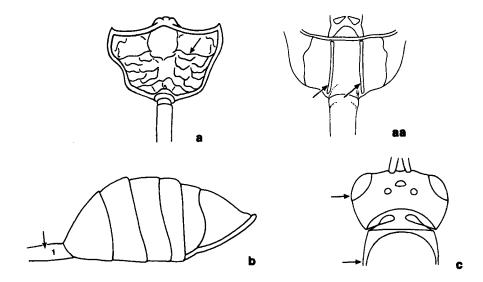
- a. Fore wing with cell R1 nine times as long as wide.
  - b. Hind leg with tarsomere 1 longer than remaining tarsomeres combined.
  - c. Metasoma from segment 2 on knife-like, strongly compressed laterally.
  - d. Female: metasomal tergum 6 longest, measured dorsally.
  - e. Body 10–30 mm long ...... **IBALIIDAE** (p. 526)
  - aa. Fore wing with cell R1 at most six times as long as wide.
  - bb. Hind leg with tarsomere 1 shorter than remaining tarsomeres combined.
  - cc. Metasoma from segment 2 on not strongly compressed.
  - dd. Female: metasomal tergum 2, 3, 4 or 5 longest, measured dorsally.
  - ee. Body usually 1-8 mm long (rarely up to 15 mm long in some Liopteridae) ...... 2



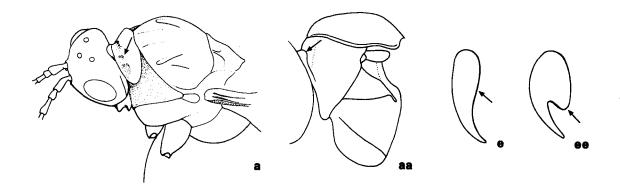




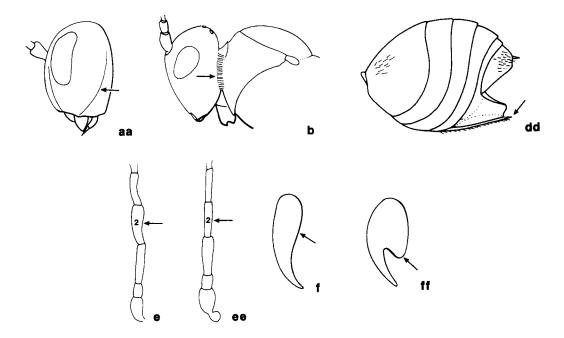




- a. Propodeum without strong lateral ridges, often with transverse ridges and 3 weak longitudinal ridges, the propodeum sometimes produced posteriorly.
  - b. Metasomal segment 1 at least 1.5 times as long as high in lateral view.
  - c. Head distinctly wider than mesosoma ...... some **FIGITIDAE** (p. 527)
  - aa. Propodeum usually with strong sublateral ridges, without transverse ridges, and usually without median longitudinal ridge.
  - bb. Metasomal segment 1 shorter than high or not apparent.



- **6(5)** a. Pronotal plate well developed, with lateral margins.
  - b. Mesoscutum smooth (except for notauli), without transverse ridges, frequently longer than wide, with only a few stout setae.
  - c. Mesoscutellum sometimes with posterior spine or ridge.
  - d. Female: hypopygium without spine.
  - e. Tarsal claws without preapical tooth.
  - f. Head with genal carina strongly developed ...... most **FIGITIDAE** (p. 527)
  - aa. Pronotal plate weakly developed (moderately developed in adults of *Euceroptres* and *Myrtopsen*, which have weakly toothed tarsal claws, females with a hypopygial spine, and at least a suggestion of transverse sculpture on the mesoscutum).
  - bb. Mesoscutum smooth or sculptured, wider than long, with or without fine and dense setae.
  - cc. Mesoscutellum without posterior spine or ridge.
  - dd. Female: hypopygium sometimes with spine.
  - ee. Tarsal claws sometimes with preapical tooth.



- 7(6) a. Head smooth and shining; posteroventral margin of gena without ridge.
  - b. Body usually without sculpture, but if with sculpture then with a distinct brush of strong seta on the gena (adults of *Lytoxysta*).
  - c. Mesotibia and metatibia often with 1 spur at apex.
  - d. Female: hypopygium without spine.
  - e. Male: flagellomere 1 or 2 frequently bent.
  - f. Tarsal claw without preapical tooth.
  - g. Body 1–3 mm long ..... CHARIPIDAE (p. 528)
  - aa. Head with rough sculpture; posteroventral margin of gena usually with ridge.
  - bb. Body with some sculpture and gena without brush of strong setae.
  - cc. Mesotibia and metatibia with 2 spurs at apex.
  - dd. Female: hypopygium usually with spine.
  - ee. Male: flagellomere 2 not bent, flagellomere 1 usually bent.
  - ff. Tarsal claw often with preapical tooth.

#### Family IBALIIDAE

(Fig. 192)

**Diagnosis** Fore wing with extremely long thin radial cell; tarsomere 1 of hind leg longer than the remaining tarsomeres combined; metasoma strongly compressed, knife-like.

Comments These are the largest Cynipoidea known, with some members reaching 30 mm in length. The family contains a single genus, *Ibalia*, parasitic on Siricidae and Anaxyelidae. The larva feeds internally in early stages, externally later. The family contains about 15 species confined to the

Holarctic region but one species has been introduced to New Zealand. Seven species occur in North America, including four in Canada.

References Maa (1949) revised the eastern Palaearctic species. Weld (1952) reviewed the Nearctic species. Kerrich (1973) revised the species associated with conifers. Fergusson (1986) revised the British species. Ronquist and Nordlander (1989) treated in detail the morphology of one species.

<sup>&</sup>lt;sup>1</sup> The family includes Himalocynipinae and Australocynipinae.

#### Family LIOPTERIDAE

(Fig. 193)

**Diagnosis** Metasomal tergum 4, 5, or 6 in dorsal view the largest tergum; metasoma petiolate. The family is divided into three subfamilies: Liopterinae, Oberthuerellinae, and Mesocynipinae. Oberthuerellinae is distinguished by the presence of a strong spine on the underside of the metafemur; Liopterinae has the metasomal petiole distinctly elongate; and Mesocynipinae has the petiole shorter than wide.

**Comments** The biology is unknown, but circumstantial evidence indicates that some are

parasitic on wood-boring insects (Coleoptera: Buprestidae; Hymenoptera: Siricidae). The family contains 13 genera and 71 species around the world but primarily in the tropics. Three species in two genera of Mesocynipinae occur in North America, none occur in Canada.

References Hedicke and Kerrich (1940) revised Liopterinae; Weld (1952) keyed genera and species of Mesocynipinae. Quinlan (1979) revised Oberthuerellinae from the Ethiopian region. Maa (1949) discussed the biology.

#### **Family FIGITIDAE**

(Fig. 194)

**Diagnosis** Metasomal tergum 3 the largest tergum; scutellum usually modified (e.g., with spines, additional pits, or ridges); female hypopygium without a spine; head and mesosoma usually strongly sculptured.

Comments The family is traditionally divided into three subfamilies: Anacharitinae, Aspiceratinae, and Figitinae. The relationships between the subfamilies are unclear, and the subfamily Figitinae is artificial; several genera appear to be intermediates between the subfamilies. The family contains 30 genera and approximately 250 described species around the world. Eighteen genera and 58 species occur in North America, including 12 in Canada.

• Anacharitinae Metasomal petiole longer than wide; head distinctly wider than mesosoma; gena with strong posteroventral ridge; mesoscutellar spine, when present, directed posterodorsally. Members of this subfamily are parasitoids of larvae of Hemerobiidae and Chrysopidae (Neuroptera). Nordlander (1982b) suggested that Anacharitinae should be given family status.

- Aspiceratinae Tergum 2 tongue-like; the posterior (inner) surface of metatibia with ridges; metasomal petiole shorter than wide; mesoscutal spine, when present, directed posteriorly. Known host records for Aspiceratinae indicate that members of this subfamily are parasitoids of Diptera puparia (Cyclorrhapha) and appear to be associated with dung. Quinlan (1979) revised the Aspiceratinae of the Ethiopian region.
- Figitinae Metasomal petiole shorter than wide; tergum 2 not tongue-like; posterior surface of the metatibia without ridges; gena usually with posteroventral ridge; mesoscutal spine (when present) directed posterodorsally. The subfamily appears to be a heterogeneous assemblage and is best defined as those Figitidae that do not belong to either Aspiceratinae or Anacharitinae. It contains mostly internal parasitoids of Diptera. The early stages of the larva are parasitized, but the parasitoid emerges from the puparium.

**References** Weld (1952) reviewed the world genera. Fergusson (1986) revised the British species.

#### Family EUCOILIDAE

(Fig. 195)

**Diagnosis** Scutellum medially with characteristic round or teardrop-shaped raised plate ("cup" of the older literature).

Comments This is the largest family of Cynipoidea. Eucoilids are internal parasitoids of the calyptrate Diptera larvae, emerging from the puparium. Many species are associated with dung or rotting fruit, but the family is not restricted to these habitats. The number of species around the

world is unknown, but most occur in the tropics, where they are very abundant. Fifteen genera and 78 species occur in North America, including 10 species in Canada. A minimum of research could double or triple the Canadian list.

**References** Eucoilidae has not been revised since Dalla Torre and Kieffer (1910) and Weld (1952). Nordlander (1976, 1978, 1980, 1981, 1982a, 1982b) revised several genera. Quinlan (1986) keyed the

Afrotropical genera. Quinlan (1967) keyed the brachypterous genera and species. Vet and Bakker

(1985) and Vet and Van Alphen (1985) studied aspects of the behavior of some species.

#### Family CHARIPIDAE

(Fig. 196)

**Diagnosis** This family is apparently defined by host association and negative morphological attributes (e.g., the lack of sculpture). Adults are usually very small (1-3 mm) and so can be difficult to identify.

Comments The family is divided into two subfamilies: Alloxystinae and Charipinae. Members of Alloxystinae are hyperparasitoids of Aphidae (Homoptera) through Braconidae (Aphidiinae) and Aphelinidae. The early stages of the hyperparasitoid are spent inside its primary host, which is inside an aphid, but after the braconid or aphelinid pupates, the last larval instar of the alloxystine feeds externally and pupates inside the inflated aphid skin. Members of Charipinae are

hyperparasitoids of Psylloidea (Homoptera) through Encyrtidae (Hérard 1986).

The family contains four genera and about 200 species around the world. Four genera and 29 species occur in North America, including 18 species in Canada.

References Weld (1952) reviewed the world genera. Hellén (1963) revised the Finnish species. Andrews (1978) revised the Nearctic species of Alloxystinae. Fergusson (1986) revised the British species. Quinlan and Evenhuis (1980) discussed the subfamily names. Menke and Evenhuis (1991) keyed the North American genera and provided a checklist of species.

#### Family CYNIPIDAE

(Fig. 197)

**Comments** All phytophagous Cynipoidea are placed in this family. Members of Cynipidae either form galls on various plants or live as inquilines in the galls of other gall-forming insects.

There is some disagreement about the limits of Cynipidae. Most European authors (e.g., Quinlan 1979) have a broad concept of the family and recognize four subfamilies: Himalocynipinae, Austrocynipinae, Pycnostigmatinae, and Cynipinae. North American authors usually have a narrower concept of Cynipidae, limiting the family to gall formers and inquilines. If this is accepted, then the other subfamilies should be given family status. However, until the higher classification is resolved, to do so here would be strictly an arbitrary decision that is unwarranted. Synerginae (inquilines), sometimes treated as a subfamily, does not warrant subfamily status.

• Himalocynipinae Yoshimoto (1970) proposed the subfamily Himalocynipinae in Figitidae for *Himalocynips vigilis* Yoshimoto from Nepal. Although the biology of *H. vigilis* is unknown, it appears to be morphologically intermediate between Figitinae and Cynipinae, and is easily distinguished from them both by the forward-projecting clypeus and by the antenna with 18 flagellomeres. The presence of a distinct hypopygial spine appears to show a closer relationship between *Himalocynips* and other Cynipidae than to Figitidae.

- Austrocynipinae Riek (1971) proposed the subfamily Austrocynipinae in Cynipidae for Austrocynips mirabilis Riek. Austrocynips is intermediate between Mesocynipinae and Cynipinae and is therefore placed in its own subfamily. It is easily distinguished by the stigma in the radial cell of the fore wing; the presence of a hypopygial spine relates Austrocynips to Cynipidae. It has been reared from the seeds of Araucaria in Australia.
- Pycnostigmatinae This subfamily contains two species, each in its own monotypic genus restricted to Africa. It is distinguished by the distinctive radial cell which is reduced in size, closed, with heavy veins, and resembles a stigma. The biology of Pycnostigmatinae is unknown, but it has been suggested that they are inquilines in the galls of other insects.
- Cynipinae Many female Cynipinae have the hypopygial spine extremely well developed; however, males are difficult to identify, and it is often impossible to place them to genus. Gall-forming species on oaks (Quercus) and roses (Rosa) can be recognized by the extremely narrow pronotum (median dorsal length less than one-seventh lateral height). Most species of Cynipinae form galls on Quercus (Fagaceae) species in warm-temperate and subtropical regions. Sexual and agamic generations alternate in many oak gall formers. A few genera form galls

on Compositae and Rosaceae, but rarely other plants. Cynipinae is restricted to the Holarctic region except for one species in South Africa (*Rhoophilus loewi* Kieffer) and eight species in South America (*Myrtopsen* spp., *Plagiotrochus suberi* Weld). The subfamily contains about 93 genera and 1200 species around the world. Forty-six genera and about 640 species occur in North America, including about 110 species in Canada.

References Weld (1952) keyed the genera of gall formers and inquilines, and Weld (1957, 1959, 1960) provided illustrated lists of the galls of the United States. Kinsey (1930, 1936) described and keyed the oak-gall formers of North America; however, these keys are difficult to use. Eady and Quinlan (1963) gave illustrated keys to the galls and gall formers of Britain; Buhr (1964) keyed the European species. Askew (1984) reviewed the biology of gall formers.

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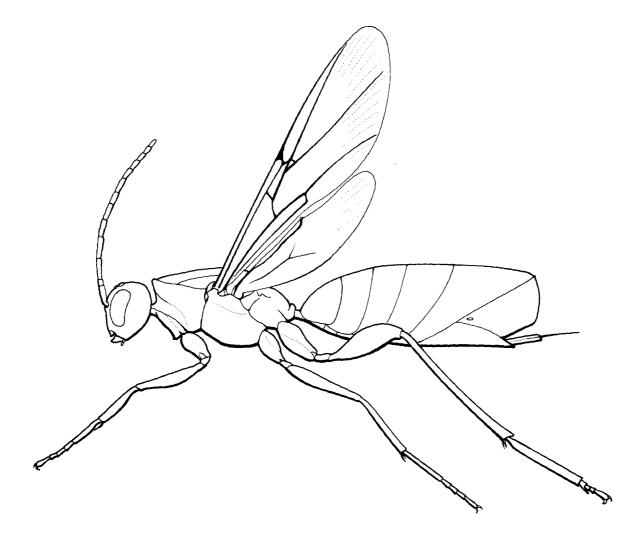


Fig. 192. Ibaliidae

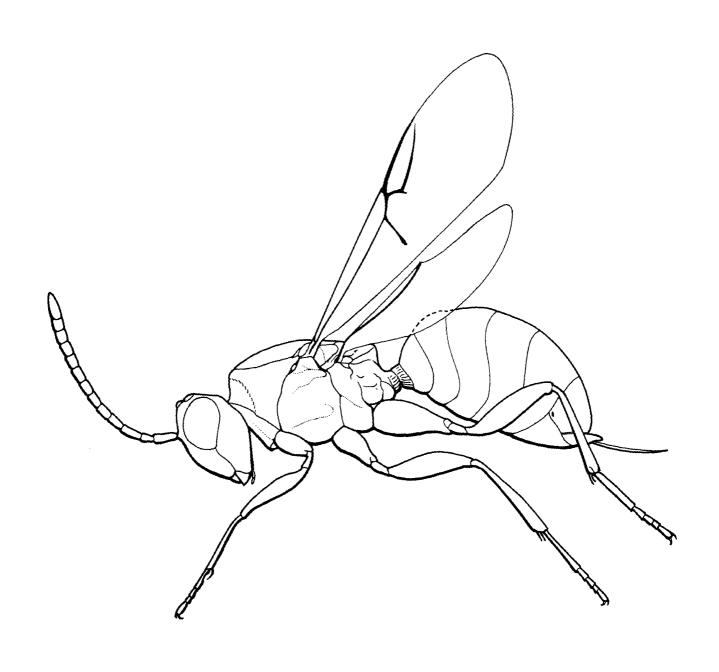
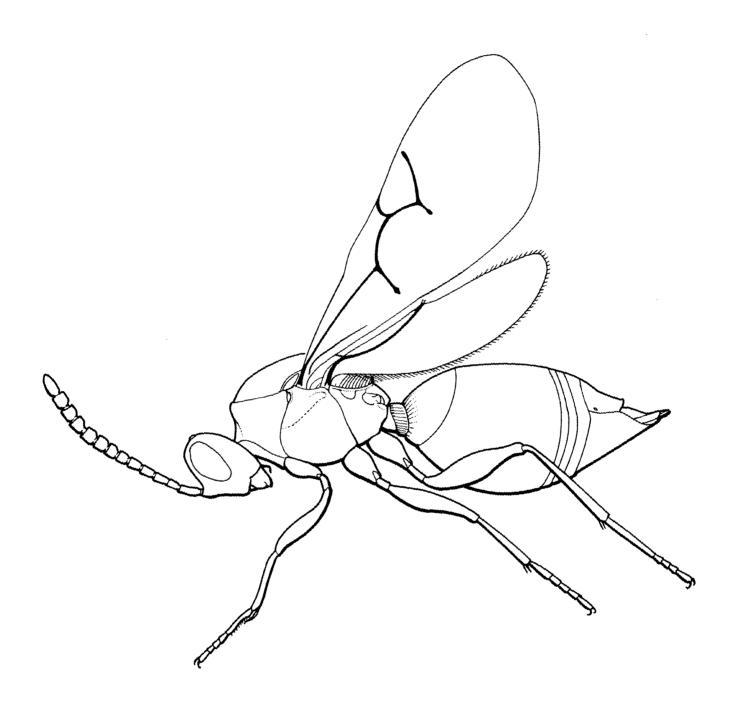


Fig. 193. Liopteridae



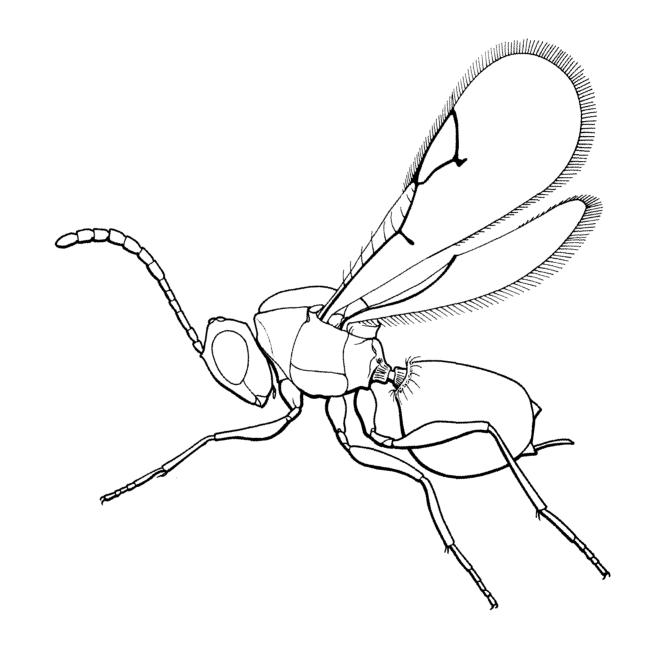


Fig. 195. Eucoilidae

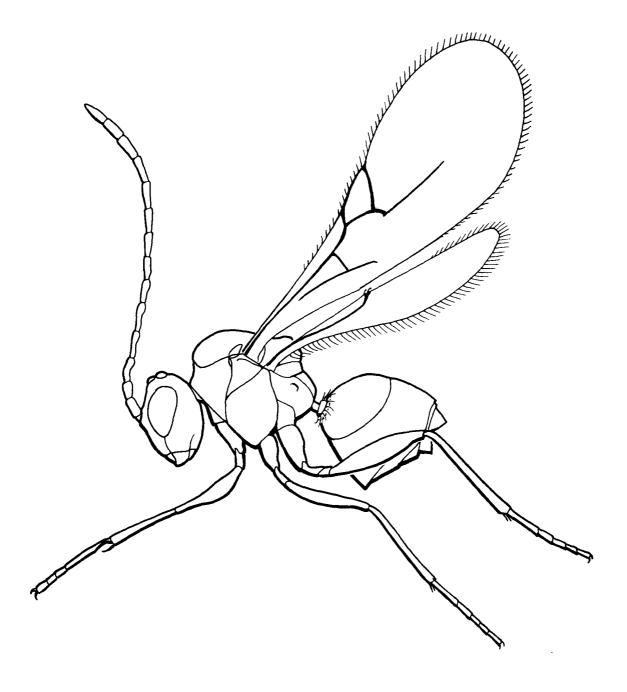


Fig. 196. Charipidae

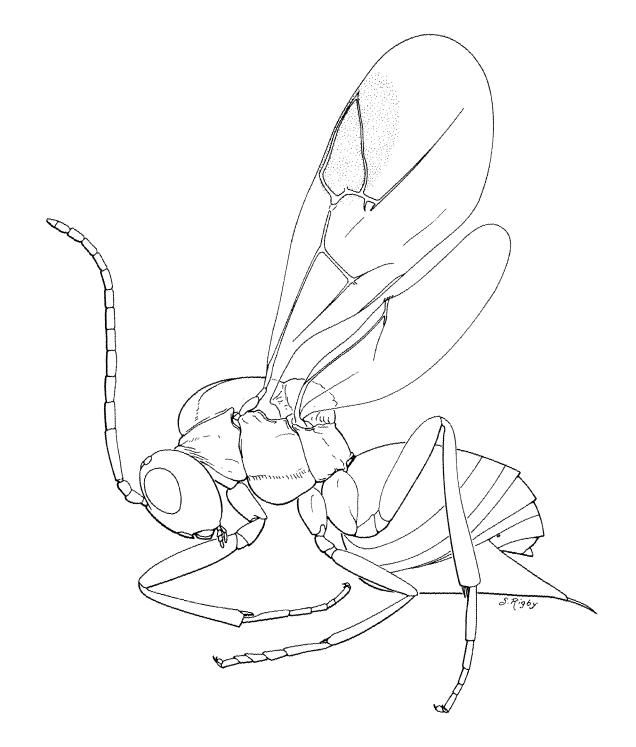


Fig. 197. Cynipidae

### Chapter 13 Superfamily PROCTOTRUPOIDEA

(Figs. 198-206)

Lubomir Masner

Included families (9): Austroniidae, Diapriidae, Heloridae, Monomachidae, Pelecinidae, Peradeniidae, Proctotrupidae, Roproniidae, Vanhorniidae.

Only two of the included families, Diapriidae and Proctotrupidae, are speciose. The rest are small, relict families, with few species. The entire superfamily is apparently very old, with some intermediate groups missing, so that the extant families are isolated from one another and therefore easy to distinguish.

Because of its taxonomic diversity this superfamily is difficult to define morphologically. However, all members are strongly sclerotized and nonmetallic; the antennae have a constant number of flagellomeres (at the specific and generic level), without longitudinal placoid sensilla; metasomal segment 2 (true or apparent) is often the largest segment; and the ovipositor is either internal, or it is external and is housed in strongly sclerotized sheaths (in *Vanhornia* it is in a ventral groove on the

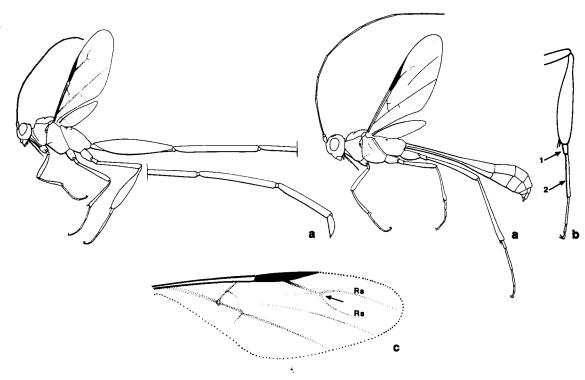
metasoma), always issuing from the metasomal apex.

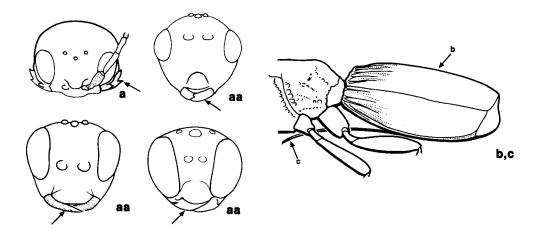
The biology and hosts of the superfamily are as diverse as its morphology. Members of most of the families are predominantly parasitoids of various Coleoptera, rarely Symphyta or Neuroptera. Diapriidae and Monomachidae seem to be confined mostly to Diptera, although a few species of the former parasitize Coleoptera or Formicidae, and *Ismarus* is hyperparasitic on Homoptera through Dryinidae.

About 2500 species are described but the world fauna is estimated at about 6000 species.

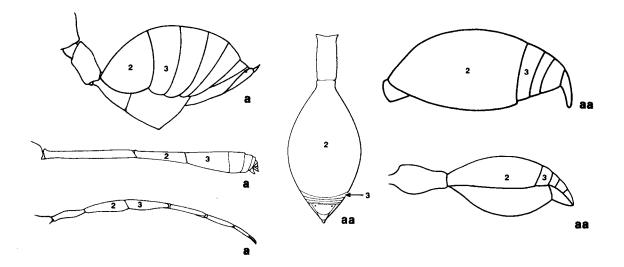
Within the superfamily two groups appear to form more natural units: Pelecinidae, Vanhorniidae, Proctotrupidae, Heloridae, Peradeniidae, and Roproniidae in one group, and Monomachidae, Austroniidae and Diapriidae in the other. Naumann and Masner (1985) keyed the families; Johnson (1992) cataloged the species.

## Key to families of PROCTOTRUPOIDEA

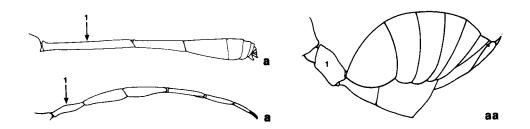


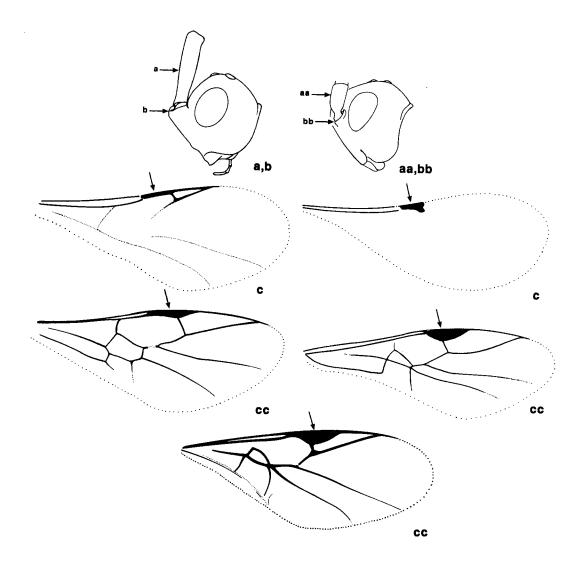


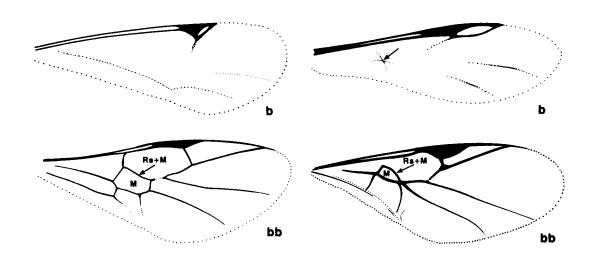
- 2(1) a. Mandibles exodont, with tips not touching when closed.
  - Metasomal tergum 1 (syntergum) distinctly the largest.
  - Ovipositor directed forward between legs and housed in ventral groove on metasoma. (Northern Hemisphere; three described species) ...... VANHORNIIDAE (p. 543)
  - aa. Mandibles endodont, with tips touching or crossing when closed, the mandibles rarely reduced or absent.
  - Metasomal tergum 1 not largest, but often long, cylindrical, in some Proctotrupidae covered bb. dorsally by syntergum and visible only at sides.



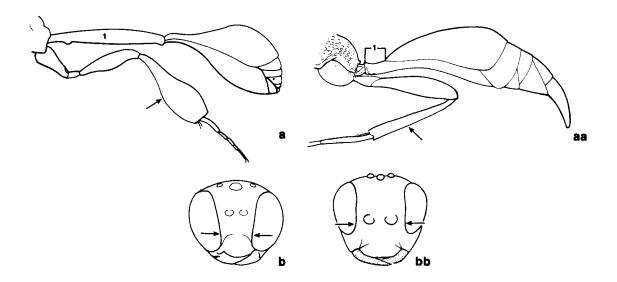
- 3(2) Metasomal tergum 2 subequal to tergum 3 ...... Metasomal tergum 2 (true or apparent) several times as long as tergum 3 ......







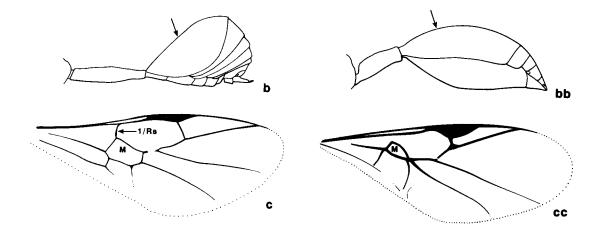
vein .....



- 7(6) a. Metasomal segment 1 as long as rest of metasoma; metatibia club-like.
  - b. Eyes with inner margins strongly convergent ventrally.

  - aa. Metasomal segment 1 and metatibia not as above.
  - bb. Eyes with inner margins not convergent ventrally.
  - cc. Lateral ocellus separated from inner orbit by more than its own diameter.

    (Worldwide; many species) ...... PROCTOTRUPIDAE (p. 544)



- **8(6)** a. Antenna with 12 flagellomeres, none ring-like.
  - b. Metasoma beyond segment 1 strongly compressed laterally, much higher than wide, in lateral view with terga much higher than sterna.

  - aa. Antenna with 14 flagellomeres, including 1 ring-like.
  - bb. Metasoma beyond segment 1 slightly wider than high, in lateral view with terga subequal in height to sterna.

### Family PELECINIDAE

(Fig. 198)

**Diagnosis** Body at least 20 mm long, up to 70 mm long in some larger females, black. Fore wing with vein Rs forked; female metasoma long and slender, male metasoma shorter and pedunculate with metasomal segment 1 forming petiole.

**Comments** The single known species, *Pelecinus polyturator* (Drury), parasitizes grubs of *Phyllophaga* (Coleoptera: Scarabaeidae) by sticking its entire flexible metasoma into the soil to reach the host.

Females are encountered fairly frequently in late summer or early fall in eastern Canada, but males are very rare. The family occurs only in the Western Hemisphere (Canada to Argentina), but one extinct genus is known from Oligocene Baltic amber.

**References** Lim et al. (1980) described the prepupa and pupa of *P. polyturator*. Mason (1984) described the structure and function of the female metasoma.

### Family VANHORNIIDAE

(Fig. 199)

**Diagnosis** Body 6-7 mm long. Mandibles exodont; antenna inserted right above clypeus; metasoma with most segments fused to form large carapace; ovipositor housed in ventral groove on metasoma, with apex projecting forward.

**Comments** The species *Vanhornia eucnemidarum* Crawford parasitizes larvae of Eucnemidae (Coleoptera) in old, dying maple (*Acer*) trees. The

family contains one genus with five species: one in Europe, two in North America (one undescribed), one in China, and one (undescribed) in Japan.

**References** Mason (1983) described the structure of the metasoma. He and Chu (1990) described a species from China. Deyrup (1985) provided information on the biology of *V. eucnemidarum*.

### **Family PROCTOTRUPIDAE**

(Fig. 200)

**Diagnosis** Body 3–10 mm long, relatively robust, usually black, with predominantly smooth sculpture except on propodeum. Mandible usually unidentate; antenna thread-like, with 11 flagellomeres in both sexes; fore wing with distinct stigma, with relatively wide closed costal cell and closed radial cell formed by tubular veins, and with other veins nebulous; transscutal suture (between tegulae) absent; metasoma in lateral view more or less curved, with apex distinctly downcurved in females; metasomal tergum 1 and sternum 1 fused to form petiole, and petiole fused posteriorly with sternum 2 (petiole sometimes overlapped by anterior margin of syntergum); terga 2-4 fused into syntergum; all terga in lateral view overlap the sterna considerably to entirely. Female ovipositor with strongly sclerotized sheaths.

Comments Most species are solitary endoparasitoids of Coleoptera larvae living in soil litter and rotten wood; some species parasitize larvae of Mycetophilidae (Diptera). Gregarious parasitism occurs and is considered a secondary adaptation. In all species a peculiar emergence pattern from the host occurs. The parasite larva pupates outside the host larva but remains connected by its posterior end to the ventral surface of the host, as in Pelecinidae. A thin membrane (but no cocoon) is formed on the parasitoid pupa. Adults are common in wet, shaded habitats. Males generally are caught in Malaise traps, females in pan or pitfall traps.

Townes and Townes (1981) recognized three subfamilies: Vanhorniinae, Austroserphinae

(= Acanthoserphinae), and Proctotrupinae. Here, Vanhorniinae is treated as a family related to Proctotrupidae.

Austroserphinae, with three genera and few species in Australia, New Guinea, and South America, represents an archaic group with the most complete wing venation, though most of the veins (M, Rs+M, Cu) are only nebulous; the scape has one or two sharp spikes; and the mandibles are almost vestigial. *Austroserphus* has the ovipositor and sheaths enclosed in a long gutter-shaped extension of the apical sternum that presumably is used for digging or for piercing during oviposition.

Heloriserphus, with two species from Chile, represents, in the author's opinion, a separate subfamily characterized mainly by the unique structure of the metasoma, which is not downcurved at the apex, is campanulate rather than laterally compressed with the sterna considerably exposed, and has the ovipositor protruding straight back in line with the longitudinal axis of the body.

Proctotrupinae is the largest subfamily, with 21 genera of very uniform habitus around the world.

The family contains 310 described species but up to 1200 are estimated for the world fauna. Seventy-five species occur in North America, including about 35 in Canada.

