

## HYMENOPTERA

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Sawflies, horntails, wasps, bees, ants, and relatives. Adults are mandibulate; most species have four membranous wings (the second pair is small) [see illustration page 653], but about a tenth of the species lack wings at some stage in one or both adult sexes, or in a neuter worker caste (ants). The antennae are well developed, filiform or geniculate, and clubbed or flabellate, with segments numbering from about 70 to as few as 3. Maxillary palpi are primitively six-segmented, although segments may vary from seven to one in different genera; labial palpi primitively comprise four segments, but vary downward to one segment, or none. The under-mouthparts are often elongate and generally modified for taking floral nectar in many bees, wasps, and parasitoids. The cervical sclerites are fused with the propiternum. An ovipositor is present in the female, except in some higher ants and bees, but it serves as a sting in most aculeates.

Metamorphosis is complete and endopterygote; the larva is eruciform (Symphyta) or grublike, apodous, and blind (Apocrita). The tracheal system most often is holopneustic or peripneustic, at least in the final instar. Pharate adults (pupae) are exarate, and enclosed in a cocoon (there are many exceptions). The nervous system usually is relatively unconcentrated in larvae and adults; there are three thoracic ganglia and three or more abdominal ganglia.

Chromosomes range from a haploid number of 4 to over 45. Species are haplodiploid (males are normally haploid, developing from unfertilized eggs; females are diploid). Some species scattered through the order are thelytokous (without males).

Adults are active; males inseminate females, but rarely play any further role in protecting the female or rearing the young. Females may limit care of the young to oviposition in or on a suitable host plant or arthropod (most Symphyta and Parasitica), or may furnish the egg or larva with a prepared nest and dead or paralyzed arthropodan prey, pollen and nectar, or other kinds of provisions (most Aculeata). Some aculeates in various taxa have evolved to the stage of progressive provisioning, in which the female returns repeatedly to her larvae after they hatch and brings them food as they develop.

Haplodiploidy (by increasing the genetic similarity between sisters and other close female relatives) and progressive provisioning (by leading to the overlap and cohabitation of adult female generations) were key adaptations that made possible the evolution of societies several times independently in the Hymenoptera.

This is a very large and important order, with 2 suborders, Symphyta (=Chalastogastra) and Apocrita (=Clistogastra), including perhaps 130,000 described species; species are distributed worldwide except for the coldest regions. The earliest known fossils are from the Lower Triassic; a sister group may be the modern panorpoid complex.

**References.** K. V. Krombein et al., *Catalog of Hymenoptera in America North of Mexico*, Smithsonian Institution Press, Washington, DC, 2 vols., 1979; E. F. Riek et al., *Hymenoptera*, in *The Insects of Australia*, Commonwealth Scientific and Industrial Research Organization, University of Melbourne Press, 1970.

## SYMPHYTA

Sawflies, horntails, and allies. Adults are thick-waisted, but more or less wasplike, insects, only occasionally showing conspicuous sexual dimorphism; they are always fully winged. The first and second abdominal segments are broadly joined, but sometimes with a more or less membranous hingelike junction between them, foreshadowing the definite constriction of Apocrita. Females have a complex ovipositor, usually sawlike, but sometimes rodlike (Siricoidea), with a pointed apex for boring.

Larvae are mostly caterpillarlike, with a well-developed head capsule, true legs, and often abdominal prolegs. They usually live and feed on leaves, but many are borers in stems or wood, or are miners in leaves. In such cases, the legs and other appendages are reduced or absent, and the body form is cylindrical, flattened, or otherwise modified in the way usual for holometabolous insects in these microhabitats. All Symphyta are feeders on plant tissues, except for the family Orussidae.

The suborder (=Chalastogastra) has a worldwide distribution, especially in temperate zones; it is rarer in the tropics. It is usually considered to contain 4 superfamilies: Megalodontoidea, Tenthredinoidea, Siricoidea, and Cephoidea. About 4700 species in perhaps 350 genera exist, mostly in the Northern Hemisphere.

**References.** H. H. Ross, A generic classification of the nearctic sawflies (Hymenoptera, Symphyta), *Ill. Biol. Monogr.*, 15(2):1-173, 1937.

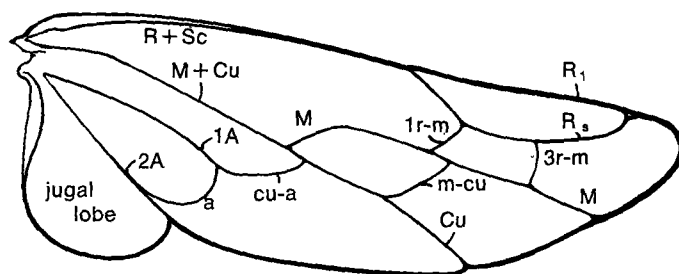
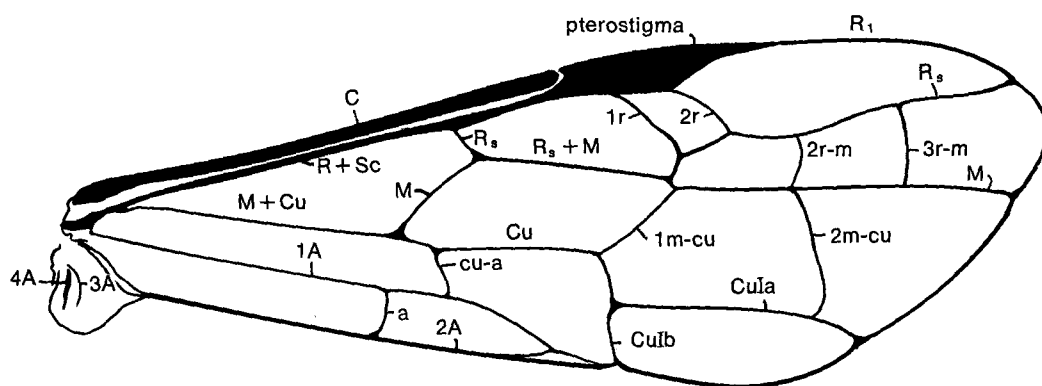
## Megalodontoidea

Sawflies with a relatively broad head and a broad abdomen, usually modest-sized (length 5-20 mm), black in color, or black and red, white, or yellow in various combinations. The underside of the head is very diverse in form: Xyelidae have an open-type head, and Pamphiliidae and Megalodontidae have a closed head. Xyelidae and Pamphiliidae have a wide presternal (episternal) bridge in front of the mesosternum, but Megalodontidae lack this bridge entirely. The genitalia of the male are uninverted (except in Xyelinae). The antennae have 12 or more segments, the number differing according to family. The fore tibiae have two apical spurs.

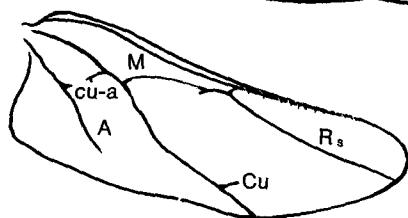
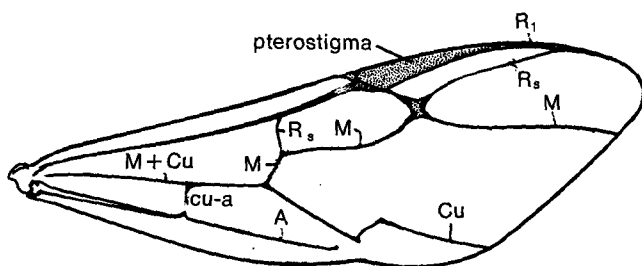
The larvae also differ according to family; thoracic legs and eyes are present, but abdominal prolegs are present only in Xyelidae; subanal appendages (cerci) are present, except in Xyelidae. The larvae live and feed free or in webs on leaves, inside rolled leaves, in holes bored in conifer shoots, or on staminate pine cones. Pupation takes place in a cell in the ground; the pharate adults climb up to the soil surface and cast their skins there.

The superfamily comprises 3 families: Xyelidae, Pamphiliidae, and Megalodontidae. It is holarctic in distribution, and includes more than 300 species in about 15 genera.

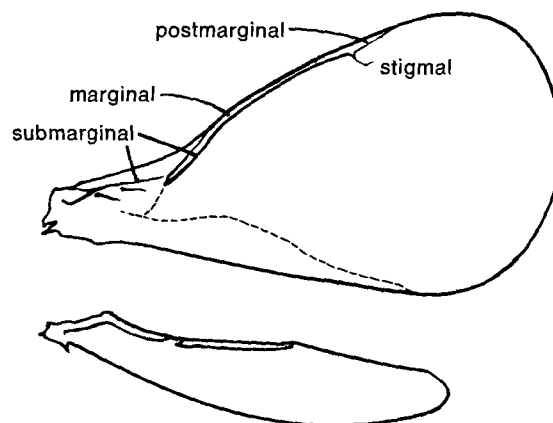
**References.** H. H. Ross, A generic classification of the nearctic sawflies (Hymenoptera, Symphyta), *Ill. Biol. Monogr.*, 15(2):1-173, 1937.



*Janus integer* (Symphyta),  
female



*Oecophylla smaragdina* (Aculeata), male



*Enaysma gahani* (Eulophidae), female

Fore and hind wings of three representative species of Hymenoptera. The letters and numbers refer to wing veins: capital initials denote longitudinal veins, lowercase abbreviations mark crossveins. C = costa, R<sub>1</sub> = first radial, R<sub>2</sub> = radial sector, M = median, Cu = (anterior) cubitus, 1A = first anal, 2A = second anal, and so on; 1r = first radial crossvein, 2r = second radial crossvein, 2 r-m and 3 r-m = second and third radiomedial crossveins (1 r-m is present in only a few primitive sawflies), 1 m-cu and 2 m-cu = first and second mediocubital (or recurrent) crossveins, cu-a = cubitoanal crossvein, a = anal crossvein.

**Xyelidae.** Primitive sawflies, considered by some authorities to link the Hymenoptera to a pre-panorpid ancestor. The body of adults is usually 5–15 mm long, and colored black, often with red or yellow markings. Females have an elongate ovipositor. The third segment of the antennae is very long and cylindrical; the remaining 9–20 or more short segments form a slender, flexible, terminal filament. Wing venation is full, the most complete in Hymenoptera; there is a radial cell with two crossveins. The abdomen is not markedly depressed; male genitalia are inverted (strophandrous) or not (orthandrous). Xyelids are pollen feeders.

In the larvae the antennae have six or seven segments; there are 10 pairs of abdominal prolegs, but cerci are lacking. The larvae feed on the staminate flowers of pines and their pollen, or bore into leaf shoots or galls on conifers, or feed externally on buds and leaves of trees such as *Carya* and *Ulmus*.

Distribution of this family is holarctic, extending to the mountains of Sumatra with *Pinus*. Xyelidae comprise about 50 species in 5 genera. Two subfamilies exist: Xyelinae (male genitalia are inverted) and Macroxyelinae (male genitalia are uninverted). [D. CHRIS DARLING]

**References.** D. J. Burdick, A taxonomic and biological study of the genus *Xyela* Dalman in North America, *Univ. Calif. Publ. Entomol.*, 17:285–365, 1961; D. R. Smith, A review of the larvae of Xyelidae, with notes on the family classification (Hymenoptera), *Ann. Entomol. Soc. Amer.*, 60:376–384, 1967.

**Megalodontidae.** Sawflies with a large head, similar to Pamphiliidae. They are distinguished by their flabellate antennae and undivided second abdominal tergite. The forewing has a costal cell without a longitudinal vein or crossvein (that is, the subcosta is obsolete); the anal cell is not contracted basally, and contains a scaly patch. The mesosternum is trapezoidal. The tongue, when extended, is usually as long as the head capsule. The abdomen is flattened dorsoventrally.

The larva is similar to that of Pamphiliidae, with segmented thoracic legs and cerci, but is distinguished by the position of the eyes, which are below but near the antennae. The larvae are often gregarious; they spin webs over herbaceous vegetation.

This is a palearctic family, with about 45 species in 3 genera. [D. CHRIS DARLING]

**References.** F. W. Konow, *Lydidae*, in P. Wytman (ed.), *Genera Insectorum*, Brussels, fasc. 27, 1905.

**Pamphiliidae.** Adults are robust and dorsoventrally flattened, with a wide head; their color is often black and yellow. The antennae are slender, multisegmented, and tapered apically. The female ovipositor is very short, not projecting beyond the apex of the abdomen. The wings have a costal cell divided by a longitudinal (subcostal) vein; the radial cell has a single crossvein. The posterior margin of the pronotum is straight; the second abdominal tergite is divided medially, like the first.

The larvae have well-developed thoracic legs, but lack abdominal prolegs. The antennae are long and have seven segments. Cerci are present as distinctly segmented appendages. The eyes are below and lateral to the antennae. Larvae are often gregarious, and are usually found in silken webs or rolled leaves; they are external leaf feeders.

Distribution is holarctic, with about 170 living species in 6 genera. The family comprises 2 subfamilies: Cephalcinae,

on conifers, and Pamphiliinae, on Rosaceae and the amenaceous woody families of angiosperms. [D. CHRIS DARLING]

**References.** W. W. Middlekauff, The North American sawflies of the genera *Acantholyda*, *Cephalcia* and *Neurotoma* (Hymenoptera, Pamphiliidae), *Univ. Calif. Publ. Entomol.*, 14:51–174, 1958; W. W. Middlekauff, The North American sawflies of the genus *Pamphilius* (Hymenoptera, Pamphiliidae), *Univ. Calif. Publ. Entomol.*, 38:1–84, 1964.

### Tenthredinoidea

Sawflies and their allies. Their body form is either slender or thick, more or less wasplike, usually ranging 3–20 mm in length. Wings are always present, with a relatively full venation. The underside of the head is of the open type. The male genitalia are rotated 180°. The pronotum is narrow and reduced to a thin strap in the middle. The mesosternum is trapezoidal. Cenchri are present. The antennae are extremely diverse in form—filiform, bifurcate, plumose, serrate, clavate, capitate, flabellate, and so on—with 3 to 13 or more segments. Adults are mostly active fliers. Some are predacious on small insects. Females use a sawlike ovipositor to open places in plant tissues for their eggs.

The larvae are eruciform (caterpillarlike), or sluglike, with thoracic legs and a variable number of abdominal prolegs (the first and ninth segments always lack prolegs), and have a pair of simple eyes, and five antennal segments, in most of the free, leaf-feeding forms; the gall-dwelling and leaf-mining or petiole-mining forms often show a great reduction in any or all of these features. Pupae either are enclosed in hard cocoons that can be formed on an open surface, or have a weak cocoon or none, with pupation taking place in the protection of a cell in the earth, in twigs, in rotting wood, or such. So far as is known, the pupae (pharate adults) are quiescent.

The food plants are diverse, but the genera of the Holarctic Region tend to feed on relatively primitive plants such as ferns, *Equisetum*, gymnosperms, grasses, amentifers, and Rosaceae, while relatively few genera live on other families, such as Myrtaceae, Ericaceae, Caprifoliaceae, and Compositae.

This cosmopolitan superfamily is by far the largest in the suborder Symphyta, with more than 270 genera and over 4000 species, and is the most actively evolving and ecologically dominant taxon at the present time. It is divided into 6 families: Cimbicidae, Tenthredinidae, Argidae, Blasticotomidae, Pergidae, and Diprionidae.

**References.** H. H. Ross, A generic classification of the nearctic sawflies (Hymenoptera, Symphyta), *Ill. Biol. Monogr.*, 15(2):1–173, 1937; R. B. Benson, On the classification of the sawflies (Hymenoptera, Symphyta), *Trans. Roy. Entomol. Soc. London*, 87:353–384, 1938.

**Cimbicidae.** Adults are large, robust, bumblebeelike sawflies distinguished by capitate or clubbed antennae. The pronotum is emarginate behind. The abdomen is dorsoventrally depressed and angled laterally, so that the terga are sharply divided into dorsal and ventrolateral surfaces. The radial cell is divided by a crossvein. The color varies with genus and species: black, black and yellow, dull metallic green, and so on.

The larvae are exposed feeders on foliage. Their thoracic legs have five segments; abdominal prolegs are present on segments II through VIII and segment X. Cerci are absent. The antennae are short and one-segmented. The labrum is divided into three parts by a pair of longitudinal sutures.

Distribution of the family is holarctic, neotropical, and

Oriental. About 140 species in 20 genera exist, in 4 subfamilies: Cimbicinae, Coryninae, Zараeinae, and Pachylostictinae. [D. CHRIS DARLING]

**References.** R. B. Benson, On the classification of sawflies (Hymenoptera, Symphyta), *Trans. Roy. Entomol. Soc. London*, 87:353–384, 1938.

**Tenthredinidae.** Sawflies. In the adults body length is mostly in the range 3–20 mm; the body form varies from slender and wasplike, with black and yellow banding and spotting, to broad and dark-colored, such as black and red. The antennae are mostly 7- to 13-merous, rarely reaching 23 or more segments; they are filiform, clavate, or rarely partly flabellate or pectinate, and the third segment is never disproportionately elongate. The scutellum is behind, with a separated, transverse, postscutellar plate. Each of the anterior tibiae has two well-developed apical spurs. The larvae are as described under Tenthredinoidea.

This is the largest family of Tenthredinoidea, with at least 150 genera and more than 3000 species. Distribution is widespread, even into the Arctic, but the family is feebly represented in Australia, where Pergidae dominate; it is absent in New Zealand. There are 7 subfamilies: Selandrinae, Dolerinae, Tenthredininae, Emphytinae, Blennocampinae, Phyllotominae, and Nematinae. [D. CHRIS DARLING]

**References.** H. H. Ross, A generic classification of the nearctic sawflies (Hymenoptera, Symphyta), *Ill. Biol. Monogr.*, 15(2):1–173, 1937; R. B. Benson, On the classification of the sawflies (Hymenoptera, Symphyta), *Trans. Roy. Entomol. Soc. London*, 87:353–384, 1938.

**Argidae.** Adults are stout-bodied, and 4–15 mm long; they may be black, yellow, black and red, metallic blue, or other colors. The antennae are three-merous, with the third segment very long, and in the males often deeply divided into a Y or V. The scutellum lacks a separated apical plate.

The larvae are diverse according to genus, and usually free-living; thoracic legs are usually well developed, with six segments; or prothoracic legs occur, with four segments, and mesothoracic and metathoracic legs are three-merous; legs are reduced in leaf-mining species. Abdominal prolegs are usually well developed, and are usually present on II–V, II–VI, or II–VII, as well as segment X. Some forms are gregarious and spin cocoons under a communal cover; in these genera, females often stand guard over the young larvae.

Ten subfamilies are recognized by R. B. Benson: Zenarginae, Arginae, Trichorhachinae, Atomacerinae, Athermantinae, Erigleninae, Dielocorinae, Pachylotinae, Theminae, and Sterictophorinae. Close to 50 genera and more than 500 species are recognized in this family; it has widespread distribution, mainly in the tropics and in warm-temperate areas. [D. CHRIS DARLING]

**References.** R. B. Benson, On the classification of sawflies (Hymenoptera, Symphyta), *Trans. Roy. Entomol. Soc. London*, 87:353–384, 1938.

**Blasticotomidae.** Monogeneric (*Blasticotoma*, including *Runaria*) family, with 3 or 4 species. These stout-bodied sawflies are about 6–10 mm long; they are black in color with partly fulvous or rufous legs, and the abdomen is black or brown. The family is distinguished by the aberrant antennae, which consist of three or four segments: the first two segments are short, the third is very long and robust, and the fourth is tiny and sometimes hardly more than a tubercle at the end of the third segment. The forewing venation is dis-

tinctive: the second free abscissa of the radial sector is absent with Rs+M+Mf2 forming one strongly arched vein that continues posteriorly as m-cu. The larvae are legless; they bore in the stems of various ferns. Members of this family range from northern Europe to eastern Asia (Ussuri area, Japan, and northern Burma).

**References.** R. Malaise, Tenthredinoidea of southeastern Asia, *Opuscula Entomol., Suppl.*, 4:90–91, 1945.

**Pergidae.** Adult body length ranges 4–25 mm; the body is thickset. The antennae have 6–13 or more segments; they are serrate, branched, flabellate, clavate, or capitate. The posterior margin of the pronotum is strongly emarginate; the abdomen has rounded lateral margins, not angled or carinate. The hindwing lacks closed discoidal and anal cells; the anal cell of the forewing is petiolate, or may be absent. The radial cell of the forewing is not crossed by a vein. The apical spur or spurs of the anterior tibiae are simple. Cenchri are stridulatory. Females commonly stand guard over the young larvae.

Larvae are gregarious on foliage; rarely, they are leaf miners. Thoracic legs are large and well developed; abdominal prolegs are often absent, preserved only on certain segments, or reduced. In some taxa, noxious secondary substances secured from host plants are stored, and are ejected by the larvae to repel threatening enemies.

There are 14 subfamilies: Philomastiginae, Perginae, Phylacteophaginae, Acordulecerinae, Paralypiinae, Styra-cotechyinae, Pteryperginae, Syzygoniinae, Lobocerinae, Pergulinae, Conocoxinae, Pterygophorinae, Euryinae, and Perreyiinae. The genera, several of which are doubtful, number close to 50, and the species probably add up to more than 300 (136 in Australia alone).

The family is mainly Australian and tropical American in distribution, with extensions through New Guinea to the Celebes; a number of species of *Acordulecera* reach into North America.

**References.** R. B. Benson, On the classification of sawflies (Hymenoptera: Symphyta), *Trans. Roy. Entomol. Soc. London*, 87:376–384, 1938.

**Diprionidae.** Conifer sawflies. Adults are 5–12 mm long, with very stout bodies. The antennae have 13 or more segments, and are serrate in females and pectinate or bipectinate in males. The radial cell lacks a crossvein. The body is usually dark in color or bicolorous. Larvae are caterpillarlike, feeding on cedars (Monocteninae) or pines (Diprioninae). Thoracic legs are five-segmented, with prolegs present on abdominal segments II to VIII and segment X. The antennae are three-segmented, erect, and peglike. Cerci are absent. The abdominal segments are divided dorsally by transverse grooves into distinct annulets. The larvae store resins and terpenes obtained from conifers and eject the substances to repel enemies.

Distribution of the family is holarctic, reaching Cuba. There are 50–100 species in 6 or 7 genera and 2 subfamilies (Monocteninae and Diprioninae). [D. CHRIS DARLING]

**References.** H. H. Ross, A generic classification of the nearctic sawflies (Hymenoptera, Symphyta), *Ill. Biol. Monogr.*, 15(2):56–58, 1937.

### Siricoidea

Horntails, wood wasps, and their allies. Adult are cylindrical wasps about 1–4 cm long. A true genaponta or bridge composed of the fused postgenae closes the underside of the head behind the mouth. The labrum is long-spatulate.

The female ovipositor is awllike, adapted for boring. The apical tibial spur formula is 1,2,2, except in Orussidae, where it is 2,2,2.

The larvae lack abdominal prolegs, and the thoracic legs are vestigial. No eyes or cerci are present. The antennae are one- or three-merous. All are wood borers, or at least live in tunnels in wood. Pupae are enclosed in a cocoon of silk and wood crumbs in the burrow.

The superfamily comprises 4 living families: Xiphydriidae, Syntexidae, Siricidae, and Orussidae. There are approximately 250 living species in 46 genera. Distribution is worldwide, in tropical to cold-temperate regions.

[D. CHRIS DARLING]

**References.** H. H. Ross, A generic classification of the nearctic sawflies (Hymenoptera, Symphyta), *Ill. Biol. Monogr.*, 15(2):1–173, 1937.

**Xiphydriidae.** Wood wasps. Xiphydriids are similar to horn-tails (Siricidae) in general appearance, but are often smaller (length 7–25 mm) and slender, with a round head set onto an elongate neck formed by a propleural extension. The pronotum has an inverted-U shape (dorsal part in dorsal view). The antennae are slender, with 11–27 segments; maxillary palpi are four- to seven-merous, and labial palpi are three- or four-merous. The mesonotum has a transverse suture. Wing venation is complete, with a crossvein in the costal cell. The last external abdominal tergite lacks a hornlike process; the sheath of the ovipositor is seldom longer than that tergite. Adults are usually black in color or testaceous, often with red, yellow, tan, or white markings; and rarely, metallic.

In the larvae the antennae are three- or four-merous. As far as is known, larvae bore in the wood of angiospermous trees and shrubs, usually in dead or rotting branches or twigs.

The family is worldwide in distribution (except for Africa and Madagascar), in tropical to cold-temperate regions. About 90 species are known, in 2 subfamilies: Derecyrtinae (4 genera, neotropical and Australian) and Xiphydriinae (18 genera, holarctic and Indo-Australian).

[D. CHRIS DARLING]

**References.** R. B. Benson, Classification of the Xiphydriidae (Hymenoptera), *Trans. Roy. Entomol. Soc. London*, 105: 151–162, 1954.

**Syntexidae.** Monotypic (*Syntexis libocedri*) family from California and Oregon. This black insect is about 8 mm long. It is similar to Xiphydriidae in the form of the head and antennae, and in wing venation, but the mesoscutum is not divided by a transverse suture. There is no subantennal groove in front of the eye; a deep, wide trench exists between the mesonotum and metanotum. The antennae are setaceous, with about 16 segments. The pronotum is broader behind than in front, with a broad, inverted-V-shaped posterior margin (not reduced to a narrow, U-shaped collar). The anterior leg has a pectinate apical tibial spur, but no preapical tibial spurs. The mesosternum is short and set off from the episterna by distinct sutures. The alaglossa of the labium partly envelopes the paraglossae from below.

The larva is similar to those of Xiphydriidae. It bores in the wood of the incense cedar (*Libocedrus*).

[D. CHRIS DARLING]

**References.** R. B. Benson, On the genera of the Cephidae, and the erection of a new family Syntexidae (Hymenoptera, Symphyta), *Ann. Mag. Natur. Hist.*, (10)16: 534–553, 1935.

**Siricidae.** Horntails. Adults are 2–4 cm long and cylindrical; they are often black and yellow, black and red, fulvous, or metallic blue. The head is large and widened behind the eyes. The pronotum is transverse in dorsal view, with a concave anterior surface and a concave posterior margin. The mesonotum has a pair of diagonal furrows. The forewing lacks a crossvein in the costal cell. The antennae are filiform, each with approximately 14–30 segments. The apical tibial spur of the anterior leg is cleft at the apex. The propodeum is divided longitudinally. The common name of these insects derives from the hornlike prolongation of the last abdominal tergite, which is short and triangular in the male, and long and spearlike in the female. The sheath of the ovipositor is very long, extending beyond the end of the abdomen. Maxillary palpi have only one segment. The females oviposit by drilling into standing trees or fallen timber.

In the larvae each of the antennae has a single segment. Metathoracic spiracles are large and functional. The abdomen has a spine at the tip. The larvae are wood-boring; they cause damage due to symbiosis with rot-producing fungi.

The family is distributed in the Holarctic, Ethiopian, Oriental, and Neotropical regions; there is 1 species introduced into Australia. There are approximately 90 living species in 8 genera and 2 subfamilies, Siricinae and Tremicinae.

[D. CHRIS DARLING]

**References.** W. W. Middlekauff, Siricid wood wasps of California, *Bull. Calif. Insect Surv.*, 6:57–77, 1960.

**Orussidae.** Adults are similar in general appearance to Siricidae, but often smaller (length 5–20 mm). The antennae are inserted far below the eyes, immediately above the mandibles, and beneath a transverse frontal ridge. The head has a curved crest of sharp tubercles on the vertex. Wing venation is reduced, and lacks a closed submarginal cell in the hindwing. The front tibia has two apical spurs, one very short, the other longer and cleft at the apex. The eyes normally are finely hairy. The foreleg of the female is modified, with a "jointing" in the swollen tibia and an apparent three-segmented tarsus; the device is probably a vibration sensor.

In the larvae each of the antennae has a single segment. Metathoracic spiracles are vestigial and nonfunctional. The abdomen lacks a spine at the apex. Larvae are found in the burrows of wood-boring beetles, apparently as parasitoids.

Orussidae have worldwide distribution. They are a relict group, with many Southern Hemisphere species. The family comprises about 75 species in 15 genera.

[D. CHRIS DARLING]

**References.** R. B. Benson, Classification of the Orussidae, with some new genera and species (Hymenoptera, Symphyta), *Proc. Roy. Entomol. Soc. London (B)*, 24:13–23, 1955.

## Cephoidea

Stem wasps; a superfamily containing the single family Cephidae, thought to lie near the ancestral stock of the apocritan Hymenoptera. Adults are slender, usually 5–25 mm in body length, typically with a compressed abdomen, and usually black, often with rufous markings. The back of the head has a maxapontal closure formed by the midline fusion of the lower maxillariae, forming a bridge between the postgenae; this feature is similar to that of the apocritan family Braconidae. The antennae are filiform to clavate,

with 15–36 segments. The anterior tibia has one apical spur, modified into a calcar. Cenchri are lacking. Abdominal segments I and II are somewhat separated by a membranous articulation, lending flexibility to the area. The costal cell of the forewing is narrow, sometimes with a thickened or darkened membrane, but usually distinguishable. The pronotum is quadrate, rather long, and loosely attached to the mesonotum. Male genitalia are unrotated. Each of the parameres is in one piece.

Larvae have vestigial thoracic legs and no abdominal prolegs. Cerci are present as minute, unsegmented appendages; eyes are present but small; the antennae have four or five segments. The tip of the abdomen has a spiniform process. The larvae are stem borers in rosaceous shrubs, poppies, *Salix*, grasses, and such. The pupa is enclosed in a transparent cocoon within the stem mine.

The family is widely distributed in the Holarctic Region, extending somewhat into the Oriental Region (subfamily Cephinae, with 10 genera and about 100 species), and Madagascar (subfamily Athetocephinae, with 1 genus and 2 species).

**References.** R. B. Benson, Classification of the Cephidae (Hymenoptera, Symphyta), *Trans. Roy. Entomol. Soc. London*, 96:89–108, 1946.

#### APOCRITA

Wasps (parasitoid, solitary, and social), bees, and ants. Adults of this suborder are distinguished from the suborder Symphyta by the true abdomen having a strong constriction ("wasp waist") between its first two segments. The first segment, consisting primarily of the tergum, is solidly fused to the true thorax, and bears the special name propodeum (=epinotum=median segment). The true thorax and the propodeum thus form the second tagma of the body, often called the thorax, but correctly known as the alitrunk, or simply, trunk, used here. The school of C. D. Michener uses "mesosoma" for trunk, but this term seems to have been put forward as a needless synonym of alitrunk, and is a confusing homonym of nonhomologous tagmata or organs elsewhere among the Arthropoda. By similar reasoning, the terminal tagma of Apocrita, having lost a segment to the trunk, is no longer equivalent to the abdomen; it is called the gaster (the "metasoma" of Michener and his students). Further complications are introduced in higher aculeates, such as ants, where additional constrictions between true abdominal segments II and III, and even III and IV, give rise to the nodiform or squamiform petiole and postpetiole; in such cases, the term "gaster" is usually applied to the terminal tagma (including segment IV and succeeding segments), which contains the midgut and reproductive organs.

The ovipositor is retained in the parasitic Apocrita as a long or short, slender, tubular organ, functioning to direct an egg into or onto arthropodan prey, into plant tissue, and so forth; in the lower aculeates, it is modified into a sting for killing or paralyzing prey or for defense. In some social bees and ants, the ovipositor loses its ability to penetrate, and is variously specialized to dispense repellents or to trail pheromones or alarm substances, or is finally lost.

The larva is legless and blind, with antennae reduced to papillae, usually passing through three or more instars; the later instars, at least in most cases, are soft, white, grublike (hymenopteriform), and sedentary, passing their days feeding within or upon the body of a host arthropod or its egg, in a plant gall, fruit, or seed, or in a nest constructed by the

adult or adults. First-instar larvae, especially of Parasitica, are very diverse in form and lifeway, in correspondence with the variety of microhabitats in which the eggs are deposited by their mothers. Malpighian tubules during larval life normally number four, so far as is known, but often are more numerous in adults.

Adults are often nectarivorous, or feed on the honeydew of Homoptera; females may also imbibe juices of arthropodan prey. Most species are very active, and range widely in body size, form, and color. Distribution is worldwide, except Antarctica and similarly severe arctic and alpine areas. The suborder (=Clistogastra) includes the vast majority of Hymenoptera: there are probably about 125,000 described species, and with the species yet remaining undescribed the total may well rise above 200,000. Apocrita contain two series of superfamilies, Parasitica and Aculeata, representing an early (Jurassic?) radiation from a symphytan ancestor, which was most likely a plant stem-feeding form close to the modern Cephioidea.

**References.** C. P. Clausen, *Entomophagous Insects*, McGraw-Hill, New York, 1940; H. E. Evans and M. J. West Eberhard, *The Wasps*, University of Michigan Press, Ann Arbor, 1970.

#### PARASITICA

Parasitic wasps, gall wasps, fig wasps, chalcid wasps, and their allies. This series is also frequently referred to as the suborder or series Terebrantia, not to be confused with the suborder of Thysanoptera of the same name. An extremely heterogeneous collection of superfamilies, Parasitica can be defined better on bionomic criteria than on strictly morphological ones. The species are internal or external parasitoids or parasites of arthropods (mostly insects and spiders) or of various living plant tissues.

Typically, the female inserts an egg into the host through a tubular ovipositor, which may be long and permanently exerted, or retractile. The ovipositor, when long, often originates from the underside of the gaster before its apex, and the apical sternite is then cleft; some groups have shorter ovipositors that issue at the apex. Wing venation is reduced in most families. The leg bases, particularly those of the posterior legs, often have an additional small segment between the trochanter and the femur, so that the trochanter appears to be two-merous, but this is by no means universal. The antennae are quite variable, often filiform, with more than 13 segments; there are fewer segments in some species-rich groups, particularly those with the elbowed configuration, as in many Chalcidoidea and Proctotrupeoidea. Forms that attack arthropod hosts do not build nests or transport the hosts, but they sometimes do inject a paralyzing or lethal poison. No forms are eusocial.

Larvae are extremely diverse, especially the first instar; later instars are often hymenopteriform.

Parasitica are worldwide in distribution, except Antarctica and similar extreme environments. This immense taxon contains more than half of the known species of Hymenoptera; this proportion will certainly increase as collecting continues. Eventually, the absolute number of species probably will greatly surpass 100,000. The classification is unstable at the moment, and will doubtless change rapidly as more is learned about the rich array of early taxa now being described from the Mesozoic, particularly from the Jurassic and Cretaceous of Central Asia and the Cretaceous Amber of North America. Parasitica may have arisen near the Triassic-Jurassic boundary. The current tendency is to rec-

ognize numerous independent lineages as superfamilies, but the array of 8 superfamilies offered here is a fairly conservative compromise: Ichneumonoidea, Trigonaloidea, Megalyroidea, Evanioidea, Proctotrupoidea, Ceraphronoidea, Chalcidoidea, and Cynipoidea.

**References.** C. P. Clausen, *Entomophagous Insects*, McGraw-Hill, New York, pp. 3–277, 1940; E. F. Riek, *Insects of Australia*, University of Melbourne Press, pp. 867–924, 1970.

### Ichneumonoidea

Parasitic wasps. The body is very small to large (2–40+ mm long), averaging larger than Chalcidoidea or Proctotrupoidea. Wing venation is usually more reduced than in Symphyta or the larger-sized Aculeata, but is more nearly complete than in most chalcidoids or proctotrupoids. There are usually four or more closed cells in the forewing, two in the hindwing (except Aphidiidae); and the pterostigma is distinct. The costal cell usually is lost by approximation or fusion of C and R; in a few species this cell is present apically, but narrow. Scattered genera contain wingless forms; in these, the tegulae are typically lost in Ichneumonidae, but are often present in Braconidae. The antennae are usually multisegmented, with 16–90 segments, but the segment count can be as low as 10 in a few genera. Typically, a minute ring segment, the annellus, follows the pedicel; the scape and pedicel are short and thick, so that the antennae are not elbowed. The gaster is very varied in form, according to family and subfamily; in the female the ovipositor is exerted, slender and elongate, or short and retractile.

Ichneumonoids are internal or external parasitoids of a wide variety of insects (mostly Holometabola and Hemiptera) and spiders. The body form of the larvae is diverse, especially in the first instars. The larvae may be solitary or gregarious within a single host individual, according to taxon.

These insects occur worldwide wherever suitable hosts exist, primarily in mesic habitats. The superfamily probably contains about 50,000 described, unchallenged species in more than 2500 genera, but the majority of existing species remain undescribed. Five families are recognized: Braconidae, Aphidiidae, Ichneumonidae, Agriotypidae, and Apozygidae; the vast majority of species are contained in the first 3 families listed.

**References.** E. F. Riek, *The Insects of Australia*, University of Melbourne Press, pp. 896–902, 1970.

**Braconidae.** Mostly small to medium-sized (2–15 mm) parasitic wasps; a few are larger. Their color is quite variable, but mostly they are black, brown, testaceous, or particolored red and black, orange and white, orange and green, and so on. Body form is extremely variable: some genera are long and slender, with a very long, filiform ovipositor; others are short and stout, with a short, retractile ovipositor; some have hard gasters, fused segments, and so on. The antennae usually have many segments (up to 90), but in rare cases there are as few as 10 segments. As a rule, braconids resemble small ichneumonids, but with a modified gaster, usually not notably petiolate. Gastric tergites II and III usually are immovably fused. Braconids differ from most winged ichneumonids in lacking a “second recurrent vein” (2m–cu) in the forewing, and in having the basal cell of the hindwing not reach beyond the base of the “marginal vein” (R<sub>1</sub>). Occasional genera have a very narrow costal cell differentiated over at least the distal half, and in some spe-

cies a minute cell occurs at the basal end of the pterostigma. An oblique Rs+M is present in many genera. A few forms are wingless.

The gregarious or solitary larvae feed as internal or external parasitoids in a wide variety of insect hosts, particularly lepidopterous larvae, dipterous larvae and pupae, and coleopterous larvae, pupae, and adults. First-instar larvae are hymenopteriform, mandibulate, caudate, vesiculate, polypodeiform, or various intermediates. Many species exert strong control on the host species, and are thus important in biological control applications.

R. D. Shenefelt, who is cataloging the Braconidae, has entries for about 1400 genera and 35,000–40,000 species, but he cannot estimate how many of these taxa are currently considered valid. He believes that less than a quarter of the existing species have so far been described. There are differing ideas about how the Braconidae should be classified, but the following 20 subfamilies are often accepted in the modern literature: Agathidiinae, Macrocentrinae, Cheloninae, Rogadinae, Microgasterinae, Ichneutinae, Opiinae, Euphorinae, Braconinae, Doryctinae, Triaspidinae, Exothecinae, Alysinae, Hybrizoninae, Calyptinae, Mimagnathidinae, Cosmophorinae, Neoneurinae, Exothecinae, and Incubinae. Distribution is worldwide, except for the most extreme environments.

**References.** P. M. Marsh, Keys to the nearctic genera of the families Braconidae, Aphidiidae and Hybrizontinae, *Ann. Entomol. Soc. Amer.*, 64:841–850, 1971.

**Aphidiidae.** Small (1–5 mm) wasps close to euphorine Braconidae. Tergites II and III of the gaster are not fused, but move freely, like other segments. Wing venation varies with the genus, but is usually more reduced than Braconidae. Aphidiidae are often treated as a subfamily of Braconidae.

Aphidiids are solitary internal parasites of ovoviviparous aphids of the families Aphididae, Hormaphididae, and Eriosomatidae. Apparently, oviparous aphids (Adelgidae, Phylloxeridae) are not attacked. The parasite larva usually develops within the middle or late aphid nymphal instars, and pupates either within the empty host skin or in a cocoon beneath it. The first-instar larvae are usually of the caudate type (having a conical caudal appendage). Most known species have distinct segmentation, with posteriorly directed serrations or setae along the posterior segmental margins; paired digitiform ventral processes are typically present near the base of the caudal appendage.

Distribution is widespread, especially in the Holarctic and Oriental regions. About 35 genera and 350 species exist.

**References.** M. Mackauer, Aphidiidae, in *Hymenopterorum Catalogus* (nova ed.), pt. 3, W. Junk, 's-Gravenhage, Netherlands, 1968; C. F. Smith, The Aphidiinae of North America (Braconidae: Hymenoptera), *Ohio State Univ. Contrib. Zool. Entomol.*, 5:1–154, 1944.

**Ichneumonidae.** Ichneumon wasps or ichneumon flies. The body is generally 3–40 mm long, and very diverse in form and color, often particolored. Most species are relatively slender, with an elongate, arched, caudally thickened gaster having a more or less differentiated petiole (=first gastric segment=second true abdominal segment); typically the second and third gastric sterna (at least) are more or less membranous. The ovipositor of the female is often very long and permanently exerted, but in many species it is short and retractile. Most species are winged (a few are apterous or brachypterous), and are distinguished from Braconidae and Stephanidae by the usual presence of the “sec-

ond recurrent vein" (2m-cu). In the few ichneumonids in which this vein is absent, the second and third gastric tergites are flexibly articulated, unlike most braconids, and each of the middle tibiae has two (rarely one) apical spurs (none in Stephanidae).

The antennae are long and filiform (or feebly thickened apically), rarely bizarrely broadened in part, with 13 or more segments, and usually more than 16. Mandibles usually have two teeth, or the upper tooth is weakly subdivided, or one tooth is missing so that only the apical tooth remains.

These are active parasitoidal insects, with the females found mostly in the relatively mesic haunts of the hosts. The hosts are mainly larvae or pupae of holometabolous insects, but also include adult spiders, or spider and pseudoscorpion egg masses. A few species place their eggs in nests of solitary bees, where the larvae first devour the contents of the host bee egg and then the beebread provisions.

Eggs are diverse in form, usually plain, but often elongate, or even with long stalks, by means of which they are attached to the host's integument. A regular plastic deformation may occur during the long passage through the mother's ovipositor.

Larvae are external or internal parasitoids, most often primary but frequently secondary, usually feeding on larval, or larval and pupal, stages of host insects (on eggs, spiderlings, or adults of spider hosts). The first-instar larva is usually hymenopteriform in external feeders; internal feeders are mostly of the caudate type, but are sometimes vesiculate, polypodeiform, or approaching mandibulate, and changing to hymenopteriform in later instars. They are most often solitary.

H. Townes counts about 1200 genera and 15,000 valid species so far known, and believes that the total may eventually reach 1800 genera and 60,000 species. The currently recognized subfamilies number 24 (without Agriotypidae): Ephialtinae, Tryphoninae, Labiinae, Adelognathinae, Xoridinae, Gelinae, Lycorininae, Banchinae, Scolobatinae, Porizontinae, Cremastinae, Phrudinae, Tersilochinae, Ophioninae, Mesochorinae, Metopiinae, Anomalinae, Acaenitinae, Microleptinae, Orthopelmatinae, Collyriinae, Orthocentrinae, Diplazontinae, and Ichneumoninae.

**References.** H. Townes, The genera of Ichneumonidae, pt. I, *Mem. Amer. Entomol. Inst.*, 11:1-300, 1969.

**Agriotypidae.** Monogeneric (*Agriotypus*) family with 3 known species, one each from Europe, the Himalayas, and Japan. All are parasitoids of the prepupae and pupae (=pharate adults) of Trichoptera. Adults are black, 6-9 mm long, with ichneumonidlike head and wings. The antennae are long, slender, and multiarticulate (about 20-40 segments). The gaster is ovoid-fusiform, attached to the trunk by a slender, rodlike petiole consisting of the completely fused, equilateral, sclerotized tergum and sternum of true abdominal segment II. The female has a short, exerted ovipositor.

The larva has a peculiar form, called by C. P. Clausen agriotypiform; the first instar has a heavily sclerotized, mandibulate head; rows of erectile, spiniform setae on the succeeding segments; and a slender, bifurcate caudal appendage—adaptations serving to maintain and change position in the water within the host caddis fly case. After consuming the host's tissues, the *Agriotypus* larva spins a cocoon and a silken tube or ribbon that is extruded from the case, and is apparently respiratory in function. After spending the winter as a pharate adult, the wasp ecloses and floats to the surface. The female walks long distances on plants and stones under water to reach the host.