**References** Townes and Townes (1981) revised the world species. Nixon (1938) keyed the British species. Pschorn-Walcher (1971) keyed the species of Switzerland, but the key can be used for all of central Europe. Kozlov (1987) keyed the species for the former USSR.

### **Family HELORIDAE**

(Fig. 201)

**Diagnosis** Body 6–8 mm long, robust, usually black. Mandibles long, sickle-shaped, and crossing over scissor-like; labrum long and narrow, finger-like, usually not exposed; flagellum with ring-like article between pedicel and flagellomere 1; fore wing with 5 closed cells including subtriangular first medial cell; tarsal claws pectinate; metasomal segment 1 distinctly elongate (petiolate); metasomal terga 2–4 fused into syntergite.

Comments Members are solitary endoparasitoids in larvae of Chrysopidae (Neuroptera). Adults emerge from the host cocoon. The family contains seven uncommon species around the world but is apparently absent from lowland tropics. Two species occur in North America, including Canada.

**References** Townes (1977) reviewed the world species.

### **Family PERADENIIDAE**

(Fig. 202)

**Diagnosis** Body 6-10 mm long, robust, black, similar in habitus to some twig-nesting

Pemphredonidae (*Pemphredon*). Eyes extremely large, with inner orbits distinctly converging below;

malar space almost absent; pronotum in lateral view strongly receding backwards; fore wing venation reduced to only 2 closed cells; metatibia strongly clavate; metasomal segment 1 extremely long and narrow (petiolate), anterior part of tergum 2 and sternum 2 constricted and neck-like, terga 2-4 fused into syntergite.

**Comments** Biology is unknown but I.D. Naumann (personal communication) observed a distinct flight period during winter. The family contains one genus (*Peradenia*) with two rare species restricted to Tasmania and Victoria, Australia.

**References** Naumann and Masner (1985) described the family.

#### Family ROPRONIIDAE

(Fig. 203)

**Diagnosis** Body 5–10 mm long, robust, with some coarse sculpture; fore wing with relatively complete venation; metasoma beyond petiole rudder-shaped, compressed, metasomal segment 1 forming long petiole; metasomal tergum 2 clearly (only moderately in *Xiphyropronia*) the longest; hypopygium plough-shaped in females.

**Comments** One species has been reared from Symphyta cocoons. The family contains two genera

with 18 species in the Nearctic, Palaearctic, and Oriental regions. Four species (one undescribed) occur in North America, including two in Canada.

**References** Townes (1948) reviewed the world species. Yasumatsu (1956), Heqvist (1959), Chao (1962), He (1983), Lin, (1987), and Madl (1991) described additional species from the Palaearctic and Oriental regions.

### Family AUSTRONIIDAE

(Fig. 204)

**Diagnosis** Body about 5 mm long, smooth, relatively robust. Metasoma almost scalpel-like, strongly compressed laterally, especially in females; ovipositor relatively long but retracted into metasoma and upcurved apically; pronotum with sharp transverse carina medially, partly covering anterior part of mesoscutum; metacoxa close to propodeal orifice; metasomal segment 1 (petiole) slightly elongate in female, more distinctly elongate in male.

**Comments** Biology and hosts are unknown. This family contains one genus with three species and is restricted to Australia.

**References** Riek (1955) described *Austronia* in the Heloridae. Kozlov (1970) proposed the family Austroniidae.

### Family MONOMACHIDAE

(Fig. 205)

**Diagnosis** Body 10–18 mm long, smooth, slender, not black; sexes very dimorphic. Female with sickle-shaped attenuated metasoma; male with pedunculate metasoma. Mandible massive; pronotum almost neck-like with sharp transverse ridge, capable of sliding over anterior part of mesoscutum; propodeum distinctly cone-shaped, without median keel; metacoxa inserted relatively far from propodeal foramen; fore wing with at least 5 closed cells and relatively narrow stigma; metasomal segment 1 (petiole) remarkably long and slender; metasomal tergum 2 composed of 1 tergum that is not the longest segment; ovipositor extremely short, concealed inside metasomal segment 8.

Comments Some Neotropical species are light green and a few are multicolored. One Australian species has been reared from Stratiomyidae (Diptera). Adults of the Australian species are active during the winter. In two undescribed Neotropical species (from Peru and Chile) the female is micropterous. The family contains two genera and about 20 rare species, mostly in the New World tropics (Guerrero, Mexico, to Argentina and Chile), with only a few others in Australia and New Guinea. The family presumably originated in the Southern Hemisphere.

**References** Schulz (1911) revised the world species. Naumann (1985) revised the Australian species.

#### Family DIAPRIIDAE

(Fig. 206)

**Diagnosis** Body mostly 2–4 mm long, exceptionally as small as 1 mm or as large as 8 mm, smooth and highly polished; antenna more or less distinctly elbowed, with moderately to strongly elongate scape inserted high above clypeus, usually on a prominent transverse ledge; fore wing without stigma but sometimes with slightly thickened marginal vein; metasoma distinctly petiolate with true or apparent tergum 2 the longest; ovipositor almost entirely retracted.

**Comments** The biological groundplan is primary endoparasitism of various Diptera (larval-pupal, or pupal parasitoids), though species in other orders are parasitized by some advanced groups. Adults are generally found in damp, shaded habitats such as in forests and marshes, near or in water, and in the soil. Four subfamilies are recognized: Belytinae, Ismarinae, Ambositrinae, and Diapriinae. These seem to form natural units well characterized both morphologically and biologically. The family contains about 150 genera and about 2300 described species, but the fauna is estimated to be 4500 species around the world. About 300 species occur in North America, including about 200 in Canada. Most taxa outside Europe are undescribed.

- Belytinae is perhaps the most primitive subfamily on the basis of morphology and hosts. The fore wing has relatively complete venation, usually with three closed cells (costal, medial, and radial), and metasomal tergum 2 is formed by 1 large tergum. Belytinae is best defined by a single synapomorphy: two longitudinal grooves on metasomal sternum 2 in which the lateral margins of tergum 2 fit. This groove may continue on the following sterna, sometimes supplemented by a ridge. The antenna of Belytinae usually has 13 flagellomeres in females (rarely 12 or only 10), 12 in males, with flagellomere 1 sexually modified; the scape is relatively long, inserted high on frons on distinct ledge. Although there are few reliable host records, Belytinae appears to be restricted to Mycetophilidae and Sciaridae (Diptera) (Chambers 1971). The subfamily occurs around the world mostly in moist habitats, with the greatest diversity and abundance in the cool southern temperate forests of Chile, New Zealand, Tasmania, and southeastern Australia.
- Ismarinae is perhaps the most aberrant subfamily, both morphologically and biologically. The female antenna has 13 flagellomeres, the male has 12, and flagellomere 2 is sexually modified; the scape is relatively short, about 2.5 times as long as wide, inserted fairly low on frons, which is not expanded into a ledge; the

- mesosoma is relatively short and highly convex dorsally, with notauli reduced to small anterolateral depressions; the metatibia is strongly incrassate; metasomal segment 1 is a very short petiole, the remainder of the metasoma is campanulate, with the terga fused to various degrees to form a carapace. In the most primitive species all the sutures between terga are superficially indicated, giving a large single tergum 2, but in more advanced species the sutures gradually become evanescent until only one suture remains between tergum 7 and 8. The unique position of Ismarinae, not only within Diapriidae but Proctotrupoidea in general, is underlined by its biology. Adults are hyperparasitoids of Cicadellidae (Homoptera) through larvae of Dryinidae (Chambers 1955, Waloff 1975, Jervis 1979). With only a few rare or infrequent species in one genus this relict subfamily is the smallest in Diapriidae.
- Ambositrinae shares the ancestral number of flagellomeres (females 13, males 12) with the previous two subfamilies. Usually, male flagellomere 2 is sexually modified, metasomal sternum 2 is divided by a deep suture from large sternum 3, and the metasomal tergites are sharply margined laterally and acutely flexed under to couple with the sterna. In most genera the large tergum 2 (syntergum) is composed of fused terga 2, 3, and 4 so that the metasoma has only five visible tergites in females and six in males (two primitive Southern Hemisphere genera have one extra free tergum visible). Wing venation is relatively reduced, with the radial cell not closed, the marginal vein usually very short, and the costal vein sometimes absent (e.g., Ambositra). The sexes are occasionally strikingly dimorphic, with females brachypterous or apterous, almost ant-like, and males macropterous. Occasionally both sexes are brachypterous. Biology is known for only one species. Hosts are assumed to be Mycetophilidae and related Nematocera (Diptera). There are about 20 genera, mostly with Gondwanan distribution. Most species occur in moist forest habitats in south temperate zones.
- Diapriinae has the derived number of flagellomeres either 11 in both sexes (Spilomicrini) or 10 in females and 12 in males (other tribes). Numerous variations occur caused by a reduction in number. The male antenna is thread-like, often with long hairs or bristles, and flagellomere 2 is modified. The female flagellum is more or less distinctly clavate or incrassate towards the apex. The fore wing has reduced venation; in some species the wing appears to be or really is veinless; and the radial cell is not

closed. Primitive Diapriinae (Psilini) have a true large tergum 2, but in most derived members (Spilomicrini, Diapriini) the apparent tergum 2 is actually composed of terga 2 and 3 fused into a syntergum. Hosts are primarily Diptera Orthorrhapha (Tabanidae, Stratiomyidae, Syrphidae) and Cyclorrhapha (e.g., Muscidae, Anthomyiidae, Tachinidae, Calliphoridae, Sarcophagidae, Chloropidae, Tephritidae). Secondarily, some species changed hosts to Coleoptera (Staphylinidae, Psephenidae), and some appear to parasitize larvae of Formicidae. Some species occur in extreme habitats, where their hosts are found, e.g., the intertidal zone of continents and subantarctic islands (Early 1978, 1980), deep in the soil, in mammal burrows, and in bird nests. Species of several highly specialized genera of Diapriini are highly integrated with army ants in the New World and termites (Dictuoptera: Termitodea) in the Old World

tropics. Huggert and Masner (1983) assumed that some of these species changed hosts gradually from parasitizing scavenging Diptera living in ant nests to the ants themselves. However, only two records are available to support this (Huggert and Masner 1983, Loiácono 1987).

References Kieffer's (1916) key to world genera is largely of historical value only. Keys by Nixon (1957, 1980) for Britain (also good for northwestern Europe), and Kozlov (1987) for the former USSR are good starting points for interested students. There are no modern keys to world genera. Masner (1976) revised the New World Ismarinae. Masner (1961) proposed the subfamily Ambositrinae. Naumann (1982, 1987, 1988) revised the Ambositrinae of Australia, New Zealand, New Guinea, and Oceania. Hellén (1963) keyed the Finnish Diapriinae.

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Fig. 206. Diapriidae

## Chapter 14 Superfamily PLATYGASTROIDEA

(Figs. 207, 208)

Lubomir Masner

Included families (2): Platygastridae, Scelionidae.

The placement of the two families Scelionidae and Platygastridae as an independent superfamily outside the classical Proctotrupoidea may appear rather avant-garde. However, an opinion about the special position of these two families was expressed some time ago (Masner 1956) and later was formally recognized in at least two major classifications (Richards and Davies 1977, Delvare and Aberlenc 1989) as Scelionoidea. Nevertheless, a thorough phylogenetic analysis supported by an in-depth morphological study is necessary to justify the superfamily and to recognize it properly. This will be done elsewhere, but a brief discussion is presented below.

The first and most important attribute of Platygastroidea is found in the unique structure of the metasoma and particularly in the operating mechanism of the ovipositor. The ovipositor is relatively weakly sclerotized, and when not in use is entirely retracted inside the metasoma, where it is housed in a tube of soft tissue (Austin 1983). The tube itself seems to be homologous to intersegmental membrane and may be folded; in some groups its parts are telescoped to achieve maximum length when extruded. Morphological adaptations for increasing the length may be internal or external. Internal adaptations are, for example, a coil-like housing of the ovipositor within the metasoma. External adaptations include a specialized horn on tergite 1, a hump on sternite 1, a sac-like extension of sternite 2, or a tail-like extension of the entire metasoma. The tube with ovipositor is extruded from the metasoma during oviposition by joint action of muscles and turgor pressure of body fluids. The turgor pressure is presumed to be created by pumping movements of the head and propleura into the mesosoma and by the bellows-like action of the metasomal tergites and sternites. To achieve maximum pumping pressure and ovipositor extension, all metasomal segments, including segment 1, have the tergites and sternites connected at the sides with either simple tissues, or more or less specialized locking mechanisms consisting of laterotergites and

laterosternites. The loss of functional metasomal spiracles in species of Platygastroidea is correlated with the presumed bellows-like functioning of the metasoma. Depending on the group (genus, tribe, subfamily) the female metasoma in Platygastroidea has only 7 (many Scelionidae) or 6 (some Scelionidae and almost all Platygastridae) visible terga; a few highly derived Platygastridae have only 3 or 2 visible terga. This anomalous situation is explained primarily by a reduction or a loss of the true abdominal tergum 8 in all groups. When reduced, abdominal tergum 8 is attached to the anterior margin of abdominal tergum 9 (= metasomal tergum 7) and is always fully internal, not visible (e.g., Teleasinae). However, in most groups it is depigmented and hyaline, or completely lost. The primitive condition of metasomal tergum 7 (= abdominal 9) is completely external, fully sclerotized, bearing a pair of cerci or sensory plates with long bristles and articulating with metasomal tergum 6 without being extruded with the ovipositor tube (Telenominae, Gryonini, Baeini). In some derived groups of Scelioninae, metasomal tergum 7 may be partly or completely invaginated under metasomal tergum 6 and extruded with the ovipositor tube at its tip during oviposition; the cerci with long bristles most probably serve as sensory organs to detect the host egg in the surrounding substrate (soil, plant tissue). In Platygastridae, abdominal tergum 8 is absent and metasomal tergum 7 (= abdominal 9) is strongly reduced, hyaline, without cerci or sensory plates, always deeply invaginated under metasomal tergum 6, and not extruded with the ovipositor tube.

The second major attribute of Platygastroidea is the presence and function of basiconic sensilla on club articles (clavomeres) of the female antenna. Each clavomere bears 1–2 sensilla on its extreme ventral margin or surface. If two sensilla are present they are parallel to each other (paired in *Nixonia*). Preliminary experiments and observations indicate that these structures may have a secretory rather than receptory function (Bin and Vinson 1986).

About 4000 species have been described, but the world fauna is estimated to be about 10 000 species.

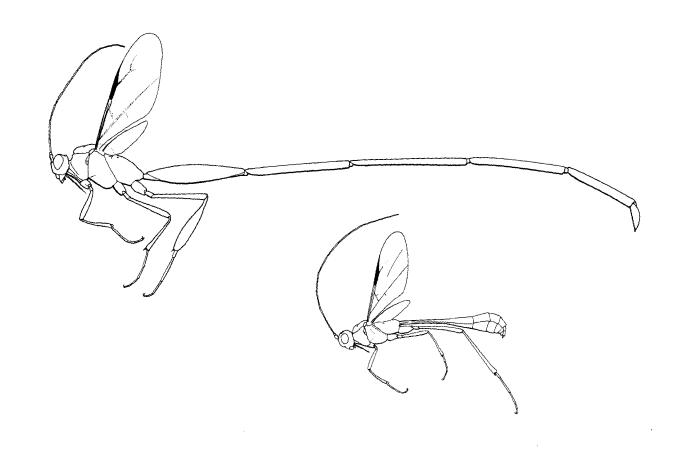


Fig. 198. Pelecinidae

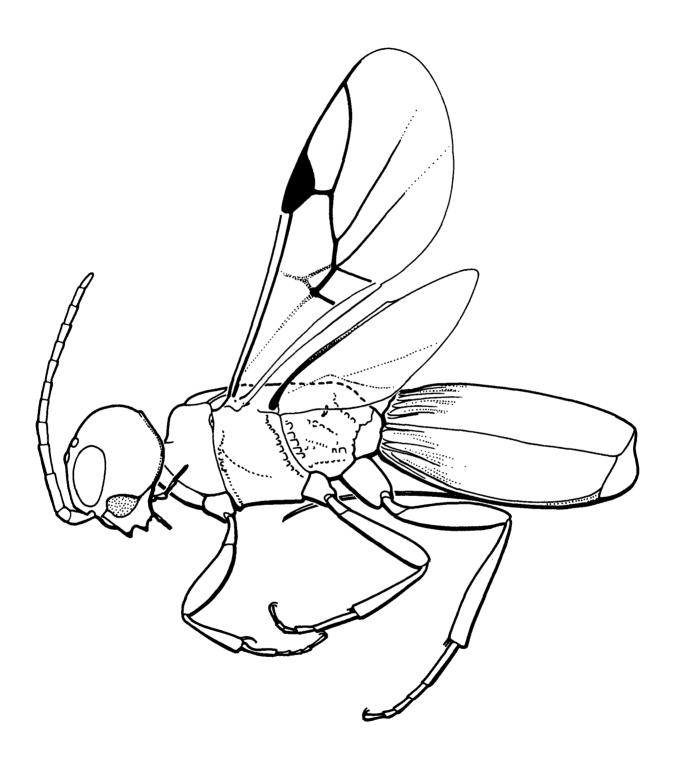


Fig. 199. Vanhorniidae

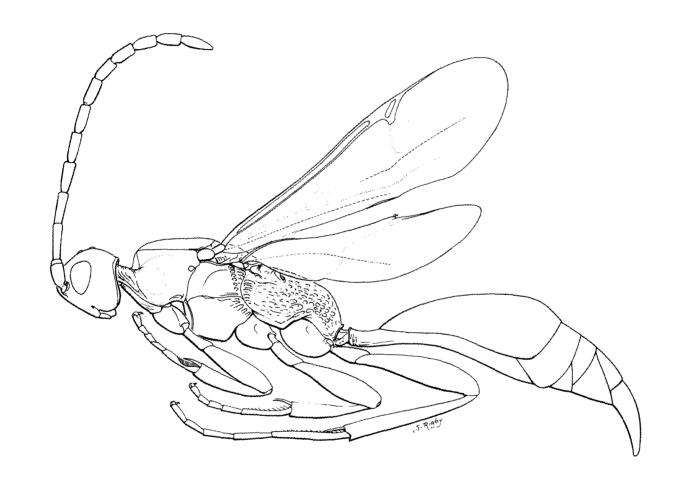


Fig. 200. Proctotrupidae

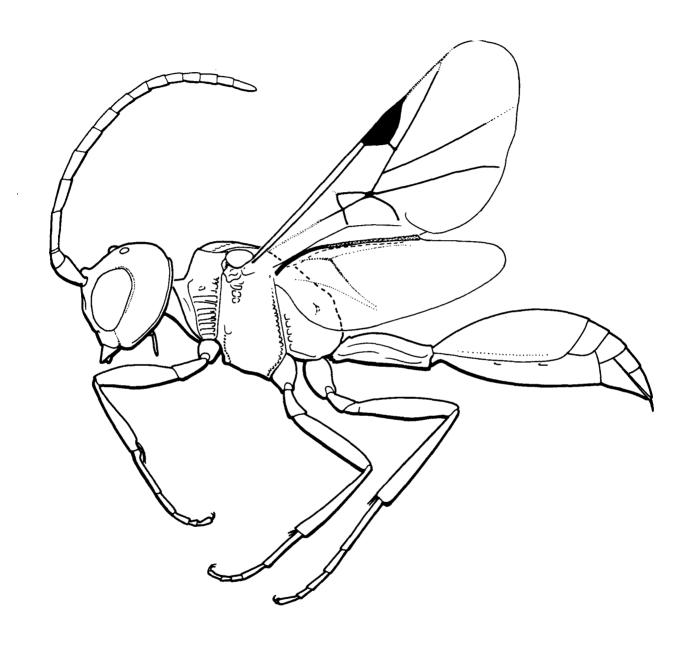


Fig. 201. Heloridae

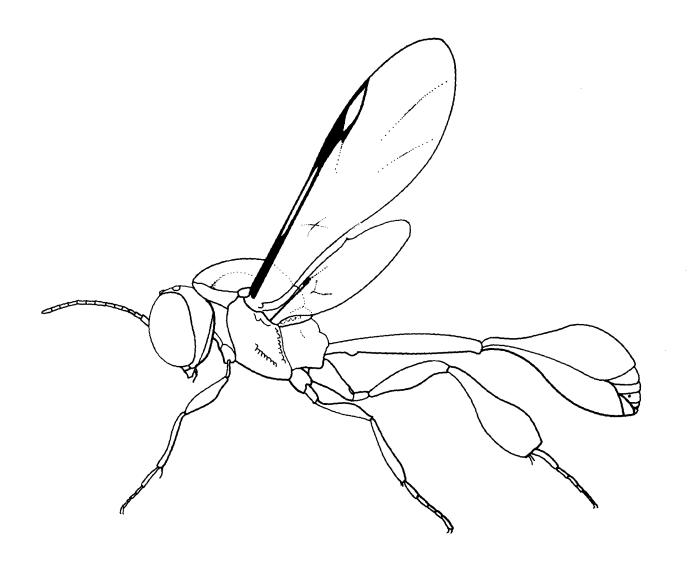


Fig. 202. Peradeniidae

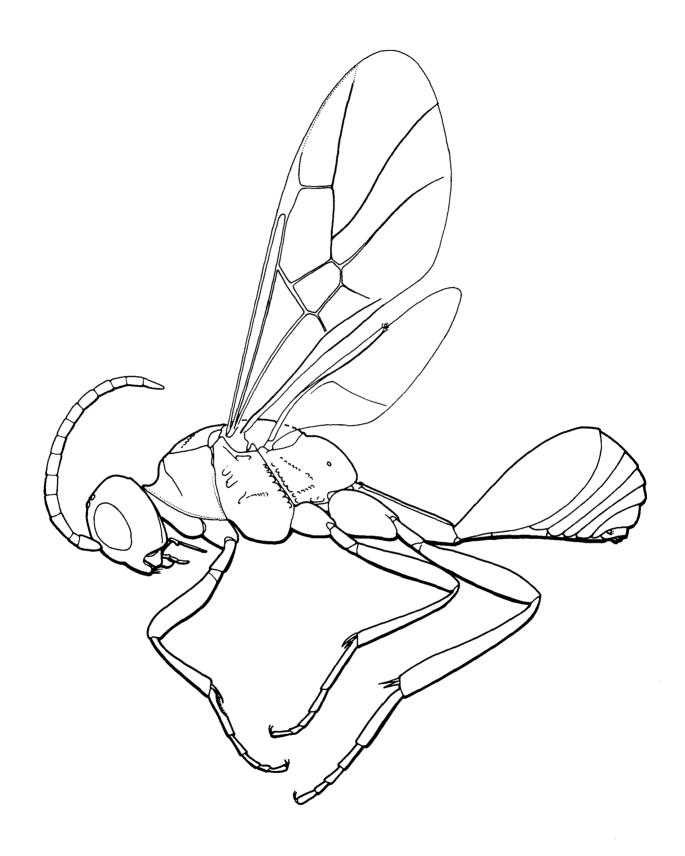


Fig. 203. Roproniidae

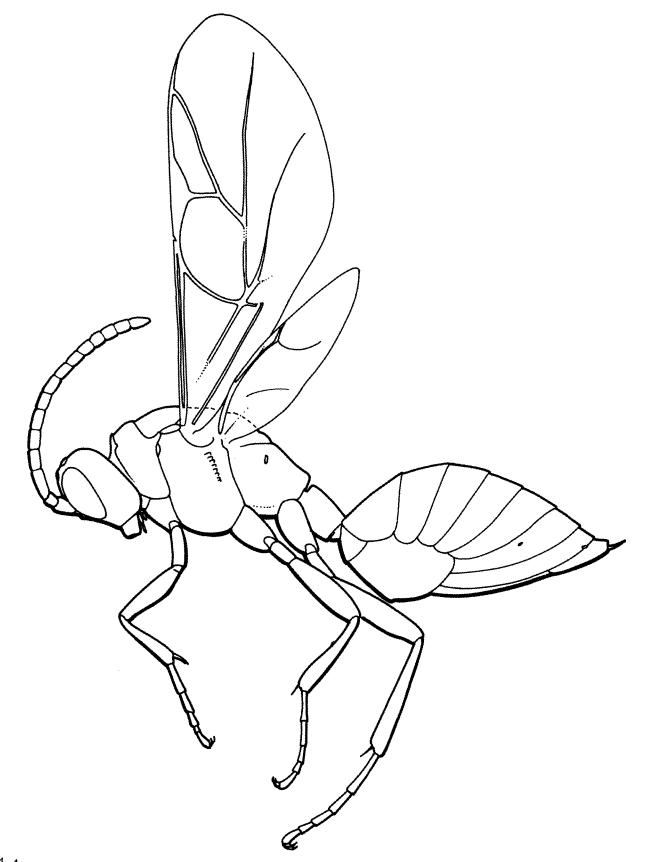


Fig. 204. Austroniidae

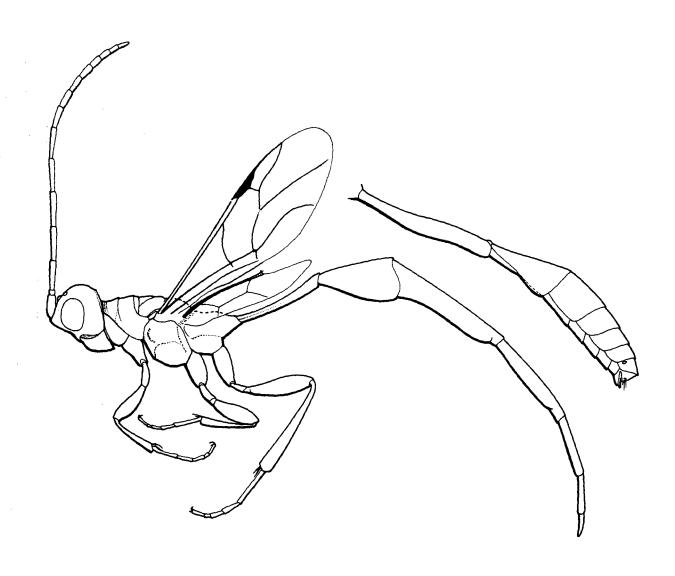
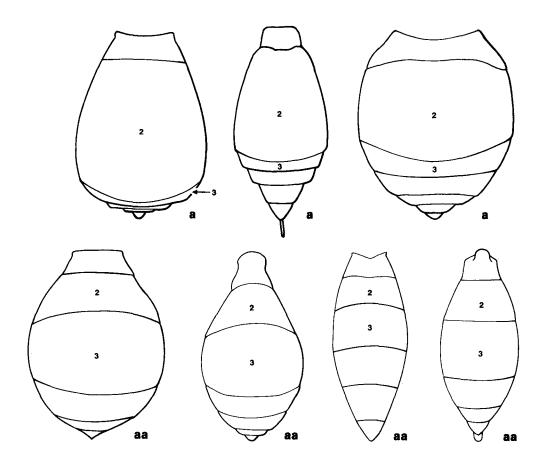
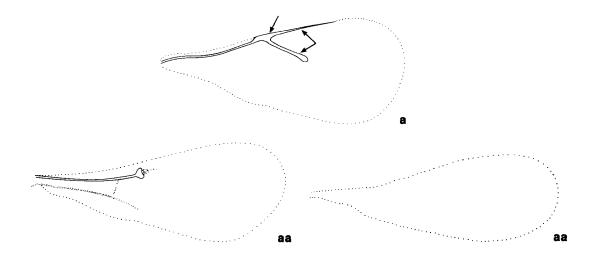


Fig. 205. Monomachidae

# Key to families of PLATYGASTROIDEA



- - aa. Metasomal tergum 2 at most slightly longer than tergum 3, almost always distinctly shorter than subsequent terga combined . . . . . . . . . . . . . most **SCELIONIDAE** (p. 560)



- 2(1) a. Fore wing with stigmal vein and usually also postmarginal vein, the veins rarely indistinct or absent.
  - b. Antenna usually with 9–10 flagellomeres, very rarely with 8 or fewer flagellomeres.
  - c. Male flagellomere 3 modified ...... some SCELIONIDAE (p. 560)
  - aa. Fore wing without stigmal and postmarginal veins, usually veinless.
  - bb. Antenna usually with 8 flagellomeres, rarely with fewer flagellomeres.
  - cc. Male flagellomere 2 or rarely 1 modified ................ PLATYGASTRIDAE (p. 561)

#### Family SCELIONIDAE

(Fig. 207)

**Diagnosis** Body 1–2.5 mm long, rarely as small as 0.5 mm or as large as 10 mm, predominantly black, sometimes yellow or multicolored, often distinctly sculptured, rarely with metallic colors. Antenna usually with 9 or 10 flagellomeres, occasionally as few as 4 or as many as 12. Male with flagellomere 3 modified; fore wing with submarginal vein usually reaching anterior margin of wing to continue as marginal vein (sometimes thickened into darker spot), the stigmal and often postmarginal veins present; hind wing in most genera with complete submarginal vein reaching to hamuli; wings rarely without veins; metasoma in most genera moderately to strongly depressed dorsoventrally; primarily, metasomal segments subequal in length, but secondarily, one of the segments may be much larger than others; if segment 2 is longest then submarginal vein reaches anterior margin of wing to continue as marginal, stigmal, and often also postmarginal veins; in female, apparent metasomal segment 7 either external or internal, with cerci or sensory plates, and may be extruded with the ovipositor during oviposition or attached to apparent tergum 6 (see superfamily discussion for explanation of segment numbering).

**Comments** Members of this large family are remarkably diverse in habitus, depending on the shape and size of the host egg from which they

emerged—cylindrical to depressed, elongate and spindle-shaped to short, squat, and stocky.

The biological ground plan is solitary endoparasitism in eggs of insects and spiders (Araneae), with hyperparasitism and superparasitism strongly avoided. Unsegmented teleaform first instar larvae kill the host embryo; all subsequent development of the parasite is completed within the single host egg (idiobiont development). Adults occur mostly in more open, sunny habitats such as grasslands, but they are also often encountered in deserts, forests, soil, marshes, and water.

The family contains about 150 genera and 3000 described species around the world, but the total fauna is estimated to be about 7000 species. In North America, 275 species have been described, including about 150 in Canada, but this number is only a fraction of the total. Three subfamilies are usually recognized: Scelioninae, Teleasinae, and Telenominae. The first two are closely related and should form one group, but the latter is very different.

• Scelioninae is the largest and most polytypic subfamily, containing more than 90% of scelionid genera, classified in 16 tribes. The primitive state of the metasoma with the segments subequal in length occurs in Sparasionini, Mantibariini, Scelionini, and most Calliscelionini. The

advanced state, with segment 2 or 3 distinctly the longest, occurs in Gryonini, Baeini, and Embidobiini. Laterosternites are well defined, and together with the sharply flexed laterotergites, they form an acute lateral margin to the metasoma. Females of Scelioninae parasitize eggs of various insects and spiders (Araneae). The geological age of each group is reflected by choice of appropriate host. The very primitive Sparasionini parasitize archaic Tettigonioidea (Orthoptera) or Grylloidea (Grylloptera). Females of the more advanced Scelioninae parasitize more advanced Tettigonioidea or Grylloidea; members of Scelionini are parasitoids of Acrididae (Orthoptera). Members of some highly derived tribes parasitize nonorthopteroid hosts such as Heteroptera or Embioptera. The tribe Baeini apparently coevolved with araneomorph spiders (Araneae) (Austin 1985). Members of Thoronini parasitize Heteroptera under water (Masner 1972), and other scelionines parasitize Grylloidea in caves. Several highly specialized phoretic species in the tribes Mantibariini, Scelionini, and Gryonini are associated with Mantidae (Dictuoptera: Mantodea), Acrididae (Orthoptera), or Hemiptera, respectively. Surprisingly, no Scelioninae evolved as associates of Formicidae or Isoptera. Maximum diversity and number of species in all groups of this subfamily occur in the tropics, where only a small fraction of the species have been described. Members of Scelioninae also flourish in dry habitats including deserts.

• Teleasinae should better be regarded as a tribe of Scelioninae. This subfamily is very homogeneous with relatively few genera, often difficult to distinguish from one another. Adults of Teleasinae are distinguished from those of Scelioninae by the apomorphic wing venation with long marginal vein, reduced palpi, and large metasomal tergite 3. In females, apparent tergite 7 is not extruded with the ovipositor during

- oviposition. Although little is known about their biology, all members of the subfamily quite probably parasitize eggs of Carabidae (Coleoptera). A high degree of wing reduction occurs in many species along with possible wing polymorphy in at least some of them, including the males. Most species occur in temperate climates.
- **Telenominae** is distinguished by the absence of laterosternites and hence the entire structure of the metasoma, which is not held so rigidly together as in the other subfamilies. The wide laterotergites overlap the sterna relatively loosely, and metasomal segment 2 is the largest. In females, apparent tergum 7 is external, not extruded with the ovipositor during oviposition, and the cerci are transformed into sensory plates studded with long hairs. Males usually have the antenna with 10 flagellomeres and females with 9, with only a few apomorphic exceptions. The subfamily is very homogeneous, with few genera but with a large number of described species and many more undescribed. During the evolution of the subfamily a host shift from Heteroptera (more primitive genera) to Lepidoptera (most *Telenomus*) occurred, with only a few species parasitizing such diverse hosts as Neuroptera, Diptera, and Homoptera. The largest genus, Telenomus, is important in biological control. The species are distributed equally in both temperate and tropical climates.

References Masner (1976, 1980) keyed the world genera and the genera of the Holarctic region, respectively. Galloway and Austin (1984) reviewed the Australian species of Scelioninae. Kozlov (1987) keyed the species of the USSR. Dodd (1930) reviewed the Australian species of Teleasinae. Fouts (1947) reviewed the Nearctic species of *Trimorus*. Johnson (1984) proposed species groups for the genus *Telenomus*. Kozlov and Kononova (1983) revised *Telenomus* for the USSR. Johnson (1992) cataloged the species.

### Family PLATYGASTRIDAE

(Fig. 208)

**Diagnosis** Body predominantly 1–2 mm long, rarely up to 4 mm, slender, usually black, rarely yellowish, with no metallic colors. Antenna strongly elbowed, usually with 8 flagellomeres, rarely with fewer (5–7); male flagellomere 2 (rarely 1) modified; fore wing usually veinless or if submarginal vein developed then only very rarely reaching anterior margin of wing, the stigmal and postmarginal veins absent; hind wing at most with short stub of submarginal vein; metasomal segment 2 always the longest and widest; female almost

always with only 6 apparent tergites, exceptionally fewer; metasomal tergum 7 (apical tergum) internal, considerably reduced and depigmented, without cerci or sensory plates, hidden under tergum 6, and not extruded with ovipositor.

Comments Adults occur in most habitats, often high on vegetation, searching for hosts such as Cecidomyiidae (Diptera). Some Platygastridae are primarily solitary parasitoids in eggs of various insects (Coleoptera, Homoptera), or they parasitize egg-like hosts such as young larvae of Coccoidea or

Aleyrodidae (Homoptera); the entire development is completed in one stage of the host (idiobionts). However, most Platygastridae are koinobionts, parasitizing the host egg (usually gall-forming Cecidomyiidae) but developing only after the host is nearly full grown (prepupa or pupa). Some of these species are polyembryonic, with two or more individuals developing from one fertilized egg.

The family contains about 1100 described species around the world but several thousand species are estimated. In North America, about 255 species are described including about 200 in Canada, but this is only a fraction of the total.

Masner and Huggert (1989) recognized two subfamilies: Sceliotrachelinae and Platygastrinae; the former subfamily Inostemmatinae was shown to be a heterogeneous assemblage. Its species were reassigned to Sceliotrachelinae or Platygastrinae.

Sceliotrachelinae comprises mostly squat to plump species. The laterotergites are relatively wide, and the general structure of the metasoma is similar to that of Telenominae. In females the club is usually abrupt, with three clavomeres, or the clavomeres are partly to completely fused into a single solid clavomere; in males the antenna is often subclavate. The fore wing in most species has a tubular submarginal vein, knobbed apically. Most members whose biology is known are idiobionts, parasitizing eggs of various insects such as Curculionidae and Cerambycidae (Coleoptera), and Flatidae (Homoptera), or parasitizing early stages of Pseudococcidae or Aleyrodidae (Homoptera). About 20 genera occur around the world but the Southern

- Hemisphere, especially Chile, Australia, and southern Africa, seems to be the centre of diversity.
- Platygastrinae comprises mostly slender to very elongate species. The laterotergites are usually narrow and tightly appressed against the sternites, making the metasoma more compact than in Sceliotrachelinae. In females the cylindrical club usually has four or five clavomeres, with the clavomeres clearly separated; in males the flagellum is usually thread-like. The fore wing submarginal vein is present in more primitive species but absent in the more numerous, derived species. Platygastrinae are biologically very cohesive, associated with Cecidomyiidae (Diptera) as koinobionts. The female parasitizes the egg or early instar larva, and the adult wasp emerges from the host prepupa or pupa. Different species seem also to be closely associated with particular host plants (or parts of the plant) where the host gall is located. About 40 genera occur around the world, with cool temperate zones apparently about as speciose as the tropics. However, the dominance of Platygastrinae in Chile and New Zealand is truly remarkable.

References Masner and Huggert (1989) revised and keyed the genera of the former subfamily Inostemmatinae. Vlug (1985) keyed and redescribed some European species described by Walker and Haliday. Kozlov (1987) treated the species in the former USSR.

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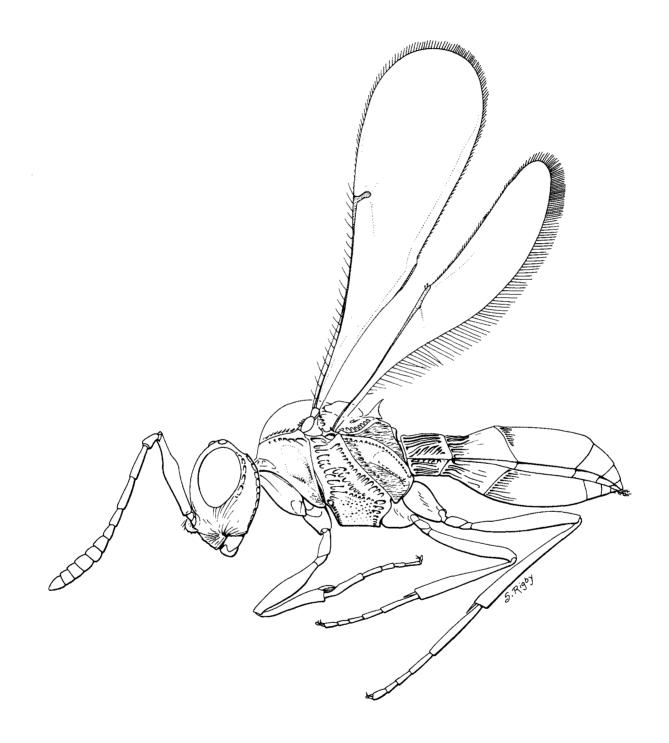


Fig. 207. Scelionidae



Fig. 208. Platygastridae

#### Chapter 15 Superfamily Ceraphronoidea

(Figs. 209, 210)

#### Lubomir Masner

Included families (2): Ceraphronidae, Megaspilidae.

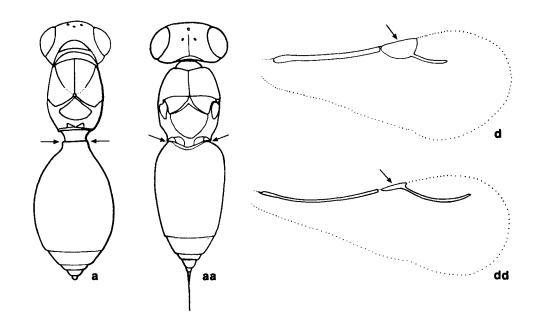
The superfamily is defined by the following combination of attributes: presence of 2 spurs on apex of protibia; fore wing with vein C + R fused into one solid bar; metasomal segment 2 very large, seemingly connected directly to propodeum. Other important attributes are: fore wing with upcurved Rs; distinctly geniculate antenna with very long scape inserted right above clypeus; mesoscutum

divided into three parts; and absence of metasomal spiracle. The species are small and superficially resemble Scelionidae, Chalcidoidea, or even Dryinidae (Aphelopinae).

Over 800 species have been described around the world, but about 2000 species are estimated.

Masner and Dessart (1967) established the superfamily and gave data on interrelationships and morphology of the major groups.

### Key to families of CERAPHRONOIDEA



- Anterior margin of metasoma in dorsal view with neck-like constriction.
- Male and female antenna each with 9 flagellomeres.
- Mesotibia with 2 spurs.
- d. Fore wing usually with large stigma.
- Mesoscutum usually with 3 longitudinal furrows or rarely reduced to narrow sclerite ......

- aa. Anterior margin of metasoma in dorsal view without neck-like constriction but bordered with strong rim.
- bb. Female antenna with 8 flagellomeres; male antenna with 9 flagellomeres (rarely with fewer).
- cc. Mesotibia with 1 spur.
- dd. Fore wing with linear stigma.
- ee. Mesoscutum at most with one median furrow, not reduced ..... CERAPHRONIDAE (p. 567)

## Family MEGASPILIDAE

(Fig. 209)

**Diagnosis** Body usually 2-3 mm long (exceptionally up to 4 mm), black or yellow; macropterous, brachypterous, or apterous; fore wing with large stigma (except in males of Lagynodinae); antenna with 9 flagellomeres in both sexes; metasoma with neck-like, constricted, anterior margin of the largest tergum (true tergum 2 = apparent tergum 1).

**Comments** Little is known about hosts and habits, but some members are primary parasitoids of Coccoidea (Homoptera), Neuroptera, and puparia of various Diptera, or are hyperparasitoids of Aphididae (Homoptera) through Aphidiinae

(Braconidae). One species from California parasitizes Boreidae (Mecoptera). Two subfamilies are recognized: Megaspilinae and Lagynodinae. The former, with worldwide distribution, comprises 12 genera; the latter comprises two genera, with sexes usually extremely dimorphic. The family contains about 450 described species around the world; about 1000 species are estimated. Fifty-two species occur in North America, including about 35 in Canada.

**References** Dessart and Cancemi (1986) keyed the world genera. Alekseev (1987) keyed the genera and species of European USSR.

### Family CERAPHRONIDAE

(Fig. 210)

**Diagnosis** Body 1–3 mm long, usually black or brown but sometimes yellow, orange, or reddish; macropterous, brachypterous, or almost apterous; if winged then fore wing with narrow linear stigma and metasoma with wide base. Female antenna with 7 or 8 flagellomeres, male antenna with 8 or 9 flagellomeres.

**Comments** Little is known about hosts and habits, but some species have been reared as endoparasitoids of Cecidomyiidae (Diptera), Thysanoptera, Lepidoptera, Neuroptera, puparia of

higher Diptera, or as hyperparasitoids from cocoons of Braconidae. Members are frequently encountered in soil; some are associated with Formicidae but with no direct integration. The family contains about 360 species around the world; about 1000 species are estimated. Fifty-two species occur in North America, including about 35 in Canada.

**References** Dessart and Cancemi (1986) keyed the world genera. Alekseev (1987) keyed the genera and species of European USSR.

#### References to Ceraphronoidea

Alekseev, V.N. 1987. Superfamily Ceraphronoidea (Ceraphronids). Pages 1213–1257 in Medvedev, G.S., ed. Keys to the insects of the European part of the USSR, Volume III, part 2. Amerind, New Delhi, India. 1341 pp.

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(Hymenoptera) avec commentaires et nouvelles espèces. Frustula entomologica, Nouvelles Séries VII–VIII (XX–XXI):307–372.

Masner, L., and P. Dessart. 1967. La reclassification des catégories taxonomiques supérieures des Ceraphronoidea (Hymenoptera). Institut Royale des Sciences Naturelles de Belgique 43/22:1-33

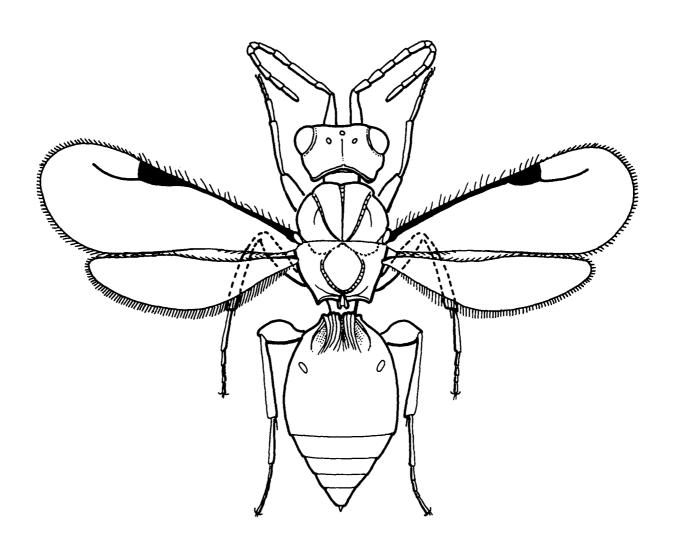


Fig. 209. Megaspilidae

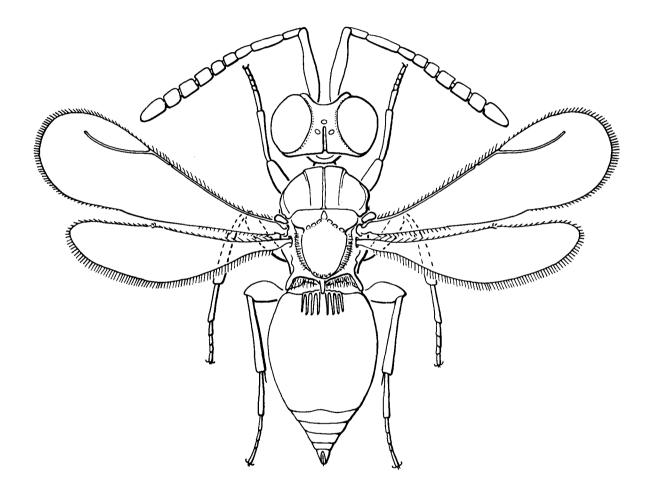


Fig. 210. Ceraphronidae

# Chapter 16 Superfamilies Mymarommatoidea and Chalcidoidea

(Figs. 211-231)

Gary A.P. Gibson

# **Superfamily MYMAROMMATOIDEA**

(Fig. 211)

Included families (1): Mymarommatidae.

Superfamily classification is discussed under the comments for Chalcidoidea. Mymarommatids are readily distinguished from other Hymenoptera by their two-segmented petiole, bizarre head structure (bellows-like structure of unknown function), and reticulate patterned fore wing.

## Family MYMAROMMATIDAE

(Fig. 211)

**Diagnosis** Body minute (less than 1 mm long), yellow to brown, without metallic luster; antennal toruli subcontiguous, high on head; antenna geniculate; flagellum without longitudinal multiporous plate sensilla, filiform in male but with club of 1 or 2 flagellomeres in female; female with 7–9 flagellomeres and males with 11 flagellomeres; mandible exodont, teeth wide and outcurved; head capsule with strongly convex frontal surface and flat posterior surface separated by pleated membrane (dorsally, head capable of expanding and contracting in bellows-like manner); pronotum triangular in lateral view, strongly reduced medially and not visible in dorsal view, but posterodorsal angle extending to tegula; prepectus absent; individuals fully winged to wingless; fore wing of fully winged specimens spatulate (spoon-shaped), with mesh-like or cell-like pattern on membrane and long marginal setae arising from within membrane; hind wing of fully winged specimens reduced to short, stalk-like, apically bifurcate vein;

protibial spur straight and simple or curved and bifurcate; tarsi with 5 tarsomeres; metasoma petiolate, with the two anterior segments tubular.

Comments Mymarommatidae occur around the world, with a single genus, *Palaeomymar*, recognized as valid at present. Nine described species are extant, but the group is ancient and specimens have been found in amber from the Cretaceous, Baltic, and Dominican periods (about 25–100 million years old).

Nothing is known about the hosts of mymarommatids, but a specimen was reared from a bracket fungus; most specimens have been collected from tropical or temperate deciduous forests, often from leaf litter or soil extractions.

References Debauche (1948) and Gibson (1986a) discussed morphology and classification; Clouâtre et al. (1989) gave information on the known habitat in Canada; Rasnitsyn and Kulicka (1990) reviewed incidence in late Cretaceous and Cenozoic amber.

# Superfamily CHALCIDOIDEA

(Figs. 212-231)

Included families (20): Agaonidae, Aphelinidae, Chalcididae, Elasmidae, Encyrtidae, Eucharitidae, Eulophidae, Eupelmidae, Eurytomidae, Leucospidae, Mymaridae, Ormyridae, Perilampidae, Pteromalidae, Rotoitidae, Signiphoridae, Tanaostigmatidae, Tetracampidae, Torymidae, Trichogrammatidae.

**Diagnosis** Fully winged chalcidoids are distinguished from most other Hymenoptera by their reduced fore wing venation. At most a single vein complex occurs, composed of the submarginal, marginal, stigmal, and postmarginal veins (Fig. 14,

Chapter 3). Most chalcidoids also have a separate sclerite, the prepectus, partly separating the mesopleuron from a more or less saddle-like or horseshoe-like pronotum. This is unlike most other parasitic Hymenoptera, which lack an exposed prepectus between the mesopleuron and pronotum, and have the pronotum highly reduced medially so as to be triangular in lateral view. Because a prepectus is present between the pronotum and the mesopleuron in most chalcidoids, the pronotum typically does not extend to the tegula, but how conspicuous this feature is depends on size of the prepectus. The position of the mesothoracic

spiracle, if visible, also distinguishes chalcidoids from other parasitic Hymenoptera. In chalcidoids the mesothoracic spiracle is at the dorsal margin of the pronotum, usually at the juncture of the pronotum, prepectus, and mesoscutum, but at least between the pronotum and mesoscutum. Other parasitic Hymenoptera have the mesothoracic spiracle situated below the dorsal margin of the pronotum, either between the pronotum and the mesopleuron (in some taxa concealed beneath a conspicuous pronotal lobe) or on the pronotum itself in this same relative position. Consequently, the spiracle and mesoscutum are separated by the posterodorsal angle of the pronotum. Virtually all chalcidoids also have longitudinal, ridge-like sensory structures (multiporous plate sensilla) on one or more flagellomeres, with the apices of the sensilla projecting above the surface, and often beyond the apex, of the flagellomere. Many chalcidoids also have a metallic luster, which differentiates them from most other parasitic microhymenoptera. Bouček (1988a) gave a comprehensive review of chalcidoid structure.

Comments Chalcidoids are found in all zoogeographic regions and in all habitats from equatorial forests to the northernmost tundra, from deserts to ponds. Despite their omnipresence they remain one of the poorest known groups of parasitic Hymenoptera, partly because of their small size (most are 3-5 mm or less in length), morphological and biological diversity, and numerical abundance. About 3300 nominal genera and 22 500 nominal species have been described, of which about 2000 genera and 18 500 species are considered to be valid (Noves 1990a). The number of species certainly represents only a fraction of the true diversity of Chalcidoidea, and estimates of 60 000-100 000 chalcidoid species do not seem to be unreasonable (Noves 1978, Gordh 1979). The approximate number of genera and species given for each family in this guide is based on Noyes (1990a).

Biological diversity of chalcidoids was reviewed in detail by Bouček (1988a), Gauld and Bolton (1988), and Bendel-Janssen (1977), and so it is only briefly discussed for each family. Most chalcidoids are parasitoids or, rarely, predators of the immature stages or, very rarely, of adults of 12 orders of Insecta, two orders of Arachnida (Araneae and Acari), and one family of Nematoda (Anguinidae). This represents about the same number of orders that are parasitized by the rest of the parasitic Hymenoptera together. Few chalcidoids are phytophagous, either as gall formers or seed eaters, or as inquilines within the galls of other species.

Members of Chalcidoidea, or Chalcidoidea plus Mymarommatidae, are readily demonstrated as monophyletic taxa. Gibson (1986a) defined Chalcidoidea on the basis of three external, putatively synapomorphic attributes. Because members of Mymarommatidae lack these three attributes, but share other putative synapomorphies with chalcidoids, they were hypothesized as the sister group of Chalcidoidea sensu stricto. Gauld and Bolton (1988) and Naumann (1991) classified mymarommatids as a family in Chalcidoidea, whereas Delvare and Aberlenc (1989) and Noyes and Valentine (1989b) classified them as a superfamily separate from Chalcidoidea. In this guide, mymarommatids are classified as a superfamilies, but they are also keyed out in the key to families of Chalcidoidea because of present instability in their classification.

Bouček (1988b) reviewed extensively the history of chalcidoid classification. Since 1952 from nine to 24 families have been recognized in the superfamily, and currently workers have not reached a consensus as to family level classification or relationships. Many of the families cannot be defined by any unique attribute or even combination of attributes if the world fauna is treated. Furthermore, using combinations of attributes to key out family level taxa results in seemingly endless, albeit often rare, exceptions or intermediate forms. These problems have long been acknowledged by chalcidologists. As stated by Gordh (1979), classifications are based on external morphology, and chalcidoids are exceedingly plastic morphologically. This has resulted in differences of opinion over the limits of higher taxa because various workers have interpreted the significance of characters differently. Grissell (1980) also noted that characters used to delimit higher taxa often work well for only one sex and generally are not disjunctive, i.e., they intergrade and crop up from time to time where least expected. As a result, many of the chalcidoid families likely represent taxa of convenience, based on overall similarity, more than they represent monophyletic evolutionary lineages.

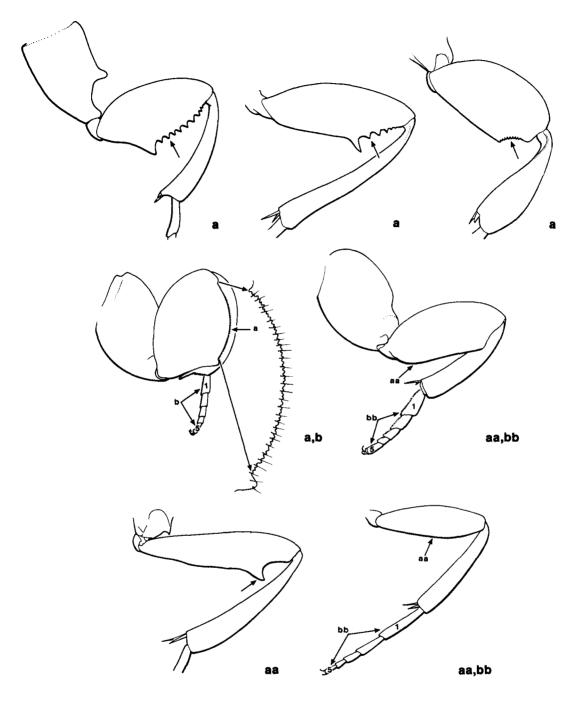
Family classification used here largely follows that of Bouček (1988a), except that delineation of Perilampidae and Eucharitidae follows Heraty and Darling (1984). Because many family diagnoses cannot be made strictly differential, diagnostic attributes of the most inclusive definable unit within each family (usually subfamily, rarely tribe) are given, except for Pteromalidae, which generally is considered to be the paraphyletic dumping ground of the Chalcidoidea. Family diagnoses are arranged primarily by degree of structural similarity between members, which may or may not reflect phylogenetic relationships. No attempt has been made to make the diagnoses strictly comparable because this would tend to obscure attributes that are important for recognition of any particular taxon. However, families with similar looking members have more comparable diagnoses.

Regional keys to families (publications with an asterisk also include keys to genera). \*Nikolskaya (1952) and \*Medvedev (1978), European USSR; \*Peck, Bouček and Hoffer (1964), Europe; Graham (1969), Europe—key to genera of Pteromalidae; Riek (1970), Australia; \*Alayo and Hernandez (1978), Cuba; Prinsloo (1980), Ethiopian region; Yoshimoto (1984), Canada; \*Subba Rao and Hayat (1985), Oriental region; \*Bouček (1988a). Australasian region—keys to genera of 14 of 21 families; Gauld and Bolton (1988), Britain; Delvare and Aberlenc (1989), tropical Africa and America; \*Noyes and Valentine (1989b), New Zealand—keys to genera of 12 of 16 families; Grissell and Schauff (1990), Nearctic region; Naumann (1991), Australia.

Use of key The key attempts to permit identification of chalcidoids, or at least female chalcidoids, to family on a world basis. This is perhaps a Sisyphean task because of the great morphological diversity found in many families even when treated on a regional basis, much less a world basis, and the indefinite family placement of some taxa. For these reasons members of some subfamilies, such as those currently assigned to Agaonidae, are distinguished in the key to families. The problem of morphological diversity has also resulted in a key replete with "usually" and

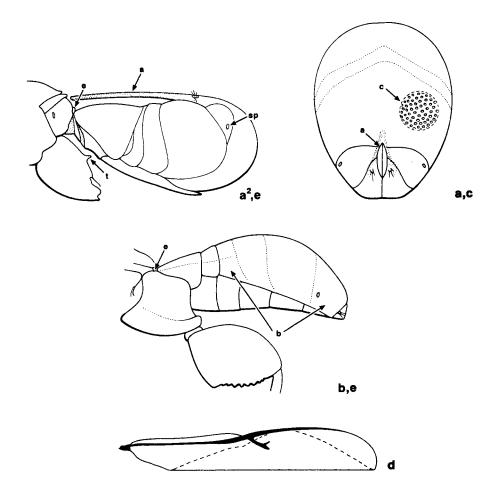
"often," and such conjunctions as "and," "or," "but." These qualifying words are important for correct identification of specimens and are in boldface type. Footnotes are used to denote exceptions or attributes that are not applicable for rare taxa, which should be keyed through the respective couplet. Additional information is given following the couplet to help recognize the problem taxa. For example, some members of Pleurotroppopsis (Eulophidae) have the metafemur toothed ventrally, but they have four tarsomeres and thus would be keyed through "aa" in couplet 1. Because the key attempts to encompass world diversity it does not ignore exceptions for easier construction, and admittedly is complicated. Users of the key should also note that because chalcidoids generally are quite small and fragile, success in keying specimens depends on how well preserved and prepared the specimens are, and whether adequate magnification and appropriate lighting are used. (Noves (1990b) gave an excellent, comprehensive review of techniques for killing, preserving, and mounting chalcidoids for taxonomic study.) Where possible, descriptors used in the key have been simplified to avoid specialized jargon; synonymous terms used in chalcidoid literature and supplemental explanatory statements for couplets are given in parentheses.

# Key to families of CHALCIDOIDEA (including MYMAROMMATIDAE)



1	a.	Metafemur toothed or serrate along at least apical third of ventral margin, usually al conspicuously enlarged.	so
	b.	Tarsi with 5 tarsomeres.	
	c.	Specimens fully winged, usually relatively large	2
	aa.¹	Metafemur at most with subapical tooth or lobe, usually not conspicuously enlarged.	
		Tarsi with 3-5 tarsomeres.	
	cc.	Specimens fully winged to wingless, sometimes very small	5

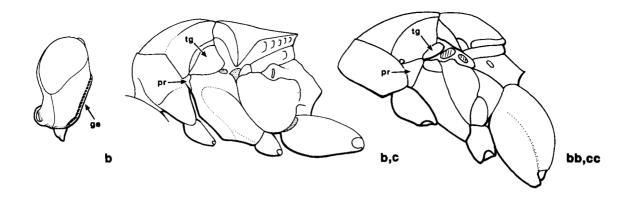
Very rare specimens with enlarged and ventrally toothed or serrate metafemur, but then tarsi with 4 tarsomeres and/or metatibia conspicuously shorter than metafemur.



- a.<sup>2</sup> Female with one or more metasomal terga longitudinally grooved for reception of upturned ovipositor sheaths (if long, sheath evenly recurved over metasoma).
  - b. Male with most metasomal terga fused into carapace.
  - c. Metasomal terga extensively, densely punctate.
  - d. Fore wing normally folded longitudinally.

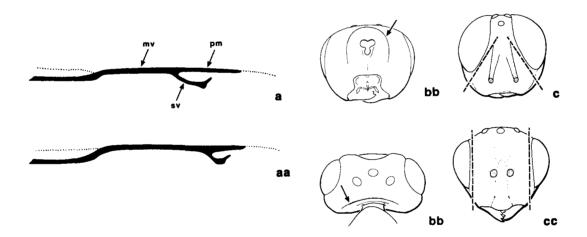
  - aa. Female with metasomal terga not longitudinally grooved (if long, ovipositor sheath projecting posteriorly or not evenly recurved over metasoma).
  - bb. Male with metasomal terga separate.
  - cc. Metasomal terga usually relatively smooth or with fine sculpture.
  - dd. Fore wing flat.

Females of Polistomorpha with metasomal terga not grooved and short ovipositor sheaths not upturned, but then tergum anterior to tergum with spiracle (sp) distinctly the largest and forming widest part of metasoma and posterior surface of metacoxa with submedial tooth (t).

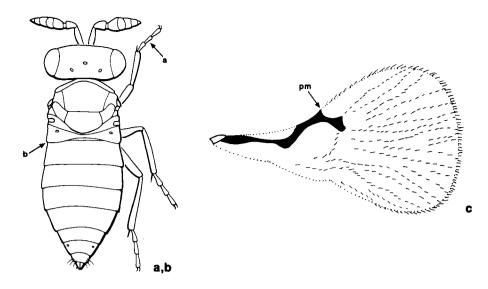


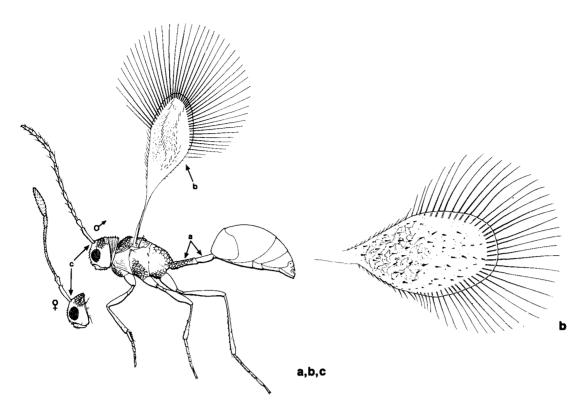
- a. Head and mesosoma only very rarely with metallic luster (if so, tegula very large and gena ridged).
  - b. Tegula (tg) usually conspicuously large (often at least twice as long as distance between pronotum and base of tegula) and/or gena (ge) distinctly ridged.

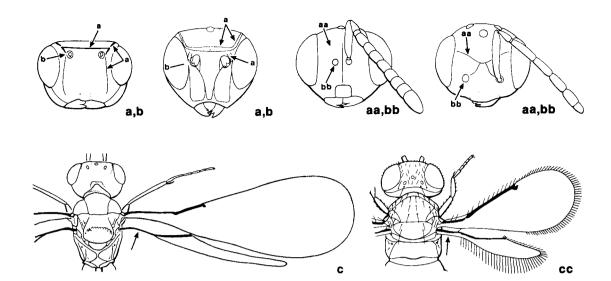
  - aa. Head and mesosoma usually with distinct metallic luster (at least entirely dark).
  - bb. Tegula (tg) not conspicuously large (only about as long as distance between pronotum and base of tegula) and gena rounded.
  - cc. Prepectus (pr) a distinct triangular sclerite extending between mesoscutum and base of procoxa



- a. Fore wing with marginal vein (mv) at most 1.5 times length of postmarginal vein (pm) and with stigmal vein (sv) relatively long.
  - b. Head without occipital carina.
  - c. Eyes in frontal view with inner margins usually diverging at least over lower half ....................... some PTEROMALIDAE (p. 608)
  - aa. Fore wing with marginal vein more than twice length of postmarginal vein **and** at least four times length of very short stigmal vein.
  - bb. Head with occipital carina (carina often fine).



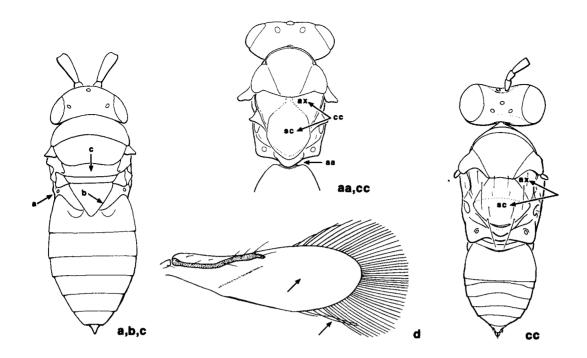




- 7(6) a. Head with H-like pattern of marks (a straight mark across face above toruli and often less conspicuous lateral marks along inner margin of eye on vertex and face).
  - b.3 Torulus usually only about its own diameter from eye, conspicuously closer to eye than to other torulus.
  - c.<sup>3</sup> Hind wing of fully winged specimen with membrane usually originating apically from stalk or rarely with stalk only.

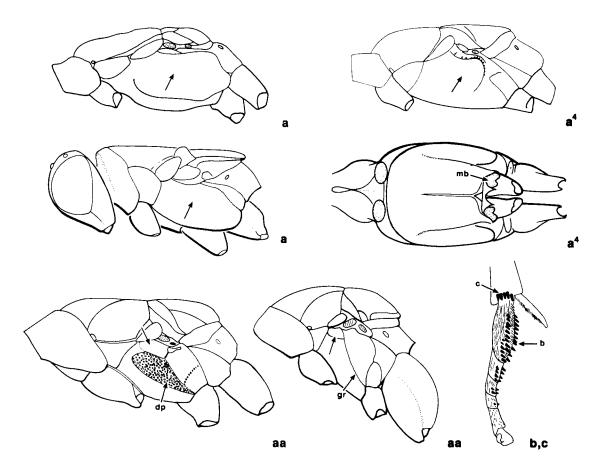
  - aa. Head without H-like pattern of marks (sometimes with membranous or light-colored transverse, V-shaped, or X-shaped mark above toruli).
  - bb. Torulus usually closer to midline of head so distance between toruli less than or equal to distance between torulus and eye.
  - cc. Hind wing of fully winged specimen with membrane extending at least narrowly to base of wing.

<sup>3</sup> Rarely with hind wing membrane narrowly extending to base and then sometimes with head wedge-like so toruli about equally spaced from each other and from each eye.



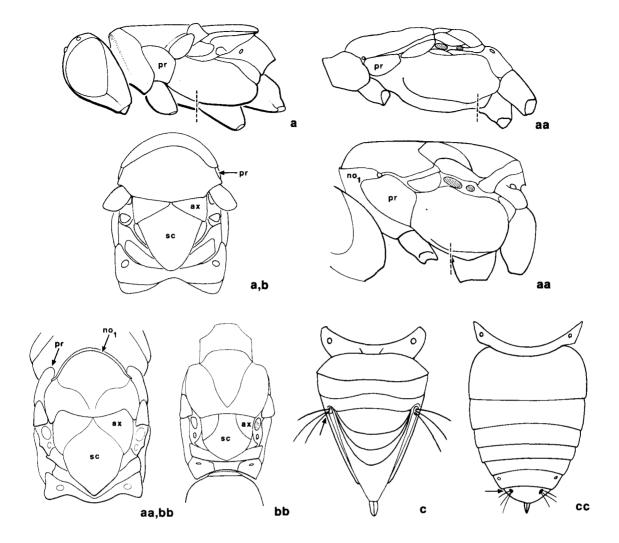
- a. Body usually 2 mm or less in length and metasoma very widely attached to mesosoma (dorsal surface flat or sclerites only slightly convex and virtually in same plane).
  - b. Propodeum with large, posteriorly pointed triangular area delineated by fine grooves.
  - c. Scutellum plus axillae narrowly transverse-rectangular (belt-like), and axilla at most obscurely delineated from scutellum.

  - aa. Body often either much longer or with metasoma separated from mesosoma by distinct constriction.
  - bb. Propodeum with areas, if any, delineated by carinae.
  - cc. Scutellum (sc) plus axillae (ax) usually at least as long as wide and axilla usually distinctly delineated.



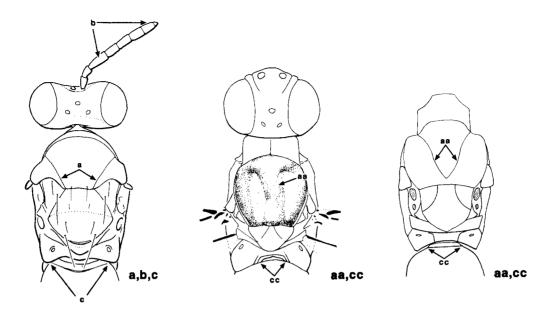
<sup>4</sup> Rare specimens from New World with flat mesopleural area occupying about half to two-thirds of region between prepectus and propodeum, and without tarsal or tibial pegs, but then in ventral view with small membranous area (mb) anterior to each mesocoxa.

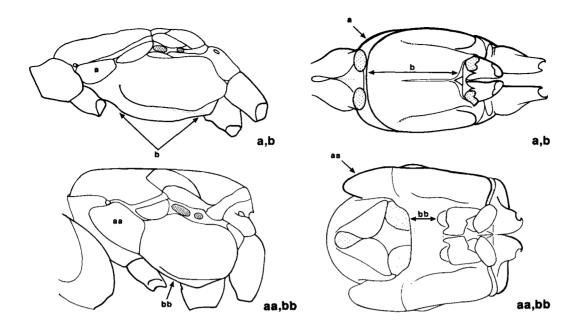
Some Aphelinidae with mesopleuron intermediate in structure between that described in statements "a" and "aa," but these specimens will key through either part of couplet.



a. Mesocoxa inserted at or anterior to midline of mesopleuron (mesosternum very short) and prepectus (pr) flat.