Some authors consider Agriotypidae to be a subfamily of Ichneumonidae, while W. R. M. Mason tentatively assigns the family to Proctotrupoidea.

**References.** C. P. Clausen, *Entomophagous Insects*, McGraw-Hill, New York pp. 14-16, 92-99, 1940; W. R. M. Mason, An Indian Agriotypus (Hymenoptera: Agriotypidae), *Can. Entomol.*, 103:1521-1524, 1971.

**Apozygidae.** Monotypic (*Apozyx penyai*) family known only from a single male collected in Chile. Total length is 2-3 mm; mandibles are bidentate; the antennae are 18-segmented; trochanters are 2-segmented. Wings are well developed, with relatively complete venation. In the forewing, C and Sc are fused (the costal cell is absent), the pterostigma is strong, Rs+M and 2m-cu are present, and the 1Rs cell is large; 2r-m intersects Sc basad of R, and 3r-m is absent. The hindwing has two closed cells. The petiole is cylindrical, and the tergum and sternum are completely fused, without a ventral membranous area occurring apically. The sterna beyond the petiole are fully sclerotized; spiracles are present on gastric segments I (=petiole) to VII. Nothing is known of the female, the immature stages, and biology.

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**References.** W. R. M. Mason, A new genus, species and family of Hymenoptera (Ichneumonidae) from Chile, *Proc. Entomol. Soc. Wash.* 80:606-610, 1978.

### Trigonalioidea

Superfamily with 1 family, Trigonalidae; medium-sized (usually 8-17 mm long), stout-bodied, big-headed wasps with a short, rounded gaster and long, slender antennae (16-20 or more segments). The body is colored black, red, or fulvous, often with extensive yellow or white markings. The wings have strong and rather complete venation; a costal cell and both 1m-cu and 2m-cu are present in the forewing; the hindwing has 2 closed cells.

All trigonalids are parasitoids, usually secondary, of sawfly larvae (Pergidae) or caterpillars, often through other dipterous or hymenopterous parasitoids of caterpillars, or vespids predators of caterpillars. The female trigonalid has a grasp-and-punch ovipositor with which she implants large numbers of tiny (microtype) eggs singly along the margins of leaves. The eggs are eaten and hatch in the gut on the sawfly or caterpillar; in the latter case, the larva seeks out and parasitizes an ichneumonid or tachinid parasite larva in the caterpillar host's body cavity. Vespids are parasitized when caterpillar prey containing trigonalid larvae is brought back to the nest and fed to the vespids larvae. Development is internal, but when attacking vespids larvae, the last-instar trigonalid larva may leave the host's body and feed externally.

There are about 100 species in 20 genera, with worldwide distribution.

**References.** W. A. Schulz, in P. Wytman (ed.), *Genera Insectorum*, Brussels, Trigonalidae, fasc. 51, 1970.

### Megalyroidea

Wasps of modest to fairly large size (4 to over 40 mm in body length). The females have very long, slender ovipositors, and superficially resemble Ichneumonidae, but short, oblique subantennal scrobes are present in front of the eyes to receive the basal segments of the antennae in repose; the long, filiform antennae (with 14 or more segments) in repose are held folded back ventrally between the legs (at

least in Megalyridae). Wing venation is more reduced than in Ichneumonidae, but the forewings usually have a narrow costal cell; the wings are especially deficient in crossveins in the apical half; closed basal cells are lacking in the hindwing. The preening mechanism on the medial apical surface of the hind tibia consists of a dense brush of short hairs. The larvae are apparently all parasitoids of wood-boring beetle larvae.

Distribution is worldwide, especially in the tropics. The superfamily probably contains 150–200 known species, with 2 families, Megalyridae and Stephanidae.

**References.** E. F. Riek, *Insects of Australia*. University of Melbourne Press, pp. 893–895, 1971.

**Megalyridae.** Stout wasps, small to medium-sized (4 to more than 20 mm long) with a very long, slender ovipositor in the female. Wing venation is strongly reduced. The medial surface of the hind tibia has a cleaning organ consisting of a dense tuft of short hairs. The antennae have 14 long, slender segments held longitudinally under the body during rest or while feeding.

Apparently, megalyrids are parasitoids of wood-boring beetle larvae. They have widespread but discontinuous distribution in the Old World tropics: South Africa, East Indies, Philippines, Melanesia, and Australia. The family includes less than 100 known species, described and undescribed, in 2 subfamilies, Megalyrinae and Dinapsinae.

**References.** E. F. Riek, *Hymenoptera, The Insects of Australia*, University of Melbourne Press, 1970.

**Stephanidae.** Adults have an attenuated body (4 to more than 40 mm long). The head is round, with a few low teeth on the vertex, forming a crest like that of orussids. The antennae have 15 or more segments. The pronotum is prolonged, forming a tapered neck cephalad. The hindlegs are modified, with long, slender coxae and swollen femora; tibiae are swollen apically, and often have a partial subdivision; tarsi have either five segments or a reduced number and basitarsal elaboration; the whole probably constitutes a receptor apparatus for sounds borne in the substrate (wood) in which the hosts are found. The petiole is long and slender, gradually broadened caudally; the gaster behind this is clavate and thickened caudally. The larvae are parasitoids of beetle larvae (Bostrychidae and such) boring in the trunk wood or twigs of trees.

The family includes over 100 species distributed worldwide, especially in the tropics.

**References.** E. A. Elliott, Monograph of the hymenopterous family Stephanidae, *Proc. Zool. Soc. London*, pp. 705–831, 1922.

## Evaniioidea

Superfamily intermediate between the series Parasitica and Aculeata. The antennae are filiform, not elbowed, and 13-merous (rarely 14-merous) in the male, 14-merous in the female. The maxillary palpi are six-merous; the labial palpi are four-merous. Three ocelli are disposed in a triangle. The pronotum extends back to the tegulae, more or less covered by a large mesonotum; the metanotum is short. The forewing has a costal cell plus at least two other cells; venation of the hindwings is strongly reduced, but the costal vein is present. Trochanters are two-merous. The propodeum is large, with the gaster inserted high up on its posterodorsal face. Gastric sternites are strongly chitinized.

Widespread in tropical and temperate regions, Evani-

ioidea comprise about 1200 species in 3 families: Gasteruptiidae and Aulacidae, which together form one branch, and Evaniidae, distinct from these in both form and lifeway. The two branches may be convergent, and could possibly deserve separate superfamily status. Evanioids are parasitoids on other insects (evaniids on blattarian egg cases).

**References.** R. W. Crosskey, The morphology, taxonomy and biology of the British Evaniioidea (Hymenoptera), *Trans. Roy. Entomol. Soc. London*, 102:247–301, 1951.

**Evaniidae.** Sometimes called ensign flies, because of the almost ridiculously small, ovate, laterally compressed gaster, attached to the top of the propodeum by a long, slender, abrupt petiole, and resembling a signal flag. Evaniidae are also distinguished from other evanioids by an unexserted ovipositor in the female, eyes remote from mandibular insertions, and a head not prolonged behind the eyes. The proepisterna do not form a long neck. Adults mostly range 2–15 mm long; they are usually colored black, red, or ferruginous, or combinations of these.

Evaniids are parasitoids in the oothecae of Blattaria. Oviposition usually occurs before the oothecal wall hardens. The larva devours the egg in which it is placed, then eats more eggs in the same ootheca. A single adult emerges from each ootheca after pupating within it.

There are about 500 species in 12 genera. The family has worldwide, mostly tropical, distribution, but a few species are widely spread as tramp species, especially in human dwellings.

**References.** H. Hedicke, Evaniidae, *Hymenopterorum Catalogus*, pt. 9, W. Junk, 's-Gravenhage, Netherlands, 1939; H. Townes, The nearctic species of Evaniidae, *Proc. U.S. Nat. Mus.* 99:525–539, 1949.

**Gasteruptiidae.** Slender, usually dark, parasitoid wasps, up to 28 mm long, with proepisterna forming a thin neck bearing the head. The antennae have 13 (rarely 14) segments in the male, 14 in the female. The forewing folds lengthwise; it lacks vein 2m–cu, but the costal cell is present; the radial cell is long and pointed; the hindwing has no closed cells, nor a jugal or anal notch. The gaster is attached high on the propodeum, far above the posterior coxae; it is narrow at the base, gradually increasing in depth toward the apex. Mouthparts are elongate for flower feeding. The first two gastric tergites are partly hinged. Hind tibiae are more or less claviform.

Adult females are often found at flowers or flying rapidly around logs or clay banks. They lay eggs in the nests of bees, or of vespid or sphecids wasps in the wood of logs or stumps, hollow twigs, or in the ground. The larvae prey upon the host larvae.

The family includes 2 subfamilies (Hyptiogastrinae and Gasteruptiinae), 10 genera, and about 500 species, described and undescribed, with worldwide distribution in tropical and temperate regions.

**References.** R. W. Crosskey, The classification of the Gasteruptiidae (Hymenoptera), *Trans. Roy. Entomol. Soc. London*, 114:377–402, 1962.

**Aulacidae.** Wasps 1–20 mm long, usually black, or black and red. Aulacidae are related to Gasteruptiidae, having similar antennae but a shorter pronotal neck. The forewing has a costal cell and a pointed radial cell; both 1m–cu and 2m–cu veins are present; wings do not fold lengthwise; the hindwing has one closed cell, or none; a very small anal notch is usually present. The first two gastric tergites are

fused; the first is inserted high up on the propodeum. Hind tibiae are not claviform.

Aulacids are parasitoids of wood-boring beetles and xiphydriid wood wasps. They occur worldwide in temperate and tropical areas. The family has perhaps 15 genera (disputed) and over 250 species, described and undescribed.

**References.** R. W. Crosskey, Two new species of *Aulacostethus* Philippi, and a new species of *Aulacus* Jurine from Australia, together with a key to the Australian species of *Aulacostethus* (Hymenoptera: Aulacidae), *Ann. Mag. Natur. Hist.*, (12)6:758–766, 1953.

## Proctotrupeoidea

Cosmopolitan superfamily of mostly black or brown wasps. Total length is 0.5–60 mm. The pronotum extends to the tegulae, without a rounded lateral lobe. The ovipositor issues from the apex of the gaster. The fore tibia has a single apical spur. The antennae are 6- to 15-segmented, filiform or elbowed.

Proctotrupeoidea are an old, highly diverse group, with fossils of recognizable living families dating from the Jurassic. All are endoparasitoids of the immature stages of arthropods (insects, spiders, possibly centipedes). The taxonomy of the superfamily has been largely neglected, so that the number of species in the larger families (Diapriidae, Scelionidae, and Platygasteridae) cannot now be estimated. In addition, the immature stages of the vast majority of species are unknown; therefore, the statements in family treatments concerning the form of the first-instar larva may not apply to all the species within each family. The term "gaster" as used for this superfamily includes all true abdominal segments posterior to the propodeum (that is, including the petiole).

There are 10 families: Peleciniidae, Monomachidae, Proctotrupidae, Heloridae, Roproniidae, Vanhorniidae, Austroniidae, Diapriidae, Scelionidae, and Platygasteridae.

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**Peleciniidae.** This group is sometimes considered as the monotypic superfamily Pelecinoidea. However, this classification has not been justified in the literature. *Pelecinus* is here retained as a family within Proctotrupeoidea.

These insects are approximately 3–6 cm in total length. The first gastric tergite and sternite are free, not fused to form a petiole. The female gaster is extremely elongate, cylindrical, and usually down-flexed; the male gaster is shorter, and clavate caudally. The antennae are 14-segmented in both sexes, filiform, and arise from the middle of the face. The first tarsomere of the hindleg is much shorter than the second.

The family is a New World group, with a reported introduction into Australia. Only a single species, *Pelecinus polyturator*, is now recognized, although more species remain undescribed. *Pelecinus* females are rather slow-flying and very conspicuous. The elongate gaster is used to reach the soil-dwelling scarabaeid larvae that are the only known hosts. Males are much more rarely collected than females in temperate regions; these populations are thought to be thelytokous, but this remains to be demonstrated. Immature stages are unknown.

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**References.** C. T. Brues, A note on the genus *Pelecinus*, *Psyche*, 35:205–209, 1928; W. A. Schulz, Beiträge zur näheren Kenntnis der Schlupfwespen Peleciniidae Hal., *Sitz. Math. Phys. Klasse K. Bay. Akad. Wiss.*, 33:451–488, 1903.

**Monomachidae.** Relict family represented by 2 small genera. Total length is 7–22 mm. The first gastric tergite and sternite are fused to form a petiole. The female gaster is about 10 times as long as wide. The antennae are 15-segmented in females, 14-segmented in males, and arise from the middle of the face. The forewing has a narrow stigma and lacks a fused Rs+M vein.

*Monomachus* (12 species) occurs in Australia and South America, and *Tetraconus* (1 species) is found in South America. Species of *Monomachus* have been reared from Stratiomyidae (Diptera). The immature stages are unknown.

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**References.** E. F. Riek, Australian Heloridae, including Monomachidae (Hymenoptera), *Austral. J. Zool.*, 3: 258–265, 1955; W. A. Schulz, Systematische Uebersicht der Monomachiden, *Mem. 1st Congr. Internat. Entomol.*, 2: 405–422, 1910.

**Proctotrupidae.** Family of rather common insects, found worldwide. Twenty-four living genera are known, with 200–300 species. Total length is usually 6–8 mm. The first gastric tergite and sternite are fused to form a petiole. The antennae are 13-segmented in both sexes, filiform, and arise from the middle of the face. The forewing has a well-developed stigma; the  $R_1$  cell is narrow; a fused Rs+M vein is absent.

These wasps are both solitary and gregarious parasitoids of the larvae of Coleoptera and Mycetophilidae (Diptera). Lithobiidae (Chilopoda) have also been reported as hosts; this requires corroboration. The first-instar larva is poly-podiform. When mature, the parasite larva emerges through the intersegmental membrane of the host, remaining attached to it by the posterior portion of the abdomen. The wasp pupates in this position without spinning a cocoon.

[NORMAN F. JOHNSON]

**References.** L. Masner, Proctotrupidae, key to the genera of the world (Hymenoptera, Proctotrupeoidea), *Expl. Parc. Nat. Upemba Miss. DeWitte*, 60:37–46, 1961.

**Heloridae.** Relict family represented now by 1 genus (*Helorus*) and 9 species. Total length is 7 mm. The first gastric tergite and sternite are fused to form a petiole; the gaster is otherwise cylindrical, not laterally compressed. The antennae are 15-segmented in both sexes, filiform, and arise from the middle of the face. The forewing has a well-developed stigma; a fused Rs+M vein is present. Tarsal claws are pectinate. The first-instar larva is polypodeiform.

Found worldwide, the helorids are solitary larval parasitoids of Chrysopidae (Neuroptera). Fossils date back to the Jurassic Period.

[NORMAN F. JOHNSON]

**References.** H. Pschorn-Walcher, *Mitt. Schweiz. Entomol. Ges.*, 28:233–250, 1955.

**Roproniidae.** Monogeneric (*Ropronia*) family of wasps with 8 species. Total length is 8–10 mm. The first gastric tergite and sternite are fused to form a petiole; the gaster is otherwise laterally compressed. The antennae are 14-segmented in both sexes, filiform, and arise from the middle of the face. The forewing has a well-developed stigma; a fused Rs+M vein is present. Immature stages are unknown.

Roproniids are found in the Nearctic, eastern Palearctic, and Oriental regions. They have been reared from Tenthredinidae (Hymenoptera).

[NORMAN F. JOHNSON]

**References.** K.-J. Heqvist, A new species of *Ropronia* from Burma (Proctotrupeoidea, Heloridae), *Entomol. Tidskr.*, 80:137–139, 1959.

**Vanhorniidae.** Family consisting of a single species, *Vanhornia eucnemidarum*. Total length is 6 mm. The antennae are 13-segmented in both sexes, filiform, and arise from the middle of the face. The forewing has a well-developed stigma; a fused Rs+M vein is present. The gaster is highly modified, with two (female) or four (male) visible tergites. The mandibles are exodont and tridentate. *Vanhornia* has been reared from eucnemid (Coleoptera) larvae in the eastern Nearctic. Immature stages are unknown.

[NORMAN F. JOHNSON]

**References.** J. C. Crawford, A new family of parasitic Hymenoptera, *Proc. Entomol. Soc. Wash.*, 11:63–64, 1909.

**Austroniidae.** Small Australian family, represented by a single genus (*Austronia*) and 3 species. Total length is 6 mm. Female antennae are 15-segmented, and male antennae are 14-segmented; the antennae do not arise from a frontal shelf. The forewing has a narrow stigma; a fused Rs + M vein is absent. The female gaster is short and laterally compressed. Hosts and immature stages are unknown.

[NORMAN F. JOHNSON]

**References.** E. F. Riek, Australian Heloridae, including Monomachidae (Hymenoptera), *Austral. J. Zool.*, 3:258–265, 1955.

**Diapriidae.** Generally the body is 3–15 mm long. The first gastric tergite and sternite are fused to form a petiole. The stigma of the forewing is linear or absent. The antennae are 12- to 15-segmented, and arise from the frontal shelf (except *Ismarus*); they are sexually dimorphic in number of segments, with male antennae usually having a sex segment or segments with a distinctive excavation or ridge (tyloid). *Ismarus* may be distinguished from other diapriids by its well-developed petiole, narrow stigma in the forewing, and relatively short, cylindrical gaster.

These parasitoids are both solitary and gregarious, primarily attacking the larvae and pupae of Diptera. Some species are myrmecophilous and termitophilous; the exact hosts in these cases are unknown. The rare monotypic *Ismarinae* are unusual in that they are hyperparasites of Homoptera (Auchenorrhyncha) through Dryinidae (Hymenoptera). The first-instar larva is mandibulate.

Very common wasps, with more than 150 living genera and over 1200 described species, many still undescribed. This family has been divided into 4 subfamilies: Ambositriinae, found mainly in the Ethiopian (including Madagascar), Neotropical, and Australian regions, with one species extending into the Nearctic; *Ismarinae*, *Diapriinae*, and *Belytinae*, with worldwide distribution. [NORMAN F. JOHNSON]

**References.** J. J. Kieffer, *Diapriidae*, *Das Tierreich*, 44: 1–627, 1976; L. Masner, A revision of the *Ismarinae* of the New World (Hymenoptera, Proctotrupoidea, Diapriidae), *Can. Entomol.*, 108:1243–1266, 1976.

**Scelionidae.** Family of wasps. Total length is 0.5–15 mm. The antennae arise close to the margin of the clypeus, are 6- to 14-segmented, and are elbowed. The first gastric tergite and sternite are free, and not fused to form a petiole.

The vast majority of Scelionidae are solitary egg parasitoids; a few species are gregarious. Scelionids attack a wide variety of arthropod hosts, including spiders, mantids, Orthoptera, Embioptera, Hemiptera, Homoptera, Coleoptera, Neuroptera, Lepidoptera, and Diptera. The first-instar larva is teleaform. Species of *Telenomus*, *Trissolcus*, and *Scelio* have been successfully used as biological control agents of their hosts.

Species of several genera are phoretic; the female parasitoid uses its mandibles or its tarsal claws to attach itself to the host. Often these structures are modified to help the wasp maintain its grip. When the host oviposits, the female wasp releases its hold to attack the eggs. *Mantibaria* is apparently also a true ectoparasite, and has been reported to feed on the body fluids of its mantid host while attached to it.

Some solitary species of *Telenomus* and *Trissolcus* have been demonstrated to avoid superparasitism of the host eggs by a behavior called host marking. After laying an egg the female “wipes” the ovipositor in a sinuous pattern over the host egg, presumably smearing a chemical on the chorion. Other females are capable of detecting that an egg has been marked, and usually do not oviposit into it.

The family is cosmopolitan; it comprises 3 subfamilies and over 125 living genera. It is commonly collected in yellow pan traps. [NORMAN F. JOHNSON]

**References.** L. Masner, Revisionary notes and keys to world genera of Scelionidae (Hymenoptera: Proctotrupoidea), *Mem. Entomol. Soc. Can.*, 97:1–87, 1976.

**Platygasteridae.** Common family of small wasps. Total length is 0.5–5 mm. The first gastric tergite and sternite are free, not fused to form a petiole. The antennae are 7- to 10-segmented, arising near the clypeal margin. The forewings are either veinless or with only an incomplete submarginal vein; the hindwings are veinless. Platygasterids may be distinguished from scelionids with 7- to 10-segmented antennae by the highly reduced venation of their wings; in apterous or brachypterous scelionids with 7-segmented antennae, the antennal club is massive and unsegmented.

Several species have the gaster highly modified to house the long ovipositor used to reach hosts in inaccessible sites. In *Leptacis hopkinsi* the gaster is extremely elongate, up to eight times the length of the thorax; *Sactogaster* species have the second gastric segment expanded ventrally to form a “sac” to contain the coiled ovipositor; *Inostemma* species retract the ovipositor into a long handlelike process (horn) of the first gastric tergite which curves up and over the mesoscutum.

Platygasterids are primarily egg-larval parasitoids of Cecidomyiidae (Diptera); other hosts include nymphs of Homoptera, cerambycid eggs (Coleoptera), and crabronine wasp larvae. The form of the first-instar larva of this family is variable: both hymenopteriform and cyclopoid types are known. Some species are polyembryonic, producing up to 18 individuals from a single egg. The female wasp may be highly selective in its choice of the host tissue in which it oviposits: some species specialize in placing the egg in the brain, others in the ventral nerve cord, gut, and so on.

There are approximately 50 known living genera in 3 subfamilies; many more genera await description. Platygasteridae are found worldwide. [NORMAN F. JOHNSON]

**References.** C. P. Clausen, *Entomophagous Insects*, McGraw-Hill, New York, 1940; M. A. Kozlov, Supergeneric groups of the Proctotrupoidea, Hymenoptera (in Russian), *Entomol. Obozr.*, 49:203–226, 1970.

## Ceraphronoidea

Cosmopolitan superfamily (=Calliceratidae) with 2 families (ceraphronidae and Megaspilidae). Total length is 0.5–5 mm. The pronotum extends to the tegulae, without a rounded lateral lobe. The ovipositor issues from the apex of the gaster. The fore tibia has two apical spurs. The antennae are 7- to 11-segmented, elbowed, and arise from the

clypeal margin. In winged forms the marginalis is distinctly separated from the stigma by a hyaline area. The species are both endoparasitic and ectoparasitic.