- b. Axillae (ax) usually transverse and with medial angles touching so that scutellum (sc) angled at transscutal articulation.
- c. Cercus **usually** conspicuously advanced anteriorly, with some terga V-like between, or M-like between and around, the cerci.
- d. Fore wing of fully winged specimen with marginal vein usually shorter than stigmal vein, sometimes point-like ..... ENCYRTIDAE (p. 621)
- aa. Mesocoxa inserted distinctly posterior to midline of mesopleuron (mesosternum relatively long) or if near midline then cercus not advanced, marginal vein conspicuous, and prepectus (pr) usually bulbous and protruding lateral to pronotum (no<sub>1</sub>).
- bb. Axillae (ax) **usually** equilateral to elongate-triangular, sometimes also with medial angles separate so that scutellum (sc) partly transverse along transscutal articulation.
- cc. Cercus not conspicuously advanced, terga more or less transverse.

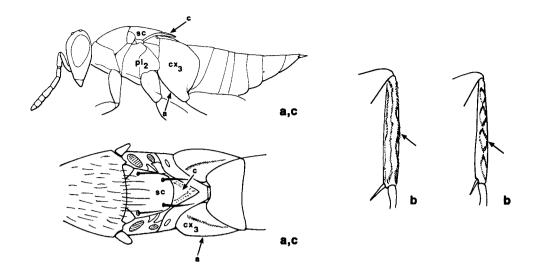




- 12(11) a. Prepectus flat.

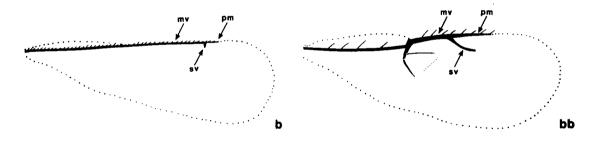
  - aa. Prepectus bulbous and protruding lateral to pronotum.

Monotypic genus from Japan with prepectus as described in statement "a" but mesosoma as described in statement "bb," such specimens without membranous area anterior to each mesocoxa and axilla transverse triangular (similar to most Encyrtidae, see Fig. b of couplet 10).



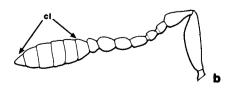
- a. Metacoxa (cx<sub>3</sub>) very large and compressed (disk-like), in lateral view flat with more or less semicircular surface conspicuously larger than mesopleuron (pl<sub>2</sub>).
  - b. Metatibia either with some very conspicuous long bristles along dorsal surface or with dense rows of short bristles in more or less wavy or diamond-like patterns.

  - aa. Metacoxa subtriangular to circular in cross section, in lateral view sometimes distinctly longer than mesopleuron but not enlarged-semicircular.
  - bb. Metatibia rarely with conspicuous long bristles but not patterned with dense rows of short bristles.
  - cc. Metanotum not protruding as horizontal triangular plate posterior to scutellum ......... 15

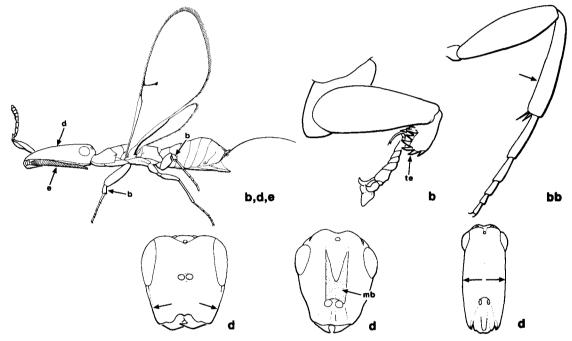


- 14(13) a. Tarsi with 4 tarsomeres.
  - b. Fore wing with very short stigmal (sv) and postmarginal (pm) veins and very long marginal vein (mv) ..... ELASMIDAE (p. 626)
  - aa. Tarsi with 5 tarsomeres.





15(13)	b.	Female (male unknown*) and: Antenna with 12 flagellomeres, of which apical 6 form compact or less conspicuously differentiated club (cl). Tarsi with 4 tarsomeres
	bb. <sup>7</sup>	Male or, if female, then: Antenna usually with 11 or fewer flagellomeres and club formed by 3 or fewer flagellomeres.  Tarsi with 4 or 5 tarsomeres
16(15)		Fully winged or fore wing at least with well-developed membranous surface extending conspicuously beyond posterior margin of mesosoma

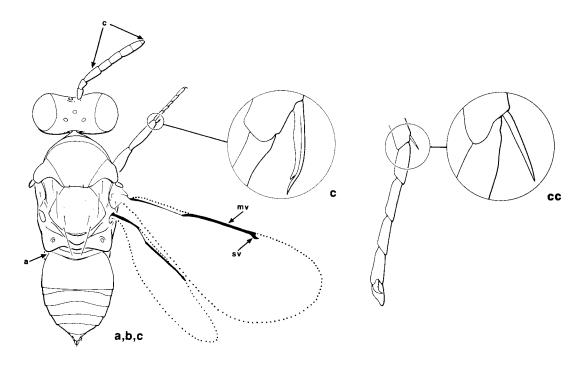


**17(16)** a. Female **and**:

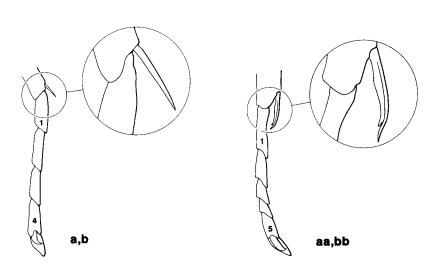
- b. Protibia and usually metatibia conspicuously smaller than respective femur (usually half or less length of femur and subtriangular, with stout spines or teeth (te) apically).
- c. Body (including head) smooth and shiny, at most with scattered micropunctures or other very obscure sculpture, and without or with only very slight metallic luster.
- d. Head flat or wedge-like in lateral view, more or less quadrate to rectangular with subparallel sides in anterior view, and often membranous (mb) above toruli.
- e. Mandible usually with ventral transversely ridged appendage or with posteriorly directed teeth ...... (Agaoninae; Sycoecinae; rare Sycophaginae; Otitesellinae) AGAONIDAE (p. 610)
- aa. Male or, if female, then:
- bb. Protibia and metatibia subequal in length to respective femur.
- cc. Body often with distinct sculpture, with distinct metallic luster, or with both.
- dd. Head usually shaped differently, never membranous above toruli.
- ee. Mandible with apical teeth only ...... 18

See note on page 624.

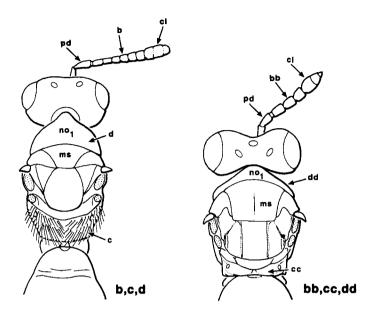
<sup>&</sup>lt;sup>7</sup> Rare specimens with 12 or more flagellomeres, but these with club formed by at most 4 flagellomeres and the tarsi with 5 tarsomeres.



- 18(17) a. Body 2 mm or less in length, without metallic luster and with metasoma widely attached to mesosoma.
  - b. Fore wing usually with long marginal vein (mv), but at least postmarginal and stigmal (sv) veins both very short (postmarginal vein absent or not extending beyond point in line with apex of stigmal vein).
  - c. Antenna with at most 6 distinct flagellomeres and protibial spur relatively long and curved ...... some APHELINIDAE (p. 622)
  - aa. Body often longer, or with metallic luster, and/or with metasoma separated from mesosoma by distinct constriction.
  - bb. Fore wing venation varied, the postmarginal and/or stigmal veins often relatively long (if stigmal vein very short then postmarginal vein usually extending beyond point in line with its apex).



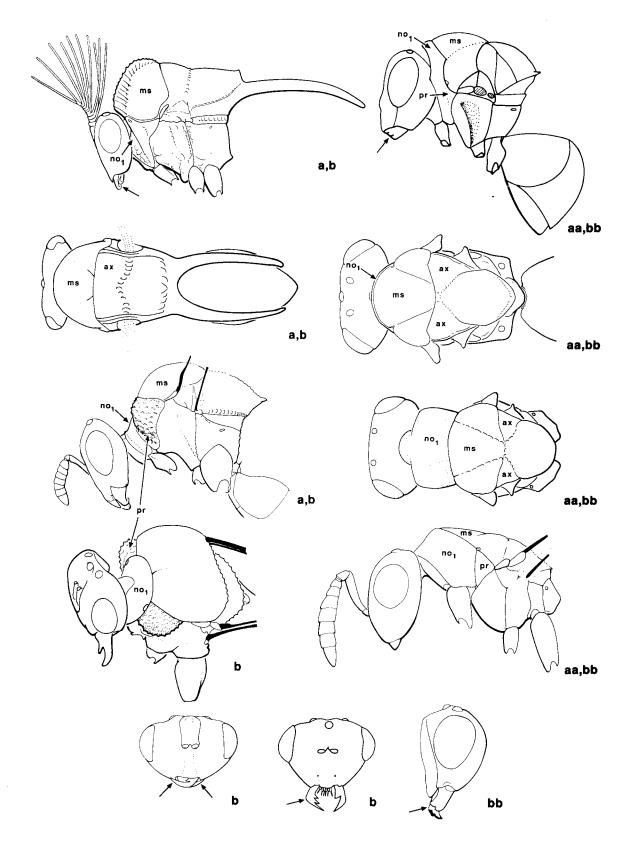
19(18)		Tarsi with 4 tarsomeres.	
	b.	Protibial spur straight, needle-like, often short and inconspicuous	20
		At least protarsus and metatarsus with 5 tarsomeres.	
	bb.8	Protibial spur usually curved, apically cleft, and distinct	21



- 20(19) a. Male (uncommon) and:
  - b. Antenna with 6 or extremely rarely 5 flagellomeres between pedicel (pd) and club (cl) (excluding any obscure basal ring-like flagellomeres).
  - c. Propodeum often setose medially, with setae of each side directed toward midline.

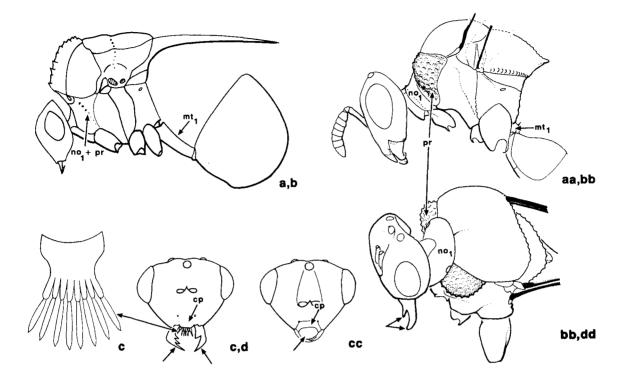
  - aa. Female or, if male, then:
  - bb. Antenna usually with 5 or fewer distinct flagellomeres between pedicel (pd) and club (cl).
  - cc. Propodeum with at least middle third bare.
  - dd. Pronotum (no<sub>1</sub>) often transverse in dorsal view and much shorter than mesoscutum ...... most EULOPHIDAE (p. 625)

Rare specimens from figs (Ficus) with long and conspicuous protibial spur but with 4 or fewer tarsomeres, but these specimens with stigmal vein long and nearly at right angle to relatively short marginal vein.



a. Mesosoma in lateral view with mesoscutum (ms) abruptly convex above pronotum (no<sub>1</sub>), with pronotum vertical and in dorsal view not visible medially.

- aa. Mesosoma in lateral view with mesoscutum (ms) not abruptly convex above pronotum (no<sub>1</sub>), with pronotum usually visible medially in dorsal view (even if only a margin).

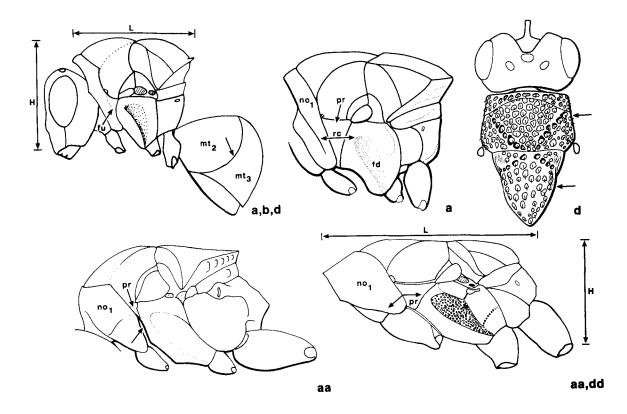


- 22(21) a. Metasomal segment  $1 (mt_1)$  tubular and usually at least as long as wide.
  - b. Prepectus (pr) either fused with pronotum (no<sub>1</sub>) or flat sclerite posterior to pronotum.
  - c. Labrum with apical margin produced into finger-like processes, each process with long, often flattened seta (labrum often concealed under clypeus (cp) but then setae usually visible as radiating row from beneath apex of clypeus).

  - aa. Metasomal segment  $1 \text{ (mt}_1)$  transverse.
  - bb. Prepectus (pr) distinctly convex, shoulder-like on either side of pronotum (no<sub>1</sub>).
  - cc. Labrum flap-like ventral to clypeus (cp), without setae as described in statement "c."

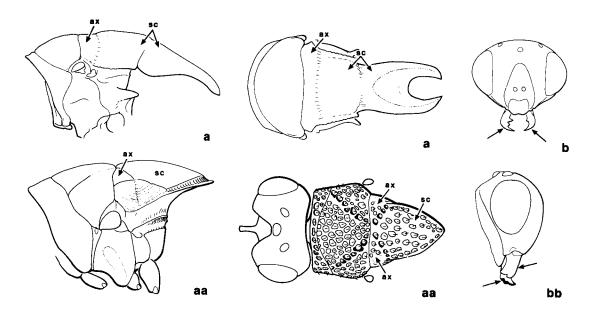
<sup>&</sup>lt;sup>9</sup> A few species with none of these attributes.

<sup>10</sup> Rare specimens with axillae widely joined and with thin sickle-like mandibles, but with distinct transverse pronotal collar in dorsal view.



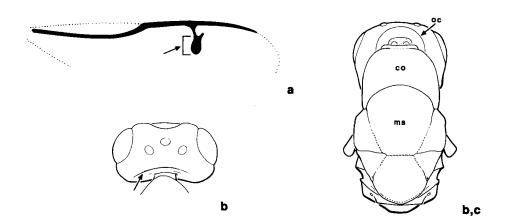
- a. Prepectus either fused (fu) with pronotum or rigidly combined (rc) with both pronotum and mesopleuron (pronotum (no<sub>1</sub>), prepectus (pr), and mesopleuron anterior to femoral depression (fd), all in flat plane).
  - b. Metasomal tergum 2 (mt<sub>2</sub>) fused dorsally to tergum 3 (mt<sub>3</sub>) (with or without visible groove), with lateral margin of tergum 2 usually free and widely curved posteriorly but with composite tergum covering at least half of metasoma.
  - c. Left mandible with 2 teeth, right mandible with 3 teeth.

  - aa. Prepectus (pr) not fused with pronotum (no<sub>1</sub>) and only **rarely** forming rigid composite structure with both pronotum and mesopleuron (mesosoma **usually** distinctly depressed **or angulate at** junction of pronotum and prepectus plus mesopleuron).
  - bb, cc. Metasoma usually with terga 2 and 3 independent but if as described in statement "b" then both mandibles with 2 teeth.
    - dd. Mesosoma often with pronotum and mesonotum reticulate or with other fine sculpture but if coarsely punctate then mesosoma usually distinctly longer than high in lateral view ..... 25

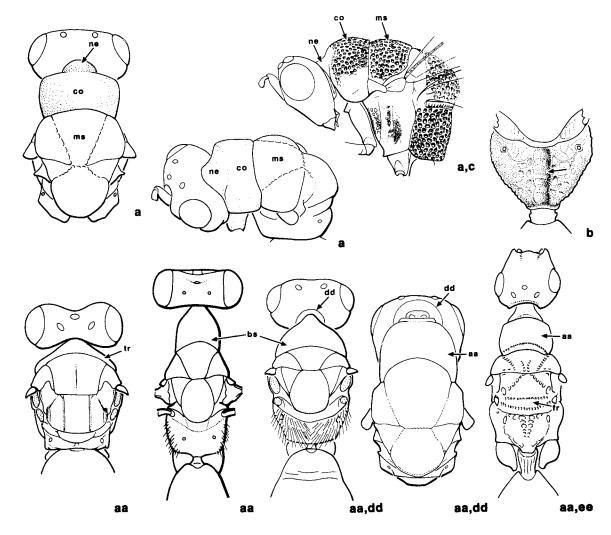


- 24(23) a. Axillae (ax) widely joined medially and scutellum (sc) extending over metasoma as a long, wide, bilobed projection.

  - aa. Axillae (ax) separated **or** with anteromedial angles just touching, and scutellum at most extending as posteriorly narrowed lobe.



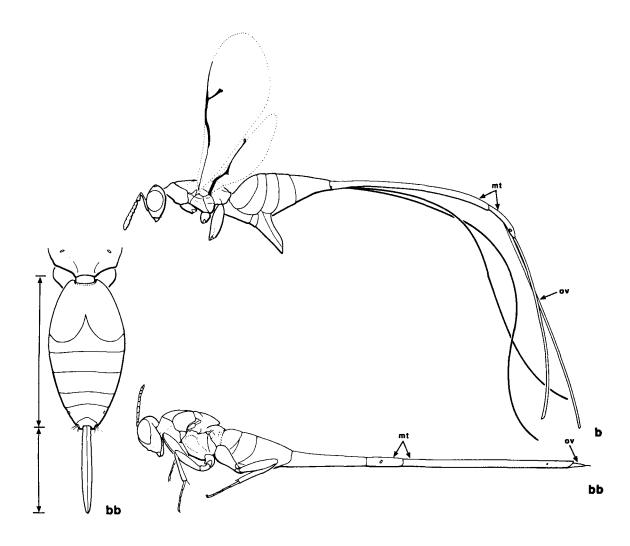
- 25(23) a. Fore wing with stigma conspicuously enlarged (knob-like).
  - b. Head with occipital carina (oc) (carina often fine).



a. Pronotum in dorsal view with large rectangular to quadrate collar (co) at least half as long as mesoscutum (ms) [posterior margin of collar often incurved but sides subparallel and anterior margin usually abruptly shoulder-like lateral to concavely narrowed neck (ne)].

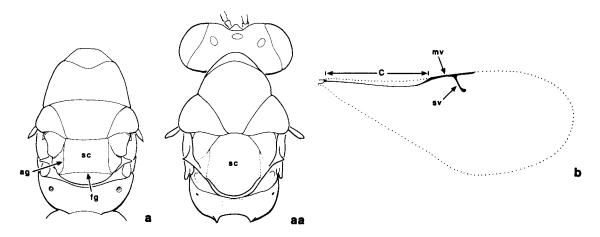
- b. Propodeum often widely depressed medially or with median longitudinal channel.
- c. Body rarely with metallic luster, usually coarsely sculptured or with distinct mesh-like or granular sculpture.
- d. Head without occipital carina (though gena often ridged).
- e. Scutellum without frenum.
- aa. Pronotum various, often conspicuously transverse (tr), or with sides evenly or sinuately convergent so as to be more or less bell-shaped (bs), but if similar to statement "a" then some to all of statements "c-f" different.
- bb. Propodeum relatively flat or evenly convex.
- cc. Body often with metallic luster or smooth and shiny with only scattered punctures.
- dd. Head sometimes with occipital carina.
- ee. Scutellum sometimes with frenum (fr) delimited by straight or curved transverse line.
- ff. Ovipositor sheath sometimes extending conspicuously beyond apex of last tergum . . . . . . 27

<sup>11</sup> New World specimens with metallic luster have ridged gena and propodeal channel.



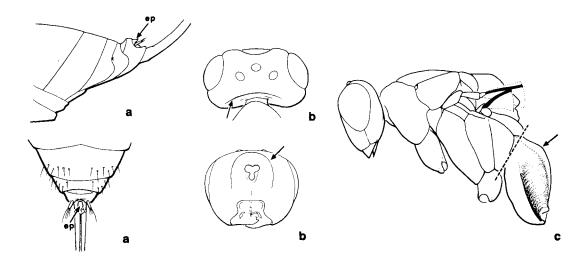
27(26)		Female and: Metasoma with ovipositor sheath, or tail-like structure, extending for distance greater than length of metasoma (excluding sheaths or tail)
		Male or, if female, then:  Metasoma with ovipositor sheath (ov) extending for distance less than length of metasoma and if posterior terga greatly lengthened then metasoma (mt) more or less evenly narrowed and/or heavily sclerotized
28(27)	a.	Metasoma with tail-like structure composed of ovipositor sheaths and posterior one or two terga
	aa.	Metasoma with only ovipositor sheaths conspicuously long

Formed by ovipositor sheaths (ov) and greatly lengthened posterior 1 or 2 metasomal terga (mt), which often look like the ovipositor sheaths fused along their midline; structure filament-like or tube-like and abruptly narrowed from anterior part of metasoma, which is relatively lightly sclerotized.

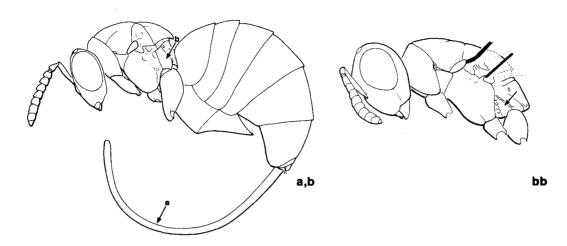


- a. Scutellum (sc) distinctly quadrate—widely truncate along transscutal articulation and with subparallel or incurved axillular grooves (ag) and transverse frenal groove (fg).

  - aa. Scutellum (sc) shield-like or teardrop-shaped.

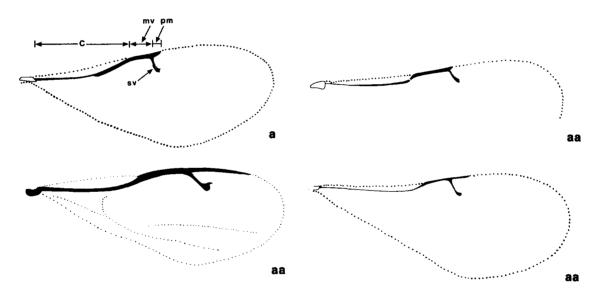


- 30(29) a. Metasoma with apical tergum transverse dorsally and with posterior margin  $\Omega$ -like, the emargination partly surrounding a small, more or less sclerotized, thumbnail-like median flap (ep, epipygium).
  - b. Head usually with occipital carina (carina often fine, very rarely absent).
  - c. Metacoxa usually conspicuously large and subtriangular in cross section (typically widely attached to metathorax-propodeum at about 45° angle) . . . . . . some TORYMIDAE (p. 614)
  - aa. Metasoma with apical tergum **usually** about as long as preceding tergum and **if** posterior margin conspicuously emarginate ( $\Omega$ -like) **then** tergum without epipygium.
  - bb. Head without occipital carina.



- **31(30)** a. Ovipositor sheath curved or coiled ventrally, thread-like.

  - aa. Ovipositor sheath straight (directed posteriorly), robust.

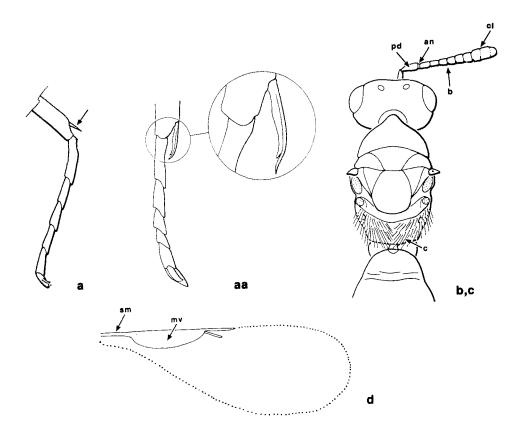


- a. Fore wing with stigmal vein (sv) longer than short to absent postmarginal vein (pm) and marginal vein (mv) one-third or less length of costal cell (C), with stigmal vein usually virtually at right angle to marginal vein.

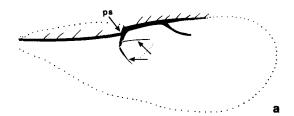
  - aa.<sup>14</sup> Fore wing venation only very rarely as described in statement "a," **usually** with marginal vein longer **or** postmarginal vein as long as or longer than stigmal vein.

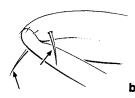
Rare males with metallic luster but these with scutellum distinctly quadrate (widely truncate along transscutal articulation, with straight or incurved axillular grooves and with transverse frenal groove).

<sup>14</sup> If venation as described in statement "a" then metapleuron triangular (angulate below base of hind wing) and body at least partly with metallic luster and/or pronotum with distinctly transverse collar.



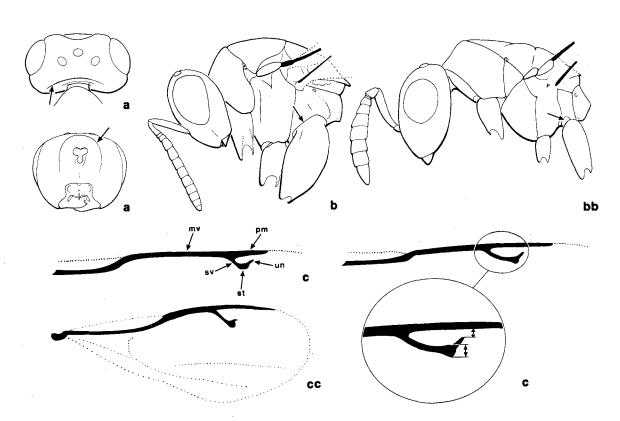
- a. Protibial spur inconspicuous (only about one-third or less length of tarsomere 1), slender and straight.
  - b. Antenna with at most 10 flagellomeres, usually with 7 distinct flagellomeres, or with 1 obscure ring-like flagellomere (an, anellus) and 5 or 6 distinct flagellomeres between pedicel (pd) and club (cl).
  - c. Propodeum often setose medially, with setae on each side directed toward midline.
  - d. Males sometimes with marginal vein (mv) enlarged as elongate, thickened, black area that is conspicuously longer than submarginal vein (sm) ...... some TETRACAMPIDAE (p. 623)
  - aa. Protibial spur robust, longer and more conspicuous than described in statement "a," often distinctly curved.
  - bb. Antenna often with 11 flagellomeres or with 2 or more ring-like flagellomeres next to pedicel.
  - cc. Propodeum with medial one-third bare, except very rarely.





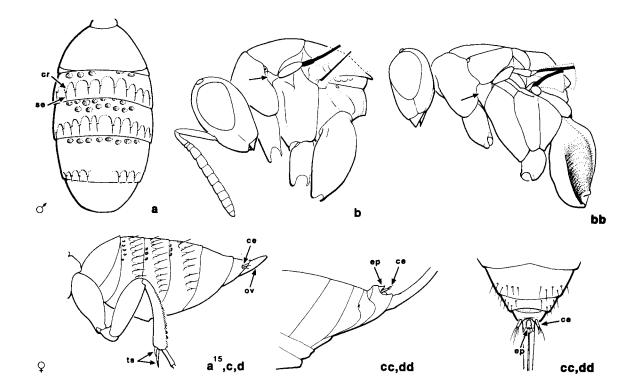
- a. Fore wing with 1-3 long bristles on parastigma (ps, curved apical part of submarginal vein), with parastigma often extending spike-like behind submarginal vein.
  - b. Mesofemur with ventrally directed subapical bristle on both anterior and posterior surfaces.
  - c. Body without metallic luster.

  - aa. Fore wing only extremely rarely with differentiated long bristles on parastigma but if so then some or all of statements "b-d" different.
  - bb. Mesofemur only rarely with subapical bristle on anterior and posterior surfaces.
  - cc. Body often with metallic luster.



- a. Head with occipital carina (carina often very fine).
  - b. Metacoxa subtriangular in cross section, widely attached to metathorax-propodeum at about 45° angle and usually conspicuously large.

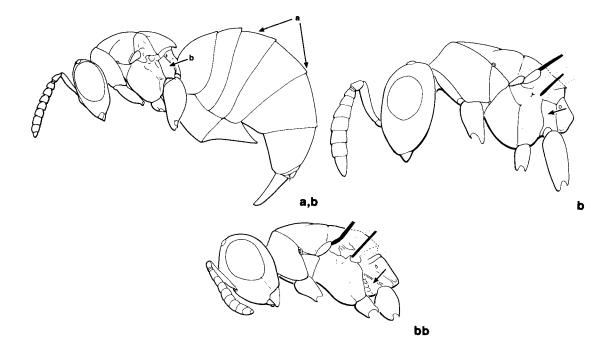
  - aa, bb. Head without occipital carina or if with carina then metacoxa usually subcircular in cross section and narrowly attached to metathorax, more or less dorsally, by sphincter-like base.



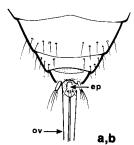
- 36(35) a.15 Metasoma usually with transverse band of coarse punctures and/or row of crenulae (cr) on one or more terga.
  - b. Prepectus small and inconspicuous, fused with mesopleuron over most of height (widely separate from procoxa if pronotum appressed against mesopleuron).
  - c. Metasoma with button-like cercus (ce) near posterior margin of apical tergum.

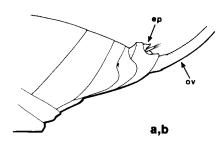
  - aa. Metasoma without differentiated sculpture.
  - bb. Prepectus large and triangular, extending ventrally to procoxa.
  - cc. Metasoma with peg-like cercus (ce) projecting from posterior margin of apical tergum.
  - dd. Female with ovipositor sheath conspicuously exserted and with posterior margin of apical tergum Ω-like and partly surrounding a small thumbnail-like median flap (ep, epipygium) ...... some TORYMIDAE (p. 614)

Rarely with crenulae reduced to small, separate, longitudinal ridges bearing a relatively long white seta (se) or very rarely with only transverse row(s) of long white setae on central terga, but then with two very robust, curved metatibial spurs (ts).



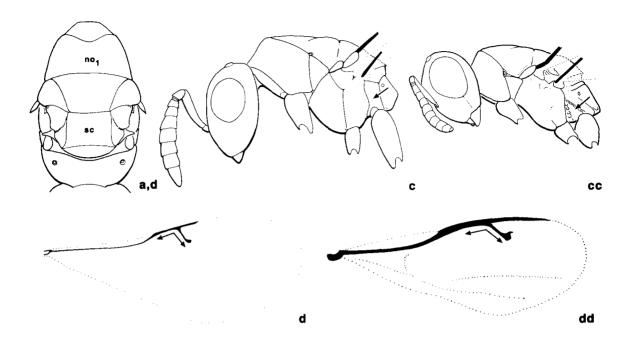
- a. Metasoma widely attached to mesosoma and more or less compressed and tapered posteriorly, with dorsum distinctly convex so that in lateral view apex usually curved down.
  - b. Metapleuron quadrate to rectangular, the dorsal margin transverse below base of hind wing (except for some rare New World taxa) ...... (some Otitesellinae) AGAONIDAE (p. 610)
  - aa. Metasoma usually petiolate, or ovate to lanceolate in dorsal view and depressed in lateral view, but if compressed then apex not curved down.
  - bb. Metapleuron subtriangular, angulate below base of hind wing (except extremely rarely) ...... 39





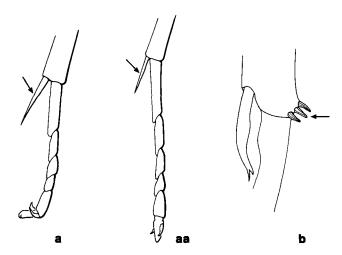
- **39(38)** a. Ovipositor sheath (ov) distinctly exserted.
  - b. Apical tergum of metasoma transverse dorsally and with posterior margin  $\Omega$ -like, the emargination partly surrounding a small, more or less sclerotized, thumbnail-like median flap (ep, epipygium) . . . . . . . . . . . some **TORYMIDAE** (p. 614)

<sup>&</sup>lt;sup>16</sup> Females of Chromeurytominae with states "a" and "b," but such females with only 6 flagellomeres between pedicel and club.



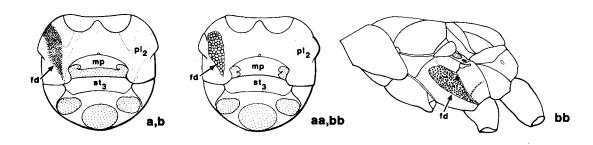
**40(37)** a. Pronotum (no<sub>1</sub>) large, rectangular to subconical.

- b. Body usually yellowish to brown, relatively lightly sclerotized with erect scattered setae.
- c. Metapleuron quadrate to rectangular, dorsal margin transverse below base of hind wing.
- d. Fore wing sometimes with stigmal vein relatively long and directed from marginal vein virtually at right angle, or with scutellum (sc) distinctly quadrate . . . . . . some AGAONIDAE (p. 610)
- aa. Pronotum often very short.
- bb. Body often with metallic luster and/or heavily sclerotized with short setae.
- cc. Metapleuron subtriangular, angulate below base of hind wing.



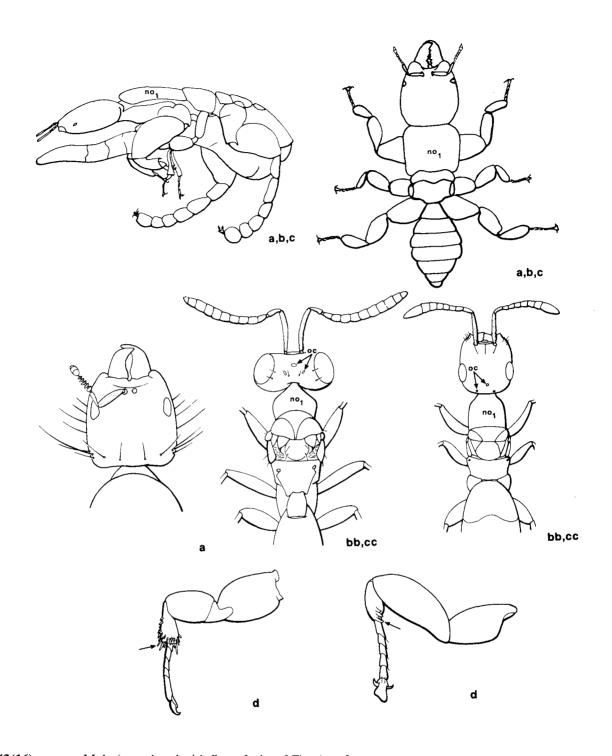
- 41(40) a. Mesotibia with distinctively long apical spur, about one-third length of mesotarsus and subequal in length to tarsomere 1.