Ceraphronoidea are distinguished from all other clitogastran Hymenoptera by the possession of two apical spurs on the fore tibiae. Reservations concerning the number of species and immature stages expressed for Proctotrupoidea apply also to this group. [NORMAN F. JOHNSON]

**References.** P. Dessart, Contribution à l'étude des Hyménoptères Proctotrupoides, I: Notes sur quelques Ceraphronidae africains et tableau dichotomique des genres, *Bull. Ann. Soc. Belge Entomol.*, 98:291–311, 1962; L. Masner and P. Dessart, La reclassification des catégories supérieures des Ceraphronoidea (Hymenoptera), *Bull. Inst. Sci. Nat. Belg.*, 43(22):1–33, 1967.

**Ceraphronidae.** Total length is 0.5–5 mm. The tibial spur formula is 2,1,2; all spurs are pectinate; the large spur on fore tibia is not bifid at the apex. In winged forms the stigma is linear. The antennae are sexually dimorphic, with males having one more antennomere than females, and are usually 11- and 10-segmented respectively; rarely, the antennae are 7- or 8-segmented—in these cases only one sex is known. Waterston's organ (a medial patch of reticulation on the fifth gastric tergite) is present. A petiole is formed from both the tergite and sternite of the first gastric segment. Ceraphronids are mostly black in color. They are often taken in Berlese funnels and in yellow pan traps. This is a very common taxon, although only 12 living genera are known; over 150 described species exist. All ceraphronids are endoparasites; their hosts include species or Diptera (Nematocera, Cyclorrhapha), Homoptera (Sternorrhyncha), and Neuroptera. Some species have been taken in ant nests, presumably parasitizing myrmecophilous Diptera.

The family includes both primary and secondary parasitoids; in most species the host is unknown. The immature stages and the function of Waterston's organ are unknown. Ceraphronids are found worldwide.

[NORMAN F. JOHNSON]  
**References.** P. Dessart, A propos du genre *Neoceraphron* Ashmead, 1893 (Hym. Ceraphronoidea Ceraphronidae), *Bull. Ann. Soc. Belge Entomol.*, 111:248–261, 1975.

**Megaspilidae.** Total length is 1–5 mm. The tibial spur formula is 2,2,2; the large spur on the fore tibia is bifid at the apex; spurs are pectinate or not. The Waterston's organ is absent. In winged forms the stigma is large and semicircular, rarely linear or absent. The antennae are 11-segmented in both sexes. A petiole is formed from the sternite of the first gastric segment.

Cosmopolitan family, with 10 genera divided into 2 subfamilies: the rare, monogeneric Lagynodinae and the Megaspilinae; there are over 250 described species. The hosts of *Lagynodes* are unknown, although some species have been collected in ant nests. Megaspilines have been reared as primary parasitoids of Diptera (Cyclorrhapha), Neuroptera, and Mecoptera, and as hyperparasites of Homoptera (Sternorrhyncha) through Hymenoptera (Ichneumonoidea, Chalcidoidea). Some species have been collected from ant nests, probably as parasites of myrmecophilous flies. The first-instar larva is hymenopteriform. With the exception of *Conostigmus quadratogenalis*, an internal parasitoid of *Boreus* (Mecoptera: Boreidae), all forms recorded are ectoparasites. [NORMAN F. JOHNSON]

**References.** P. Dessart, Contribution à l'étude des Lagyn-

odinae (Hym. Ceraphronoidea Megaspilidae), *Bull. Ann. Soc. Belge Entomol.*, 113:277–319, 1977.

## Chalcidoidea

Chalcid wasps, fig wasps, and their allies. This is an enormous and varied taxon of mainly small or minute wasps, with body length mostly in the range of 0.2–5 mm, but a small minority of species, especially in Chalcididae, Leucospidae, and leptofoenine Pteromalidae, may range up to 15, 20, or even 30 mm long. The color is often metallic green or blue, or black, brown, yellow, or straw-colored, or particolored combinations of these. Most species are winged in both sexes (male fig wasps lack wings), the wings devoid of veins, except for the compound marginal-stigmal vein in the forewing and its counterpart in the hindwing. The antennae are elbowed (except in Mymaridae), with a scape and usually 5–12 additional (flagellar) segments, either filiform or forming an apical club; they are rarely flabellate (Eucharitidae) or otherwise bizarre in males. The pronotum does not reach the tegulae (but almost reaches in some Mymaridae and Leucospidae), and the (mesothoracic) spiracles under the prothoracic lobes are at or above the level of the tegulae.

Distribution of apical tibial spurs is one on each fore tibia (none in Agaonidae), one on each mid tibia (some male fig wasps lack middle legs), and one or two on each hind tibia. Middle and hind legs sometimes have enlarged femora and other modifications for jumping.

Larvae are internal or external parasites or predators of a wide variety of other insects or their eggs, or else live in galls, seeds, or other plant tissues, such as figs. Some are hyperparasites on other insects, and some encyrtids develop polyembryonically, with dozens, hundreds, or even thousands of adult parasites arising in one host from one egg. First-instar larvae take a wide variety of forms, including hymenopteriform, sacciform, encyrtiform, caudate, mymariform, vesiculate, and planidium; later instars often become hymenopteriform.

Chalcidoids have worldwide distribution in many climates. Classifications of this superfamily vary widely; some families accepted here are subfamilies in other systems, but several families of other classifications are here considered only as subfamilies or tribes. Nineteen families are recognized here: Chalcididae, Leucospidae, Eurytomidae, Torymidae, Agaonidae, Pteromalidae, Perilampidae, Eucharitidae, Eupelmidae, Ormyridae, Encyrtidae, Tanaostigmatidae, Aphelinidae, Signiphoridae, Tetracampidae, Elasmidae, Eulophidae, Trichogrammatidae, Mymaridae. According to J. S. Noyes (1977), together they contain over 2100 unchallenged genera and about 16,500 species, but the number of species may well eventually increase to five times this figure.

**References.** E. F. Riek, Superfamily Chalcidoidea, in *The insects of Australia*, University of Melbourne Press, 1970; O. Peck, Z. Bouček, and A. Hoffer, Keys to the Chalcidoidea of Czechoslovakia (Insecta: Hymenoptera), *Mem. Entomol. Soc. Can.*, 34:1–120, 1964.

**Chalcididae.** Bizarre wasps, heavily sclerotized, mostly between 2–12 mm long, and colored black, brown, red, or yellow, often striped or particolored, rarely metallic. The femur of the hindleg is grossly expanded, its lower (inner) margin curved, dentate, serially denticulate or pectinate, with the tibia curved to fit against the armed femoral margin; the coxa is elongate, so that the leg forms a powerful

grasping organ, said to be used to hold prey larvae, but its function calls for further investigation. The ovipositor is short, extending only slightly beyond the gastric apex, and not recurved. The prepectus is very small. The forewings do not fold longitudinally at rest. The antennal club is about as wide as neighboring segments of the funiculus. There are seven (rarely six) funicular segments; the first segment beyond the pedicel (antennal segment III) may form a small anellus, or may be larger and form a funicular segment.

Chalcids are primary solitary parasites of Lepidoptera, Diptera (especially Sarcophagidae), Hymenoptera, Coleoptera, ant lions, and so on. Most species are internal in mature larvae and pupae; other species are hyperparasites through tachinid and other Diptera, and ichneumonid or braconid wasps. First-instar larvae are hymenopteriform in external feeders and lepidopterous pupal endoparasites, while those developing in dipterous puparia are of the caudate type.

The family is found worldwide, with over 1400 species in 115 genera in 5 subfamilies: Brachymeriinae, Haltichellinae, Dirhininae, Epitraninae, and Chalcidinae.

**References.** A. Habu, *Fauna japonica, Chalcididae, Leucospidae and Podagrionidae* (Insecta: Hymenoptera), Biogeographical Society of Japan, Tokyo, 1962.

**Leucospidae.** Rather larger chalcids, approximately 2–16 mm in total length. They are usually black to red with yellow or whitish markings. All tarsi are five-merous. The fore tibial spur is large and curved. The hind coxae are greatly enlarged. The hind femora are swollen, 1.5–3.5 times as long as broad and toothed ventrally. The hind tibiae are arcuate, with two apical spurs. A mesopleural scrobe is present. Tegulae are very large, nearly reaching the pronotum. Notauli are absent or only weakly indicated. Axillae are small and widely separated. The glossa is elongate and projects beyond the mandibles. The antennae are 13-merous. The ovipositor is often recurved, lying in a groove on the gastric dorsum. The gaster is sessile.

Leucospids are primary parasitoids of solitary Aculeata (Hymenoptera), mainly Apoidea, but also Eumenidae and Sphecidae. Mouthparts are apparently adapted for nectar feeding; adults are often collected on flowers. Many species appear to mimic local aculeates; a single widely distributed leucospid species may use different models.

The family includes 4 genera, *Leucospis*, *Polistomorpha*, *Neleucospis*, and *Micrapion*, with 123 described species. It is found in all major biogeographic realms, although limited to warmer parts of temperate areas. [NORMAN F. JOHNSON]

**References.** Z. Bouček, A revision of the Leucospidae (Hymenoptera: Chalcidoidea) of the world, *Bull. Brit. Mus. (Natur. Hist.), Entomol. Suppl.*, 23:1–241, 1974.

**Eurytomidae.** Seed chalcids and their allies. They are usually 3–5 mm in total length, occasionally larger, and colored black or yellow, rarely orange or metallic. The antennae are inserted in the middle of the frons, and are 6- to 13-merous. The clypeus is fused with the frons. The pronotum in dorsal view is quadrate. Axillae are separated. The mesopleural scrobe is well developed. The thorax is coarsely sculptured. The tarsi are five-merous. The hind coxae are slender, not enlarged. The hind femora are not both enlarged and dentate. The hind tibiae are straight. The fore-tibial spur is large and curved. The hind tibiae have two apical spurs. The gastric petiole is usually well developed, although sometimes small and hidden; the gaster

then appears sessile. The ovipositor sheaths reach or surpass the apex of the gaster.

Eurytomids probably derived from a parasitoid stock, but are often secondarily phytophagous, feeding within seeds, galls, and stems of a variety of plants. Many species remain as primary and secondary parasitoids, having been reared from Coleoptera (larvae, pupae), Hymenoptera (larvae), Diptera (larvae), Orthoptera (eggs), and Hemiptera (eggs). Some species of *Eurytoma* may represent a transitional stage between these two forms of life: they are parasitoids early in life, attacking a gall-maker (such as Cynipidae). After the host has been killed, the *Eurytoma* larva feeds on the plant tissue of the gall.

A large, common family distributed worldwide, Eurytomidae contain about 70 genera and 1100 described species in 8 subfamilies: Rileyinae, Harmolitinae, Eudecatominae, Aximinae, Heimbrinae, Prodecatominae, Philolemina, and Eurytominae. [NORMAN F. JOHNSON]

**References.** B. D. Burks, A synopsis of the genera of the family Eurytomidae (Hymenoptera: Chalcidoidea), *Trans. Amer. Entomol. Soc.*, 97:1–89, 1971.

**Torymidae.** Mostly small wasps, with body length usually 1–6 mm, but occasionally as much as 10–15 mm. The female commonly has a long, exerted ovipositor. Metallic species are common, mostly green, but plain black, brown, yellow, or straw-colored forms are the rule in some megastigmine and other genera. Females are usually distinguished by the epipygium, a small, hinged flap attached in the caudal emargination of tergum IX. Both sexes usually have first, or first and second, gastric terga mesally emarginate, and prominent cerci, longer than broad. The pronotum is usually movable on the mesothorax. The midlegs are not adapted for jumping, and sometimes are weak. The hind tibia often has two apical spurs, though one may be very small. Podagrionines have enlarged hindlegs, like those of Chalcididae; most are green, with a very long ovipositor and thickened antennal clubs.

Torymids are mostly associated with galls or other plant tissues, in which they may be primary gall-formers, inquiline, or parasites of tephritid fly larvae or other primary gall-formers. Podagrionines are parasitoids in mantid oothecae, while Idarninae (including Sycophaginae) are parasites or inquilines in figs, often attacking Agaonidae. Idarnine males are sometimes wingless, pale, and aberrant, somewhat like those of agaonids, while others are winged. Female idarnids can be distinguished from those of agaonids by their lack of mandibular saw appendages.

The family is widespread in tropical and temperate regions, and includes about 1000 species in about 100 genera, distributed in 6 subfamilies: Thaumatoryminae, Monodontomerinae, Megastigminae, Toryminae, Idarninae, and Podagrioninae; the last is often considered to be a separate family.

**References.** M. N. Nikol'skaya, The chalcid fauna of the U.S.S.R., translation of Opred. Faune CCCP 44(1952), Israel Program for Scientific Translations, Jerusalem, 1963; A. Habu, *Fauna japonica, Chalcididae, Leucospidae and Podagrionidae* (Insecta: Hymenoptera), Biogeographical Society of Japan, Tokyo, 1962.

**Agaonidae.** Fig wasps. Agaonids are small phytophagous wasps, 1–3 mm long, that pass most of their lives symbiotically in the syconia (compound flower receptacles, later compound fruits) of various species of *Ficus*. They are sexually dimorphic. Females are winged and pigmented, with

a more or less bizarre, longitudinally grooved head that shelters the backwardly directed, rasplike or serrate mandibular appendage; antennal segments III or IV have spiniform processes; fore tibiae usually are very short, without an apical spur. Males are all apterous and usually depigmented (yellowish) and blind, with the midlegs often very spindly or even absent; the abdomen tapers caudally, and is downcurved. The males normally spend their entire lives within syconia. Females fly from their home syconium and enter a new one through a pore, using the mandibular appendages, and eventually oviposit in flowers there to form flower galls, after apparently introducing a secreted tissue-stimulating allomone via the ovipositor. Pollination is effected by the fig wasps, so these must be introduced to new countries along with their partner fig species in order for the trees to mature their fruit (except in some self-pollinating cultivated fig varieties).

The family includes a single subfamily with about 160 described species in 12 genera, found worldwide in the warm countries where figs grow. The subfamily Sycophaginae, formerly included in Agaonidae, is now placed in Torymidae subfamily Idarninae.

**References.** G. Grandi, The hymenopterous insects of the superfamily Chalcidoidea developing within the receptacles of figs: Their life histories, symbioses and morphological adaptations, *Boll. Ist. Entomol. Univ. Bologna*, 26:1–13, 1961.

**Pteromalidae.** Mostly small (1–4 mm) wasps, with a few species larger. They are metallic green or bronze, or black, yellow, brown, or particolored. The family is exceedingly heterogeneous, and as now constituted, impossible to define for all genera. The tibial spur of the foreleg is long and strong, usually curved; the midlegs have tibial spurs which are not unusually large or thick. The antennae are 8- to 13-merous, with or without one or more anelli. Axillae are limited in front (dorsal view) by an imaginary line connecting the tegulae. The midlegs are attached nearer to the rear of the mesepisternum than to the front; the mesepisternum has a scrobe or groove to receive the folded femur. The tarsi are all five-merous, except for the female *Macromesius*, in which the midlegs have four-merous tarsi. The last (ninth true abdominal) tergite is triangular, and not deeply divided. The ovipositor is usually short.

Larvae are mostly stout-hymenopteriform. They attack a wide variety of hosts as gregarious or solitary, internally or externally feeding parasitoids, mainly lepidopterous and coleopterous larvae and puparia of cyclorrhaphous Diptera, although some are egg parasites; and others attack a wide variety of insect hosts, either as primary parasites or hyperparasites.

The family includes about 2800 species in 565 genera worldwide, but this is only a fraction of the taxa remaining to be described. M. W. R. Graham recognizes 15 subfamilies: Cleonyminae, Macromesinae, Ceinae, Spalangiinae, Cerocephalinae, Diparinae, Neodiparinae, Eunotinae, Asaphinae, Chrysolampinae, Panstenoninae, Miscogasterinae, Pteromalinae, Cratominae, and Colotrechninae. The tropical Leptofoeninae, which are elongate, metallic green or blue, stephanidlike wasps, probably belong here.

**References.** M. W. R. Graham, The Pteromalidae of northwestern Europe, *Bull. Brit. Mus. (Natur. Hist.), Entomol. Suppl.*, 16:1–908, 1969.

**Perilampidae.** Compact wasps (1.5–7 mm long), colored black, coppery, or metallic green or blue. They have a large

trunk and a short subsessile gaster, with a very short, transverse petiole (which is difficult to see). The second and third gastric terga are largely fused together, often covering most or all of the gaster. The pronotum is clearly visible from the dorsal view; notauli are complete. The antennae are 11- to 13-merous, with a single anellus and seven funicular segments. The midleg has a tibial spur not much enlarged; all tarsi are five-merous. The head in front view is not triangular; the mandibles are curved, but not falcate, usually with two or three teeth. Adults are often found around flowers (particularly Compositae) and around aphids, feeding on honeydew or on plant juices.

The eggs are larger than those of Eucharitidae, and without stalks; they are laid on foliage, sometimes in special incisions made by the female, or on chrysopid eggs stalks and such. The first-instar larva is a planidium that perches on its tail end and awaits the passing of a caterpillar, sawfly larva, chrysopid larva, or a wide variety of other insects, which it enters through the skin. Many species are hyperparasites, attacking hymenopterous or dipterous parasitoids of this first host, usually waiting until pupation to feed.

The family is distributed worldwide; there are over 200 species in about 25 genera. Perilampidae and Eucharitidae are sometimes placed as subfamilies of Pteromalidae.

**References.** Z. Bouček, A generic key to Perilampinae (Hymenoptera, Chalcidoidea), with a revision of *Krombeinius* n. gen. and *Euperilampus* Walker, *Entomol. Scand.*, 9: 299–307, 1978; Z. Bouček, Mediterranean Perilampinae: *Euperilampus* and genera allied to *Chrysomalla*, *Mitt. Münch. Entomol. Ges.*, 61:90–107, 1972.

**Eucharitidae.** Ant chalcids. These bizarre wasps, mostly 3–10 mm long, are often metallic-colored, black, green and yellow, red and green, and so on, and are close to Perilampidae and Pteromalidae. The gaster, often somewhat laterally compressed, is attached to the trunk low down by a slender petiole; the following (true third abdominal) tergum is large and covers most of the gaster. The trunk is high; the scutellum is often produced as a pair of massive spines. The mandibles are long, falcate, or straight and porrect. The antennae are sometimes flabellate in males. The pronotum is usually reduced dorsally to accommodate the mobile head. Axillae are usually fused to form a transverse sclerite separating the scutum from the scutellum. Adults are frequently found flying above ant nests or around foliage where ants are foraging; all are believed to be parasitoids on various genera of ants.

The first-instar larva is, as far as is known, a planidium, hatching from eggs deposited on or in foliage, buds, or fruits (such as bananas), and attaching to foraging worker ants to be transported to the nest. There the parasite larva transfers to an ant larva and feeds upon it externally or internally as a prepupa, pupa, or pharate adult, eventually killing it or producing an emaciated pharate adult ant (phthisergate). Host specificity at genus level seems to be the rule.

The family (=Eucharidae) is widely distributed in tropical and temperate parts of the world; about 330 species are known in 55 genera.

**References.** C. P. Clausen, *Entomophagous Insects*, McGraw-Hill, New York, pp. 221–230, 1940.

**Eupelmidae.** Mostly rather slender, usually metallic-colored wasps, 1–8 mm long. The female antennae have 10 segments plus an apical club, basically of 3 segments, often more or less completely fused. The midleg is adapted for

jumping, with a membranous area separating its coxa from the trochantal lobe of the mesosternum, so that it can be swung forward. As in Encyrtidae, the midleg usually has a stout tibial spur, and a thickened basitarsus with double-ranked stout setae beneath, but with the coxa inserted behind the midlength of the mesepisternum, much nearer to the hindleg than to the foreleg. The mesepisternum is greatly enlarged and swollen and lacks a femoral scrobe, although a suture separates it from the mesosternum. The pronotum is often divided by a medial groove, line of weakness, or carina. Wings are developed and functional, atrophied, or lacking.

Eupelmids as larvae are predators or parasites, internal or external, solitary or gregarious, of an exceptionally wide variety of insects hosts, in developmental stages from egg to pharate adult. Many eupelmid species are facultatively primary parasites or hyperparasites. Eggs are usually slender, bearing an anterior stalk of variable length. The first-instar larva is often of a particular type, which may be called eupelmiform, consisting of a segmented body with a prominent but narrowed head and vestigial mandibles, and a tapered abdomen, often ending in a pair of bent-under spines; the segments usually have transverse rows of stiff setae, much as in planidia.

This is a widespread family, particularly in the tropics. There are more than 700 known species in about 60 genera, placed in 2 subfamilies: Eupelminae and Calosotinae.

**References.** C. P. Clausen, *Entomophagous Insects*, McGraw-Hill, New York, pp. 191–199, 1940; K.-J. Hedqvist, Hymenoptera (Chalcidoidea): Eupelmidae, in B. Hanström et al. (eds.), *South African Animal Life*. Swedish Natural Science Research Council, Stockholm, 1970.

**Ormyridae.** Small (mostly 1.5–3 mm long), usually green to black or brown wasps. They are distinguished by the peculiar sculpture and pilosity of the middle terga of the gaster, which have sparse, transverse rows of stiff, caudally directed, reclinate setae, partly or completely arising from or between coarse punctures or half-punctures, also arranged in rows; in some species, the punctures are restricted to the anterior zone of each tergum, and may be covered in death by the preceding tergum. The gaster tapers apically, with the female ovipositor only slightly exerted, but the basal part coiled within. The tarsi are five-merous. The hind tibiae have two apical spurs, one or both of which are long, stout, and curved. The hind coxae are much enlarged, each having a fine carina along the dorsal border. The prepectus is small. The antennae are 13-merous, including two anelli, of which the distal is sometimes much larger than the proximal.

Ormyrids are parasites of gall-forming cynipids, chalcids, and so forth, on different tissues (such as seeds or stems) of various plants.

The family is widespread (including Europe, North America, and Australia), but full distribution is poorly known. About 50 species have been described in 3 valid genera. *Megormyrus*, a parasite of stem-dwelling bees, was formerly placed in Ormyridae, but is now a synonym of the genus *Ptinobius* in Pteromalidae.

**References.** O. Peck, A catalogue of the nearctic Chalcidoidea (Insecta: Hymenoptera), *Can. Entomol.*, Suppl. 30, pp. 591–595, 1963.

**Encyrtidae.** Small to minute wasps (mostly 0.5–5 mm long). Their form and color (metallic or not) are exceedingly varied. The tarsi are five-merous. The midlegs have coxae fit-

ted for jumping, inserted about even with the midlength of the mesepisternum, or in front of the midlength. The mesopleuron is enlarged, smoothly swollen, and lacks a femoral scrobe. The mid tibial spur is thick, and the basitarsus of the midleg is more or less thickened, with two rows of short, stout spines beneath. Notauli are absent, incomplete, or very shallow. Encyrtids are sometimes apterous, but usually are winged in both sexes; the marginal vein is short, even punctiform. The antennae are five- to seven-merous, usually six-merous, without an anellus; the club usually is solidly fused.

Most species are parasites or hyperparasites of sternorhynchous Homoptera (scales, aphids, cercopids, psyllids), but dipterous pupae (Syrphidae, Cecidomyiidae, large calyptrates) are also attacked, as well as eggs and larvae of Lepidoptera, larvae and pupae of chrysomelid and coccinellid beetles, pupae of *Chrysopa* and other Neuroptera, eggs of pentatomid bugs, nymphs of ixodid ticks, immature dryinid wasps, chalcids, and so forth.

Certain genera, such as *Litomastix*, *Ageniaspis*, and *Copidosoma*, and their relatives, exhibit polyembryony in lepidopterous larval hosts, a single egg producing tens, hundreds, or even thousands of adult chalcids. Larvae of encyrtids arise from eggs with stalks; when the stalk bears a surface rib called the aeriform plate, the egg is classed as encyrtiform. Some larvae, also called encyrtiform, hatch from these eggs, and their posterior ends remain attached to the eggshell and stalk, which serve to convey air from the point where the stalk pierces the host integument, trachea, or such. Other kinds of encyrtid first-instar larvae are hymenopteriform, vesiculate, and caudate. Encyrtidae have been used successfully in biological control, particularly against a variety of coccids.

The family is found worldwide; about 2800 valid species are known in over 500 genera, distributed in 3 subfamilies: Encyrtinae, Arrhenophaginae, and Antheminae. Some authors include Eupelmidae, Tanaostigmatidae, Aphelinidae, and Signiphoridae as subfamilies.

**References.** C. P. Clausen, *Entomophagous Insects*, McGraw-Hill, New York, pp. 169–188, 1940; C. Ferrière, Encyrtides paléarctiques (Hym. Chalcidoidea), *Mitt. Schweiz. Entomol. Ges.*, 26:1–45, 1953.

**Tanaostigmatidae.** Minute wasps, mostly 2–3 mm long, compact, usually black, with metallic reflections. The mesopleuron is large and swollen. The prepectus is also enlarged and swollen, extending forward to cover much of the lateral wall of the pronotum. The midleg has a stout tibial spur, and the hind tibiae have one or two spurs; tarsi are all five-merous. The notauli meet mesially to form a V or Y. The antennae are usually 11-merous, including two anelli; in males, they often have whorls of long hairs, and are flabellate. Some species have broad squamiform hairs on the body.

The biology of Tanaostigmatidae is little known. Adults have been reared from galls, particularly on leguminous flowers and seeds; one specimen has been recorded from a weevil.

The family (=Tanaostigmodinae of Encyrtidae) includes about 33 known species in 14 genera, distributed widely but discontinuously in the warmer parts of the world, except Africa. In the United States, they occur in Florida, Arizona, and California.

**References.** L. O. Howard, A new and remarkable encyrtid: Is it parasitic?, *Insect Life*, 3:145–148, 1890.

**Aphelinidae.** Minute wasps, with stout bodies, about 0.35–2.5 mm long; their color is mostly yellow, brown, or black, rarely with greenish or bluish metallescence, but often with dark, white, or yellow segments or markings. Wings are usually present; they may be hyaline, clouded, or streaked with dark, or have patterns of microtrichiation, and have more or less well-developed marginal fringes of hairs.

The pronotum is short, from a dorsal view hardly more than a semicircular anterior rim around the mesoscutum; the latter has strong, complete notauli. Axillae are well advanced cephalad of the scuto-scutellar suture into the area of the parapsides. The femoral groove is lacking on the mesepisternum. The legs have four or five tarsal segments; rarely, the midlegs have four segments, while the other two pairs have five; the midlegs have a tibial spur generally moderately well developed and varying in length. The wings have poorly developed marginal venation; the forewing stigmal vein is short, and the postmarginal vein is very brief or absent. The gaster is broadly attached to the trunk. The ovipositor arises well before the apex, but sometimes extends well beyond.

The antennae are short, with three to nine segments (not counting the one or two extremely small anelli often following the pedicel, which may or may not be discernible); usually six, seven, or eight segments are present. Maxillary palpi have one, two, or three segments; labial palpi are vestigial, with one or two segments.

Aphelinids are best known as primary parasites of aphids, scales, and aleyrodids, but some feed externally on scale insects or their eggs. In addition, aphelinid species have been recorded as primary parasites or hyperparasites of a wide variety of other insects or their eggs in the orders Hemiptera, Lepidoptera, Hymenoptera, Orthoptera, and Diptera, among others. A number of species have proved valuable in the control of sternorrhynchous homopteran pests.

Adults feed on honeydew or on host fluids obtained after puncture by the ovipositor. Eggs are deposited on, near, or within the host, and the larva may feed internally, externally, or both, according to the species. Some species show a remarkable sexual dimorphism: unmated females seek out hosts parasitized by their own species, and the (haploid) male larvae resulting from the unfertilized eggs then develop within the conspecific larvae, which in some species are always (diploid) females.

First-instar larvae are hymenopteriform, caudate, sacciform, or various modifications of these.

The family is distributed worldwide. There are 3 subfamilies—Calesinae, Aphelininae, and Coccophaginae—with over 800 species in 42 genera. Aphelinidae have been included along with Signiphoridae in Eulophidae by some authors.

**References.** L. De Santis, Estudio monográfico de los afelinidos de la República Argentina (Hymenoptera, Chalcidoidea), *Rev. Mus. La Plata* (n. s.), 5:23–280, 1948.

**Signiphoridae.** Minute wasps, with body length as short as 0.5 mm, and rarely much over 1 mm; they are blue-black to brown or yellow, sometimes particolored. The antennae are five- to seven-merous, including two to four short ring segments and a long, undivided apical club. Axillae are not (or only weakly) set off from the scutellum, forming with it a transverse band; the propodeum has a triangular midsection.

The gaster is broadly based; a petiole is not discern-

ible. The forewing has a conspicuous marginal fringe of hairs; the stigma is vestigial. The mid femur is short and broad, the outer face having short, stout setae, and a longer subapical seta on the inner side. The mid tibia has a large, pectinate apical spur and two or more stout setae on the outer face. The tarsi are five-merous. Mandibles are two- or three-toothed; maxillary palpi are two- or three-merous; labial palpi are one-merous.

Most species emerge from scales, aleyrodids, and psyllids, and are parasites of encyrtid and other primary hymenopterous parasites of the Homoptera; but a few signiphorids have been reared from the puparia of parasitic Diptera species.

The family (=Thysanidae) is distributed worldwide; there are about 75 species in 6 currently accepted genera. It is closely related to Aphelinidae.

**References.** C. P. Clausen, *Entomophagous Insects*, McGraw-Hill, New York, pp. 190–191, 1940; G. J. Kerrich, Report on Encyrtidae associated with mealybugs on cacao in Trinidad, and on some other species related thereto. *Bull. Entomol. Res.*, 44:789–810, 1953.

**Tetracampidae.** Small, rare family of chalcidoids, with characteristics intermediate between those of the large families Eulophidae and Pteromalidae. Tetracampids may be distinguished by the following combinations of characteristics (C. M. Yoshimoto, 1978): The antennae are 12-merous, with one anellus. The pronotum is campanulate or conical. The parapsidal furrows are distinct and complete. The marginalis of the forewings is long. The legs are slim. The foretibial spur is small and straight. Female tarsi are five-merous, and male tarsi four- (Platynocheilinae) or five-merous (Tetracampinae).

The family is found in all major biogeographical realms, but only 2 known species are native to the New World. Members are primary parasitoids of eggs of Coleoptera and Hymenoptera (Symphyta) and larvae of mining Diptera (Agromyzidae). Tetracampids are very common in Cretaceous amber of Canada.

There are 2 subfamilies, Platynocheilinae and Tetracampinae, 13 genera, and 35 described species. A third subfamily, Mongolocampinae, has recently been added for the aberrant genus *Mongolocampe*. [NORMAN F. JOHNSON]

**References.** Z. Bouček and R. R. Askew, *Index of World Tetracampidae*, Le François, Paris, 1968; C. M. Yoshimoto, Two new species of *Epiclerus* from the New World (Hymenoptera, Chalcidoidea, Tetracampidae), *Can. Entomol.*, 110: 1207–1211, 1978.

**Elasmidae.** Small wasps, with body length 1–3 mm, colored black to dull yellow, often with metallic blue or green luster, and yellowish or brownish legs or markings. They are related to Eulophidae. The tarsi are four-merous. The antennae of the female are basically 10-merous, if the club is counted as 3-merous and the one or two minute anelli are also counted, but various fusions or reductions occur to modify this count; the first three funicular segments of the male are strongly flabellate. The hindlegs have greatly expanded, flattened coxae; the outer surfaces of the hind tibiae have curious closed figures or lines formed of short, black setae (*Elasmus*). The mid and hind femora are flattened and broadened, each with a large, spurlike bristle near the apex. The forewing is narrow and subcuneiform, with a very long marginal vein and short stigmal and postmarginal stubs. The vertex is sharply margined posteriorly and the posterior ocelli are very close to the margin.

Species of the genus *Elasmus* are either primary external parasitoids of lepidopterous larvae or hyperparasites of them through other Hymenoptera, especially ichneumonids and braconids. Most of the larval hosts are enclosed in leaf mines, webs, larval cases, or cocoons, or are otherwise concealed. Species of other genera, such as *Euryschia* and *Myiocnema*, have been reared from coccoids or from dipterous parasites or predators of these or aphids. The larvae, as far as is known, are hymenopteriform, with distinct segmentation in all (three or four) instars.

It has been suggested that Elasmidae is a compound taxon, with *Elasmus* representing an aberrant group of eulophids, while the remaining genera are perhaps Aphelinidae.

The family, as it stands, is listed as containing about 220 species in 8 genera, distributed worldwide.

**References.** M. S. Mani and G. G. Saraswat, On some *Elasmus* Hymenoptera: Chalcidoidea from India, *Oriental Insects*, 6:459–506, 1972.

**Eulophidae.** Wasps less than 5 mm in total length. Color is variable, often metallic. All tarsi are four-merous. The foretibial spur is small and straight. The hindlegs are slender, not enlarged. A mesopleural scrobe is present. Axillae often extend cephally of the tegulae; the antennal funicle has five or fewer segments.

Eulophid biology is extremely variable. Eulophids have been reared as predators of insect eggs and gall mites; egg parasitoids of Odonata, cockroaches, Orthoptera, Hemiptera, Coleoptera, and Hymenoptera; egg-larvae parasitoids of Coleoptera; parasitoids of immature Lepidoptera, Coleoptera, Hymenoptera, Diptera, Neuroptera, cockroaches, Hemiptera (Homoptera), and Thysanoptera; and hyperparasites of spider eggs through Ichneumonidae (Hymenoptera) and of immature spiders through Acroceridae (Diptera). They are both solitary and gregarious, often depending on the size of the host. They have been used as biological control agents.

This is a common family, with cosmopolitan distribution. There are 5 subfamilies—Elachertinae, Eulophinae, Euderinae, Entedontinae, and Tetrastichinae—323 described genera, and about 3000 described species.

[NORMAN F. JOHNSON]

**References.** Z. Bouček, Descriptions of *Tachinobia* gen. n. and three new species of Tetrastichinae (Hymenoptera: Eulophidae), with a tentative key to genera, *Bull. Entomol. Res.*, 67:17–30, 1977; Z. Bouček and R. R. Askew, *Index of Palearctic Eulophidae (excl. Tetrastichinae)*, Le François, Paris, 1968.

**Trichogrammatidae.** Minute (mostly 0.5–1 mm long), stocky wasps with wings fringed with long hairs. Wing venation is reduced to at most an anterior marginal-stigmal element in the forewing. The hindwing is very narrow, either with a short costa or no veins at all. Venation never reaches beyond the midlength of the wing. The pubescence of the forewing is often arranged in lines. The tibial spur of the anterior leg is straight; there is no strigil. The tarsi are three-merous.

Trichogrammatids are parasites of the eggs of a wide variety of insects. First-instar larvae are modified hymenopteriform, sacciform, or mymariform, the last with a long tail, which is apparently flailed about to disorganize host egg contents. The life cycle in *Trichogramma*, from egg to adult, is only 3–10 days at summer temperatures, but may extend for 2 months in other genera. Depending on the

species, and size of host, 1 to more than 75 parasite adults may emerge from a single host egg.

There are about 70 genera and 440 species in the family, but *Trichogramma* especially seems to contain more sibling species, mostly undescribed. Distribution is widespread; some species are apparently dispersed by human commerce, and live in human habitations or gardens. Trichogrammatids are important in biological control.

**References.** R. L. Doutt and G. Viggiani, The classification of the Trichogrammatidae (Hymenoptera: Chalcidoidea), *Proc. Calif. Acad. Sci.*, 35:477–586, 1968.

**Mymaridae.** Minute (0.2–2 mm long), delicate wasps with narrow, straplike or oar-shaped wings, typically bearing a conspicuous marginal fringe of long setae, and thus often resembling a feather. Hindwings are sometimes filiform or vestigial. The marginal + stigmal vein of the forewing is short, usually not reaching wing midlength, and scarcely if at all reaching into the wing membrane. The antennae are slender, with up to 13 segments, and filiform in the male; there are fewer segments in the female, which has a distinct apical club of 1–3 segments. Legs are long; tarsi are four- or five-merous. The gaster is sessile on the propodeum, or distinctly petiolate.

Mymarids are parasitic in insect eggs. The first-instar larva is mymariform, that is, with a downcurved anterior beak; there are strong, mostly dorsal setae in rows, posteriorly inclined; and a long, tapered caudal appendage, thought to be used to stir and disrupt the host egg contents. More rarely, the first-instar larva is sacciform or modified-hymenopteriform. The larval and pupal stages are passed within the host egg. Mymaridae parasitize eggs of a wide variety of insect hosts, particularly of Homoptera, but also Odonata, Lepidoptera, psocids, beetles, Neuroptera, and Heteroptera. Some mymarids can either swim with their legs or walk down plant stems to reach submerged egg masses of aquatic hosts. Mymarids are used in biological control of pest insects.

The family is widespread and abundant in many habitats, from arctic to tropical and south temperate lands. The Mymaridae are made up of 3 subfamilies—Alaptinae, Eubroncinae, and Mymarinae—with about 95 genera and nearly 1200 species.

**References.** D. P. Annecke and R. L. Doutt, The genera of the Mymaridae, Hymenoptera: Chalcidoidea, *Entomol. Mem. Rep. S. Afr. Dep. Agr. Tech. Serv.*, Pretoria, 5:1–71, 1961; C. P. Clausen, *Entomophagous Insects*, McGraw-Hill, New York, pp. 99–106, 1940.

## Cynipoidea

Gall wasps and their parasitic and inquiline relatives. They range from about 1 mm to over 20 mm in body length. They may be black, red, amber, yellow, or particolored. The integument may be either shining or dull, but is never metallic. In the female the antennae are usually 13-merous, but may have from 12 to 20 segments. In the male, the usual number of segments is 14 or 15, but the number ranges up to 24 in known species. The pronotum reaches the tegulae. The mesoscutum and the scutellum are variously sculptured. The forewings almost always lack a pterostigma, but they usually have a radial cell, which may be open or closed, on the front margin. Some females are wingless. The gaster is usually more or less laterally compressed, especially in parasitic forms. The ovipositor issues ventrally and is retractile. Mature larvae are hymenopteriform.

form; they live in plant galls or as internal parasites of insects. Early-stage larvae are diverse and are often polypodeiform, eucoiliform, and so forth, in parasitic genera.

This superfamily comprises a large group, with 2000 or more species in about 180 genera distributed among 4 families and 13 or 14 subfamilies, found worldwide in warm and temperate regions. The higher classification is unsatisfactory, with the subfamilies apparently more "natural" (that is, monophyletic and more easily defined) than the families. The Figitidae, with mostly parasitic species, and the Cynipidae, including parasitic, gall-forming, gall-inquilinous, and seed-inhabiting taxa, are particularly confused. Attempts to place all parasitic genera in Figitidae and all plant-feeding ones in Cynipidae appear to be contraindicated both on morphological grounds and because the biology of some key taxa remains unknown.

**References.** L. H. Weld, *Cynipoidea (Hym.) 1905–1950*, privately printed, Ann Arbor, MI, 1952.

**Ibaliidae.** The family includes 1 subfamily (Ibaliinae) with the single genus *Ibalia*. These are large cynipoids, with the female 8–25 mm long. The female has a long, strongly compressed gaster with a conspicuous ovipositor. The forewing has three closed cells and the most complete venation in the superfamily. The radial cell is closed. It is nine or more times as long as it is broad. In both sexes, the sixth tergite is the largest one. The antennae are filiform, 13-merous in the female, 14-merous in the male. The scutellum is truncate or emarginate. The hind basitarsus is twice as long as tarsal segments II through V taken together. The second segment has a reclinate spur on the outer side. These wasps are often boldly colored with fulvous or rufous and black markings; the wings often bear fuscous clouds or bands.

The Ibaliidae are parasitoids of siricid wood wasps. They are polypodeiform in the first instar. Segments I–XII each have a pair of digitiform processes; segment XIII is elongate. The egg is deposited either in the host egg or in the first-instar larva, and feeds internally. The fourth instar burrows to the log surface. The life cycle may extend for 3 years or more.

There are 12–15 species, widespread in the Holarctic Region, reaching Mexico and Japan.

**Liopteridae.** Members of this family are 4 to 15 mm long, with the radial cell of the forewing less than eight times as long as it is broad. The hind basitarsus is less than twice as long as the rest of the tarsus. The largest tergite of the gaster, as seen in the side view, is the fourth, fifth, or sixth; there are two or three preceding small tergites. In the monotypic *Xenocynips* from Africa, there is only one small basal tergite (=second, third, and fourth indistinguishably fused together) in front of the very large one, which is the true fifth. The petiole is distinct; it may be long or short, and is usually longitudinally fluted. These wasps may be black, red, yellow, brown, or combinations of these.

The larvae are unknown, as are the hosts, although females of the sole species of *Kiefferiella*, *K. rugosa* from California, are said to have emerged from tunnels leading to a fresh *Acmaeodera* (Buprestidae) tunnel.

This family includes about 65 valid described and undescribed species known in 13 genera distributed among 3 subfamilies: Liopterinae (South and Central America), Oberthuerellinae (sub-Saharan Africa, Madagascar), and Mesocynipinae (Oriental to Australian regions, and 2 species in western North America). Some species based on one

sex or the other remain to be associated, and undoubtedly many species remain uncollected.

**References.** H. Hedicke and G. J. Kerrich, A revision of the family Liopteridae (Hymenopt. Cynipoidea), *Trans. Roy. Entomol. Soc. London*, 90:177–225, 1940.

**Figitidae.** The petiole is a distinct segment, though sometimes small. The tergite of the succeeding segment (tergum II) takes up much less than half of the gaster. The scutellum sometimes has a spine. The antennae are filiform, sometimes slightly clavate at the apex in the female; they are 13- to 20-merous in the female, 14-merous in the male. These are mostly medium-sized to small wasps. The body length is usually between 1.5 and 5 mm. Their color is usually black.

They are parasitic in larvae of Diptera and Neuroptera, where the hosts are known. They are usually reared from host pupae: subfamily Aspicerinae (worldwide, on Syrphidae), subfamily Anacharitinae (worldwide, on Chrysopidae and Hemerobiidae), and subfamily Figitinae (worldwide, on cyclorrhaphan Diptera). The subfamily Himalocynipinae, a Himalayan taxon with a single monotypic genus, has an unknown biology. A species of *Figites* proved to have modified eucoiliform first-instar larvae, while the second instar is polypodeiform and the third is hymenopteriform with bidentate mandibles.

The great majority of the approximately 30 genera and 250 species of the family are known from Europe and North America, but this no doubt reflects only the intensity of collecting so far. A great many more species are to be expected from the rest of the world.

**Cynipidae.** Gall wasps (Cynipinae) and allied forms. They have the second, or the combined second and third, tergites longest, usually forming half or more of the gaster. The petiole (primitive segment I of the gaster) is reduced, vestigial, or lost through fusion. In females the antennae are 12- to 19-merous, usually 13- to 15-merous; in males they are usually 15-merous, but occasionally have 14 or 16 segments, even more rarely as many as 24. The antennae are filiform but often form an apical club of one to several segments in the female. The body length ranges from 7–8 mm to less than 1 mm.

E. Riek separated Cynipidae from Figitidae as follows: In the former, the hypopygium of females is produced at the apex; these wasps are gall-formers or inquiline in galls or are reared from seeds (biology unknown in the Pycnostigmatinae). In Figitidae, the hypopygium of the female is not produced at the apex; these wasps are parasites. However, there appear to be important exceptions to the hypopygial character in Riek's classification, which assigns Eucoilinae and Charipinae to Figitidae. The parasite versus gall-former or inquiline dichotomy may hold, but there are still numerous species, including the pycnostigmines, whose biology is totally unknown. For the time being, the classification of Cynipoidea must be considered as unsettled at the family level; and the most natural groups seem to be the subfamilies. L. H. Weld's system is followed here, but without enthusiasm.