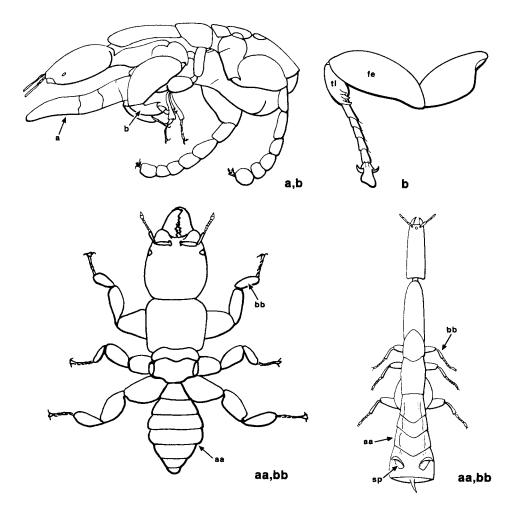
  - aa. Mesotibia with relatively short apical spur, about one-quarter length or less of mesotarsus and usually distinctly shorter than tarsomere 1.
  - bb. Protibia only very rarely with dorsoapical spines ...... most PTEROMALIDAE (p. 608) ...... very few TORYMIDAE and AGAONIDAE (pp. 610, 614)

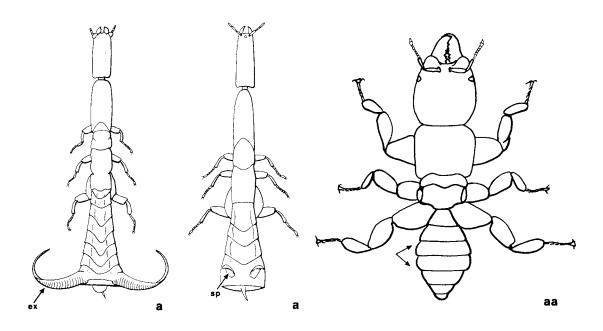


- a. Mesotrochantinal plate (mp) separated from metasternum (st<sub>3</sub>) by distinct membranous area (requires removal of mesocoxa to observe structure).

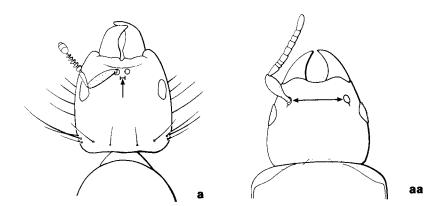
  - aa. Mesotrochantinal plate (mp) extending to metasternum (mt<sub>3</sub>).
  - bb. Mesopleuron (pl<sub>2</sub>) with femoral depression (fd) usually distinctly reticulate or punctate ...... some **PTEROMALIDAE** (p. 608)





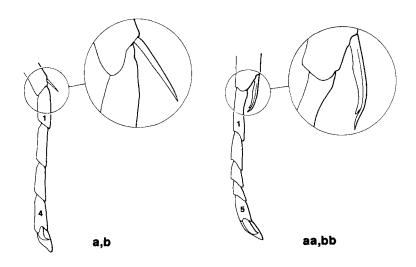


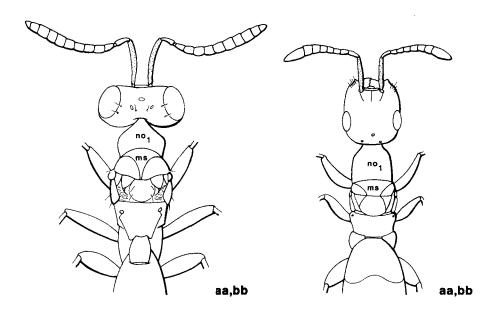
- a. Metasoma relatively long, with subparallel or diverging sides and with more or less truncate posterior margin, and usually either with long posterolateral extension (ex) or with extremely large and conspicuous spiracle (sp).
  - b. Antenna with 1-3 flagellomeres ...... (most male Sycophaginae) AGAONIDAE (p. 610)
  - aa. Metasoma relatively short and tapered posteriorly.



- - aa. Toruli near middle of head or higher **but** if only about one-third height of head from oral cavity then far apart ............................... (male **Otitesellinae**) **AGAONIDAE** (p. 610)
- 47(43) a. Tarsi with 3 tarsomeres.

  - aa. Tarsi with 4 or 5 tarsomeres.





#### Family CHALCIDIDAE

(Fig. 212)

(C = Chalcidinae, D = Dirhininae, E = Epitraninae, H = Haltichellinae, S = Smicromorphinae)

**Diagnosis** Body without metallic luster (except *Notaspidium*), mainly black or brownish to entirely yellow or reddish; head and mesosoma heavily sclerotized, usually coarsely punctate at least in part; head dorsally sometimes with projection (horn) between scrobal depression and each eve (D); gena carinate or ridged; antenna inserted below (E, H, some D) or at or above level of ventral margin of eye (C, S, some D); flagellum shorter than length of eye and with 5-7 flagellomeres (S) or conspicuously longer than eve and with 9-11flagellomeres, the first flagellomere ring-like or not; pronotum with quadrate to transverse subrectangular collar (posterior margin often conspicuously incurved) or rarely (S) almost linear in dorsal view, but with lateral margin straight and not extending to tegula (cf. Leucospidae): prepectus small, often difficult to distinguish; mesopleuron with shallow femoral depression over most of height; individuals fully winged; fore wing not folded lengthwise, with venation sometimes reduced to oblong spot at apex of submarginal vein but usually with marginal and stigmal veins distinct, with marginal vein usually longer than stigmal vein, and with postmarginal vein absent to long; tarsi with 5 tarsomeres; metacoxa long and in cross section subcircular to very large and subtriangular; metafemur large, compressed, and ventrally serrate or dentate over at least apical third; metatibia usually distinctly curved, either truncate with 2 apical spurs (H) or obliquely pointed with 1 spur or none; metasoma with petiole transverse to long and slender, rarely inserted high on propodeum adjacent to metanotum (S) or longitudinally carinate (E); postpetiolar terga separate; ovipositor sheath exserted only very slightly.

Comments Chalcidids are widely distributed, with about 195 nominal genera and 1875 nominal species. Members are readily distinguished, even with inclusion of the bizarre subfamily Smicromorphinae, but Chalcididae could well be paraphyletic relative to Leucospidae. Subfamily classification follows Bouček (1988a); a sixth subfamily (Brachymerinae) often has been distinguished from Chalcidinae based on a transverse petiole. The subfamilies can be recognized by using a combination of the attributes given above.

**Biology** Chalcididae are primary parasitoids or hyperparasitoids, mostly of Lepidoptera (primarily of young pupae) and Diptera (primarily of mature larvae), though some parasitize other Hymenoptera or Coleoptera, and a few are known from a wide variety of other insect hosts. The modified hind legs apparently have several functions, at least in females. Females of some species grab the host between the toothed femur and curved tibia during oviposition, whereas others stand upright on the hind legs so that the front and middle legs are free to manipulate the host; females are also known to use the hind legs in back-to-back fighting, and females of Lasiochalcidia igiliensis Masi use their hind legs to hold apart the mandibles of ant-lion larvae (Neuroptera: Myrmeliontidae) while ovipositing into the membrane between the head and the thorax.

References Bouček (1988a) keyed the subfamilies known from the Australasian region and listed published keys to genera from other regions. Delvare and Bouček (1992) revised the genera of the family and the species of the Chalcidini from the New World.

## Family LEUCOSPIDAE

(Fig. 213)

**Diagnosis** Body usually black or brownish to extensively yellow or reddish (slight metallic luster in some species); mesosoma and metasoma heavily sclerotized and conspicuously, densely punctate; antenna inserted at or above mid height of head, with 11 flagellomeres (suture between terminal 2 flagellomeres sometimes indistinct), the first flagellomere not ring-like; pronotum with quadrate to transverse subrectangular collar that often is transversely carinate, and with more or less sinuate lateral margin partly surrounding and extending over spiracle to base of elongate tegula; prepectus

small and inconspicuous along anterodorsal margin of mesopleuron; mesopleuron with deep, well-delineated femoral depression ventrally; individuals fully winged; fore wing normally folded longitudinally, with submarginal and postmarginal veins very long but with marginal vein shorter than stigmal vein; tarsi with 5 tarsomeres; metacoxa very large; metafemur large and compressed, ventrally serrate or dentate over at least apical half; metatibia distinctly curved or not, apically truncate with 2 spurs or obliquely pointed with 1 spur; petiole transverse; males with metasomal terga

more or less fused into carapace except for anterior 1 or 2 postpetiolar terga and apical tergum; females with metasomal terga separate, the second postpetiolar tergum mostly or entirely concealed under first tergum (at most visible only as small disc laterally), the third postpetiolar tergum very short in dorsal view, and the fifth postpetiolar tergum (preceding spiracle-bearing tergum) usually largest and forming widest part of metasoma; females with one or more metasomal terga medially grooved for reception of ovipositor sheaths (except *Polistomorpha*); ovipositor sheaths, if long, evenly recurved over metasoma.

**Comments** Leucospids are primarily tropical and subtropical. Although 11 genera have been described, only four are considered to be valid (*Leucospis*, *Micrapion*, *Neleucospis*, and

Polistomorpha). About 240 nominal species are described. Leucospids are among the largest of chalcidoids (2–17 mm) and are often quite striking in appearance because they usually mimic various wasps, though usually not the species they parasitize. The family undoubtedly is monophyletic, even with inclusion of Polistomorpha, which has more plesiomorphic-looking females, but classifying leucospids separately from chalcidids may render Chalcididae paraphyletic.

**Biology** Leucospids are all ectoparasitoids of solitary aculeate Hymenoptera, primarily of solitary bees (Apiformes) but also of Eumeninae (Vespidae) and Sphecidae.

**Reference** Bouček (1974a) revised the world fauna.

### Family EURYTOMIDAE

(Fig. 214)

**Diagnosis** Body without metallic luster (except Chryseida and Nikanoria), usually black or partly to entirely yellow or reddish; head and mesosoma usually heavily sclerotized and coarsely sculptured. but at least with distinct mesh-like or granular sculpture, and metasoma usually relatively smooth and shining; head without occipital carina, but with gena often carinate or ridged; antenna almost always inserted at or above level of ventral margin of eye; flagellum sometimes with 11 flagellomeres of which basal 1-3 flagellomeres usually ring-like, but more often with first flagellomere ring-like and with only 4-6 subsequent flagellomeres, these in males often with whorls of long setae; pronotum with quadrate to transverse subrectangular collar (posterior margin often distinctly incurved) at least half as long as mesoscutum; prepectus large to very small; individuals fully winged (except rare wingless forms in *Tetramesa*); fore wing with marginal vein sometimes conspicuously thickened or enlarged into a pseudostigma, and then often with brownish area behind parastigma, but with stigmal vein directed from marginal vein at distinctly obtuse angle—cf. Agaonidae (Epichrysomallinae); tarsi with 5 tarsomeres (except males of Boucekiana tetracampoide De Santis); metacoxa usually relatively small and subcircular in cross section; metafemur relatively slender (metacoxa and metafemur conspicuously enlarged in Masneroma, but metafemur not ventrally dentate—cf. Chalcididae); propodeum often more or less depressed medially or longitudinally channelled; metasoma with apical tergum sometimes elongate-tapered, but ovipositor sheath not conspicuously exserted (except Exeurytoma).

**Comments** Eurytomids are widely distributed, with about 135 nominal genera and 1425 nominal species. Subfamily classification currently is unstable. Burks (1971a) divided the genera into eight subfamilies, but without giving any characters to recognize them. Stage and Snelling (1986) recognized three subfamilies (Rileyinae, Heimbrinae, Eurytominae), giving a character matrix by which members could be distinguished. Zerova (1988) reviewed previous classifications and proposed a new classification of seven subfamilies (Rileyinae, Burmesiinae, Heimbrinae, Eurytominae, Harmolitinae, Aximinae, Eudecatominae). Each subfamily was diagnosed, and all previously described genera were assigned to subfamily based on the classification.

**Biology** Members of Eurytomidae have extremely diverse host associations. Some species are phytophagous, others are entomophagous, and still others are both, feeding on plant tissue before and/or after consuming an insect host. The phytophagous species are stem miners, gall formers, or seed eaters, whereas almost all of the entomophagous species are primary ectoparasitoids or hyperparasitoids of larvae concealed within plant tissue, such as stems, galls, and seeds.

References Burks (1971a) presented a synopsis of the world genera, including a key to 49 genera but listing an additional 15 taxa as unplaced. Stage and Snelling (1986) characterized the three recognized subfamilies and keyed the known genera and species of Heimbrinae. Zerova (1988) did not include keys.

### Family PTEROMALIDAE

(Fig. 215)

**Diagnosis, Comments, Biology** Pteromalidae is not defined by any unique attribute or combination of attributes. Membership is largely determined by elimination; the family is composed of chalcidoids that have tarsi with 5 tarsomeres but not the entire suite of attributes that define any other family whose members have tarsi with 5 tarsomeres. Pteromalids are widely distributed, with about 845 nominal genera and 4115 nominal species.

Graham (1969) recognized 15 pteromalid subfamilies, whereas Bouček (1988a) recognized 28 subfamilies. Readers are referred to those two works for diagnostic attributes and keys to separate the subfamilies. A list of subfamilies that are, or have recently been, recognized as subfamilies in Pteromalidae are given below. Unless otherwise indicated, Graham refers to Graham (1969) and Bouček to Bouček (1988a).

- Akapalinae Established as a subfamily of Eucharitidae by Bouček (see "Comments" for Eucharitidae), but recognized here as a subfamily of Pteromalidae because I accept the concept of Eucharitidae presented by Heraty and Darling (1984); one genus, Akapala, restricted to Australia; hosts unknown.
- Asaphinae Cosmopolitan; primary parasitoids or more often hyperparasitoids of Homoptera, especially Aphidae and Coccoidea, but also of Neuroptera (Chrysopidae, Hemerobiidae) and Siphonaptera.
- Austrosystasinae Established by Bouček for Austrosystasis atricorpus Girault; restricted to Australia; found in galls on Eleocarpus.
- Austroterobiinae Established by Bouček for Austroterobia partibrunnea Girault from Australia and for undescribed taxa from Africa and South Asia; one African species recorded as a parasitoid of *Icerya* (Homoptera: Margarodidae).
- Brachyscelidiphaginae Classified as the tribe Melanosomellini in Ormocerinae by Bouček; key to genera by Gahan and Ferrière (1947) included all pteromalid genera that were known to be gall makers or that had been reared from galls and thus also included genera currently assigned to Coelocybinae and Epichrysomallinae.
- Ceinae Composed of Spalangiopelta (world species revised by Darling 1991) and Cea; hosts little known but records indicate leaf-mining Diptera (Agromyzidae and Drosophilidae).
- **Cerocephalinae** Primarily tropical in distribution, with keys to genera by Gahan (1946)

- and Hedqvist (1969a); parasitoids of small wood-boring Coleoptera.
- Chalcedectinae Recognized as a subfamily by Graham, but as a tribe in Cleonyminae by Bouček; mostly parasitoids of wood-boring Coleoptera.
- Chromeurytominae Established by Bouček for *Chromeurytoma* and *Asaphoideus* (both from Australia) and for an undescribed genus from Burma (see also "Comments" for Torymidae).
- Chrysolampinae Recognized as subfamily of Pteromalidae by Graham but as subfamily of Perilampidae by Bouček; phylogenetic relationships analyzed by Heraty and Darling (1984) and Darling and Miller (1991); key to New World genera by Darling (1986); parasitoids of Coleoptera.
- Cleonyminae Cosmopolitan, but most diverse in tropics; parasitoids, mostly of wood-boring Coleoptera but some of stem-nesting or mud-nesting aculeate Hymenoptera; Bouček (1958b) keyed the world genera and Hedqvist (1961) the tribes of Cleonymini.
- Coelocybinae Established by Bouček; southern hemisphere in distribution; associated with galls on various trees.
- Colotrechninae Including, as a synonym, Dvaliniinae (Hedqvist 1978); cosmopolitan; often associated with galls, also some parasitoids of Coleoptera.
- Cratominae Single genus *Cratomus*, in Europe and North America; hosts unknown, probably wood-boring Coleoptera.
- Diparinae Cosmopolitan; hosts little known, but one species reared as a parasitoid of Curculionidae (hosts may include Coleoptera on roots or parts of plants close to the ground); in addition to the keys to genera by Graham and by Bouček, Yoshimoto (1977) keyed the Nearctic genera and Hedqvist (1969b) the African genera.
- Ditropinotellinae Established by Bouček for Ditropinotella, restricted to Australia and New Guinea; associated with galls on trees and shrubs.
- **Dvaliniinae** Established by Hedqvist (1978) for four genera from South America, but synonymized with Colotrechinae by Grissell (1985).
- Elatoidinae Established by Bouček for Elatoides; known from Japan and Far East

- Province of USSR; species revised by Kamijo (1983); parasitoids of Coccoidea (Homoptera).
- Epichrysomallinae See Agaonidae.
- Erotolepsiinae Established by Bouček for Erotolepsia (Neotropical), and Eunotopsia and Papuopsia (Australia); hosts unknown.
- Eunotinae Cosmopolitan; associated with Homoptera, as predators of eggs of Coccidae, or more rarely from Psyllidae and Aphidae, sometimes as hyperparasitoids.
- Eutrichosomatinae Composed of Eutrichosoma and Peckianus (New World), and Collessina (Australia); genera revised by Bouček (1974b); one species recorded as a parasitoid of Curculionidae.
- Herbertiinae Established by Bouček for *Herbertia*, a cosmopolitan genus; species revised by Burks (1959); parasitoids of leaf-mining Diptera.
- **Keiraninae** Established by Bouček for his new genus and species *Keirana longicollis*; restricted to Australia; parasitoid of *Callipappus rubiginosus* Maskell (Homoptera: Margarodidae).
- Leptofoeninae Often included as part of Cleonyminae, but recognized as subfamily by Bouček; two genera: Leptofoenus (New World; species revised by LaSalle and Stage 1985) and Doddifoenus (Australia); hosts unknown, but probably parasitoids of wood-boring Coleoptera.
- Louricinae Often included as part of Cleonyminae, but recognized as subfamily by Bouček; single genus *Callimomoides* (= Louricia) restricted to the Old World tropics; parasitoids of eggs of Cerambycidae (Coleoptera).
- Macromesinae Single genus Macromesus (differentiated from other pteromalids by having mesotarsus with 4 tarsomeres); known from all continents except South America; parasitoids of Scolytidae and Curculionidae in twigs.
- Miscogasterinae Graham included in this subfamily the tribes Miscogasterini, Sphegigasterini, Trigonoderini, Micradelini, Termolampini, Ormocerini, and Pirenini; Bouček treated the last two tribes as subfamilies, transferred the Trigonoderini to Pteromalinae, included Sphegigasterini within Pteromalini, and retained only the Miscogasterini as Miscogasterinae; under Bouček's classification, members are parasitoids of Diptera that mine or burrow into the soft tissue of plants.

- **Nefoeninae** Established by Bouček for his new genus and species *Nefoenus pilosus* and for one undescribed species; restricted to Australia; hosts unknown.
- Neodiparinae Single genus Neodipara; Askew (1970, 1975) described the females and males; hosts unknown.
- Ormocerinae Recognized as a tribe in Miscogasterinae by Graham but as a subfamily by Bouček (including Brachyscelidiphaginae as the tribe Melanosomellini); gall makers or parasitoids of gall makers.
- Otitesellinae See Agaonidae.
- Panstenoninae Single genus *Panstenon*; known from all continents except South America; associated with grasses (hosts apparently insect eggs and larvae developing in internodes of grass stems).
- Parasaphodinae Established by Bouček for *Parasaphodes*; known from Africa, Australia, and Oriental region; parasitoids of Stictococcidae and Eriococcidae (Homoptera).
- Philomidinae Classified as a subfamily of Eucharitidae by Bouček (see "Comments" for Eucharitidae); hosts unknown (suggested as parasitoids of ground-nesting Apidae by Bouček).
- Pireninae Cosmopolitan; parasitoids of Cecidomyiidae (Diptera); recognized as a tribe of Miscogasterinae by Graham.
- Pteromalinae Largest of the subfamilies, comprising those pteromalids not assigned to other subfamilies; including the Sphegigasterini and Trigonoderini sensu Bouček, which were included in Miscogasterinae by Graham.
- Spalangiinae Cosmopolitan; primary parasitoids of cyclorrhaphous Diptera (some species used in biological control programs against synanthropic flies and sheep-maggot flies); two genera: Spalangia (revised by Bouček 1963) and Playaspalangia (Yoshimoto 1976).
- Storeyinae Established by Bouček for his new genus and species, *Storeya paradoxa*, from Australia, and an undescribed species from Nepal; hosts unknown.

References Graham (1969) and Bouček (1988a) reviewed subfamily classification for Europe and the Australasian region, respectively; Bouček and Rasplus (1991) provided an illustrated key to the West-Palaearctic genera; other regional keys to genera are listed under "Regional keys to families."

## Family AGAONIDAE

(Fig. 216)

**Diagnosis, Comments** Membership and subfamily classification of Agaonidae are extremely unstable. Bouček et al. (1981) classified Agaoninae and Blastophaginae as the only two subfamilies of Agaonidae; in the same work they classified Sycophaginae (Sycophagini and Apocryptini) in Torymidae and Otitesellinae and Epichrysomallinae in Pteromalidae, but left unplaced to family Sycoecinae and Sycoryctinae (Philotrypesini and Sycoryctini). More recently, Bouček (1988a) classified all the above taxa in Agaonidae but treated the Sycophagini as a subfamily and transferred Apocryptini to Sycoryctinae. Bouček's (1988a) concept of Agaonidae included chalcidoids that are associated with figs and that have a postgenal bridge but that lack an occipital carina and/or that have a short, nonexserted ovipositor. This combination of attributes was used to delimit agaonids from torymids. Torymidae and Agaonidae share a postgenal bridge (along with some other chalcidoids, including Ormyridae and some Pteromalidae and Eurytomidae), but with rare exceptions torymids have an occipital carina. The only agaonids (sensu Bouček 1988a) with an occipital carina are some Epichrysomallinae, but females of this subfamily have a nonexserted ovipositor, whereas female torymids have an exserted, usually long ovipositor. Partly for this reason Epichrysomallinae was hypothesized as the most primitive agaonid clade by Bouček (1988a). In partial support of his classification, Bouček (1988a) noted that studies of the female reproductive structures of Torymidae and Agaonidae by Copland and King (1972) and Copland et al. (1973), respectively, indicated that the reproductive systems of epichrysomallines and sycophagines were similar in several attributes to that of agaonids (sensu stricto). However, no classification of Agaonidae/Torymidae will be valid phylogenetically until critical studies are made to determine the following: which shared attributes are plesiomorphic and which are apomorphic, which attributes are shared because of inheritance from a common ancestor, and which shared attributes result from convergence because of similar selection pressures within the fig-gall niche. For example, Wiebes (1981: 553) classified Sycoecinae in Torymidae, considering that the resemblance between sycoecines and agaonines was the result of convergence because of similar habits, "particularly the entering of the fig receptacle through the narrow ostiole."

Bouček's (1988a) classification is followed here for Agaonidae, simply as one that is as well substantiated as any other. The subfamilies are diagnosed below so that at least most members can be differentiated from each other and from other

chalcidoids. Some females of Agaoninae, Sycoecinae, Sycophaginae, and Otitesellinae are convergent in structure and easily confused, and many female Otitesellinae, particularly those from the New World tropics, are easily confused with Pteromalidae. Apterous agaonid males are relatively easy to distinguish to subfamily, but winged males are easily confused with pteromalid males. Agaonids are tropical and subtropical, with about 120 nominal genera and 650 nominal species.

**Biology** Members of the subfamily Agaoninae are the "true" fig wasps, all developing within the syconia, or figs, of Ficus species. Figs and fig wasps may have co-evolved because agaonines are the sole agents for the pollination of the internal flowers, because related figs have related pollinators, and because each species of agaonid has its own species of fig. A female agaonine finds a suitable fig of the correct species and enters the syconium through the ostiole, forcing apart the bracts that fill the ostiole with the help of her modified legs, antennae, and mandibles. Once in the syconium the female searches among the florets for a gall flower, which is adapted for oviposition by the wasp and development of the agaonid larva. The ovipositor is inserted into the stigma, through the style, and into the ovary, into which the egg is deposited. Parthenocarpic development of the ovule endosperm is stimulated to produce a gall, which becomes the larval food source. Males mature first and escape from the gall by biting their way through the thin wall of the ovary. A male then finds a gall containing a female, chews a hole through the ovary wall, inserts his recurved metasoma through the hole, and copulates with the relatively immobile female. The female escapes from the ovary by enlarging the hole made by the male. The anthers of male flowers in the syconium ripen by the time the female agaonine emerges, and pollen collects in pollen pockets on the mesosoma, in corbicula on each foreleg, or in folds of intersegmental membrane of the metasoma. The female then completes the cycle by leaving the fig and flying to a new fig of the proper species. After entering the fig the sticky stigma of female flowers, which are unsuitable for oviposition, are pollinated during the female's search for a fig flower in which to oviposit.

Members of the other agaonid subfamilies often were said to be parasitoids of agaonines, but Bouček (1988a) indicated that this probably is incorrect and that many, perhaps all, are phytophagous, competing for food and space with the pollinating agaonines.

 Agaoninae Male and female body without metallic luster, shiny and smooth, or at most sparsely micropunctate or alutaceous; head prognathous; antenna inserted near oral cavity; pronotum subequal in length or longer than mesoscutum, or with posterior margin variously incurved or emarginate; protibia and metatibia much shorter and usually much less massive than respective femur, most often subtriangular with 2 or more stout spines or denticles apically. Female fully winged; fore wing venation sometimes obsolescent except for submarginal vein, though usually complete and then marginal vein relatively short, with stigmal vein virtually at right angle to marginal vein and usually relatively long (stigmal vein often subequal in length to marginal vein); head flattened or more or less wedge-like in lateral view, usually partly membranous above toruli (then head often medially collapsed in air-dried specimens); mandible with ventrally toothed or serrated appendage, or with transversely ridged lamellar appendage fused to base; scape robust and often compressed, and/or with one or more surfaces angulate; first flagellomere not ring-like, often apically produced into spine or appendage; scutellaraxillar complex with straight or incurved axillular groove (groove sometimes very fine, rarely obsolete), the scutellum therefore usually quadrate to more or less hourglass in shape and with large lateral axillula between scutellum and axilla; metasoma very widely attached to mesosoma; metasomal tergum 7 (tergum with spiracle) with posterior margin usually distinctly emarginate and membranous medially, with spiracle sometimes conspicuously large and/or more or less ovoid; tergum 8 entirely membranous or reduced to small thumbnail-like sclerotized flap between peg-like cerci (exact structure usually concealed or difficult to discern in air-dried specimens but cerci often appear to originate from posterior margin of tergum 7, or cerci and tergum 8 separated from tergum 7 by membrane); ovipositor sheath exserted, usually long and often partly coiled. Male wingless, yellowish, with body highly modified; eyes very small or vestigial; ocelli absent; antenna with 2-6 flagellomeres; tibiae stout, with spines; metasoma long, with posterior 4 or 5 segments tubularly lengthened and tapered apically (telescoping), normally recurved U-like under mesosoma.

• Sycoecinae Female with body as described for Agaoninae except metatibia normal (not shortened like protibia) and antenna inserted near mid height of head in some taxa; fully winged; fore wing with marginal vein distinctly longer than stigmal vein (also often conspicuously thicker than other venation), with postmarginal vein subequal in length or shorter than stigmal vein and tapered to point, and with stigmal vein at distinctly obtuse angle to marginal vein; head in frontal view more or less parallel-sided (subquadrate to elongate rectangular), in lateral

view flattened to more or less wedge-like, completely sclerotized, though often with median groove or channel above toruli; mandible usually with one or more small, posteriorly pointing teeth along ventral posterior margin; antenna with scape unmodified (spindle-like) and first flagellomere ring-like; scutellum without axillular groove, thus not distinctly quadrate nor with axillula; metasoma widely attached to mesosoma; metasomal tergum 7 completely sclerotized, with posterior margin transverse and with spiracle unmodified; tergum 8 sclerotized and not conspicuously modified, the posterior margin neither emarginate nor with thumbnail-like flap (epipygium); cerci peg-like; ovipositor sheath distinctly exserted or not. Male fully winged or very rarely wingless; fully winged males with venation as described for females; antenna with 9 flagellomeres; wingless males with antenna inserted below line drawn between ventral margin of eyes, with metasoma neither elongate nor recurved under mesosoma.

**Comments** Female sycoecines can be confused with female agaonines because of their highly modified protibia, smooth and shiny body, and similar shape of head. Most females are also similar to female agaonines because the mandibles usually have posteriorly pointing teeth along the ventral posterior margin. However, female agaonines are distinguished from sycoecine females by described differences in antennal and scutellar structure, wing venation and conspicuously small metatibia. Female agaonines also usually have the head partly membranous above the toruli and they differ in the structure of metasomal tergum 8, though this latter difference usually is difficult to distinguish in air-dried specimens. Female sycoecines can also be confused with some female sycophagines and with otitesellines (see "Comments" for these latter two subfamilies).

• Otitesellinae Female fully winged; dark, usually with at least obscure metallic luster and usually with distinct, often reticulate sculpture, very rarely smooth and shiny; head only very rarely prognathous and flattened, usually hypognathous and oval to lenticular in lateral view; antenna inserted near ventral margin of eye or nearer mid height of head; antenna with basal 1-3flagellomeres ring-like, with 4 or 5 flagellomeres not ring-like, and with club of 3 flagellomeres; mandible without ventral teeth (except Grasseiana); pronotum very short to as long as mesoscutum; mesoscutum with notauli usually entire, though often fine, or obsolete in some taxa with smooth mesoscutum; scutellar-axillar complex without axillular groove, with shield-like scutellum, and with widely separated subtriangular axillae; fore wing surface often relatively sparsely setose to almost glabrous;

marginal vein conspicuously longer than stigmal vein (not conspicuously thicker than other venation), with postmarginal vein often longer than stigmal vein, and with stigmal vein at obtuse angle to marginal vein; protibia often distinctly shorter than profemur but only very rarely conspicuously modified as in Agaoninae or Sycoecinae; metatibia not modified (except Grasseiana); mesocoxae inserted virtually between metacoxae, often forming almost straight line; metacoxa only about as long as height of mesothorax; metafemur not conspicuously long, often compressed spindle-like; metasoma sessile, usually more or less compressed cylindrical and/or posteriorly tapered, with dorsum convex and sternum relatively flat so metasomal apex usually downcurved; metasomal tergum 7 unmodified, with spiracle unmodified; tergum 8 distinct, with posterior margin not conspicuously emarginate and without epipygium (rarely with depigmented band from each cercus to posterior margin of tergum delineating median epipygium-like area); cercus button-like to peg-like but extending from surface of tergum near posterior margin; ovipositor sheath at least slightly exserted, usually relatively short, thick and downcurved, but sometimes about as long as body and then more thread-like and coiled. **Male** usually wingless or with filamentous fore wing and then: yellowish, without metallic luster, smooth and shiny; head and mandibles usually conspicuously large; ocelli absent; antenna inserted near mid height of head or higher, or if only about one-third height of head from oral cavity then inserted widely apart; tibiae stout, with spines; metasoma relatively short and tapered to apex.

Comments Depending on the taxon, females of Otitesellinae are easily confused with females of Sycoecinae, Apocryptini, or Pteromalidae. Females of two Old World genera (Eujacobsonia and Grasseiana) have a flattened head, the head and mesosoma relatively smooth and shiny with obscure metallic luster, and a large pronotum, and therefore are very similar to sycoecine females (males of the two genera exhibit a structure that is typical for apterous otitesellines). Most female sycoecines are readily distinguished from Eujacobsonia and Grasseiana females by wing venation and conspicuously exserted ovipositor sheath, but Bouček (1988a) should be consulted for accurate identification. Female otitesellines from the New World often have quite long ovipositors and are very similar to females of Apocrypta. This latter genus is not known from the New World, but females are differentiated from otitesellines by their ventrally projected plowshare-like anterior metasomal sterna (not just the hypopygium), by cerci that extend from within thickened, grooved, posterolateral margins of tergum 8, and by very

long subcylindrical metacoxa and metafemur. Most female otitesellines are much more similar to various pteromalids and can only be differentiated with difficulty by a combination of attributes, including head with a postgenal bridge but without occipital carina, body with metallic luster, structure of the antenna, position of the mesocoxa, often complete notauli, nonpetiolate metasoma, usually exserted ovipositor sheath, and generally downcurved, cylindrically tapering metasoma.

Except for males of two species of Walkerella (see Bouček 1988a), Otiteselline males from the Old World are wingless and are readily distinguished from other wingless agaonid males by position of the toruli (widely spaced and in dorsal two-thirds of head). Males of two New World genera (Aepocerus and Heterandrium) are fully winged.

• Sycophaginae Female fully winged, with or without metallic luster, usually with distinct sculpture but rarely smooth and shiny; head rarely prognathous and flattened, usually hypognathous and oval to lenticular in lateral view; antenna with basal 1 or 2 flagellomeres ring-like, with 6 flagellomeres not ring-like, and with club of 3 flagellomeres; scutellar-axillar complex with straight or incurved axillular groove and transverse frenal groove (grooves sometimes very fine or obsolete when mesonotum smooth), the scutellum therefore usually quadrate to more or less hourglass-shaped, with oval to subtriangular axillula between scutellum and axilla; fore wing with relatively short marginal vein (one-third or less length of costal cell) that usually is subequal in length or shorter than stigmal vein, and with postmarginal vein absent to longer than stigmal vein; protibia and metatibia rarely modified as described for Agaoninae; metacoxa only about as long as height of mesothorax; metasoma sessile to petiolate; metasomal spiracle rarely conspicuously enlarged; tergum 8 with posterior margin deeply, sinuately ∧-like, with small sclerotized thumbnail-like medial flap (epipygium) and with peg-like cercus from within membrane on either side of epipygium; ovipositor sheath long. Male of Pseudidarnes fully winged, with venation and scutellar-axillar complex as for female; males of other known taxa wingless. Wingless males yellowish to brown, smooth and shiny; antenna inserted adjacent to oral cavity, often on transversely subdivided anterior portion of head; scape compressed and flagellum with 2 or 3 flagellomeres; head and body flattened (ribbon-like); metasoma relatively long, with subparallel sides and more or less truncate posterior margin (except Idarnes); tibiae stout, with spines; metasomal spiracle usually very large, usually with long membranous extension.