Eucoilinae are very small wasps. The adult body length ranges from 0.75 to 5 mm, but is usually 1 to 3 mm. These wasps are distinguished by the ornamentation of the scutellar disk, which consists of bilaterally paired foveae anteriorly and a posteromedian pit or "cup" with raised margin. The body is mostly smooth and shining. The larvae are parasitic in dipterous fly larvae and puparia; the first larval

instar is eucoiliform and the second may be polypodeiform or modified hymenopteriform. Weld (1952) recognized 700 species in 55 genera, distributed worldwide.

Pycnostigminae are small, slender wasps with reduced venation. The anteromedian part of the forewing has a very thick-veined subcircular cell, probably the modified radial cell, which is said to resemble a pterostigma. The antennae are 12- to 24-merous. There are about 4 species in 2 genera, one from northern Africa and the other from South Africa. Their biology is unknown.

Charipinae are very small wasps, under 2 mm long, with smooth, shining sculpture. The scutellum is smooth, rarely with paired foveae at its base. The wings are sometimes reduced. There is no areolet. The antennae are filiform. So far as is known, all are secondary parasites of aphids through their aphidiid parasites. There are 9 genera, which are widespread, with over 150 species.

Cynipinae are a subfamily that includes the true gall-makers as well as forms that are inquiline in cynipid or other galls. The body length can be as much as 7.5 mm. These wasps may be fully winged, brachypterous, or apterous. They have no pterostigma. The radial cell may be open or closed. The larvae inhabit plant galls, mainly on oaks and Rosaceae, but also on Compositae and some other angiospermous families. They are modified hymenopteriform. On oaks, galls may occur on any part of the plant, including roots, leaves, stems, staminate flowers, acorns, and acorn cups; many species living on oaks have alternating sexual and asexual (thelytokous) generations, the latter consisting of wingless females, in some genera active in fall and winter. For many species only one or the other form is known. About 70 genera are known worldwide, and over 1200 "species," but the past description of very many of these as "varieties" makes a fair estimate of species numbers impossible for the present.

Austrocynipinae are a subfamily based on the female of a single species (4 mm long) reared from seeds of *Araucaria cunninghamii* in Queensland, Australia. A distinct pterostigma is present in the forewing, but there is no areolet. The antennae are 15-merous. Tergite II of the gaster is the largest. The hypopygium is slightly produced at the apex.

**References.** E. F. Riek, A new subfamily of cynipid wasps (Hymenoptera: Cynipoidea) from Australia, *Entomological Essays to Commemorate the Retirement of Professor K. Yasumatsu*, Hokuryukan, Tokyo, 1971.

## ACULEATA

Wasps, bees, and ants, encompassing an enormously diverse array of families, best defined biologically. The true ovipositor of Symphyta and Parasitica has been modified into a sting in most aculeates, and is even lost in some higher taxa of ants and bees. In most aculeates, the sting is no longer used to transfer the egg, but serves to inject poisons from glands at its base into prey or, for defense, into predators or other enemies; in some ants, it functions to dispense enemy-repellent allomones or to draw pheromone trails for its nest mates.

In primitive aculeates, such as Tiphidae, the host is sought by the female and stung and paralyzed (or killed) where it is found. An egg is deposited upon it there, underground or in some other cryptic situation, and then the mother leaves the egg to hatch and the larva to feed and develop by itself. More advanced solitary wasps transport the prey to a natural or actively constructed cavity or burrow (nest) in the soil, in rotten wood, or in a hollow twig or

such, then lay an egg on it or near it, seal the nest entrance, and leave it. Further evolution has led to progressive provisioning (where the mother continues to provision the nest while the larva hatches and develops), and eventually to social systems in which the adult offspring overlap the maternal generation and share the nest with one or more maternal females, developing some polyethism (division of labor) and correlated caste differences near this point in the evolution of eusociality.

The combination of haplodiploidy (the hymenopterous norm) and progressive provisioning has apparently led to the evolution of eusociality in at least six, and probably more, independent lineages and about 15,000 species among the aculeates. It occurs, for instance, in Vespoidea, Formicoidea, Apoidea, and Sphecoidea, although all of these superfamilies except the ants consist mainly of solitary species.

The larvae of the Aculeata are basically hymenopteriform, though often with added tubercles, appendages, setae, or spicules in ants and some other families; frequently the thoracic region is tapered cephalad into a necklike region. They are mostly external feeders on the arthropod prey or nectar-pollen provisions furnished by the mother. In social forms, particularly ants, the larval provisions vary widely according to taxon, and sometimes extend to foods such as plant seeds, fungal hyphae, homopteran honeydew, adult glandular secretions, and even special trophic eggs laid by the queen or workers.

The series Aculeata includes perhaps 50,000 to 60,000 species in 8 superfamilies: Chrysidoidea, Tiphioidea, Pompiloidea, Formicoidea, Scoliidea, Vespoidea, Sphecoidea, and Apoidea. They exist worldwide, even in arctic regions, but the species are concentrated in the warm parts of the world.

**References.** D. J. Brothers, Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae, *Univ. Kans. Sci. Bull.*, 50:483-648, 1975.

## Chrysidoidea

Heterogeneous assemblage of wasps, mostly small or medium-sized, which are parasitoids or, rarely, cleptoparasites of other insects. The antennae are 10- to 30-merous, the same number in both sexes, 10- or 13-merous being most common. The antennal socket is simple, with no distinct tubercle. The palpi are segmented 6,4 (that is, maxillary palpi have six segments, and labial palpi have four) or less. The pronotum articulates freely with the mesonotum. Wings are usually present in males, but they are absent or strongly reduced in females in roughly a third of the known species. In the latter cases the sexual dimorphism is usually marked in other ways as well, so that conspecific males and females have often been placed in different genera. The mesosternum has no posterior projections. Except in the Plumariidae, wing venation is more or less reduced; the hindwing has one closed cell, or none (two or three closed cells in plumariids). The anal lobe is distinct and there is no jugal lobe. The legs typically have apical tibial spurs 1,2,2, but may be reduced to 1,0,1; usually each claw has a submedian tooth.

The larvae, where known, are hymenopteriform, and are mostly external solitary parasitoids of the immature stages of other insects or egg parasites of stick insects. The larvae and prey of Plumariidae and Scolebythidae remain unknown.

A large taxon, this superfamily (=Bethylidae) probably

contains more than 5000 described species in nearly 250 genera. It occurs worldwide in both tropical and temperate countries. Eight families are recognized: Plumariidae (which may or may not belong here), Chrysididae, Dryinidae, Embolemidae, Sclerogibbidae, Scolebythidae, Bethylinidae, and Loboscelidiidae. Problems of distinctness exist between two of the main families: the subfamily Mesitiinae (Bethylinidae) may actually belong in Chrysididae, next to or in the subfamily Cleptinae.

**References.** D. J. Brothers, Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae, *Univ. Kans. Sci. Bull.* 50:483–648, 1975.

**Plumariidae.** Small family related to Bethylinidae, containing 5 genera and about 20 known species, described and undescribed. The males are 3–10 mm long, or longer. They are testaceous to black, with 13-segmented antennae and peculiar wing venation, featuring four free apical abscissae (or their stubs continued as vein shadows) in the forewing, the first (Rs) issuing from a short marginal (radial) cell. The pterostigma is large and thick. The hindwing is large, with a prominent anal lobe. The jugal lobe is undifferentiated and there are three or four free apical abscissae, not counting R in the anterior margin. There are two large, closed basal (median and submedian) cells; a costal cell may or may not be present. The gaster has no constriction between the basal and following segments; it is usually somewhat depressed. The maxillary palpi are five- or six-merous, while the labial palpi are two- to four-merous.

The female is known only from 1 species of *Plumarius* or *Plumaroides* from Peru. It is depressed, wingless, bethylinid-like, and light castaneous in color, but with rather large compound eyes. The antennae are 13-merous; there are no ocelli. The palpi are segmented 5.3. The trunk has a strong promesonotal suture. It is widest across the mesothorax and sharply and deeply constricted between the mesonotum and the propodeum. The petiole is very short but narrow; the platelike parts of the first gastric segment are short and are included in the body of the gaster without constriction. The legs are stout, with stout fossorial setae. The claws are simple, and the integument is largely smooth and shining.

This family is found predominantly in dry areas. Both nocturnal and diurnal species occur. The prey is unknown; it is most likely hypogaecic beetle larvae.

This family contains 5 known genera: *Plumarius* and *Plumaroides* (circum-Andean), *Myrmecopterina* and *Myrmecopterinaella* (South Africa), and *Heterogyna* Nagy, not Chapman 1898 (Levant).

**References.** D. J. Brothers, The genera of Plumariidae, with description of a new genus and species from Argentina (Hymenoptera: Bethyloidea), *J. Entomol. Soc. S. Afr.*, 37: 351–356, 1974; M. C. Day, A new genus of Plumariidae from southern Africa, with notes on Scolebythidae (Hymenoptera: Chryridoidea), *Cimbebasia, Windhoek*, (A)4: 171–177, 1977.

**Chrysididae.** Cuckoo wasps, gold wasps, and allies. They are mostly robust, heavily sclerotized, and strongly sculptured wasps. The body length ranges from 2.5 to perhaps 20 mm. The great majority of species are metallic green, blue, copper, or purple, but a few are nonmetallic black, red, orange, or particolored. They are usually winged, although some Amiseginae, mostly females, are apterous or brachypterous. The forewing has a strong, curved stigmal vein (2r.Rsf 4·5), arising from the pterostigma but otherwise typically

isolated from distinct intersecting veins; there are four to six closed cells in full-sized wings. The hindwing usually has no distinct veins (except marginal), although weak vestiges may occur; it usually has no closed cells. A distinct excision sets off a lobe at the base of the hindwing, often called the jugal lobe, but probably really the anal lobe. The antennae are 13-merous, geniculate, filiform, and gradually clavate or incrassate. The eyes are large, and compound, and three ocelli are present. Except in a few primitive Amiseginae, the posterodorsal angles of the pronotum fail to reach the tegulae, and the propodeum has posterodorsal angles which are rectangular, acute, or even produced as slender teeth. The gaster usually has two to five visible tergites in females (occasionally V or VI are exerted in males); but the apical segments of the female are tubular and telescoping, usually held retracted, but extensible and forming a functional unit with a true ovipositor. The gaster is more or less flattened beneath, and in Chrysidinae it is margined and concave so that the head and trunk can be folded into the hollow and thereby protected when the wasp assumes the doubled defensive position.

The larvae live as parasitoids or, more rarely, cleptoparasites, of other insects after the mother chrysidid places the egg in the host cocoon or brood cell. They are hymenopteriform. The first instar has a large head; the second through the fifth have tridentate mandibles.

Three subfamilies are currently recognized in this family: Cleptinae, with 1 genus (*Cleptes*) and about 70 species, is mainly holarctic; species parasitize prepupal sawflies. Amiseginae occur worldwide, with about 16 genera and close to 50 species; they parasitize phasmatid eggs. Chrysidinae are found worldwide, and are parasitic on solitary bees, sphecids and vespids wasps, and lepidopterous prepupae and pupae; this subfamily includes the vast majority of Chrysididae, with 40 to 50 genera and perhaps close to 3000 species. Chrysidine classification is in confusion, partly because many of the species are both closely related and phenotypically very variable, due partly to allometry affected by different host nutritional resources, and partly to an excessive resort to the ambiguous subgenus and subspecies categories by some taxonomists working in this family. Revision is sorely needed.

**References.** H. Bischoff, Hymenoptera Fam. Chrysididae, in P. Wytsman, *Gen. Insect.*, 151:1–86, 1913; K. V. Krombein, A generic review of the Amiseginae, a group of phasmatid egg parasites, and notes on the Adelphinae (Hymenoptera, Bethyloidea, Chrysididae), *Trans. Amer. Entomol. Soc.*, 82:147–215, 1957.

**Dryinidae.** Small wasps, 1.5–10 mm long. They vary in color from dull fulvous, brown, or black to particolored red, black, and white. The males are winged, while the females may be either winged or apterous and are often antlike. The wings, when present, are frequently patterned with black or brown. Venation of the forewing is reduced, especially in the middle of the wing, but a costal cell is present; 2r and the apex of the radial sector form an angled or curved stigmal vein. Hindwing venation is obsolete except for the marginal vein, but the anal lobe is distinct. The antennae are 10-merous. In the female, the fore tarsi are modified into a chela which consists of the strongly produced fifth tarsal segment opposed by an enlarged claw; the other claw may be reduced or lost. The empodium is present as a sclerotized lateral piece at the joint of the chela. In females of Aphelopinae and in males of all subfamilies, the fore tarsi are normal, not chelate.

The females attack nymphal or adult auchenorrhynchous Homoptera, particularly Fulgoroidea and Cicadellidae, seizing them with the chelae (if present) and stinging the prey in the abdomen, often causing a paralysis of brief duration. The first-instar larva of dryinids is usually sacciform and develops inside the host, but with few exceptions later instars are hymenopteriform and external, borne on the host abdomen in a sac formed of the parasite's exuviae. Some species have several larvae on one host individual. Adult females sometimes capture prey and feed upon them or their honeydew without ovipositing.

Dryinidae have received attention because of their potential as control agents for pest species, particularly leafhoppers or plant hoppers on sugarcane, and some have been introduced into Hawaii for this purpose.

The family contains several hundred, perhaps nearly a thousand, species in about 60 genera and 4 subfamilies: Aphelopinae, Anteoninae, Gonatopodinae, and Dryininae. They are distributed worldwide in the tropics and the temperate regions.

**References.** O. W. Richards, The classification of the Dryinidae (Hym.) with descriptions of new species, *Trans. Roy. Entomol. Soc. London*, 104:51–70, 1953.

**Emboleminidae.** Small wasps, 1.3–5 mm long. The males are winged; their color is black or piceous. The females may be winged, wingless, or nearly so; they are fulvous to black. The antennae are 10-merous, and arise from a prominence at the anterodorsal end of the head, widely separated from the ventrally placed clypeus and mandibles. The forewing has four to six closed cells: r-m is present, but often weak or interrupted; the curved stigmal vein ( $2r+Rs_4+5$ ) is prominent; it may or may not reach the wing margin. The hindwing is veinless or has feeble longitudinal remnants; the anal lobe is well developed. Wingless females have small eyes placed high up on the head behind the antennal insertions.

*Ampulicomorpha confusa* of North America parasitizes the nymphs of *Epiptera*, a fulgoroid living on bracket fungi, much in the same way that dryinids do. Adult females of *Embolemus* have been taken from ant nests harboring scales or aphids.

Emboleminids are rare insects, with less than a dozen known, described and undescribed, species from widely separated localities in the Holarctic Region, South Africa, Chile, Australia, and Java; they no doubt occur elsewhere. Largely due to the difficulty of recognizing and associating the sexes, the classification has been confused and still needs revision. The species are referable to *Embolemus*, *Ampulicomorpha*, and possibly 1 or 2 additional genera. The family is sometimes placed as a subfamily of Dryinidae.

**References.** O. W. Richards, The British Bethylinidae (s.l.) (Hymenoptera), *Trans. Roy. Entomol. Soc. London*, 89:293–297, 1939.

**Sclerogibbidae.** Small wasps (3–7 mm long) resembling Bethylinidae. Their color is black, brown, rufous, or black and rufous. They are sexually dimorphic. The antennae have 17–30 segments. The frontal area of the head forms a short, projecting shelf anteriorly; mouthparts and antennal insertions are situated close below this shelf, and so are not visible from above. The antennal scape is distinctly longer and thicker than the succeeding antennomeres. The female is apterous, with a slender (narrower than the head) tripartite trunk which consists of pronotum, short mesonotum, and propodeum, and is slightly constricted near the promesonotal suture. The head is depressed and subcordate (narrowed anteriorly, the posterior margin concave).

Very large eyes occupy most of the posterior half of the sides of the head, or more. There are two or three ocelli. The fore femora are strongly broadened and flattened; the apical spurs of tibiae occur 1,2,2 or 1,1,2. The tarsal claws have one or two preapical teeth. The male is winged, with five or six closed cells, including the radial cell, in the forewing.

These wasps are external parasitoids of Embiidina. The larvae are hymenopteriform, with long, acute mandibles. They have been found attached to the thoracic dorsum of the nymphal web spinners (*Probethylus*), or several at a time on the abdominal segments of adults (*Caenosclerogibba*).

The Sclerogibbidae are found worldwide in the tropics and warm temperate lands inhabited by Embiidina, especially Africa. The family includes 15–20 species described in 3 genera: *Sclerogibba* (Old World tropics to southern Europe), *Probethylus* (South America to Arizona, Australia), and *Caenosclerogibba* (Japan). A number of species in collections remain undescribed.

**References.** O. W. Richards, The Bethylinidae subfamily Sclerogibbidae (Hymenoptera), *Proc. Entomol. Soc. London*, (B), 8:211–223, 1939; K. Yasumatsu, A new addition to the genera of the Sclerogibbidae (Hymenoptera), *Kontyu*, 26:20–24, 1958; A. Yokoyama and M. Tsuneyoshi, Discovery of a hymenopterous ectoparasite of *Oligotoma japonica* Okajima (Embioptera), *Kontyu*, 26:25–28, 1958.

**Scolebythidae.** Family of only 3 rare genera, each with a single known species. These modest-sized, stout, black or brown wasps resemble Bethylinidae, with the proepisterna forming a prominent, projecting pedestal upon which the head is placed. The sexes are much alike, both with 13-segmented antennae. The maxillary palpi are six-segmented; the labial are four-segmented. The proepimera are separated from the proepisterna by sutures; the prosternum is large, flat, and diamond-shaped. The wings are rather short and bethylinidlike. The hindwing has no closed cells, but does have an anal lobe.

The larvae, prey, and habits of these wasps are unknown. The larvae are found in dead or rotten wood. Equivocal evidence suggests that one species (*Scolebythus madecassus*) may be social or subsocial to some degree. The genera which compose this family are *Scolebythus* (Madagascar), *Chystopsenella* (Brasil), and *Ycaploca* (South Africa, Australia).

**References.** H. E. Evans, A new family of wasps, *Psyche*, 70:7–16, 1963.

**Bethylinidae.** Small wasps, ranging in length from about 1 to 20 mm, but mostly under 10 mm. They are black to testaceous, or bicolored; sometimes they are metallic green, blue, and so on. The head is often elongate and depressed; in females it is usually elongate and prognathous. Sexual dimorphism is moderate where both sexes are winged, but females are often brachypterous or apterous and very different from males, so that conspecific males and females are often described in different species or even genera. The antennae have 12 or 13 segments in both sexes. The palpal formula is 6.3 or less. The pronotum reaches the tegulae. The forewings have no closed submarginal cells (rarely, one), and one or no closed discoidal cells. The hindwings lack closed cells but have an anal lobe. The gaster has seven or eight visible segments. The wingless females are often mistaken for ants, although they lack the petiolar node characteristic of ants.

The larva is known for very few species. The mandible is usually denticulate; 10 pairs of fully developed spiracles are present.

These wasps are predators of small holometabolous insect larvae, particularly those of Coleoptera, more rarely Lepidoptera, usually living in cryptic situations such as in the soil, in stems, seeds, or wood, under bark, or in rolled leaves. Some bethylids attack larvae much larger than themselves, paralyzing or killing them by repeated stinging, and then lay several eggs on them. The female often feeds on hemolymph oozing from the prey's wounds and may stay with the developing larvae to achieve a subsocial condition and sometimes interesting kinds of polyphenism involving winged, wingless, and subapterous adult forms. Many Bethyidae may carry or drag their prey to a preexisting beetle burrow or crack, which they may or may not close. A number of species are found in ant nests, but it is not yet definitely known whether they prey on the ant larvae or on inquiline beetle larvae. Adults of winged species often feed on homopteran honeydew.

A number of bethylid species inhabit human dwellings or buildings infested with dermestid or grain-feeding beetles, where the females may become abundant and annoy humans with their potent stings.

The family occurs worldwide in the tropics and temperate regions. It is composed of probably more than 1000 described, valid species in 70–90 genera, but the number of undescribed species is much greater than 1000—perhaps 2000 to 4000 for the world. It contains 4 subfamilies: Bethylinae, Pristocerinae, Epyrinae, and Mesitiinae.

**References.** H. E. Evans, A synopsis of the American Bethyidae (Hymenoptera, Aculeata), *Bull. Mus. Comp. Zool. Harv.*, 132:1–222, 1964.

**Loboscelidiidae.** Small (2–5 mm), smooth, rufous to black wasps of very peculiar form: the back of the head is produced behind in the middle, and this projection is bordered laterally by broad, foliaceous laminae on each side. Laminae also grace the pronotum and propleura and protect the cervix; the femora and tibiae are broadened and bear laminae. The eyes are large; three ocelli are present. The antennae are geniculate and 13-merous in both sexes, inserted on a strong facial shelf. The wings are well developed, their bases covered by very large tegulae. The pterostigma and costal vein are absent. Distinct veins occur only in the basal half of the forewing. At most, one cell is present, the basimedial, and this may be closed or open at the apex. The anal lobe of the hindwing is distinct.

The gaster has a short petiole consisting of the fused tergum and sternum of abdominal segment II. Terga III and IV are fused, as are sterna III and IV; segment V is fairly large; VI is smaller; the rest are small and retracted. There are no cerci.

The larvae remain undescribed. Some Australian species have been reared from phasmatid eggs, and one specimen has been taken in an ant nest. The laminar protection also suggests that part of the life cycle may be passed in ant nests.

This family includes 2 genera, *Loboscelidia* and *Scelidoloba*, with about 20 species which range from the Oriental Region to the Australian Region.

**References.** T. C. Maa and C. M. Yoshimoto, Loboscelidiidae, a new family in Hymenoptera, *Pacif. Insects*, 3: 523–548, 1961.

## Tiphioidea

Very varied wasps, mostly within the range from 3 to 30 mm long. The sexes differ widely in most species. The males are winged, while the females of more than half of

the species are wingless. There are 12 antennal segments in the female, 13 in the male. There are primitively six maxillary and four labial palpal segments, but these are reduced to as few as two and two in a few lines. The integument is often thick and hard; compound eyes are present and are usually well developed. Color and pilosity vary to extremes with genus and species, but the hairs are simple. The sting is well developed and downcurved in females. The legs of females often have spines to aid in digging. Wing venation, when wings are present, is usually nearly complete for aculeates, with at least two cells in the hindwing.

The larvae are hymenopteriform, with 9 or 10 pairs of well-developed spiracles. They are parasitoids of immature insects, especially the larvae of scarabaeoid beetles and of solitary bees and wasps. For many species, genera, and even certain families, the hosts are unknown. Progressive provisioning is unknown in this superfamily.

These wasps are found worldwide in tropical and temperate countries. The superfamily contains about 270 genera and probably over 7000 described and undescribed species in 5 families: Tiphidae, Sapygidae, Mutillidae, Sierolomorphidae, and Bradynobaenidae.

**References.** D. J. Brothers, Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae, *Univ. Kans. Sci. Bull.*, 50:483–648, 1975.

**Tiphidae.** Wasps of variable form, color, and size (body length mostly 4 to 30 mm). The males are always winged and have 13-merous antennae. The females are apterous in about half of the species (all Thynninae, Brachycistidinae, and Methochinae), with 12-merous antennae; (the pedicel is sometimes reduced and hidden in the end of the scape). The trunk is divided into three sections by strong sutures: a movable suture between the pronotum and mesonotum, and one between the mesonotum (or metanotum) and propodeum. The middle coxae are separated and their bases overlapped by the mesosternal lobes or tubercles. The propodeum is simple, that is, not trisected by two longitudinal sutures. The wings, when present, have a smooth (not corrugated) membrane. The hindwing has closed cells and an anal lobe. The gaster is never furnished with felt lines. The first segment (true abdominal segment II) is often partly pinched off as a distinct petiole. The male hypopygium is frequently produced as a sharp, upcurved spine or aculeus, probably a false sting.

The larvae are hymenopteriform, living attached to, and feeding upon, single prey insects that have previously been stung and paralyzed by the mother wasp. The prey are usually mature beetle larvae, in most cases scarabaeid larvae in the earth or in rotten wood; also attacked are the larvae of cicadeline tiger beetles, cerambycid wood borers, and (by the thynnine *Diamma* in Australia) adults of gryllotalpid mole crickets. After stinging, the prey is usually left where found, but in some cases the prey is buried, usually in its own or another preformed burrow or crevice. In most cases, prey larvae live in and are attacked in soil burrows or other cryptic situations.

Adults feed extensively on homopteran honeydew or nectar from the floral and extrafloral nectaries of plants. In forms with apterous females, the females are often carried in flight by males during mating.

The family contains 6 subfamilies: Anthoboscinae, Tiphinae, Myzininae, Methochinae, Thynninae, and Brachycistidinae, comprehending nearly 100 genera and perhaps 1500 or more known species, distributed worldwide. The Anthoboscinae and Thynninae tend to replace the remaining subfamilies in the Southern Hemisphere.

**References.** V. S. L. Pate, A conspectus of the Tiphidae, with particular reference to the nearctic forms (Hymenoptera, Aculeata), *J. N. Y. Entomol. Soc.*, 60:115–145, 1947.

**Sapygidae.** These wasps are colored black, black and red, or black marked with white, orange, or yellow. The body is cylindrical, 6–22 mm long. The sexes are much alike. Both are always winged. The wings have complete aculeate venation; some longitudinal veins extend to or nearly to the wing margin in both pairs. The anal lobe is set off by a weak notch, the jugal lobe by a deep notch. The head is suborbicular. The eyes are large, reaching or nearly reaching the mandibular insertions. The front of the head is broad. The mandibles have tridentate apices. The pronotum is elongate, coplanar with the mesonotum and reaching back to the tegulae. The mesosternum is simple, with no plates or denticles before or overlying the middle coxae. The propodeum is simple, rounded, and undifferentiated. The coxae are large, bilaterally contiguous or approximate. Apical tibial spurs occur 1,2,2; the tarsal claws each have a submedian tooth. The larva has 10 pairs of well-developed spiracles.

The family contains 2 subfamilies: Fedtschenkiinae has 1 genus, *Fedtschenkia*, with 4 species in the arid lands of central Asia and the Middle East, and 1 species in western North America. It is fossorial, parasitizing eumenid wasps. Sapyginae has about 8 genera and 80 species, and is widespread except for the Australian Region. Its larvae are cleptoparasitic in the nests of bees, particularly Megachilidae and Xylocopinae, made in a variety of sites. After the mother pierces the wall of the host bee's cell with her ovipositor-like sting and lays her egg on or near the host egg, the parasite larva hatches first, devours the host egg, and then the stored provisions.

**References.** V. S. L. Pate, Neotropical Sapygidae, with a conspectus of the family (Hymenoptera: Aculeata), *Acta Zool. Lilloana*, 4:393–426, 1947.

**Mutillidae.** Velvet ants, cow killers, and allies. These are strongly sexually dimorphic wasps. The body length of most species is between 3 and 30 mm. The female is apterous; the male is winged. Color is variable. The female often has brilliant red, orange, yellow, and black or white hair arranged in an aposematic pattern; rarely, the integument is metallic blue, green, or purple. The male is usually dark, often with black pilosity and wings, but sometimes with red, orange, or white bands on the gaster, which is used in some species to signal other males, but may also be aposematic. The integument is thick and hard, and is often coarsely foveolate, rugulose, or otherwise sculptured; it frequently has a dense covering of pubescence and also longer hairs. The female trunk is fused into a single box, except in the Myrmosinae, in which the promesonotal suture is complete and functional. Gastric tergum III has a median stridulitrum at its anterior margin; the tergum or the sternum of the second gastric segment often has a longitudinal "felt line" secretory groove on each lateral surface. The female sting is very long and strong. The final-instar larva has nine pairs of well-developed spiracles. The second pair is reduced.

Males and females may mate quickly on the ground surface, but in some genera the female is carried in flight by the male, and mating may take place during or after the flight. The females parasitize solitary bees and wasps, and some are known to utilize chrysomelid and other beetles, Diptera, Lepidoptera, and even blattarian oothecae, the

main requirement apparently being that the host stage is in a relatively immobile state and enclosed in a cell, cocoon, puparium, or ootheca. Female Mutillidae are especially familiar objects running quickly over dry, bare, often sandy ground, but they are also often found climbing trees in wet tropical forests.

These wasps occur worldwide in temperate and tropical countries. The family contains about 5000 species, described and undescribed, in about 150 genera and subgenera, distributed among 7 subfamilies: Myrmosinae, Pseudophotopsidinae, Ticoptinae, Rhopalomutillinae, Sphaerophthalminae, Myrmillinae, and Mutillinae.

**References.** D. J. Brothers, Phylogeny and classification of the aculeate Hymenoptera, with special reference to the Mutillidae, *Univ. Kans. Sci. Bull.* 50:483–648, 1975.

**Sierolomorphidae.** Small family with a single genus, *Sierolomorpha*, containing about 10 known species, described and undescribed (holarctic distribution, mainly North American, but also Hawaii and Panama). These are black wasps, sometimes with yellowish legs, 3.5–6 mm long. They are robust, superficially similar to Bethyridae or small *Tiphia*, but with two closed cells in the hindwing. The forewing has seven closed cells; 2 r-m and 2 m-cu are absent. The sexes are alike, both winged. The male has 13 antennomeres, while the female has 12. There are no gastric felt lines; the petiolar (second abdominal) segment may or may not be constricted behind. Tibial spurs occur 1,2,2; the tarsal claws each have a submedian tooth. There is vestiture of simple, short, decumbent pubescence, not hiding the mostly shining integument. The larvae and larval habitat and prey are unknown.

**References.** H. E. Evans, *Breviora Mus. Comp. Zool. Harv.*, 140:1–12, 1961.

**Bradynobaenidae.** Wasps mostly between 3 and 20 mm in body length. Their color may be dull yellow, red, brown, or black. The male is winged; the female is apterous, resembling either mutillid or wingless tiphid females, and often (except in Bradynobaeninae) with felt lines on the lateral faces of the second gastric tergum. The female trunk has a flexible articulation between the pronotum and mesonotum. The hairs may be simple, plumose, barbate, or scale-like. There are paired stridulitra on the base of tergum IV of the gaster in Chyphotinae and Typhoctinae; these are absent in the other 2 subfamilies. The true second abdominal segment (petiole) is more or less constricted behind (nodose) and pedunculate in front, and in Aptergyninae the third segment also is constricted behind to form a nodose postpetiole.

The larva, life history, and prey are still not known for any bradynobaenid species. The family contains more than 200 known species, described and undescribed, in 5 or 6 genera distributed among 4 subfamilies, concentrated in the dry parts of the north and south temperate zones and Africa. Bradynobaeninae consist of less than 10 species in southern South America. Typhoctinae have about 10 species which extend from the arid regions of the southeastern United States southward to southern South America. Aptergyninae have up to 100 species in southern Europe, Asia, and Africa. Chyphotinae consist of about 100 species from the western United States and Mexico.

**References.** D. J. Brothers, Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae, *Univ. Kans. Sci. Bull.*, 50:483–648, 1975.

### Pompiloidea

Slender solitary wasps, 2.5 to over 60 mm long, usually winged (and active fliers), but in a few genera brachypterous or apterous in one or both sexes. The antennae are slender and 12-merous (rarely 13-merous) in the female, 13-merous in the male. The prothorax is flexibly linked to the mesothorax. The legs are long, especially the hind tarsi; the middle and hind tibiae have prominent paired apical spurs. On the hindlegs, one of the spurs of each tibial apex is pectinate, forming a preening comb opposed to a basitarsal strigil. When wings are present, venation is relatively full; there is at least one closed basal cell in the hindwing, and the jugal and anal lobes are developed.

The larvae are hymenopteriform, and parasitoidal on spiders (Pompilidae) or crickets (Rhopalosomatidae). There are over 2000 species, mostly spider wasps, widespread in tropical and temperate lands. This superfamily includes the 2 families mentioned.

**References.** E. F. Riek, Hymenoptera, in *The Insects of Australia*, University of Melbourne Press, 1970.

**Rhopalosomatidae.** Cricket wasps. These are slender wasps with a body 2.5 to 20 mm long. They are ferruginous, tan, or black and yellow in color; they may be fully winged, brachypterous or apterous, according to genus. In females, antennae are always 12-merous; in males they are 13-merous. In general the Rhopalosomatidae are similar to the Pompilidae, but they lack the transverse-oblique mesopleural groove. The petiole (abdominal segment II) is separated from the succeeding segment by a distinct constriction.

The larvae, living in sacs formed from their own shed exuviae, are attached to the abdomens of crickets, particularly Eneopterinae and Trigonidiinae, upon whose tissues and juices they feed. They are hymenopteriform, with 10 pairs of spiracles, all apparently functional. Body setae are absent, and there are no pleural bosses or lobes. The mandibles are finely denticulate along the masticatory margins (*Rhopalosoma*).

The family includes perhaps 20–25 species, described and undescribed, distributed among 5 or 6 genera. It is widespread, but occurs sporadically in the temperate and tropical parts of the world, and is uncommon in collections.

**References.** C. T. Brues, The American species of *Rhopalosoma*, *Ann. Entomol. Soc. Amer.*, 36:310–318, 1943.

**Pompilidae.** Spider wasps. These active wasps are 3–60 mm or more long. They are often black or metallic blue, with orange or yellow wings (*Pepsis*), but otherwise they vary widely in color with the genus and species. In death, the antennal apices often form distinctive circular curls as seen from above. The long legs, with long, paired apical spurs on the middle and hind legs, are good identification marks. The mesopleuron is crossed by a "horizontal" groove or "suture," actually somewhat oblique.

Females lay their eggs on spiders (rarely on Opiliones) which they first hunt and sting to death or paralysis. (*Ceropales* and other cleptoparasites oviposit on the prey that another spider wasp has secured as provender for her own larva.) The hunting female characteristically flips her wings as she rapidly walks about, as do some spider-hunting sphecids. The prey spider may be left, with egg attached, in its own burrow, or it may be left in a burrow dug by the female wasp either before or after she secures the spider prey, this behavior differing according to wasp genus. Some species use curled bark or preformed beetle bur-

rows as nests for the larvae, and others build mud cells. Each larva has a single spider.

The larva is hymenopteriform, with lateral pleural lobes or bosses on most segments. The second thoracic spiracle is vestigial. The mandibles have paired apical teeth and a blunt or truncate subapical tooth; more rarely, they may have just one apical point, and be otherwise unarmed. (The larva of *Ceropalinae* is unknown.)

Classification is incomplete and partly in disarray, burdened with ill-defined and shifting "subgenera" and "subspecies," but there exist an estimated 2000–3000 known, described and undescribed species in perhaps 150 good genera. Three subfamilies are now recognized in this family: Pompilinae, Pepsinae, and Ceropalinae. However, the first two of these are only weakly separated and probably should be merged.

**References.** H. E. Evans, Comparative ethology and the systematics of spider wasps, *Syst. Zool.*, 2:155–172, 1953.

### Formicoidea

Superfamily of aculeate Hymenoptera containing a single family, Formicidae, the ants, characterized by the familiar antlike form in the worker, or neuter female, caste. The pinched waist of the Aculeata, separating the trunk from the petiole (=abdominal segment II), is in ants usually augmented by a second constriction between abdominal segments II and III, so that II is left as a nodiform or squamiform petiole. In about half the ants, for instance, Myrmicinae, Pseudomyrmecinae, *Eciton*, and so on, segment III is also constricted behind and forms a postpetiole. The final tagma, consisting of the joined true abdominal segments III or IV through VIII (and the vestigial apical segments VIII–X), is the gaster. The antennae are elbowed, with a broad, usually elongate scape and 3–11 additional segments, which are collectively the funiculus (in the queen and worker); they are varied in form, with 10–13 segments (rarely fewer) in the male. Primitively there is a complex metapleural gland opening above the metacoxa, but this is secondarily lost in a variety of species scattered through the superfamily. Wings are most often present in males and unmated queens. They are eventually shed in fertilized queens, but many species have wingless queens, or even substitute fertile workers for normal queens.

All species form perennial societies living in nests made in the soil, in rock crevices, in rotten wood, under bark, and in hollow stems and other plant cavities, or fashioned from agglutinated plant fibers on leaves or branches; a few ants use larval silk to build leaf nests or line hollows in the earth. A nest normally consists of one or more fertile, ovipositing queens, ten to millions of neuter workers, and brood, plus seasonally produced males, or drones, that serve to fertilize the queens, usually during a mass nuptial flight.

Ant societies, or colonies, reproduce independently by two principal means: dispersal and subsequent isolation of newly mated foundress queens in an incipient-nest chamber; and swarming or nest division, polarized around dealate fertile queens that depart, each drawing a retinue of workers from the parent colony. A third (dependent) class of colony foundation includes various kinds of inquilinism, in which specialized queens gain entrance to the nests of host species and subdue or appease the workers, parasitizing or eventually replacing the host colony.

Ecological studies, especially in the tropics and temperate arid lands, are increasingly revealing the astonishingly high biomass of ants and their potent role in the transformation of energy and the mixing of the soil.

Their food is varied. Many ants are specialized predators of arthropods, and many are scavengers, feeders on nectar, homopteran honeydew, and so forth. Several genera of the subfamily Myrmicinae harvest seeds, while the New World Attini cultivate fungi on leaves or other vegetable matter.

This superfamily is worldwide and abundant, except in high arctic and alpine areas and wet tropical forest above about 2000 m. There are about 14,000 known species in about 240 valid genera, but these numbers will probably rise to at least 15,000 and 300.

**References.** E. O. Wilson, *The Insect Societies*, Belknap/Harvard University Press, Cambridge, 1971.

### Scoliioidea

Superfamily containing 1 family, Scoliidae. They are large, robust wasps (length 8–60 mm). The males are smaller and more slender than the females. Both sexes are covered with black, golden, or otherwise richly pigmented pilosity. The integument may be black, fulvous, red, or strikingly part-colored. Wings are always present; they may be hyaline, fuscous, metallic blue-black, yellowish, or coppery. The membrane of the apical fields of both wings is finely longitudinally corrugated (striolate). The anal lobe of the hindwing is distinct; there is no jugal lobe. The antennae are 13-merous in the male and 12-merous in the female. The inner margins of the eyes are deeply notched. The apical spurs of the tibiae occur 1,1,2. The tarsal claws are simple. The extensor surfaces of the middle and hind tibiae often have oblique conical teeth or setae in females. The propodeum is divided into three parts by two longitudinal sutures. The male hypopygium is trispinose.

The females seek out scarabaeid (more rarely, large curculionid) larvae in the soil, rotten wood, palms, and so forth. They sting them and oviposit upon them much in the manner of *Tiphia*, and the wasp larvae develop singly as external parasitoids. Male and female adults spend much time at flowers and other sources of nectar or honeydew.

Scoliioidea has long been considered to include such families as Tiphidae and Mutillidae, but D. J. Brothers considers Scoliidae and Tiphidae to be convergent.

Scoliidae are found worldwide; they are widespread in the temperate and tropical regions. This family is one more taxon suffering from excessive splitting into genera and "subgenera" and, at a lower level, the description of many "subspecies," most of which are based on minor geographical variation in color, sculpture, and pilosity. Such hemitaxa tend to obscure species relationships and adaptive trends, and make tidy inventory very difficult. The family is estimated to contain about 20 genera and over 300 species. Some authors have recognized 2 subfamilies, but this division does not seem to be called for.

**References.** C. P. Clausen, *Entomophagous Insects*, pp. 302–307, McGraw-Hill, New York, 1940.

### Vespoidea

Both sexes are winged. The eyes are usually medially emarginate. The antennae are 13-merous in the male and 12-merous in the female. The pronotum is reduced and constricted mesally; the posterolateral corner is somewhat produced above the anterior margin of the tegula. The mesonotum is enlarged and produced anteriorly. The coxae are contiguous. The first tergum of the gaster overlaps the sternum and is often partly fused with it. There is a marked constriction between sterna I and II. Tergum VII

is reduced. The parameres in the male are generally spine-like. The majority of species also have an elongate median cell in the forewing, and fold the wings longitudinally at rest.

These wasps are common in disturbed habitats and dry areas, as well as rain forests. The female constructs nests consisting of burrows in soil or twigs, free mud cells, or paper combs. One egg is laid per cell before provisioning; provisions consist either of arthropod prey or nectar and pollen. The adults are nectar-feeding.

This large cosmopolitan superfamily of aculeate Hymenoptera is most diverse in tropical regions. The behavior of these wasps ranges from solitary to eusocial. There are more than 4000 species in 3 families (Masaridae, Eumenidae, and Vespidae).

[JAMES M. CARPENTER]

**References.** O. W. Richards, *A Revisional Study of the Masarid Wasps*, British Museum (Natural History), London, 1962.

**Masaridae.** Uncommon melliferous wasps. The labrum is short and broad in most species. The paraglossae are short, lacking acroglossal "buttons". The labiomaxillary complex is retractile in some Masarinae. The mandibles are short and broad. The mid femur has no basal ring, except in *Euparagia*; usually there are two mid-tibial spurs; claws may be either simple or toothed. The forewing has two submarginal cells in the Masarinae and three in the Gayellinae and Euparagiinae. The median cell is rarely elongate; the wings are not longitudinally folded at rest (except in *Celonites* and *Quartinia*). The first tergite and sternite are not fused in the gaster; segments after II are not retractile.

These are solitary wasps. Their nests are constructed in the ground or as a series of mud cells attached to rocks or plants. Provisions consist of a mass of nectar and pollen in all genera except *Euparagia*, which utilizes larval chrysome-

This is a small and relictual family with 19 genera and about 230 species arranged in 3 subfamilies (Gayellinae, Euparagiinae, and Masarinae).

[JAMES M. CARPENTER]

**References.** O. W. Richards, *A Revisional Study of the Masarid Wasps*, British Museum (Natural History), London, 1962.

**Eumenidae.** Solitary wasps. The labrum is flat and narrow; the glossae and paraglossae have sclerotized pads or acroglossal "buttons" (except *Raphiglossa*). The malar space is very short. The mandibles are elongate, crossing in Eumeninae. The mid femur has a basal ring, and the mid tibia has one apical spur (some Zethinae have two). The claws are almost always bifid. The forewing has three submarginal cells, and the median cell is elongate. At rest the wings are folded longitudinally. The gaster usually has the first tergite and sternite partly fused; segments after II are retractile.

These wasps have predatory and melliferous habits. Their nests consist of a few cells constructed in the soil, twigs, or old aculeate bores in wood, or of variously shaped mud cells attached to plants or rocks. Their prey consist predominantly of lepidopteran larvae; some species use coleopteran larvae. Certain species of the genera *Zethus* and *Synagris* are subsocial.

This is the most diverse family in the Vespoidea, with more than 120 genera and 3000 species; there are 3 subfamilies (Zethinae, Raphiglossinae, and Eumeninae). Zethinae are pantropical; they are diverse in arid re-

gions. Raphiglossinae are a small group with limited, primarily African distribution. Eumeninae are cosmopolitan and speciose.

[JAMES M. CARPENTER]

**References.** F. D. Parker, A revision of the North American species in the genus *Leptochilus* (Hymenoptera: Eumenidae), *Misc. Publ. Entomol. Soc. Amer.*, 5:151–229, 1966.

**Vespidae.** The labrum is narrow and often reduced. The glossae and paraglossae are short and equal in length, with acroglossal "buttons" (except in Stenogastrinae). The malar space is often long, and the mandibles do not cross. There is a basal ring on the mid femur or fore femur or both (lost in *Mischocyttarus*). The mid tibia usually has two apical spurs. The claws are simple or, rarely, toothed. The forewing has three submarginal cells, and the median cell is elongate. At rest the wings are folded longitudinally (except in the Stenogastrinae). The gaster has the first tergite and sternite partly fused; the segments after II are retractile.

The habits of this family are predatory and melliferous. The degree of sociality of Stenogastrinae and some Polistinae is very slight. Nests are constructed of masticated plant fibers; they consist of a few to many cells arranged in combs. The colonies consist mostly of sterile females; they are annual in temperate zones and may be perennial in the tropics. The larvae are fed a masticated paste of arthropod prey.

Mostly eusocial and socially parasitic wasps; the family consists of 3 subfamilies (Stenogastrinae, Polistinae, and Vespinae), with about 36 genera and more than 800 species.

Distribution is worldwide. The primitive Stenogastrinae are confined to the Indo-Malayan region. The Vespinae are centered in the Oriental tropics, with a number of holarctic species. The Polistinae are concentrated in the American tropics.