Comments Some female sycophagines can be confused with sycoecine or agaonine females because of a smooth and shiny body, flat head, similarly modified front and hind legs, and enlarged metasomal spiracle, but they are distinguished by structure of metasomal tergum 8, which is characteristic for the subfamily. Most female sycophagines are much more readily distinguishable by the structure of their scutellar-axillar complex. The wingless males are most like those of Apocryptinae, but the latter have a subcylindrical scape.

• Sycoryctinae – Sycoryctini Female fully winged, vellowish to black, with or without metallic luster or distinct sculpture; stigmal vein distinct to very long, at obtuse angle to marginal vein; postmarginal vein relatively long, it and often marginal vein distinctly longer than stigmal vein; metasomal tergum 8, or 7 and 8, conspicuously elongated, tubularly (tail-like) protracted over ovipositor sheaths (often appearing as ovipositor sheaths fused along midline); tergum 8 without epipygium; cercus absent or button-like; metasomal sterna forming relatively flat venter or many New World taxa with anterior sterna ventrally projected plowshare-like (variedly deep) and then metacoxa and metafemur more conspicuously elongate-slender, subcylindrical. Male fully winged to wingless; wingless or subapterous males without metallic luster, but some fully winged males with metallic luster; antenna with 6-11 flagellomeres; pronotum quadrate to rectangular; fully winged males with stigmal vein relatively long and at distinctly obtuse angle to marginal vein, with marginal and postmarginal veins both relatively long, longer than stigmal vein; subapterous to wingless males with antenna inserted near oral cavity, the toruli usually subcontiguous or at least closer to each other than to eyes, the tibiae stout, with spines, the metasoma relatively small, tapered posteriorly to acute angle, and the metasomal spiracle small and unmodified.

**Apocryptini** Female fully winged, at least in part with metallic luster, and with distinct sculpture; antenna with basal 2 flagellomeres ring-like, with 5 flagellomeres not ring-like, and with club 3 having flagellomeres; metacoxa and metafemur conspicuously elongate-slender, subcylindrical; metasoma compressed, with anterior sterna deep and ventrally projected plowshare-like; metasomal tergum 8 dorsally extensive (subequal in length to tergum 7), with posterior margin conspicuously ∩-like, but not emarginate and without epipygium; cercus peg-like, originating from within thickened, grooved, posterolateral margin of tergum 8; ovipositor sheath very long. Male wingless; yellowish, smooth and shiny; antenna inserted adjacent to oral cavity; scape subcylindrical; flagellum composed of single

flagellomere partly fused to pedicel; tibiae stout, with spines; metasoma relatively long, with subparallel sides and more or less truncate posterior margin; metasomal spiracle very large but without membranous extension.

**Comments** Members of this subfamily are characterized only by the relatively typical chalcidoid wing venation, the long ovipositor of females, and the absence of attributes that are used to characterize the other agaonid subfamilies. Apocrypta Coquerel is the only genus assigned to Apocryptini, and it is restricted to the Old World. Many New World Sycoryctini have more or less plowshare-like metasomal sterna and, correlated with this, long hind legs, similar to females of Apocrypta. Female Apocrypta are also very similar to some New World otitesellines, as is discussed under the latter subfamily. Males of Apocrypta are quite similar to most males of the subfamily Sycophaginae; fully winged, metallic-hued male sycoryctines can also be confused easily with male torymids, except for the different fore wing venation.

• Epichrysomallinae Female fully winged, without metallic luster, yellowish to black, rarely densely punctured (Ascobia), usually relatively smooth, with only fine striae or reticulation; occipital carina present or absent, often fine; head hypognathous to prognathous; toruli near mid height when head hypognathous but at or near oral margin when prognathous; antenna with number of flagellomeres highly varied; pronotum transverse-rectangular to elongate-subconical but without distinctly delineated collar and neck; fore wing with stigmal vein relatively long (often subequal in length or longer than relatively short marginal vein and almost always longer than postmarginal vein) and at nearly right angle to marginal vein; protibia and metatibia not reduced or highly modified; tarsi with 4 or 5 tarsomeres; metacoxa inserted conspicuously above mesocoxa; metasoma sessile to petiolate; metasomal tergum 8 not emarginate, without epipygium; cercus button-like to slightly elongate; ovipositor sheath not exserted. Male wingless to fully winged; wingless males with tibiae normal, not conspicuously widened apically, and without stout spines; fully winged males with color, sculpture, pronotum, and fore wing venation similar to that described for females and with antenna often inserted near oral margin.

Comments Members of this subfamily were restricted to the Old World until recent introductions. Some females with a prognathous head could be confused with agaonine or sycoecine females because of their smooth and shiny body, but the protibia is unmodified. Most female epichrysomallines are much more easily mistaken

for eurytomids because of their nonexserted ovipositor sheath, usually transverse to quadrate pronotum, and nonmetallic luster. The fore wing venation and usually smooth head and mesosoma differentiate epichrysomallines from eurytomids. Though the ovipositor is not exserted, it is long and coiled within the metasoma.

References Alternative classifications of Chalcidoidea associated with figs were provided by Bouček (1988a) and Bouček et al. (1981); the former included a key to the subfamilies, tribes, and genera of Agaonidae of the Australasian region, including important general references. Grandi (1963) cataloged the world species of Agaonidae. Hill (1967a) provided a synoptic catalog of the genera of chalcidoids associated with figs, as well as an extensive bibliography on figs and fig insects,

and (1967b) keyed some genera and subgenera of Agaoninae. Wiebes (1966b) keyed some genera of Sycoryctini, cataloged the genera and species of Otitesellinae (1967, 1974), keyed the African genera of Agaoninae (1974), analyzed the phylogeny of Agaoninae relative to the phylogeny of Ficus (1982b), and provided excellent accounts of the biology of fig insects and the history of fig wasp research (1977, 1982a). Morphological studies have been made of *Blastophaga psenes* (L.) (Agaoninae) (Grandi 1929), Idarnes (Sycophaginae) (Gordh 1975), and Apocrypta (Sycoryctinae) (Ulenberg 1983); Wiebes (1966a) studied the structure of the terminal metasomal terga and ovipositor of Sycophaginae and Sycoryctinae, and Copland et al. (1973) studied structure of the female reproductive system of Agaoninae.

## Family TORYMIDAE

(Fig. 217)

**Diagnosis** Head with postgenal bridge and, except rarely, occipital carina; antenna with 11 flagellomeres, with basal 0-4 flagellomeres ring-like, and the club with 3 flagellomeres; mesoscutum with notauli entire, usually distinct; tarsi with 5 tarsomeres; prepectus relatively large, ventral angle extending at least to base of procoxa; cercus peg-like, originating from posterolateral margin of metasomal tergum 8; tergum 8 of female very short dorsally, with posterior margin conspicuously emarginate (Ω-like) and partly surrounding small, more or less sclerotized, thumbnail-like setose flap (epipygium); ovipositor sheath exserted, usually long.

**Comments** As discussed under Agaonidae, concepts of the limits and membership of this family are not stabilized. Except for inclusion of the Echthrodapinae within Monodontomerinae (see under Eucharitidae), Bouček's (1988a) classification is used here for Torymidae; the four subfamilies that he recognized are discussed separately below. Female torymids usually are quite easy to recognize because of their distinctly exserted ovipositor sheath, peg-like cerci, and structure of tergum 8, though the last two attributes often are difficult to observe in air-dried specimens. As well, females of Chromeurytominae (Pteromalidae) possess all the diagnostic attributes given above for Torymidae, except that the antenna has only 9 flagellomeres (6 funicular articles plus club of 3 articles). Bouček (1988a) should be consulted for additional attributes to differentiate chromeurytomines. Male torymids, particularly those that lack an occipital carina, are even more readily confused with male pteromalids. Fore wing venation coupled with other attributes, such as the peg-like cerci and relatively large metacoxae (of

most subfamilies), will distinguish most males. Torymids are widely distributed, with about 120 nominal genera and 1150 nominal species.

• Toryminae Body usually with metallic luster at least in part; individuals fully winged (except for some males of *Physothorax*); fore wing venation usually distinctive, with long marginal vein (almost always longer than half length of costal cell), relatively short postmarginal vein (often one-third or less length of marginal vein), and usually very short stigmal vein (though stigma itself sometimes quite enlarged); groove separating mesopleuron and metapleuron distinctly sinuate; metacoxa usually 2-3 times as long as and distinctly more massive than procoxa, more or less triangular in cross section, and widely attached to metathorax-propodeum at about 45° angle; propodeal spiracle not elevated, near anterior margin of propodeum; metasoma usually with 1 or more anterior terga emarginate at midline; female with metasomal tergum 7 and 8 often separated medially by membranous area, and with ovipositor sheath usually at least one-third length of metatibia (usually much longer); male antenna without whorls of setae.

**Comments** Members of this subfamily are distinguished from those of Monodontomerinae only by the sinuate groove separating the mesopleuron and metapleuron.

**Biology** Most torymines are ectoparasitoids of gall-forming insects (particularly Cynipidae and Cecidomyiidae) or are phytophagous inquilines in the galls, but a few are primary parasitoids or hyperparasitoids of various Holometabola or Coccoidea.

**Reference** Bouček (1988a) listed regional keys to genera.

• Monodontomerinae Females and males as described for Toryminae except groove separating mesopleuron and metapleuron straight, and more commonly with marginal vein shorter and stigmal and postmarginal veins longer. If the stigmal vein is relatively long, i.e., more pteromalid-like, then the distance between the apex of the uncus and the postmarginal vein is equal to, or less than, the width of the stigma. Members of some taxa also exhibit one or more of the following attributes: ovipositor not exserted or only slightly so; metacoxa of comparable size to procoxa and/or subcircular in cross section; metafemur massively enlarged and ventrally serrate or dentate, and metatibia curved and extending apically into acute angle or spine (similar to many Chalcididae).

Comments, Biology Taxa with the metafemur and metatibia modified as described above were often classified as the subfamily Podagrioninae in Torymidae, or even as their own family. Members are now classified in three tribes of Monodontomerinae: Podagrionini-world-wide, parasitoids of egg cases of Mantidae (Dictuoptera); Chrysochalcissini—Old World, parasitoids of Heteroptera eggs; and Chalcimerini—one known species from Mediterranean region parasitic on Äylax (Cynipidae) larvae. Other monodontomerines (Monodontomerini, Erimerini, Palachiini) can also have hind legs quite similar to those described above, but the metatibia is truncate apically. Members of Monodontomerini are parasitoids of various Diptera, Hymenoptera, Lepidoptera, and Coleoptera; those of Erimerini are parasitoids of various insects in grass stems; and those of Palachiini are parasitoids of eggs of Mantidae (Dictuoptera).

References Szelényi (1957) provided a key to the then known world genera of Monodontomerini (Monodontomerinae sensu Szélenyi). Bouček (1978b) gave a key to the world genera with greatly enlarged and toothed hind femora (except non-African Podagrionini) in a key to the African genera of Torymidae. Grissell and Goodpasture (1981) provided a key to the three monodontomerine tribes known in the Nearctic

region and revised the Nearctic species of Podagrionini.

• Thaumatoryminae Females and males as described for Toryminae except as follows: marginal vein short, less than half length of costal cell and only about twice length of postmarginal vein; groove between mesopleuron and metapleuron slightly sinuate; propodeal spiracle on mound-like convexity distant from anterior margin of propodeum; male antenna with whorls of setae.

Comments, Biology This subfamily was established in Peck et al. (1964) for the single species, *Thaumatorymus notanisoides* Ferrière and Novicky, from the Mediterranean region. The host is unknown.

**References** Peck et al. (1964) and Bouček (1978b) gave attributes to differentiate this subfamily from other torymid subfamilies.

• Megastigminae Body often partly or entirely without metallic luster, usually yellowish and/or brownish to black, with scattered, bristle-like setae; male antenna with or without whorls of setae; pronotum and/or mesoscutum usually transversely striate, aciculate, or punctate-rugose; fore wing with stigma conspicuously knob-like enlarged; postmarginal vein usually as long as, or longer than, marginal vein; metacoxa of similar size to procoxa, subcircular in cross section; groove separating mesopleuron and metapleuron straight; ovipositor sheath long and upcurved.

**Comments** Members of this subfamily are readily identified by the enlarged stigma of the fore wing.

**Biology** Most megastigmines are phytophagous in seeds of Rosaceae, Pinaceae, and Cupressaceae, though some are gall formers, or are parasitoids of gall-forming or seed-feeding Hymenoptera and Diptera.

**References** Milliron (1949) keyed the known genera of Megastigminae and cataloged the world species; he also revised the Nearctic species of *Megastigmus* and gave a host list and summary of the known biology for the world species of this genus. Kamijo (1962) revised the Megastigminae of Japan, and Bouček (1970) revised the species from western Europe.

## Family ORMYRIDAE

(Fig. 218)

**Diagnosis** Body relatively heavily sclerotized, with metallic luster at least in part; in lateral view anterior and dorsal surface of head plus mesosoma usually distinctly convex, with frontal surface of

head often faced more or less ventrally; head with postgenal bridge and occipital carina; antenna with 11 flagellomeres, basal 1–4 flagellomeres ring-like; prepectus small, fused ventrally with mesopleuron,

the external ventral angle of prepectus separated from base of procoxa by posterolateral margin of pronotum; mesoscutum with or without fine notauli; fore wing with relatively long marginal vein, short postmarginal vein, and sessile stigmal vein; tarsi with 5 tarsomeres; metacoxa large, as long as or almost as long as metafemur, subtriangular in cross section and attached to metathoraxpropodeum at about 45° angle; metatibia usually with spine-like setae along posterior surface and with 2 stout sometimes very long apical spurs, one or both spurs curved; metasoma usually moderately compressed in female, moderately flattened in male; petiole transverse; second postpetiolar tergum usually very short, in some males and many females concealed under first tergum or visible only laterally, and then with only 6 visible postpetiolar terga; one or more terga usually with large, deep punctures in transverse row(s), and/or transverse row(s) of crenulate sculpture, but at least with long, often bristle-like setae arranged in transverse row(s); metasomal tergum 8 not emarginate, without epipygium, with button-like cercus near posterolateral margin; ovipositor sheath not greatly exserted.

**Comments** Ormyrids sometimes are classified in Torymidae because of their similar fore wing venation and metacoxal structure. Members of the two families also share a postgenal bridge and

occipital carina but are separated by structure of the cerci, and in females by structure of the apical metasomal tergum and ovipositor sheath. Exact relationships are unknown, but recognition of ormyrids as a family-level taxon most likely makes Pteromalidae or Torymidae paraphyletic. Doğanlar (1991) recognized four genera, Avrasyamyrus, Cyrtosoma, Ormyrus and Ormyrulus, based primarily on the number of rows of punctures on the metasomal terga. The only speciose genus, Ormyrus, contains about 90 species distributed widely in the Old World but primarily north temperate in the New World. Records of the genus are extremely rare south of Central America; Ormyrus brasiliensis Ashmead is the only described species from South America.

Biology Ormyrulus gibbus Bouček was reared from galls of Cecidomyiidae (Bouček 1986). Species of Ormyrus are primary parasitoids or hyperparasitoids in galls of other insects, primarily Cynipidae (Hymenoptera) and Tephritidae (Diptera), though two species in North America are known to parasitize a pteromalid that forms galls on blueberries (Vaccinium). Some tropical species are known to develop in figs (Ficus) as facultative or obligatory parasitoids of fig wasps.

Reference Doğanlar (1991) keyed the genera.

# Family PERILAMPIDAE

(Fig. 219)

**Diagnosis** Body black or with metallic luster, usually distinctly plump in habitus; head and/or pronotum and mesonotum usually with coarse thimble-like (umbilicate) punctures or transverse arcuate wrinkles, but with metasoma polished and shiny; antenna relatively short, with 11 flagellomeres, the first flagellomere ring-like; mandible deep in lateral view, robust, the right mandible with 3 teeth, the left mandible with 2 teeth, one mandible crossed in front of other when closed; labrum often concealed under clypeus but if visible then with apical margin produced into finger-like processes, each process with long, sometimes spatulate seta (setae usually visible in radiating row from beneath apex of clypeus when labrum concealed); pronotum with distinct, transverse collar that is abruptly angled relative to vertical or concave neck; prepectus usually fused to pronotum but if visible as distinct sclerite then posterolateral surface of pronotum, prepectus, and anterior margin of mesopleuron rigidly combined in flat plane; tarsi with 5 tarsomeres; metasoma usually more or less triangular in lateral view, with first and second postpetiolar terga fused dorsally (with or without visible groove) but with lateral

margin of the first postpetiolar tergum free and widely curved posterior to dorsal line of fusion, and with the composite sclerite covering half or more of metasoma; ovipositor sheath only slightly exserted.

Comments Perilampids are widely distributed, with about 260 nominal species. Six of 30 nominal genera have generally been recognized as valid (keyed by Bouček 1978a), but Argaman (1990, 1991) recently described 26 new genera. Though most of Argaman's genera may well fall into synonymy, a comprehensive study is needed to determine if the paper constitutes anything more than taxonomic terrorism.

Perilampids sometimes are classified as a subfamily of Pteromalidae or if as a separate family then with or without the Chrysolampinae included as a subfamily. Chrysolampines are classified here as a subfamily of Pteromalidae because members lack a digitate labrum, the mandibles each have 2 teeth, and the prepectus is moveable and does not form a rigid, composite structure with the pronotum and mesopleuron. Other taxa that are similar in appearance to perilampids, and the hypothesized relationships of the family, are discussed under Eucharitidae.

**Biology** Most perilampids are hyperparasitoids of Lepidoptera through Tachinidae (Diptera) or Ichneumonoidea, or are primary parasitoids of wood-boring Coleoptera (primarily Anobiidae and Platypodidae). A few species are known to be primary parasitoids or hyperparasitoids of various Hymenoptera, Orthoptera, and Neuroptera. An unusual attribute of Perilampidae, and of Eucharitidae, is that host-finding is done by the larva rather than the adult female. Females deposit their eggs away from the host in or on leaves or buds, in cracks of bark, or under lichens on trees. An egg hatches into a specialized planidium type of larva that is mobile and that attempts to attach itself by its mandibles to almost any moving object. Thus, attachment to an appropriate host, or to an intermediate carrier that will transport the planidium into a gallery or nest where there are appropriate larvae, is serendipitous. A planidium that attaches itself to a secondary host burrows into the body and searches for a primary tachinid (Diptera) or ichneumonoid host, which if found will also be entered. A planidium that attaches itself to

a primary host may remain external, but in either instance the planidium then becomes dormant until the primary host pupates. Once this occurs the planidium, if internal, exits the host body and initiates feeding and further development as an ectoparasitoid. Development is hypermetamorphic, with the second and subsequent larval instars being hymenopteriform.

References Bouček (1978a) and Argaman (1990) present keys to genera. Bouček (1978a) also revised the species of Krombeinius and Euperilampus, and Bouček (1980) revised the species of Monacon. Smulyan (1936) revised the Nearctic species of Perilampus, and Argaman (1991) gave an annotated checklist of the world species of Perilampus that he assigned to his new genera. Darling (1983, 1988) revised the New World species of Euperilampus and described labral structure of members of Perilampidae and Eucharitidae, respectively. Heraty and Darling (1984) described and compared the planidial type of larvae of Perilampidae and Eucharitidae.

## Family EUCHARITIDAE

(Fig. 220)

(E = Eucharitinae, O = Oraseminae)

**Diagnosis** Body with or without metallic luster: head often appearing small relative to mesosoma and/or thin in lateral view and more or less transverse triangular to oval in anterior view; antenna with 8-24 flagellomeres, these sometimes modified (serrate, ramose, or otherwise), with first flagellomere similar to others (E) or ring-like (O); mandible usually large and thin in lateral view, widely crossed over when closed (one on top of other) and sickle-like when open, but rarely mandible absent or reduced peg-like; right mandible with 3 teeth and left mandible with 2 teeth when not reduced; labrum often concealed under clypeus, but if visible then with apical margin produced into digit-like processes, each process with long, sometimes spatulate seta (setae usually visible in radiating row from beneath apex of clypeus if labrum concealed); pronotum vertical, not visible medially in dorsal view; mesonotum abruptly convex above pronotum; scutellum often with posterior projection(s); prepectus fused to pronotum (E) or separate sclerite posterior to pronotum (O); axillae usually narrowly to widely contiguous medially; tarsi with 5 tarsomeres; metasoma with petiole usually at least as long as wide, often much longer, very rarely transverse; postpetiolar segments often more or less compressed, with first tergum often covering following terga; ovipositor sheath not exserted.

**Comments** Eucharitids are widely distributed but are most diverse in the tropics and subtropics. About 70 nominal genera and 380 nominal species are described. Concepts of limits and relationships of this family are unsatisfactory. Traditionally, two subfamilies are included in Eucharitidae: Eucharitinae and Oraseminae. On the basis of larval morphology, Heraty and Darling (1984) hypothesized that Eucharitidae is the sister group of Perilampidae and that Chrysolampinae (Pteromalidae) is the sister group of Eucharitidae plus Perilampidae. Darling (1988) further hypothesized Eucharitidae and Perilampidae as sister taxa based on the digitate labrum, which was hypothesized as derived from a chrysolampine-like labrum. Bouček (1988a) recognized five subfamilies in Eucharitidae: Eucharitinae, Oraseminae, Akapalinae, Philomidinae, and Echthrodapinae. Members of Akapalinae have a digitate labrum, whereas members of Philomidinae and Echthrodapinae have a flap-like labrum. Akapalines are also like many eucharitids because they have thin mandibles, widely joined axillae, and a scutellum that extends posteriorly as a wide, bilobed appendage. However, akapalines are also similar to perilampids because they have a transverse pronotal collar and the first 2 postpetiolar terga are fused. Members of Philomidinae are superficially like eucharitids because they share a similar pronotum and a highly convex mesonotum, modified flagellomeres, and more or less sickle-like mandibles, though each

mandible has only 2 teeth and one mandible is crossed in front of the other when closed. The labrum is also nondigitate and the axillae are vertical and widely separate. Members of Echthrodapinae are least like eucharitids, similar only in having very narrowly contiguous axillae (mandibles reduced and lobe-like). Except for the nonexserted ovipositor sheaths of females, echthrodapines are more like torymids because they have an occipital carina as well as a setose epipygium and peg-like cerci articulated with metasomal tergum 8. In addition, the metafemur has a subapical ventral lobe, and one species is known to be an ectoparasite of bee pupae, as are some Monodontomerinae (Torymidae). Because of these attributes, in this guide ecthrodapines are included in the subfamily Monodontomerinae of Torymidae. The combination of attributes possessed by members of the other taxa discussed above also indicates convergence in one or more of the attributes that are used to define or to relate Eucharitidae and Perilampidae. Akapalinae and Philomidinae are therefore classified as subfamilies in Pteromalidae until relationships can be resolved by an analysis of character-state homology and distribution.

**Biology** Adult eucharitid females deposit their eggs into plant tissue, such as leaves and buds, away from the ant nest. Once hatched the mobile planidium type of larva attempts to attach itself by its mandibles to almost any moving object. The planidium is carried into an ant (Formicidae) nest if it fortuitously attaches itself to a foraging worker ant or perhaps to some ant-nest associate. In at least some instances the planidium feeds on an intermediate carrier, such as a Thysanoptera, thereby extending the planidium's life until it can transfer to a worker ant. Once in an ant nest the planidium transfers to a larva and ceases further development until the larva pupates, whereupon it initiates feeding and subsequent hypermetamorphic development as an ectoparasitoid.

References Heraty (1985) keyed the genera and revised the species of Eucharitinae for North America, and Heraty (1989) established the monophyly of Eucharitinae on the basis of skeletomusculature of the mesosoma. Clausen (1940, 1941) gave detailed observations on eucharitid behavior and life history. Heraty and Darling (1984) described and compared the planidial type of larvae of Eucharitidae and Perilampidae.

## Family EUPELMIDAE

(Fig. 221)

**Diagnosis, Comments** It is not possible to diagnose this family by any single attribute or combination of attributes without excluding some taxa whose members possess one or more of the attributes and without including some taxa whose members lack one or more of the attributes. Many of the attributes used to define Eupelmidae are primitive and are shared with other chalcidoids: tarsi with 5 tarsomeres; fore wing with relatively long marginal vein; mesocoxa inserted posterior to midline of mesopleuron so that procoxa and mesocoxa separated by quadrate to long mesosternum; mesoscutum and scutellar-axillar complex articulated along entire width (except *Neanastatus*); prepectus not bulbously protruding exterior to pronotum; and cerci not conspicuously advanced anteriorly. Other attributes shared by members, including male eupelmines, are derived but are shared with some other chalcidoids: one or more small, curved spicules on dorsoapical margin of protibia (inconspicuous and requiring high magnification to see on small specimens); relatively long and microsetose mesotibial spur; and eyes with inner margins, or at least ventral inner margins, diverging in anterior view. Protibial spicules are characteristic of many chalcidoids that parasitize wood-boring Coleoptera, and the last two attributes are shared with members of Cleonyminae

(Pteromalidae). Other structures that traditionally are used to characterize the family not only are shared with some other chalcidoids but are not possessed by all eupelmids: convex mesopleuron (enlarged acropleuron), modified structure of mesocoxal articulation, and presence of mesotibial and mesotarsal pegs. Gibson (1989) concluded that these features were derived convergently to similar features in Encyrtidae and Tanaostigmatidae, and that Eupelmidae likely represents a grade level taxon. The three subfamilies currently assigned to Eupelmidae are diagnosed below to characterize distribution of attributes within the family. The primitive and derived attributes that are listed above are not included in the following diagnoses.

Eupelmids are widely distributed, but are most diverse in the tropics and subtropics. About 90 nominal genera and 900 nominal species are described.

References Kalina (1984) revised the subfamilies and the genera of the Palaearctic Region, and Bouček (1988a) keyed the subfamilies and genera of the Australasian region. Gibson (1989) analyzed monophyly and relationships of the family, and gave keys to distinguish eupelmid subfamilies from other chalcidoids.

• Calosotinae Females and males not conspicuously dimorphic in mesosomal attributes; pronotum conspicuous in dorsal view, the sides subparallel posteriorly and abruptly convergent to head anteriorly; mesoscutum with notauli sulcate or as obscure lines, either V-shaped or subparallel in anterior half of mesoscutum; axillae either subtriangular with anteromedial angles contiguous or axilla variously reduced, sometimes to a linear strip along each side of scutellum; mesopleuron in lateral view with or without distinct mesepisternum and/or mesepimeron; acropleuron flat or convex, occupying at least half length of pleuron and usually extending to metapleuron at least dorsally; mesothorax in ventral view with membranous area anterior to each mesocoxa; mesocoxa able to rotate anteriorly out of fossa; mesotibia almost always without row of pegs along anteroapical margin; mesotibial spur elongate-slender to robust; mesotarsus without pegs, or with row of pegs along posteroventral margin, or with rows along both anteroventral and posteroventral margins; individuals fully winged.

**Comments** Members of Calosotinae are highly varied in structure. The most derived members are most similar to female eupelmines, whereas the most primitive members intergrade in structure with various Cleonyminae (Pteromalidae). Calosotinae is most diverse in the Old World, but the most primitive members are in the New World.

**Biology** Members of Calosotinae are mostly ectoparasitoids of wood-boring Coleoptera. Some species of *Calosota* are known to be primary parasitoids or hyperparasitoids of other chalcidoids in grass stems, or of Diptera or Lepidoptera; some have also been reared from the nests of solitary bees and wasps.

**Reference** Gibson (1989) revised the world genera.

• Neanastatinae Females and males not conspicuously dimorphic in mesosomal attributes; pronotum conspicuous in dorsal view, conical or rhomboidal; mesoscutum without notauli; axillae varied in shape, with anteromedial angles contiguous to widely separate; mesopleuron with acropleuron conspicuously convex and enlarged; mesothorax in ventral view without membranous area anterior to each mesocoxa: mesocoxa unable to rotate anteriorly out of fossa; mesotibia almost always with row of pegs along anteroapical margin and with conspicuously elongatethickened spur; mesotarsus with row of pegs extending along anteroventral and anteroapical margins of each tarsomere so that rows appear curved or oblique; individuals fully winged.

**Comments** Neanastatines are most notable among eupelmids for the absence of a membranous area anterior to each mesocoxa, so that the mesocoxae are unable to rotate anteriorly. Neanastatinae is most diverse in the Old World.

**Biology** Members of the Old World genus *Neanastatus* are parasitoids of larvae of Cecidomyiidae (Diptera) or are hyperparasitoids through Platygastridae. Other members of the subfamily whose biology is known are parasitoids of the larvae of wood-boring Coleoptera, primarily Cerambycidae and Buprestidae.

**References** Kalina (1984) established the subfamily name Neanastatinae, which was not realized by Bouček (1988a) when he proposed Metapelmatinae or by Gibson (1989) when he revised the world genera under that name.

Eupelminae Females and males highly dimorphic in most mesosomal attributes (males are pteromalid-like in appearance). Female with pronotum usually conspicuous in dorsal view, often as described for Calosotinae but usually medially divided or with longitudinal white line; mesoscutum with notauli V-shaped but usually furrow-like, very rarely sulcate; axillae equilateral to elongate subtriangular, with anteromedial angles usually subcontiguous; mesopleuron with acropleuron convex and extending to metapleuron; mesothorax in ventral view with membranous area anterior to each mesocoxa; mesocoxa able to rotate anteriorly out of fossa; mesotibia often with row of pegs along anteroapical margin, with elongate-thickened spur; mesotarsus with one or more rows of pegs along both anteroventral and posteroventral margins or if pegs reduced in size and/or number then ventral surface of tarsomere 1 conspicuously pad-like setose; individuals fully winged or brachypterous to various extents. Male with pronotum distinct or almost vertical and not visible medially in dorsal view; mesoscutum with linear notauli usually present (often obscure), and then complete and widely separate at transscutal articulation; mesopleuron without conspicuously enlarged acropleuron, with shallow femoral groove between mesocoxa and prepectus; mesothorax in ventral view without membranous area anterior to each mesocoxa; mesocoxa unable to rotate anteriorly out of fossa; mesotrochantinal plate extending only about half distance to metasternum, the intervening area membranous (internal attribute visible only if mesocoxae removed); metacoxa relatively small, only about twice size of mesocoxa; mesotibia without pegs along anteroapical margin, with elongate-slender spur; mesotarsus slender, not differentiated from protarsus and metatarsus, without pegs ventrally; individuals fully winged.

Comments Males and females of Eupelminae are highly dimorphic, the pteromalid-like males being very primitive in structure and the females very derived in structure. This either—or situation contrasts with Calosotinae, in which males and females are similarly structured but there are transformation series from primitive to derived structures within the subfamily.

Taxonomy of Eupelminae is based on females; male eupelmines are so different from females that most cannot currently be assigned confidently to genus. Males are most similar to male Cleonyminae (Cleonymini, Chalcedectini) because of the elongate-slender mesotibial spur, divergent or ventrally divergent inner margins of the eyes, and dorsoapical spicules on the protibia. Male chalcedectines are easily separated from male eupelmines by an enlarged and dentate metafemur, but male cleonymines are much more difficult to distinguish. Male cleonymines often have conspicuously large metacoxae, and the sculpture of the femoral groove often is coarsely reticulate relative to the finer sculpture of most male eupelmines. However, the only absolute attribute known to distinguish males of the two groups is an internal structure. Male cleonymines have the mesotrochantinal plate extending to the metasternum, completely separating the mesocoxal fossae from each other. In male eupelmines the mesotrochantinal plate extends only partly to the metasternum so that the mesocoxal fossae are connected posteriorly by a transverse membranous area (males of some other noncleonymine pteromalids have a similar structure).

Female eupelmines often die in a contorted U-shape, with the head and metasoma reflexed dorsally relative to the mesosoma, and, if so, are readily distinguished. This unusual shape results from the way females jump. Most chalcidoids jump

with their middle legs, powered by a large dorsoventral tergal muscle inserted into each mesotrochanter. Jumping by eupelmine females is powered by a large longitudinal muscle that occupies each acropleuron. Contraction of the acropleural muscles stretches pads of resilin (a rubber-like protein) inserted into the anterolateral margins of the mesoscutum. The resilin pads are thought to store the energy produced by muscle contraction until some unknown lock mechanism is triggered. The resilin pads then contract and pull the mesoscutum back, resulting in the mesonotum being arched along the transscutal articulation. Arching the mesonotum shortens it, which results in the pronotum being pulled back up over the anterior margin of the mesosternum so that the prothorax and head are rotated upward. Arching also rotates the scutellar-axillar complex so that the posterior margin pushes down on the base of the metasoma, thereby reflexing the apex of the metasoma upward. Arching the scutellar-axillar complex also rotates the sides of the axillae, pulling up on a tendon-like ligament that connects each axilla and mesotrochanter and changing a horizontal force of muscle contraction into a vertical force for jumping.

**Biology** Eupelminae is most diverse in the New World tropics; it is by far the most speciose as well as morphologically and biologically the most diverse subfamily. Members are primary parasitoids or hyperparasitoids of the egg or larval stages of various insect and spider (Araneae) hosts in a wide variety of niches.

**Reference** Gibson (1986b) compared the skeletomusculature of males and females, explaining differences as the result of differences in muscles used for flight and jumping.

#### Family TANAOSTIGMATIDAE

(Fig. 222)

Diagnosis (excluding Cynipencyrtus) Body with pronotum vertical, only linear margin visible in dorsal view; mesoscutum without notauli or notauli sinuately V-shaped convergent, and if convergent then notauli either meeting at transscutal articulation or extending at least half length of mesoscutum; mesoscutum with sinuate posterior margin, articulated with scutellar-axillar complex only laterally, with conspicuous membranous area between sclerites if mesonotum roof-like arched; axillae subtriangular with contiguous anteromedial angles; prepectus bulbous and protruding anteriorly beside pronotum; individuals fully winged; fore wing with relatively long marginal vein; acropleuron convexly enlarged to metapleuron; mesothorax in ventral view with membranous area anterior to each

mesocoxa; mesocoxa able to rotate anteriorly out of fossa; mesocoxa inserted posterior to, or near midline of, acropleuron; mesosternum transverse-rectangular; protibia without dorsoapical spicule, though cuticle sometimes dorsoapically produced into a denticle; mesotibia without pegs along anteroapical margin, with robust spur; tarsi with 5 tarsomeres; mesotarsus either without pegs ventrally or with row of pegs along posteroventral margin; cercus not conspicuously advanced anteriorly and with at least one cercal seta very long and kinked.

**Comments** Tanaostigmatidae is primarily tropical and subtropical, with about 15 nominal genera and 90 nominal species. The family diagnosis does not

include the genus *Cynipencyrtus*, which initially was described in Encyrtidae but was transferred to Tanaostigmatidae by LaSalle and Noyes (1985). Placement of *Cynipencyrtus* in Tanaostigmatidae is problematical because specimens differ from Tanaostigmatidae (sensu stricto) in numerous attributes, including the following: axillae transverse-triangular; mesoscutum and scutellar-axillar complex only inconspicuously separated when flexed; pronotum transverse-rectangular in dorsal view and covering anterior portion of each prepectus; membranous area anterior to each mesocoxa absent; mesotibial apical pegs present; and pattern of mesotarsal pegs different. In most of these attributes specimens of

Cynipencyrtus more closely resemble typical encyrtids than tanaostigmatids, but they lack the apomorphic mesocoxal position of encyrtids. Tanaostigmatidae, Cynipencyrtus, and Encyrtidae likely form a monophyletic assemblage, but exact relationships among the taxa are unresolved.

**Biology** The only known species of *Cynipencyrtus* (from Japan) is parasitic on Cynipidae on *Quercus*. Other tanaostigmatids are phytophagous, forming galls in stems, leaves, seeds, or flower ovules.

**References** LaSalle (1987) revised the New World fauna. LaSalle and Noyes (1985) and Gibson (1989) analyzed family placement and phylogenetic relationships of *Cynipencyrtus*.

#### Family ENCYRTIDAE

(Fig. 223)

**Diagnosis** Body with pronotum usually visible and most often transverse in dorsal view; mesoscutum usually without notauli but if present then linear and more or less sinuately V-shaped; mesoscutum articulated to scutellar-axillar complex only laterally, with very slender membranous area and/or depressed anterior margin of scutellar-axillar complex visible between sclerites if mesonotum arched; axillae almost always transverse-triangular, usually with contiguous anteromedial angles (sometimes appearing separate because of overhanging posteromedial curvature of mesoscutum); prepectus flat posterior to pronotum but internally with prepectal strut between ventral angle of prepectus and mesoscutum; individuals fully winged to wingless; fully winged specimens with marginal, stigmal, and postmarginal veins relatively short, the marginal vein usually very short to punctiform; acropleuron convexly enlarged to metapleuron; mesothorax in ventral view with or without membranous area anterior to each mesocoxa but mesocoxa unable to rotate completely out of fossa; mesocoxa inserted at or anterior to midline of acropleuron; mesosternum transverse; protibia without dorsoapical spicules, with relatively long, curved tibial spur; mesotibia with row of pegs along anteroapical margin, with robust, usually elongate spur; tarsi usually with 5, less commonly with 4, tarsomeres; mesotarsus usually with pegs in various patterns along ventral or anteroventral surfaces of tarsomeres; metasoma with cercus advanced anteriorly, usually distinctly so, and then apical tergum large, triangular or U-shaped, and/or with one or more terga M-like between and around

**Comments** This is one of the largest and structurally most diverse chalcidoid families, particularly in structure of the head and antennae.

About 745 nominal genera and 3825 nominal species are described. Members are easily recognized by the completely enlarged acropleuron in conjunction with the advanced position of the mesocoxae. Most members are also characterized by their very short marginal vein and conspicuously advanced cerci. Two subfamilies often are recognized, Encyrtinae and Tetracneminae, but their members are differentiated by attributes that are usually difficult to observe and that are not possessed by all members of each subfamily (dentition of mandibles, presence or absence of metasomal paratergites, and presence or absence of differentiated setae along linea calva of fore wing).

**Biology** Encyrtidae is one of the most important chalcidoid families for biological control. Species are endoparasitoids, mostly of Coccoidea (Homoptera), but also of the eggs or larvae of Coleoptera, Diptera, Lepidoptera, Hymenoptera (as primary parasitoids or hyperparasitoids), Neuroptera, Orthoptera, Hemiptera, and Arachnida. One tribe, Copidosomatini, whose members are primary parasitoids of Lepidoptera, has an unusual process of multiplication of specimens from one egg within the host larva. The egg in this polyembryonic type of development divides into an irregularly branched chain of cells, each of which becomes a separate embryo. The resulting endoparasitic larvae consume the host larva and pupate within its swollen and distorted skin, with the emerging adults being all of one sex, unless more than one egg was deposited initially.

References Trjapitzin and Gordh (1978a, 1978b) keyed the females and males, respectively, of the genera of North America; Trjapitzin (1971, 1989) keyed the Palaearctic genera; Noyes (1980, 1988) keyed the Neotropical genera and the New Zealand genera and species, respectively; Noyes and Hayat

(1984) keyed the genera from the Indo-Pacific region; and Prinsloo and Annecke (1979) keyed the genera from the Ethiopian region. Trjapitzin (1973*a*, 1973*b*) discussed subfamilial and tribal classification, and Trjapitzin (1977) gave a

comprehensive analysis of known morphological diversity within the family. Tachikawa (1963) monographed the family for Japan, and Tachikawa (1981) provided a list of the known hosts for members of encyrtid genera.

### Family APHELINIDAE

(Fig. 224)

(A = Aphelininae, E = Eriaporinae)

**Diagnosis** Body 2 mm in length or less, relatively lightly sclerotized, often dark but at most with obscure metallic luster; antenna usually with at most 6 distinct flagellomeres (rarely with 7-9flagellomeres including obscure ring-like basal flagellomeres); females with at most 4 distinct flagellomeres between pedicel and club; males without distinct club; pronotum usually distinctly shorter than half length of mesoscutum and often linear in dorsal view; mesoscutum with notauli more or less straight, complete and widely separated at transscutal articulation near anteromedial angles of axillae; axillae relatively small, with anteromedial angles widely separated, usually partly advanced anterior to scutellum; prepectus flat posterior to pronotum, with anterodorsal point of articulation anterior to (E) or posterior to (some A) insertion of pl<sub>2</sub>-t<sub>2</sub>c muscle, sometimes also with internal prepectal strut between ventral angle of prepectus and mesoscutum (some A); individuals usually fully winged but some females subapterous; fore wing with marginal vein relatively long; stigmal vein short and postmarginal vein either absent or not extending beyond point in line with apex of stigmal vein (A), or stigmal and postmarginal veins both long but then parastigma (curved apical part of submarginal vein) usually extending spike-like onto membrane behind submarginal vein and with 1 or 2 conspicuously long bristles (E); mesopleuron usually with distinct mesepisternum and mesepimeron separated by fine groove and then with or without small subalar acropleuron, but acropleuron sometimes enlarged and very rarely comprising entire mesopleuron; mesothorax in ventral view without membranous area anterior to mesocoxa (except Coccobius); mesotrochantinal plate and metasternum abutting (requires removal of mesocoxae to observe) and either with metasternum extending anteriorly and ventrally to mesotrochantinal plate (then metasternal pit widely separated from anterior margin of metasternum) (A) or mesotrochantinal plate extending dorsally to transverse margin of metasternum (then metasternal pit very near anterior margin of metasternum) (E); protibia with relatively long, curved apical spur; mesotibia dorsoapically, and mesotarsus ventrally, without pegs (except some Eutrichosomella); mesotibial spur relatively long,

often robust; metatibia sometimes with long and conspicuous bristles (most E); tarsi usually with 5, less commonly with 4, tarsomeres; propodeum almost always conspicuously transverse, with metasoma widely attached to mesosoma; cercus not conspicuously advanced anteriorly.

**Comments** Aphelinids are widely distributed. Though about 100 nominal genera have been described, only about 40 are recognized as valid; about 1120 nominal species are described. Concepts of family membership and relationships are unsatisfactory, and aphelinids have been classified as a subfamily in both Encyrtidae and Eulophidae. Woolley (1988) hypothesized that Aphelinidae is paraphyletic relative to Signiphoridae, with the latter family most closely related to Azotus and Ablerus. Genera that sometimes are classified as the subfamily Eriaporinae (these genera also sometimes classified as a separate family, Euryischidae) present a special problem. Specimens differ from Aphelinidae (sensu stricto) in having well-developed stigmal and postmarginal veins. Also, one of the included genera (Euryischia) has disc-like compressed metacoxae, the metanotum extending posteromedially into a flat triangular plate, the propodeum relatively long medially, and two robust metatibial spurs, similar to members of Elasmidae. Specimens of other eriaporine genera are less elasmid-like and more typically aphelinidlike, except for the wing venation. Gibson (1989) hypothesized that Aphelinidae and Signiphoridae are sister taxa, based on the structure of the metasternum, and that this and the structure of the prepectus indicate that eriaporines are incorrectly classified in Aphelinidae. However, exact relationships with Aphelinidae and Elasmidae are uncertain, and eriaporines are here included as a subfamily of Aphelinidae as a matter of convenience. Bouček (1988a) also suggested that the subfamily Mongolocampinae, currently assigned to Tetracampidae, might be better classified in Aphelinidae.

**Biology** Along with Encyrtidae, Aphelinidae is one of the most important chalcidoid families for biological control. Species are primary endoparasitoids or ectoparasitoids, or hyperparasitoids, mostly of Aleyrodoidea, Aphidoidea, Auchenorrhyncha, Psylloidea, and

especially Coccoidea (Homoptera), but also of the eggs of Lepidoptera and Orthoptera, the eggs, larvae, and pupae of Diptera, and the larvae of other chalcidoids and Dryinidae. The family is renowned for its often complicated modes of differential development and parasitism of the sexes. In some species the females are endoparasitoids and the males ectoparasitoids of the same host species, whereas in others the males are hyperparasitoids of females of their own species (obligate adelphoparasitism or autoparasitism), of other aphelinid species (facultative adelphoparasitism), or of other primary parasitoids.

References Hayat (1983) and Jasnosh (1983) each keyed the world genera (Jasnosh did not include the eriaporine genera); Jasnosh (1976, 1979) reviewed subfamily classification and summarized the hosts for aphelinid genera, respectively; Ferrière (1965) revised the aphelinid fauna of Europe and the Mediterranean Basin, Nikolskaya and Jasnosh (1966) of the European USSR and the Caucasus, and De Santis (1948) of Argentina; Rosen and DeBach (1979) monographed the world *Aphytis*. Compere (1947), Shafee (1975), and Hayat and Verma (1980) discussed classification of the eriaporine genera. Flanders (1967) related adelphoparasitism with ovipositional behavior.

### Family SIGNIPHORIDAE

(Fig. 225)

**Diagnosis** Body 2 mm in length or less, shiny with very fine sculpture, rarely with very slight metallic luster, usually black, brown, or with yellow to orange markings; body compact and streamlined, usually elliptical in dorsal view, mesosoma and metasoma very widely attached to each other, with sides continuous in dorsal view and with dorsal surfaces more or less flattened and in one plane; antenna with 2-5 flagellomeres, with 1-4 quadrate to ring-like funicular articles, and with large, usually elongate-slender unsegmented club in both sexes; mesoscutum transverse, without notauli; scutellaraxillar complex transverse-subrectangular, with axilla not differentiated or only obscurely so, and then small and widely separated; propodeum relatively large, with posteriorly pointed medial triangular area delineated by fine grooves; individuals fully winged to wingless; wings usually with marginal fringe of long setae, but surface of membrane glabrous except possibly for isolated setae; fore wing with marginal vein short to long, with stigmal vein sessile, and without postmarginal vein; protibial spur relatively long, curved, sometimes pectinate; mesotibia usually with 2-4long bristles along dorsal margin and with long, usually spinose spur; tarsi with 5 tarsomeres; metasoma with terga transverse and subequal in length.

**Comments** This family is most diverse in the New World tropics and subtropics. Four genera are

recognized as valid, with about 80 nominal species. Signiphorids have been included as a subfamily of Encyrtidae or Aphelinidae in some classifications, but their distinctive habitus makes them among the easiest chalcidoids to recognize at family level. Woolley (1988) hypothesized that signiphorids are most closely related to two genera within Aphelinidae, i.e., that Aphelinidae is paraphyletic relative to Signiphoridae. However, Gibson (1989) hypothesized that Signiphoridae and Aphelinidae sensu stricto (excluding Eriaporinae) are sister taxa. The family has sometimes been divided into two subfamilies, Signiphorinae and Thysaninae, based primarily on wing and antennal characters; both Signiphoridae and Thysanidae have been used for the family name.

**Biology** Most signiphorids are parasitoids of Homoptera, primarily of Coccidae and Aleyrodidae but also of Aphidae and Psyllidae, either as primary parasitoids or, more commonly, as hyperparasitoids through other Hymenoptera and Diptera.

**References** Woolley (1986) gave a detailed historical account of family level classification; Woolley (1988) analyzed monophyly and relationships of the family, revised the genera, and keyed the species groups of *Signiphora*; and Woolley (1990) diagnosed the family and keyed the genera.

#### Family TETRACAMPIDAE

(Fig. 226)

(M = Mongolocampinae, P = Platynocheilinae, T = Tetracampinae)

**Diagnosis** Body usually with metallic luster; head usually with occipital carina (P, T except *Niticampe*);

antenna with 9 or 10 flagellomeres (if club composed of 3 flagellomeres); flagellum with 5–7 funicular articles and usually with club of 3 flagellomeres (rarely, articles of club fused and not distinguished by sutures) (M: antenna with 9

flagellomeres, but at least first flagellomere ring-like and easily overlooked so funicle appears to be composed of 5 flagellomeres; P: antenna with 10 flagellomeres, with first flagellomere distinct, so funicle with 7 flagellomeres; T: antenna usually with 10 flagellomeres, but first flagellomere ring-like and easily overlooked, so funicle appears to be composed of 6, or extremely rarely 5, flagellomeres, and rarely with 3 flagellomeres of club indistinguishably fused); pronotum sometimes transverse-linear in dorsal view (most M) but usually transverse-conical to elongate-conical or bell-shaped (P, T, M: Eremocampe); mesoscutum usually with complete linear notauli; propodeum with median third glabrous (M, P, some T) or setose with setae directed toward midline from each side (many T); individuals fully winged; fore wing usually with very long, thin marginal vein, and with postmarginal vein extending beyond apex of very short stigmal vein (T), but sometimes marginal vein greatly widened or cylindrically to foliately enlarged and darkened (then much longer than short submarginal vein), with postmarginal vein either extending beyond point in line with apex of stigmal vein (male P), or not (M); protibial spur short and straight but apically furcate; tarsi with 5 (M, P, female T) or 4 (male T) tarsomeres; metasoma separated by distinct constriction from mesosoma; petiole transverse to longer than wide.

**Comments** About 15 nominal genera and 50 nominal species are described, but monophyly and relationships of Tetracampidae are uncertain. In addition to the three extant subfamilies, three extinct subfamilies have been described from Cretaceous amber. Bouček (1988a) suggested that Mongolocampinae more likely is the plesiomorphic sister-group of all the other forms traditionally

classified in the Aphelinidae. Tetracampids and rotoitids are similar in having the protibial spur relatively short and straight (derived state, as in eulophids) but apically furcate (primitive state, as in pteromalids). Tetracampids are also intermediate in structure between most pteromalids and eulophids in number of flagellomeres; as well, most tetracampids have tarsi with 5 tarsomeres but males of Tetracampinae (and one extinct subfamily) have tarsi with 4 tarsomeres. Most members of the most common subfamily, Tetracampinae, have a distinctive mesosomal setation. The dorsum of the mesosoma, usually including the propodeum and axillae, is conspicuously setose, except most often for the scutellum, which is virtually glabrous except for one or two pairs of very long paralateral setae (similar to some eulophids).

**Biology** Species of Mongolocampinae are parasitoids of the larvae of *Aphaniosoma* (Diptera: Chiromyidae), which form gall-like swellings on the leaves of *Nitraria* species. Species of Platynocheilinae and some species of Tetracampinae are parasitoids of Diptera larvae that mine leaves and twigs; other Tetracampinae are endoparasitoids of the eggs of Chrysomelidae (Coleoptera) and Diprionidae.

References Yoshimoto (1975, 1978) described the extinct subfamilies, and the only two endemic New World tetracampids, respectively. Bouček (1958a) established the subfamily Platynocheilinae and revised the Palaearctic Tetracampidae, and Bouček and Askew (1968a) cataloged the world species. Sugonyaev (1971) established the subfamily Mongolocampinae, discussed subfamily classification, and keyed the three subfamilies.

#### Family ROTOITIDAE

(Fig. 227)

**Diagnosis** Body without metallic luster, lightly sclerotized (usually shriveled if air-dried); antenna with 12 flagellomeres, the first flagellomere not ring-like and the apical 6 flagellomeres forming a more or less compact club; prepectus linear, usually concealed beneath posterolateral margin of pronotum in air-dried specimens; mesoscutum with notauli obscure or absent; individuals fully winged or brachypterous; fore wing of fully winged specimens with postmarginal vein very long, much longer than relatively long stigmal and marginal veins; protibial spur short and straight but apically furcate; tarsi with 4 tarsomeres; metasomal spiracle present or absent.

Comments, Biology This family was described for *Rotoita basalis* Bouček and Noyes, from New Zealand, but the family diagnosis includes a second undescribed genus from Chile. The family is known only from females\*; based on the number of tarsomeres and structure of the protibial spur, members probably are related to Tetracampidae and/or Eulophidae. The hosts of rotoitids are unknown.

**Reference** Bouček and Noyes (1987) established the family and discussed family relations.

\*Note: After the key was completed, a male of the underscribed genus was collected in Chile. It is similar to females (Fig. 227) except that the moniliform flagellum has only 11 articles and lacks a differentiated club.

#### Family EULOPHIDAE

(Fig. 228)

**Diagnosis** Body with or without metallic luster. usually lightly sclerotized (often collapsed or shriveled if air-dried); antenna with 5-10flagellomeres; females usually with funicle of 2-4 nonring-like flagellomeres and with club of 3 or fewer flagellomeres; males with antenna of 6 or fewer distinct flagellomeres, often without distinct club; prepectus conspicuous, usually subtriangular; mesoscutum with notauli absent to complete; scutellum sometimes with pair of submedian longitudinal lines and/or with 1-3 pairs of long paralateral setae; axillae often partly advanced anterior to scutellum; individuals usually fully winged; protibial spur short, straight, simple; tarsi with 4 tarsomeres; mesosoma and metasoma separated by distinct constriction; petiole transverse to elongate.

**Comments** Eulophidae is one of the largest chalcidoid families, with about 540 nominal genera and 3900 nominal species. Infrafamily classification is unstable, but four subfamilies (discussed below) generally are recognized.

**Biology** This is one of the economically most important chalcidoid families. Most species are primary parasitoids of concealed larvae, particularly leafmining Lepidoptera, Diptera, Hymenoptera, and Coleoptera, but the host range is extremely diverse. Some species are phytophagous.

**References** Graham (1959) provided keys to the genera of Britain, and Graham (1987, 1991) revised the European genera and species of Tetrastichinae. Miller (1970) keyed the North American genera of Eulophinae, and Schauff (1991) revised the Holarctic genera of Entodoninae. Domenichini (1966) cataloged the Palaearctic Tetrastichinae, and Bouček and Askew (1968b) cataloged the remainder of the family for the Palaearctic region.

• Eulophinae Scutellum mostly without submedian longitudinal lines, with 2 or more pairs of sublateral setae; axillae not advanced anterior to scutellum, or only slightly so; mesoscutum with notauli absent to entire; fore wing with venation not interrupted at base of parastigma, with submarginal vein smoothly joining marginal vein; submarginal vein usually with 3 or more setae; postmarginal vein at least as long as stigmal vein; male antenna often branched.

**Biology** Species are mostly solitary or gregarious external parasitoids of Diptera, Lepidoptera, Coleoptera, Hymenoptera (usually of the larvae but rarely of the pupae of members of these orders), Homoptera, and Heteroptera; leafminers and free-living caterpillars are the most common hosts; a few species are phytophagous. Species of

Euplectrus are unusual in two ways: first, the gregarious external larvae feed dorsally on a lepidopterous host that often is freely moving about; and second, once the host contents are consumed the larvae move below the emaciated host to pupate, each larva spinning a silk cocoon to hold the host down and to separate itself from other larvae.

• Tetrastichinae Scutellum usually with pair of submedian longitudinal lines and with 2 or more pairs of long sublateral setae; axillae usually distinctly advanced anterior to scutellum; mesoscutum with notauli entire, linear; fore wing venation more or less interrupted at base of parastigma, the latter projected basally to tapered apex of submarginal vein; submarginal vein usually with 3 or more setae, rarely fewer; postmarginal vein absent or distinctly shorter than stigmal vein.

**Biology** Species are mostly internal primary parasitoids of the eggs, larvae, or pupae of Lepidoptera, Coleoptera, and Diptera, but they have been reared from members of 10 insect orders; a few species are known to be phytophagous, predaceous on gall-mites (Acari) or Nematoda, or parasitoids of thrips larvae (Thysanoptera). Members of *Melittobia* are parasitoids of aculeate Hymenoptera; their biology has been relatively well studied because of their strong sexual dimorphism, the development of two dimorphic generations on a single host, and the existence of fighting males.

• Euderinae Scutellum without submedian longitudinal lines, extensively setose or with 2 or 3 pairs of sublateral setae; axillae usually distinctly advanced anterior to scutellum; mesoscutum with notauli entire; fore wing venation indistinctly interrupted at base of parastigma; submarginal vein usually with 3 or more setae, rarely less; postmarginal vein at least as long as stigmal vein.

**Biology** Species are internal parasitoids of the eggs or larvae of Lepidoptera, Coleoptera, Tephritidae (Diptera), and Cephidae.

• Entedoninae Scutellum mostly without submedian longitudinal lines, usually with 1 pair of sublateral setae; axillae usually not distinctly advanced anterior to scutellum; mesoscutum with notauli usually incomplete, rarely extending to transscutal articulation, and if so then usually as relatively shallow, wide impressions posteriorly; fore wing venation distinctly interrupted at base of parastigma; submarginal vein with 2 setae; postmarginal vein at least as long as stigmal vein.

**Biology** Species are mostly internal parasitoids of Lepidoptera or Coleoptera larvae that are hidden in mines, stems, rolled leaves, or other places.

Ectoparasitism, or hyperparasitism through Diptera and Hymenoptera, or parasitism of eggs or pupae occur but are not common.

#### Family ELASMIDAE

(Fig. 229)

**Diagnosis** Body brown or black to extensively yellow, usually with slight metallic luster; mesosoma and metasoma wedge-like in cross section; head more or less lenticular, with occiput sharply margined; antenna with 7 flagellomeres in females and 8 flagellomeres in males, the basal flagellomere ring-like and the club with 3 flagellomeres; males with long ramus from basal 3 flagellomeres of funicle; mesoscutum conspicuously setose, without notauli; axillae relatively small and widely separated, more or less advanced anterior to scutellum; scutellum usually glabrous except for 2 pairs of long sublateral setae, but rarely more or less evenly setose with sublateral setae not conspicuously differentiated; mesopleuron almost flat, with only very fine mesopleural groove and with posteroventral angle extending slightly over base of metacoxa; metanotum extending medially over propodeum as flat, triangular, usually yellowish or translucent lamina; fore wing distinctively elongate-narrow, the length about three times or more greatest width; marginal vein very long; postmarginal vein short; stigmal vein sessile; protibial spur short and straight; mesofemur and metafemur compressed, more or less elongate-oval; metacoxa greatly enlarged and compressed, disc-like; metatibia with conspicuous, short black bristles, the bristles usually in more or less undulatory rows or diamond-like pattern; tarsi with 4 tarsomeres; mesotarsus and metatarsus

conspicuously elongate-slender, slightly tapered to apex; metasoma with transverse petiole.

Comments Elasmus is the only genus generally recognized, though Riek (1967) established a second genus based on differences in the setal pattern of the mesotibia and metatibia and relative length of the sublateral scutellar setae. Elasmus is most diverse in the Old World tropics, but about 260 nominal species occur around the world. The family sometimes is classified as a subfamily of Eulophidae because of the number of tarsomeres and because of the structure of the protibial spur, but members are also similar in structure to some Aphelinidae—see diagnosis and comments concerning Aphelinidae (Eriaporinae).

**Biology** Elasmids are mostly either primary external parasitoids of Lepidoptera larvae or hyperparasitoids of their larvae through various Hymenoptera, particularly Ichneumonidae and Braconidae; a few species also have been reared from the nests of *Polistes* (Vespidae), as primary parasitoids of their larvae.

**References** Burks (1965) revised the North American species of *Elasmus*, and Burks (1971b) described one additional species; Riek (1967) revised the Australian species; Ferrière (1929) revised the Asiatic and African species, and Ferrière (1947) the European species.

#### Family TRICHOGRAMMATIDAE

(Fig. 230)

**Diagnosis** Body usually 1 mm or less in length, lightly sclerotized (usually shriveled when airdried), without metallic luster; antenna distinctly shorter than combined length of head and mesosoma, with 3-7 flagellomeres (including at most two ring-like and two nonring-like funicular articles) and with club with 1-5 flagellomeres (some flagellomeres forming club may be mistaken for additional funicular articles in males with a noncompact club); individuals usually fully winged; fore wing varying from very wide (with apical margin almost truncate) to very narrow (and then with long marginal setae), the setae on membrane often partly aligned in longitudinal or radiating rows; fore wing with marginal vein, stigmal vein, and postmarginal vein variable, but often lacking

postmarginal vein, and with short marginal vein and relatively long stigmal vein (then venation more or less S-shaped)—and if postmarginal vein present then very short and not extending past the point in line with apex of stigmal vein; hind wing almost always with membrane extending to base, rarely stalked; protibial spur short and straight; tarsi with 3 tarsomeres; metasoma widely attached to mesosoma.

Comments About 75 genera are recognized as valid, with about 675 nominal species. The family most likely is monophyletic based on the number of tarsomeres. Viggiani (1971) recognized two subfamilies within Trichogrammatidae (Trichogrammatinae and Oligosetinae) based on

male genitalia. Differences in male genitalia have also been used to help delimit genera, and species in various genera, thus necessitating good slide mounts for taxonomic study.

**Biology** Trichogrammatids are all egg parasitoids of the large holometabolous orders and of Homoptera, Hemiptera, Orthoptera, and Thysanoptera. Species appear to be more habitat-specific than host-specific, and females of some species attempt to oviposit into virtually anything of an acceptable size and shape. Species of *Trichogramma* have been used extensively in biological control programs of various pests

(particularly Lepidoptera), resulting in an enormous economic literature of questionable value because of taxonomic confusion in species identification.

References Doutt and Viggiani (1968) revised and keyed the world genera, and Viggiani (1971) presented a key based on male genitalia for 27 of the 72 genera they recognized. Nagarkatti and Nagaraja (1977) reviewed the biosystematic literature on *Trichogramma* and *Trichogrammatoidea*, and Yousuf and Shafee (1986) gave a checklist and bibliography for the world species of the family.

## Family MYMARIDAE

(Fig. 231)

**Diagnosis** Body usually less than 1.5 mm, but rarely up to 5 mm in length, at most with obscure metallic luster; antennae inserted closer to each eve than to each other (except if head wedge-like in lateral view) and almost always distinctly longer than combined length of head and mesosoma; first flagellomere very rarely ring-like in male; antennal club distinct in female, absent from male; head with H-like (often dark) set of marks (transverse mark across head above toruli and lateral mark along inner margin of each eye on vertex and face); individuals usually fully winged; hind wing usually either with membrane arising apically from stalk formed by submarginal vein or with wing composed only of stalk, but rarely with membrane narrowly extending to base of wing; protibial spur relatively long and curved; tarsi with 4 or 5 tarsomeres; metasoma widely attached to mesosoma (sessile), or separated by distinct constriction (subsessile) or tubular petiole (petiolate).

Comments Mymarids are widely distributed, with about 100 genera recognized as valid and with about 1400 nominal species. The family usually is divided into two subfamilies in two different classifications. In one classification the number of tarsomeres is used to characterize the subfamilies Mymarinae (with 4 tarsomeres) and Gonatocerinae (with 5 tarsomeres). In the alternative classification, the manner of attachment of the metasoma to the mesosoma is used to distinguish Alaptinae (widely attached) and Mymarinae (subsessile or petiolate).

A third subfamily, Eubroncinae, based primarily on a wedge-like head structure, was established by Yoshimoto et al. (1972). Though not all eubroncines have the head conspicuously wedgelike, members differ from other mymarids in having the membrane of the hind wing narrowly extending to the base of the wing so that it is not stalked. Mymaridae is indicated to be a monophyletic group based on the pattern of lines on the head plus other features listed by Schauff (1984). Because mymarids are so distinct structurally from other chalcidoids they sometimes have been considered to be the sister group of the rest of the superfamily. However, Chalcidoidea excluding Mymaridae lack known synapomorphic features, so that it is equally likely that Mymaridae represents the sister group of only some part of the superfamily.

**Biology** Mymarids are all parasitoids of insect eggs, mostly of eggs laid in concealed situations, such as in plant tissue, under scales, or in the soil; hosts are primarily Homoptera and Hemiptera, though Psocoptera, Coleoptera, Orthoptera, and Diptera are also used.

References Annecke and Doutt (1961) revised the world genera, Schauff (1984) the North American genera, Noyes and Valentine (1989a) the New Zealand genera, and Yoshimoto (1990) the New World genera. Huber (1986) gave a historical review of mymarid classification and recorded hosts, and included an extensive bibliography.

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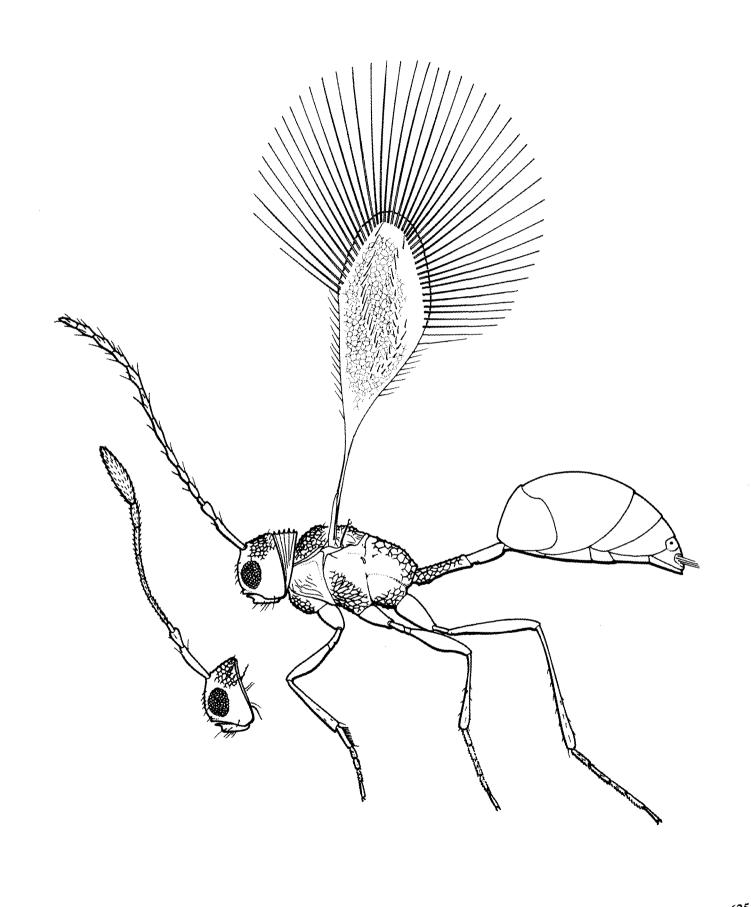