[JAMES M. CARPENTER]

**References.** J. P. Spradbery, *The Wasps*, University of Washington Press, Seattle, 1973.

## Sphecoidea

Digger wasps and allies; a superfamily with 1 family, Sphecidae. These are minute (2 mm) to large (5 cm) aculeate wasps, always winged, with a stigma and seven or more closed cells in the forewing, and at least two in the hindwing; the jugal lobe is distinct. The antennae have 13 (rarely 12) segments in the male and 12 in the female. The sexes are usually alike, although the legs often differ in conjunction with sexual behavioral differences. The pronotum is immovably fused to the mesothorax, but there is usually a ridge or collar and a suture near their dorsal junction. Each side of the pronotum has a posterior lobe covering the spiracle, but usually not extending to the tegula. The posterior margin of the pronotum is usually straight in the dorsal view.

Sphecids are most frequently associated with definite nests, dug or prepared by the female, usually alone, but in a few genera the nests are fashioned cooperatively by two or more females in a subsocial, or even (*Microstigmus*) eusocial, effort. Nests are dug in the soil, in rotten or sound wood, and in hollow twigs or other plant cavities, or they are built of mud or plant fibers in a variety of other places. A few species are cleptoparasites of other wasps. Adult sphecids feed on flower nectar, homopterous honeydew, and other free sources of sugar; some females take hemolymph oozing from sting punctures in the prey they capture. This prey in most cases consists of a live insect or spider, which is stung and paralyzed or killed, and carried to the nest,

where an egg is deposited on it. The female may then close the cell and nest and leave her larva alone to hatch, feed on the prey, and pupate. In some genera, however, she continues to provision each cell with new prey items during larval life. Progressive provisioning of the larva is evidently a step necessary in the evolution of social life in aculeate Hymenoptera.

Most species of sphecid wasps choose their prey from a fairly narrow taxonomic range, such as a single suborder, family, or even genus, but there are also scavengers, such as *Microbembex*, which gathers a wide variety of dead arthropods for larval food.

Sphecoidea (Sphecidae) include 11 subfamilies, 226 genera, and about 7700 described species, but many species remain undescribed. These wasps are worldwide in distribution, with the exception of Antarctica and other extremely cold areas. The subfamilies are: Larrinae, Nyssoninae, Crabroninae, Philanthinae, Pemphredoninae, Sphecinae, Ampulicinae, Astatinae, Laphyragogaenae, Xenosphecinae, and Entomosericinae.

**References.** R. M. Bohart and A. S. Menke, *Sphecid Wasps of the World*, University of California Press, Berkeley, 1975.

## Apoidea

Bees. These are minute (2 mm) to large (4 cm) flower-visiting aculeate Hymenoptera which form a sister group with the Sphecoidea, and sometimes are united with them in 1 superfamily. The adults differ from sphecid wasps by having at least a few plumose (branched) hairs, the hind basitarsus at least slightly broader than the more distal tarsomeres, and the seventh gastral tergum of the female fully separated into two hemitergites.

All bees feed on pollen and nectar both as larvae and as adults. Many solitary species are oligolectic, restricting their pollen collecting to a few closely related plant species, although such bees are usually less restricted in their nectar sources. Other solitary species and all social species are polylectic, visiting a wide variety of plant species for pollen, although individual bees typically remain constant to a given plant species for many successive foraging flights.

All nonparasitic bees construct nests in which the immature stages develop. Nests may be dug in the soil or in rotten or sound wood, or may be constructed within hollow twigs and a wide diversity of other cavities. They may also be freestanding structures built of mud, resin, or wax produced by the bee itself. Most species build multi-cellular nests, and cells are frequently lined with Dufour's gland secretions or with foreign materials brought to the nests. Most bees nest solitarily and mass-provision cells before oviposition with a mixture of pollen and honey (concentrated nectar). Nectar is carried to the nest in the crop, and pollen is carried on special hairs (scopa) on the hindlegs or the gaster or (in some Colletidae) in the crop. After oviposition the cells are closed, and no larval-adult interactions occur. Communal nesting, in which several adult females share a nest and all lay eggs, has evolved multiple times in the Apoidea. Semisocial nesting, in which related bees of the same generation share a nest and some do not reproduce but instead act as workers, frequently occurs in the founding of colonies that will later be eusocial. This is a terminal strategy in some Halictidae. Truly social or eusocial nesting, with overlap of generations, the mothers becoming reproductive queens and some adult daughters becoming nonreproductive workers, has evolved inde-

pendently at least five times in the Apoidea, in 2 tribes of sweat bees (Halictidae), in Old World carpenter bees (Anthophoridae), and two times in the Apidae, in the stingless bees, and in the bumblebees and honeybees. Progressive provisioning is characteristic only of the carpenter bees, bumblebees, and honeybees.

Cleptoparasitism, or cuckoo behavior, in which eggs are laid in the cells of other species and the adult female or modified first-instar larva kills the immature host and the cleptoparasitic larva consumes the host's provisions, has evolved repeatedly among the Apoidea. Adult cleptoparasites lack scopae and superficially resemble sphecids wasps. Social parasitism has evolved among the sweat bees, carpenter bees, and bumblebees.

This superfamily includes 8 families and over 400 genera and 20,000 species, distributed worldwide except for the coldest regions.

[GEORGE C. EICKWORT]

**References.** C. D. Michener, A classification of the bees of the Australian and South Pacific regions, *Bull. Amer. Mus. Natur. Hist.* 130:1–362, 1965; C. D. Michener, Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera), *Bull. Amer. Mus. Natur. Hist.* 82:151–326, 1944; C. D. Michener, *The Social Behavior of the Bees*, Harvard University Press, Cambridge, 1974; T. B. Mitchell, *Bees of the Eastern United States*, vols. 1 and 2, N.C. Agr. Exp. Sta. Tech. Bull. no. 141, 1960, and no. 152, 1962.

**Colletidae.** The labial palpal segments are similar and subcylindrical. The postpalpal portion of the galea is much shorter than the stipes. The glossa is short, broad, truncate or bilobed (except in a few males); the exposed portion of the middle coxa is much shorter than the distance from the summit to the posterior wing base.

A suite of plesiomorphic characters, especially the wasplike glossa, characterizes the Colletidae as the most primitive family of bees. They vary from the small, slender, wasplike Hylaeinae and Euryglossinae that carry pollen to the nests in the crop, to the other subfamilies of more robust, hairy bees with a pollen-collecting scopa on the gaster or hindlegs or both. All known species are nonparasitic and nest solitarily or, rarely, communally. Many species construct nests in the soil, and others, especially among the Hylaeinae and Xeromelissinae, nest in hollow twigs and other cavities. All nest cells are lined with a translucent or transparent, cellophanelike Dufour's gland secretion that holds the semiliquid provisions.

The family contains about 45 genera and probably over 3000 species. Colletidae are distributed worldwide, with the greatest representation in the Southern Hemisphere, especially Australia. The subfamilies are: Colletinae (worldwide), Diphaglossinae (New World, principally neotropical), Hylaeinae (worldwide), Xeromelissinae (=Chilicolinae; neotropical), and Euryglossinae (Australian). The Australian Stenotritinae are usually placed in the Colletidae, although they differ in having a blunt glossa and a waxlike rather than cellophanelike cell lining coupled with a firm provision mass.

[GEORGE C. EICKWORT]

**References.** C. D. Michener, The classification of the Diphaglossinae and North American species of the genus *Caupolicana* (Hymenoptera, Colletidae), *Univ. Kans. Sci. Bull.*, 46:717–751, 1966; R. R. Snelling, Studies on North American bees of the genus *Hylaeus*, 3: The Nearctic subgenera (Hymenoptera, Colletidae), *Bull. S. Calif. Acad. Sci.*, 65:164–175, 1966; W. P. Stephen, A revision of the bee genus *Colletes* in America north of Mexico (Hymenoptera,

Colletidae), *Univ. Kans. Sci. Bull.*, 36:149–527, 1954; H. Toro, and C. D. Michener, The subfamily Xeromelissinae and its occurrence in Mexico (Hymenoptera: Colletidae), *J. Kans. Entomol. Soc.*, 48:351–357, 1975.

**Halictidae.** The prepupal portion of the galea is usually as long as the postpalpal portion and evenly tapered to a slender basal point. The mentum and submentum are virtually absent. The glossa is acute, and may be short or long. The exposed portion of the middle coxa is much shorter than the distance from the summit to the posterior wing base.

Halictidae are a very large family of small to medium-sized bees, and in many areas are second only to honeybees in their abundance. Many species of Halictinae are called sweat bees because of their habit of lapping perspiration from human skin. Most Halictidae are polylectic and are common visitors to alien weeds, although some are oligolectic, and one, the alkali bee *Nomia melanderi*, is an important pollinator of alfalfa (lucerne). Nests are built in the soil or, more rarely, in rotten wood, and cells are lined with waxlike Dufour's gland secretions.

While most species are solitary, all intermediates between solitary and primitively eusocial nesting occur within the Halictidae, especially in the Halictinae. The evolutionary steps that have led to the appearance of a sterile worker caste, and the selective pressures that have produced each intermediate stage, can be better seen in the Halictinae than in any other insect taxon. Intensive studies of the sweat bee *Dialictus zephyrus* have provided especially valuable insights into primitive eusocial behavior. Species in several genera are cleptoparasites in nests of other bees, and a few social parasites in the nests of eusocial Halictinae are known.

The family contains about 60 genera (many more if the subgenera of *Lasioglossum* and *Nomia* are recognized as genera) and probably over 5000 species in 3 subfamilies: Halictinae, Nominae, and Dufoureae. Halictidae are distributed worldwide.

[GEORGE C. EICKWORT]

**References.** G. C. Eickwort, A comparative morphological study and generic revision of the augochlorine bees (Hymenoptera: Halictidae), *Univ. Kans. Sci. Bull.*, 48:325–524, 1969; C. D. Michener, A generic review of the Dufoureae of the Western Hemisphere (Hymenoptera: Halictidae), *Ann. Entomol. Soc. Amer.*, 58:321–326, 1965; C. D. Michener, The parasitic groups of Halictidae (Hymenoptera, Apoidea), *Univ. Kans. Sci. Bull.*, 51:291–339, 1978.

**Andrenidae.** The labial palpal segments are similar and cylindrical, or the first (rarely also the second) segment may be elongate and flattened. The glossa is acute, and may be short or long. There are two (rarely one) subantennal sutures from each antennal socket to the clypeus; the first antennal flagellar segment is shorter than the scape. The exposed portion of the middle coxa is much shorter than the distance from the summit to the posterior wing base. A stigma is present. The apices of the posterior femora of the female are unmodified.

Andrenid bees are rather generalized, soil-nesting species, with no cleptoparasitic forms. Andreninae are among the most abundant spring bees of the Holarctic Region and range from polylectic to oligolectic, while Panurginae are especially diverse in arid regions and are typically oligolectic. Andrenid bees produce a wax-like cell lining from Dufour's gland secretions. These secretions are also used to coat the provision mass by Panurginae; some Panurginae

have coated provision masses and unlined cells. Andrenid nests may be solitary or communal.

The family contains 2 subfamilies, Andreninae and Panurginae, with about 20 genera and probably over 4000 species. Members are distributed worldwide except for Australia.

[GEORGE C. EICKWORT]

**References.** J. G. Rozen, Jr., Review of the biology of panurgine bees with observations on North American forms (Hymenoptera, Andrenidae), *Amer. Mus. Novitates*, 2297: 1-44, 1967.

**Oxaeidae.** The first labial palpal segment is elongate and flattened, and the remaining segments are short and subcylindrical. The glossa is acute and short. There are two subantennal sutures from each antennal socket to the clypeus. The first antennal flagellar segment is at least as long as the scape. The exposed portion of the middle coxa is much shorter than the distance from the summit to the posterior wing base. The stigma is virtually absent. The apices of the posterior femora of the female are flattened, and enlarged plates are associated with the basitibial plates.

Oxaeidae are a very small family of large, fast-flying bees, sometimes placed as a subfamily of Andrenidae because of the two subantennal sutures. These bees dig deep solitary or communal soil nests and are narrowly polylectic. The males have large eyes, and conspicuously guard territories.

The family includes 4 genera and 20 species. Oxaeidae are found in the New World, principally in the Neotropical Region.

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**References.** P. D. Hurd, Jr., and E. G. Linsley, *The Bee Family Oxaeidae with a Revision of the North American Species (Hymenoptera: Apoidea)*, Smithsonian Contrib. Zool. no. 220, 1976.

**Melittidae.** The labial palpal segments are similar. The galea is short, and the prepalpal portion is shorter than the postpalpal portion. The submentum is V-shaped, and the mentum is tapered basally. The glossa is acute, ranging from short to long. The exposed portion of the middle coxa is much shorter than the distance from the summit to the posterior wing base.

Melittidae are a small but diverse family with mouthparts intermediate between those of the more plesiomorphic "short-tongued" bees (Colletidae, Halictidae, Andrenidae, and Oxaeidae) and the apomorphic "long-tongued" bees (Megachilidae, Anthophoridae, and Apidae). The species dig nests in the soil or build nests in preexisting cavities, especially in wood, and all are solitary and nonparasitic. Some, but not all, melittid larvae spin cocoons.

The family contains about 12 genera and several hundred species. Melittidae are distributed worldwide except for South America. The subfamilies are: Melittinae (holarctic and African), Dasypodinae (holarctic and African), Macropidinae (holarctic), and Ctenoplectrinae (Oriental, African, Australian).

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**References.** J. G. Rozen, Jr., The relationships of the bee subfamily Ctenoplectrinae as revealed by its biology and mature larva (Apoidea: Melittidae), *J. Kans. Entomol. Soc.*, 51:637-652, 1978.

**Megachilidae.** The first two labial palpal segments are elongate and sheathlike. The galea is greatly elongated; the submentum is V-shaped, and the mentum tapered basally. The glossa is elongate, with a flabellum (apical expansion). The labrum is longer than broad, and the middle coxa is over two-thirds as long as the distance from the summit to

the posterior wing base. The scopa of nonparasitic females is restricted to the venter of the gaster.

Megachilidae are a large, rather distinctive family of long-tongued bees whose females carry pollen only on the hairs of the venter of the abdomen. Many species are broadly to narrowly oligolectic and are efficient at gathering pollen from particular flowers, as is the alfalfa leaf-cutter bee, *Megachile rotundata*. In contrast to most bees in other families, megachilids do not line their cells with glandular secretions, but instead bring foreign materials to the nest to line the cells, or at least to close them. Such materials include cut leaves, chewed leaf material, plant hairs, resin, mud, and pebbles. While some species excavate nests in the soil or in wood, many "rent" hollow stems and other cavities and some build freestanding masonry or resin nests. Megachilid larvae spin cocoons, unlike most other noneusocial bees. Most species nest solitarily, although a few, especially the mason bees, nest communally. None is eusocial. Several genera contain species that are cleptoparasites in nests of other megachilid bees.

The family contains about 95 genera and probably over 3000 species. Megachilidae are distributed worldwide. The subfamilies are Megachilinae, Lithurginae, and Fidelinae. Until recently, Fidelinae had been placed as a subfamily of Apidae or as a separate family.

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**References.** P. D. Hurd, Jr., and C. D. Michener, The megachilid bees of California, *Bull. Calif. Insect Surv.*, 3: 1-248, 1955; C. D. Michener, The generic classification of the anthidiine bees (Hymenoptera, Megachilidae), *Amer. Mus. Novitates*, 1381:1-29, 1948; J. J. Pasteels, La systématique générique et subgénérique des Anthidiinae (Hymenoptera, Apoidea, Megachilidae) de l'Ancien Monde, *Mem. Soc. Roy. Entomol. Belg.*, 31:1-148, 1969; J. G. Rozen, Jr., The ethology and systematic relationships of fidelid bees, including a description of the mature larva of *Parafidelid* (Hymenoptera, Apoidea), *Amer. Mus. Novitates*, 2637:1-15, 1977.

**Anthophoridae.** The first two labial palpal segments are elongate and sheathlike. The galea is greatly elongated. The submentum is V-shaped, and the mentum is tapered basally. The glossa is elongate, usually with a flabellum (apical expansion). The labrum is broader than long (except in some cleptoparasites). The middle coxa is over two-thirds as long as the distance from the summit to the posterior wing base. The scopa of nonparasitic females is restricted to the hind tibia and the basitarsus, and does not form a corbicula.

Anthophoridae are a very large family consisting of three distinctive subfamilies that older classifications often considered to be subfamilies of Apidae or to be separate families.

Anthophorinae are generally rather large, hairy, fast-flying bees. Many are oligolectic. Most species nest in soil, although a few nest in wood, and the cells are lined with a waxlike secretion. Anthophorine nests may be solitary or communal, and species in 2 tribes are cleptoparasites in the nests of other anthophorines.

Nomadinae are all cleptoparasites and are diverse and wasplike in appearance. The subfamily is considered to be monophyletic on the basis of larval and behavioral characters. Females of all species lay their eggs inside the cell lining of their host nests, and the modified first-instar larvae kill the host egg or larva. Hosts include most taxa of soil-nesting bees.

Xylocopinae are the carpenter bees, and nearly all species

nest in vegetation, the small carpenter bees (Ceratinini) using pithy or hollow stems, and the large carpenter bees (Xylocopini) using solid wood or sometimes large stems. The nest cells are unlined. Adults are typically long-lived, and prolonged contact of adults and their larvae, with some elements of subsocial care, occurs commonly. Subsocial care is best developed in the paleotropical and Australian allodapine group of genera of the Ceratinini, in which eggs and larvae are reared in a common cavity in a stem, and the larvae are fed progressively in most species. Semisocial associations are common in allodapine nests and occur in other Xylocopinae, and primitively eusocial colonies are known for several species of allodapines. A few species of allodapine bees are cleptoparasites in the nests of other allodapines. Synapomorphic behavioral and morphological traits suggest that the Xylocopinae share a common ancestor with the Apidae.

The family contains over 170 genera and probably over 4000 species in 3 subfamilies: Anthophorinae, Nomadinae, and Xylocopinae. Anthophoridae are distributed worldwide.

[GEORGE C. EICKWORT]

**References.** P. D. Hurd, Jr., An annotated catalog of the carpenter bees (genus *Xylocopa* Latreille) of the Western Hemisphere (Hymenoptera: Anthophoridae), Smithsonian Institution Press, Washington, 1978; W. E. LaBerge, The genera of bees of the tribe Eucerini in North and Central America (Hymenoptera, Apoidea), *Amer. Mus. Novitates*, 1837:1-44, 1957; C. D. Michener, A taxonomic study of African allodapine bees (Hymenoptera, Anthophoridae, Ceratinini), *Bull. Amer. Mus. Natur. Hist.*, 155:67-240, 1975; J. G. Rozen, Jr., K. R. Eickwort, and G. C. Eickwort, The bionomics and immature stages of the cleptoparasitic bee genus *Protepeolus* (Anthophoridae, Nomadinae), *Amer. Mus. Novitates*, 2640:1-24, 1978.

**Apidae.** The first two labial palpal segments are elongate and sheathlike, and the galea is greatly elongated. The submentum is V-shaped, and the mentum tapers distally. The glossa is elongate, with a flabellum. The labrum is broader than long. The middle coxa is over two-thirds as long as the distance from the summit to the posterior wing base. The scopa of the nonparasitic females forms a corbicular (a smooth area surrounded by long hairs) on the hind tibia.

Apidae are the only family of Apoidea in which most species are eusocial, and include all of the advanced eusocial bees. The 3 subfamilies (Bombinae, Meliponinae, and Apinae) are distinctive, and older classifications sometimes gave them familial status. Apidae construct cells of wax or resin, typically within natural cavities, or sometimes free-standing; they do not dig nest burrows. The larvae spin cocoons.

Bombinae include the orchid bees (Euglossini) and bumblebees (Bombini). Euglossini are large, beautiful, very long-tongued bees, resembling bumblebees or with metallic greens, blues, purples, and reds. Many orchids depend on male euglossines for pollen transfer; the male bees in turn collect secretions from the orchids and apparently use them as pheromones. Euglossine bees construct cells of resin,

often supplemented by mud, mammalian feces, or bark. Euglossine nests are solitary or communal. A few Euglossini are cleptoparasitic in the nests of other euglossines. Bumblebees are familiar to nearly everyone. All nonparasitic species of Bombini are primitively eusocial and are among the more important pollinators of many temperate plants. Bumblebees construct cells of secreted wax inside various natural shelters such as abandoned rodent nests. In nearly all species several eggs are laid in a single cell, and the larvae are fed progressively. The endothermic abilities of bumblebees allow them to fly at colder temperatures than most other bees and to incubate their brood. Some Bombini are social parasites in the nests of other bumblebees. Bombini are primarily holarctic, with some neotropical and Oriental species, while Euglossini are neotropical.

Meliponinae are the highly eusocial stingless bees. All form perennial colonies with well-differentiated queen and worker castes, and new colonies are produced by swarming. Brood cells are mass-provisioned and built of wax mixed with resin; they are arranged in combs that are separate from the differently shaped provision storage pots. The nest cavity is variously surrounded by plates of wax mixed with resin and any of a huge variety of foreign substances. In their highly advanced social behavior and sophisticated communication systems, the stingless bees rival the honeybees. A few species are robber bees that obtain their provisions from nests of other species. Meliponinae are undoubtedly important pollinators in the tropics, and have been a source of honey for native Americans. Meliponinae are pantropical, and are probably the most common bees in tropical America. Meliponinae have been considered to be a tribe of the Apinae in many classifications, but recent studies by M. L. Winston and C. D. Michener indicate that highly advanced eusocial behavior arose independently in the honeybees and stingless bees and that the two groups do not form a monophyletic taxon.

Apinae include only the honeybees of the genus *Apis*, with 4 species. All *Apis* species are highly eusocial, and most species are restricted to Asia. *Apis mellifera*, the common honeybee, is also native to Africa and Europe, and has been spread by humans throughout the world. It is the most common bee in many parts of the world and usually is the most important pollinator from a human viewpoint. *Apis mellifera* is the best studied of all insects, and many people are familiar with some aspects of its communication system and social biology.

Apidae are distributed worldwide. The family contains 13 genera and probably less than 1000 species.

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