Fig. 211. Mymarommatidae

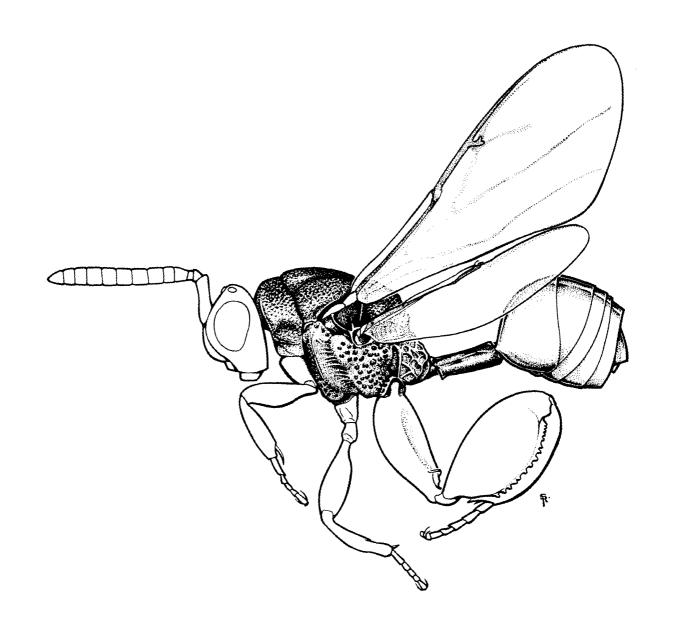


Fig. 212. Chalcididae

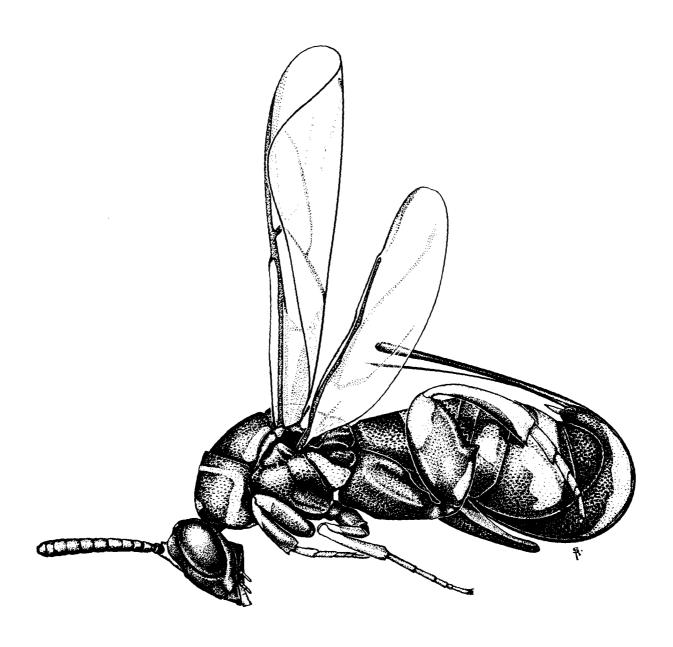


Fig. 213. Leucospidae

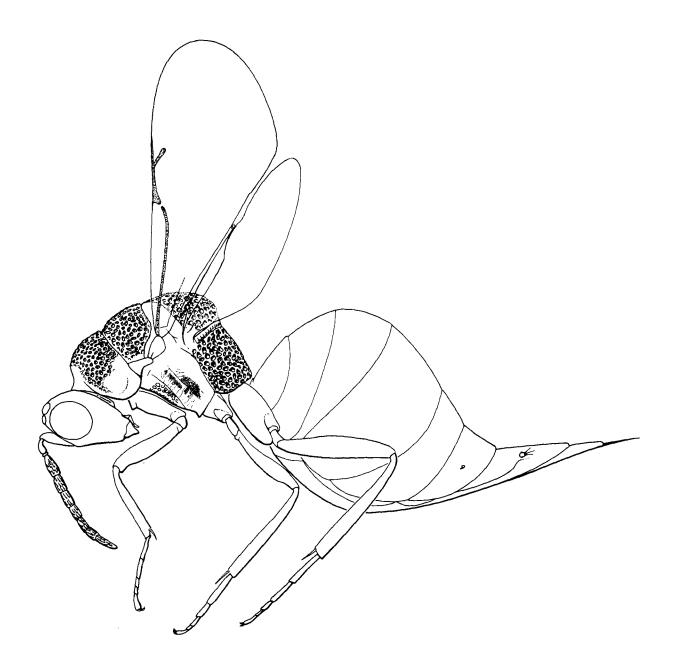


Fig. 214. Eurytomidae

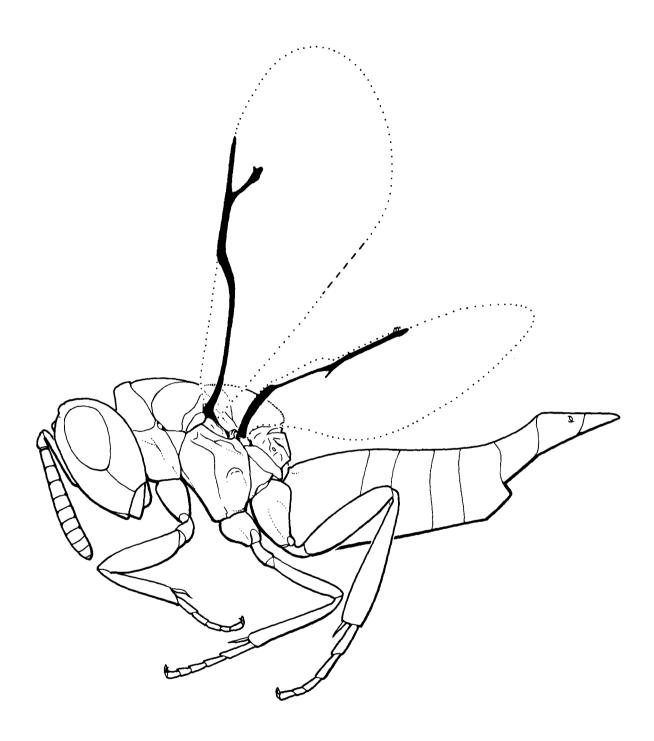


Fig. 215. Pteromalidae

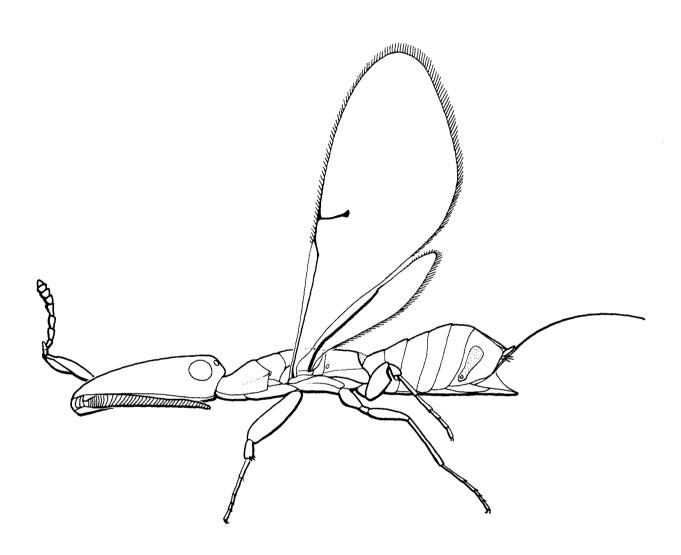
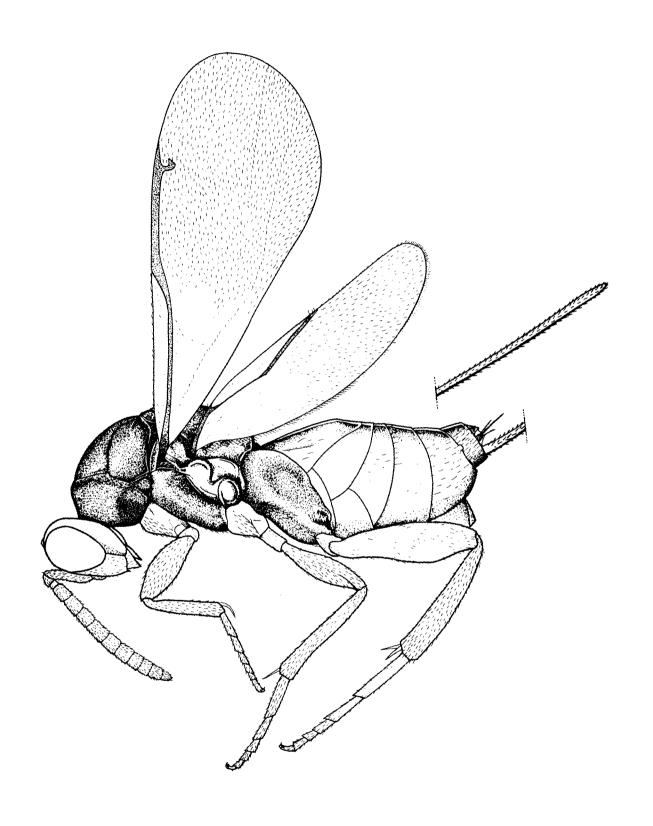


Fig. 216. Agaonidae



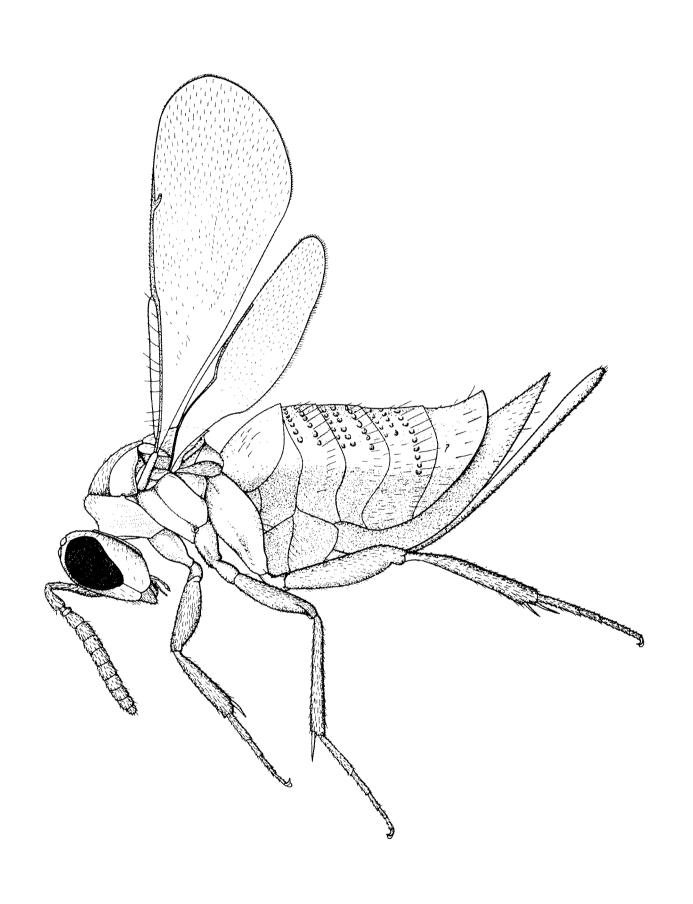


Fig. 218. Ormyridae

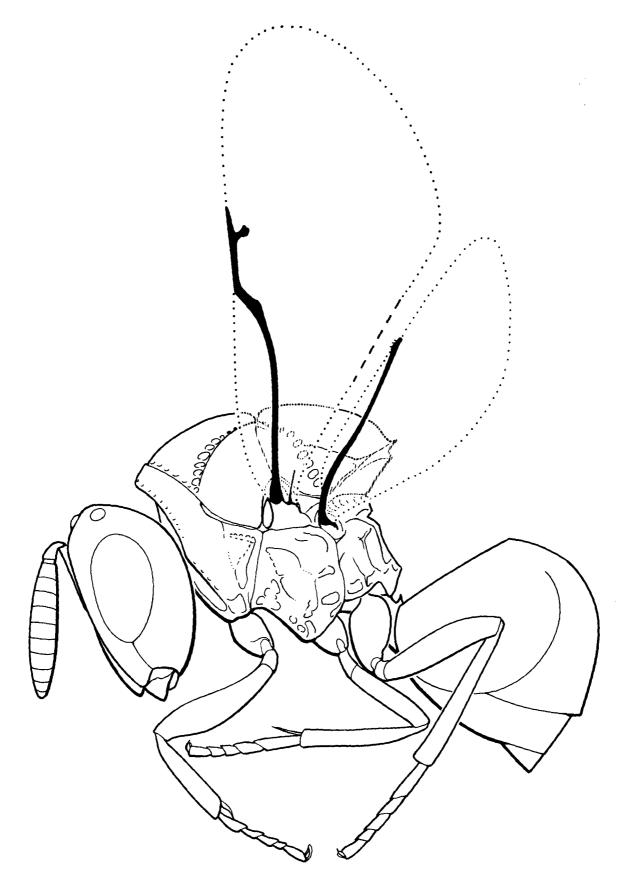
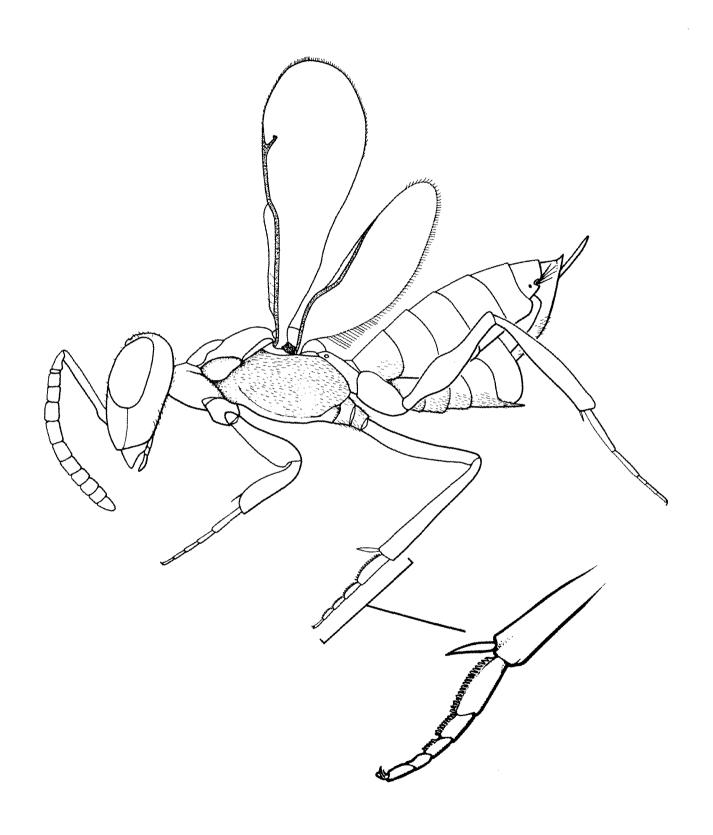


Fig. 219. Perilampidae



Fig. 220. Eucharitidae



645

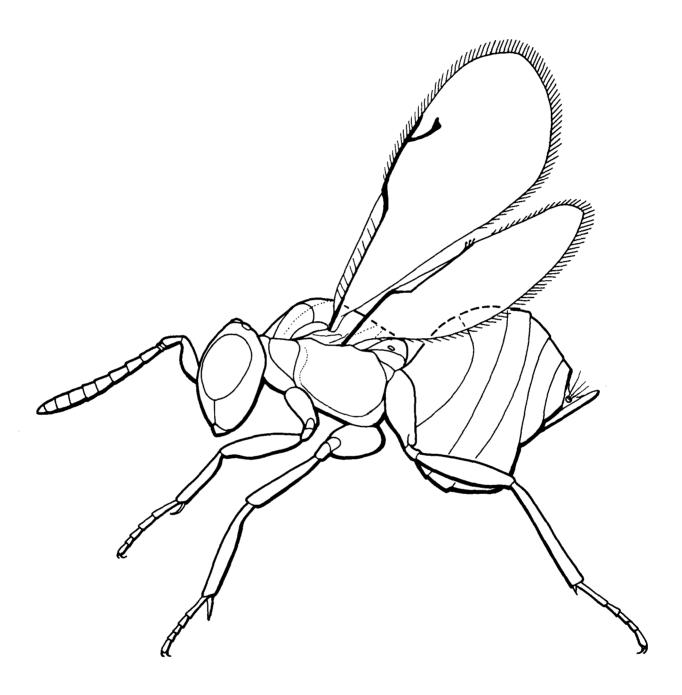


Fig. 222. Tanaostigmatidae

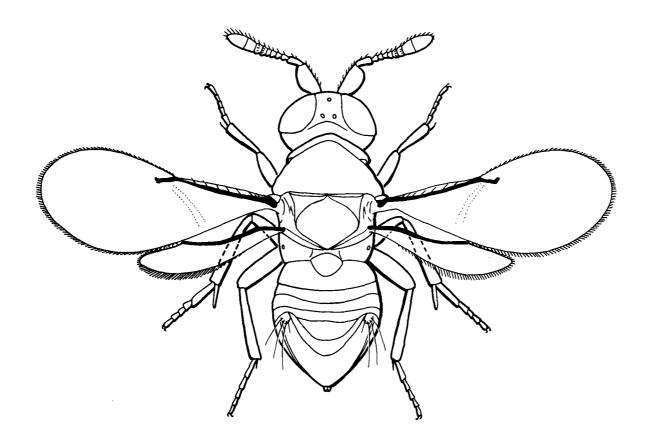


Fig. 223. Encyrtidae

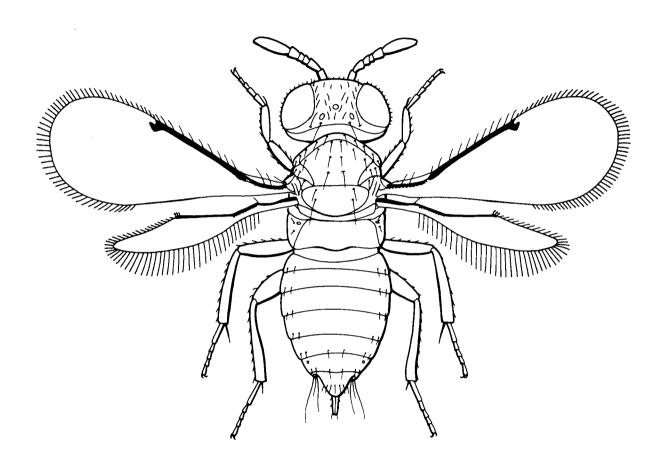


Fig. 224. Aphelinidae

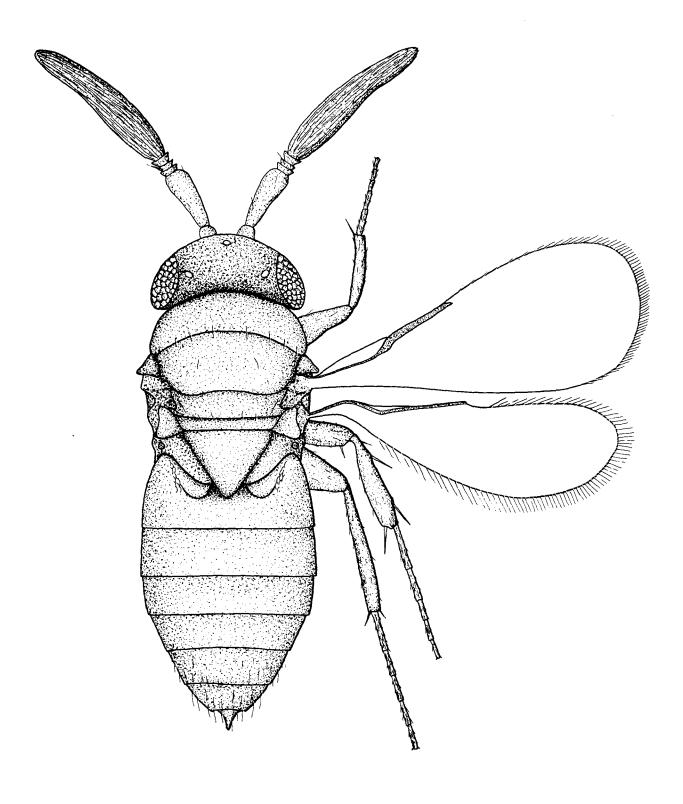


Fig. 225. Signiphoridae

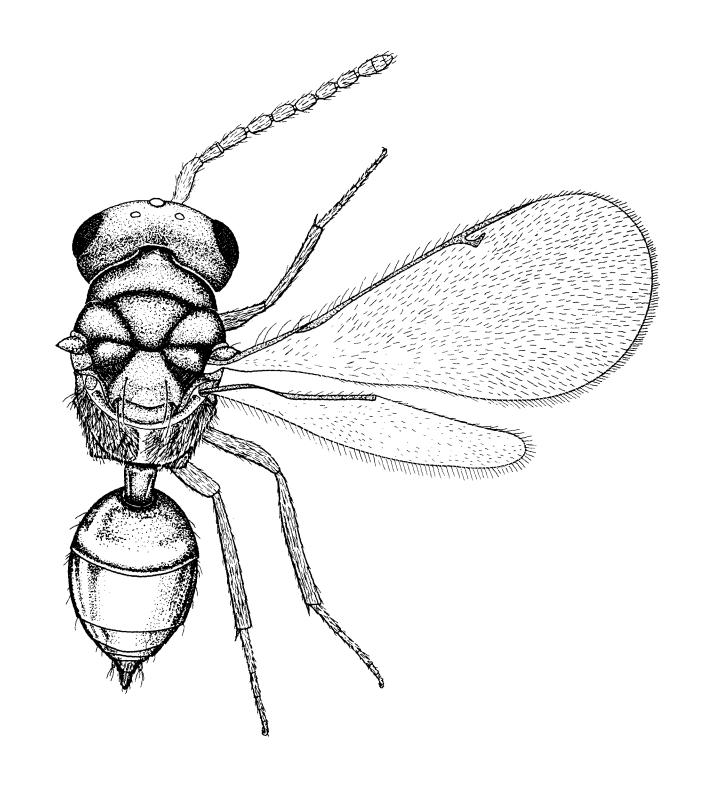


Fig. 226. Tetracampidae

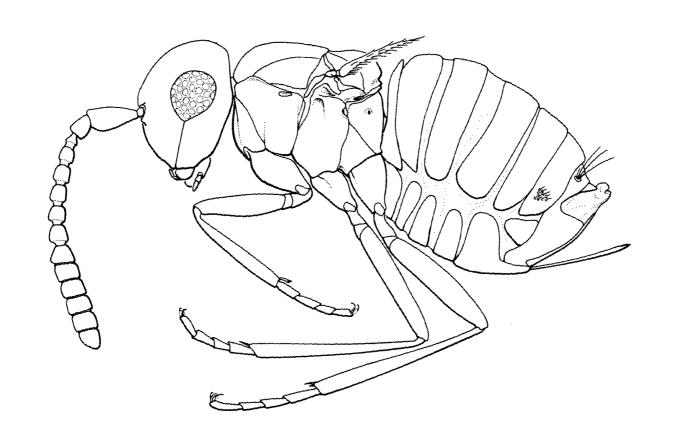


Fig. 227. Rotoitidae

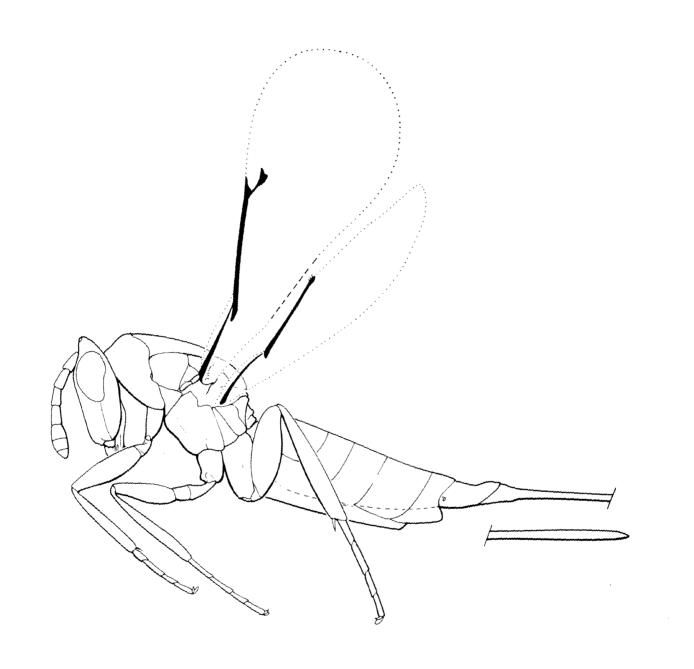


Fig. 228. Eulophidae

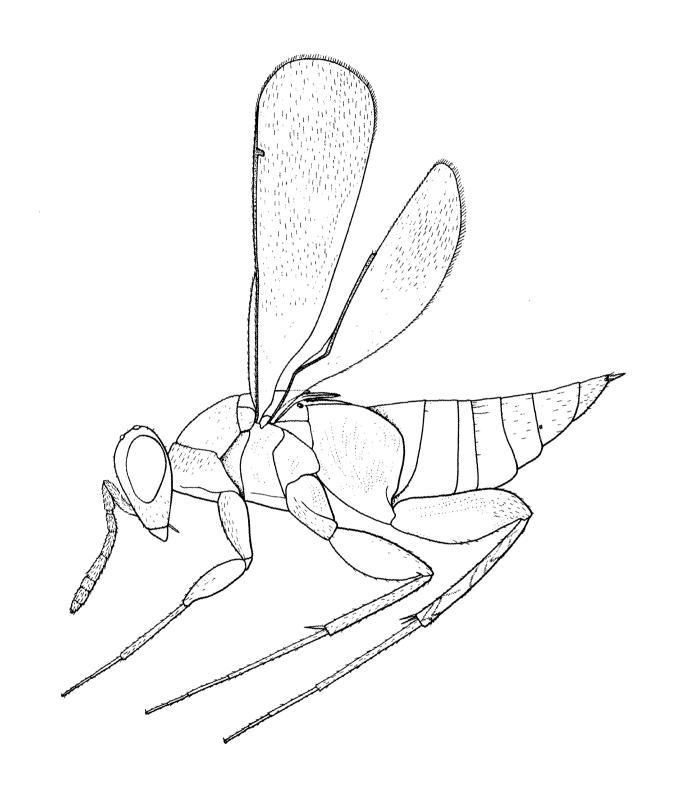


Fig. 229. Elasmidae

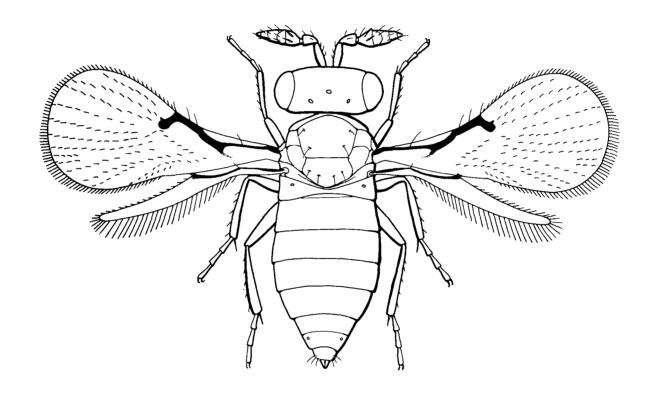


Fig. 230. Trichogrammatidae

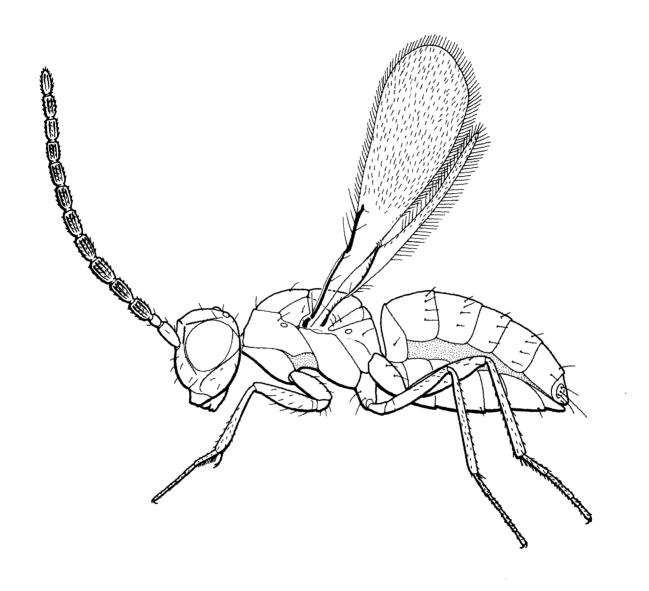


Fig. 231. Mymaridae

## Appendix 1 List of habitus drawings, with generic names

Numerical list of habitus illustrations in order of appearance in text. Subfamilies given only when they are keyed and discussed separately.

Cephoidea   CEPHIDAE   Megalodontes   Megalodonte	Fig.	Superfamily	Family	Subfamily	Genus
23					
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67 Mutillinae female Timutilla					
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70 POMPILIDAE Pepsinae Priocnemella				Pensinae	
71 Pompilinae Arachnospila					
72 Ceropalinae Ceropales					
73 RHOPALOSOMATIDAE Rhopalosoma			RHOPALOSOMATIDAE	<b>r</b>	
74 BRADYNOBAENIDAE Chyphotinae Chyphotes	74			Chyphotinae	

Fig.	Superfamily	Family	Subfamily	Genus
75			Apterogyninae female	Apterogyna
76			Apterogyninae male	Apterogyna
77 70		SCOLIIDAE	Proscoliinae	Proscolia
78 70		TABODID A.E.	Scoliinae	Campsomeris
79 80		VESPIDAE	Euparagiinae	Euparagia
81			Masarinae	Pseudomasaris Ancistrocerus
82			Eumeninae	Parischnogaster
83			Stenogastrinae Vespinae	Provespa
84			Polistinae	Polybia
85		FORMICIDAE	Myrmeciinae	Myrmecia
86			Pseudomyrmeciinae	Pseudomyrmex
87			Ponerinae	Pachycondyla
88			Dorylinae	Aenictus
89			Myrmicinae	Atta
90			Dolichoderinae	Monacis
91			Formicinae female (worker)	Formica
92			Formicinae male	_
93	Apoidea	HETEROGYNAIDAE		Heterogyna
94		AMPULICIDAE	Dolichurinae	Dolichurus
95			Ampulicinae	Ampulex
96 97		SPHECIDAE	Sceliphrinae	Chalybion
97			Sphecinae	Sphex
98 99		DEMBLIDEDONIDAE	Ammophilinae	Ammophila
100		PEMPHREDONIDAE	Pseninae Pemphredoninae	Pseneo
101		ASTATIDAE	Astatinae	Pemphredon Dryudella
102		CRABRONIDAE	Larrinae	Liris
103		CREDIONIDAE	Crabroninae	Crossocerus
104		MELLINIDAE	Mellininae	Mellinus
105		NYSSONIDAE	Alyssoninae	Alysson
106			Nyssoninae	Zanysson
107			Gorytinae	Neoplisus
108			Stizinae	Bembicinus
109			Bembicinae	Microbembex
110		PHILANTHIDAE	Eremiasphecinae	Eremiasphecium
111			Philanthinae	Philanthus
112			Aphilanthopinae	Aphilanthops
113			Cercerinae	Eucerceris
114 115		COLLETIDAE		Hylaeus
116		STENOTRITIDAE ANDRENIDAE		Ctenocolletes Andrena
117		OXEIDAE		Protoxaea
118		HALICTIDAE		Halictus
119		MELITTIDAE		Macropis
120		CTENOPLECTIDAE		Ctenoplectra
121		FIDELIIDAE		Neofidelia
122		MEGACHILIDAE		Megachile
123		ANTHOPHORIDAE		Anthophora
124		APIDAE		Bombus
125	Ichneumonoidea	BRACONIDAE	Adeliinae	Adelius
126			Agathidinae	Bassus
127			Amicrocentrinae	Amicrocentrus
128			Cardiochilinae	Cardiochiles
129			Cheloninae	Chelonus
130			Dirrhopinae	Dirrhopus
131 132			Euphorinae	Syntretus
132			Helconinae Homolobinae	Wroughtonia Homolobus
133			пошоющае	HOMOIODUS

Fig.	Superfamily	Family	Subfamily	Genus
134			Ichneutinae	Ichneutes
135			Khoikhoiinae	Khoikhoia
136			Macrocentrinae	Macrocentrus
137			Meteoridiinae	Meteoridea
138			Meteorinae	Meteorus
139			Microgastrinae	Promicrogaster
140			Miracinae	Mirax
141			Neoneurinae	Neoneurus
142			Orgilinae	Orgilus
143			Sigalphinae	Sigalphus
144			Trachypetinae	Trachypetus
145			Xiphozelinae	Xiphozele
146			Alysiinae	Gnathopleura
147			Aphidiinae	Ephedrus
148			Apozyginae	Apozyx
149			Braconinae	Digonogastra
150			Doryctinae	Spathius
151			Gnamptodontinae	Ĝnamptodon
152			Opiinae	Opius <sup>1</sup>
153			Rogadinae	Āleoides
154		ICHNEUMONIDAE	Acaenitinae	Arotes
155			Adelognathinae	Adelognathus
156			Agriotypinae	Agriotypus
157			Anomaloninae	Barylpa
158			Banchinae	Lissonota
159			Campopleginae	Diadegma
160			Collyrinae	Collyria
161			Cremastinae	Temelucha
162			Ctenopelmatinae	Synoecetes
163			Cylloceriinae	Cylloceria
164			Diplazontinae	Diplazon
165			Eucerotinae	Euceros
166			Ichneumoninae	Ichneumon
167			Labeninae	Grotea
168			Lycorinae	Toxophorides
169			Mesochorinae	Stichtopisthus
170			Metopiinae	Exochus
171			Microleptinae	Microleptes
172			Neorhacodinae	Neorhacodea
173			Ophioninae	Enicospilus
174			Orthocentrinae	Stenomacrus
175			Orthopelmatinae	Orthopelma
176			Oxytorinae	Oxytorus
177			Paxylommatinae	Hybrizon
178			Phrudinae	Phrudus
179			Phygadeuontinae	Attractodes
180			Pimplinae	Coccigomimus
181			Stilbopinae	Stilbops
182			Tatogastrinae	Tatogaster
183			Tersilochinae	Heterocola
184			Tryphoninae	Polybastus
185	Description	ALILACIDAE	Xoridinae	Xorides
186	Evanioidea	AULACIDAE		Pristaulacus
187		GASTERUPTIIDAE		Gasteruption
188	C4	EVANIIDAE		Prosevania
189	Stephanoidea	STEPHANIDAE		Megischus
190	Megalyroidea	MEGALYRIDAE		Megalyridea
191 192	Trigonalyoidea	TRIGONALYIDAE		Poecilogonalos
172	Cynipoidea	IBALIIDAE		Ibalia

Fig.	Superfamily	Family	Subfamily	Genus
193		LIOPTERIDAE		Mesocynips
194		FIGITIDAE		Xyalophora
195		EUCOILIDAE		Heptamerocera
196		CHARIPIDAE		Charips
197		CYNIPIDAE		Diplolepis
198	Proctotrupoidea	PELECINIDAE		Pelecinus
199	•	VANHORNIIDAE		Vanhornia
200		PROCTOTRUPIDAE		Exallonyx
201		HELORIDAE		Heloridus
202		PERADENIIDAE		Peradenia
203		ROPRONIIDAE		Ropronia
204		AUSTRONIIDAE		Austronia
205		MONOMACHIDAE		Monomachus
206		DIAPRIIDAE		Spilomicrus
207	Platygastroidea	SCELIONIDAE		Trimorus
208		PLATYGASTRIDAE		Trichacoides
209	Ceraphronoidea	MEGASPILIDAE		Megaspilus
210		CERAPHRONIDAE		Ceraphron
211	Mymarommatoidea	MYMAROMMATIDAE		Palaeomymar
212	Chalcidoidea	CHALCIDIDAE		Chalcis
213		LEUCOSPIDAE		Leucospis
214		EURYTOMIDAE		Eurytoma
215		PTEROMALIDAE		Habrocytus
216		AGAONIDAE		Pleistodontes
217		TORYMIDAE		Torymus
218		ORMYRIDAE		Ormyrus
219		PERILAMPIDAE		Perilampus
220		EUCHARITIDAE		Pseudochalcura
221		EUPELMIDAE		Anastatus
222		TANAOSTIGMATIDAE		Tanaostigmodes
223		ENCYRTIDAE		_
224		APHELINIDAE		Aphytis
225		SIGNIPHORIDAE		Signiphora
226		TETRACAMPIDAE		Epiclerus
227		ROTOITIDAE		_
228 229		EULOPHIDAE		Aprostocetus
229		ELASMIDAE	=	Elasmus
230		TRICHOGRAMMATIDAL		Ophioneurus Compto comp
231		MYMARIDAE		Gonatocerus

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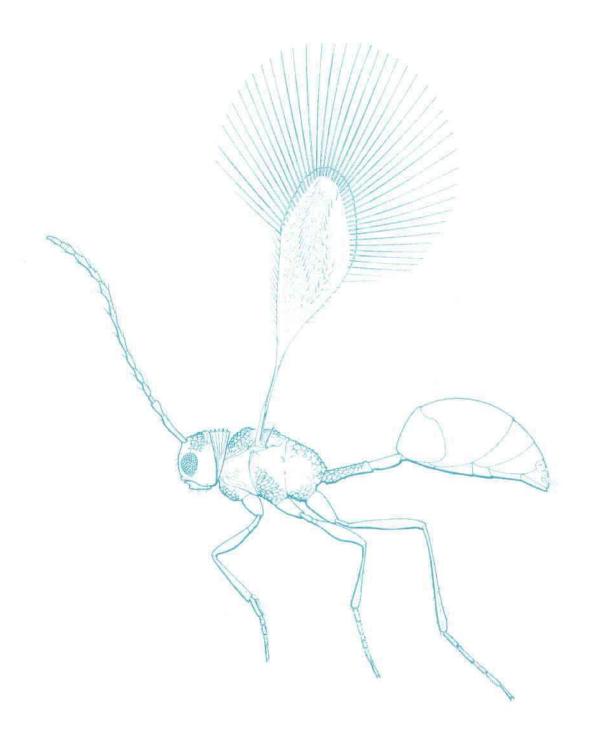
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