Unit 10 - Holometabolous development, Hymenoptera

Open Entomology Project

18 October 2016

Introduction

Today we begin looking at a taxon named **Holometabola**, which all exhibit a form of development called **holometaboly**. The immature stage (**larva**) is quite different, usually, from the imago, and the transition to adulthood takes place in a stage we refer to as the **pupa**. We'll discuss this life cycle in more detail in a later lecture. This lecture focuses on **Hymenoptera**, a lineage of almost indescribable diversity (155,000 known species and probably at least a million that need names). Is this the largest order? Possibly. These species, commonly known as sawflies, wasps, bees, and ants, exhibit a broad array of morphologies and life histories. Their ecological and economic importance, as predators (*e.g.*, ants), pollinators (bees), pests (*e.g.*, some herbivorous sawflies), and bio-control agents (numerous parasitic wasps) is enormous.

The predominant parasitoid/predatory lifestyle amongst the derived lineage, Apocrita, is arguably impacted by the appearance of an evolutionary novelty, the wasp waist. The wasp waist separates the locomotory tagma, the mesosoma, from the tagma of reproduction and digestion, the metasoma; it allows for an exceptionally flexible mechanism to maneuver the sting or egg-laying device (ovipositor). Members of this order can be readily separated from other insects based on the following characteristics:

- haplodiploidy (males are haploid)
- smaller hind wings connected to larger fore wings by hook-like spurs (hamuli)
- transverse and longitudinal veins cannot be differentiated (compare with Odonata and Plecoptera, *e.g.*, where transverse veins are usually less sclerotized and more flexible than longitudinal veins)
- protibial apical spur and the first basitarsus is modified into an antenna cleaning device
- abdominal tergite I at least partly fused with metanotum

Materials

- specimens (provided)
- fine forceps, probes (provided)
- sorting tray, watch glasses, gloves, safety glasses, glycerine, ethanol (provided)
- pencil/paper for sketches

Safety

We will be working with sharp tools and insects on pins. Wear your personal protective gear at all times. Specimens are to be returned to their vials after lab, and glycerine and ethanol will be collected for proper disposal or reuse.

Methods

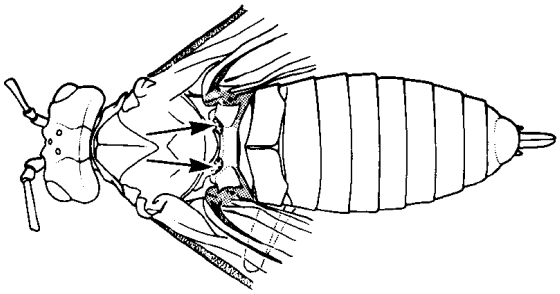
Working with a partner, organize your space, specimens, tools, and microscope. Use your probe and forceps to manipulate the specimen. In this lab, however, we will not be dissecting specimens (unless otherwise noted). You can start anywhere in the handout.

1 Hymenoptera

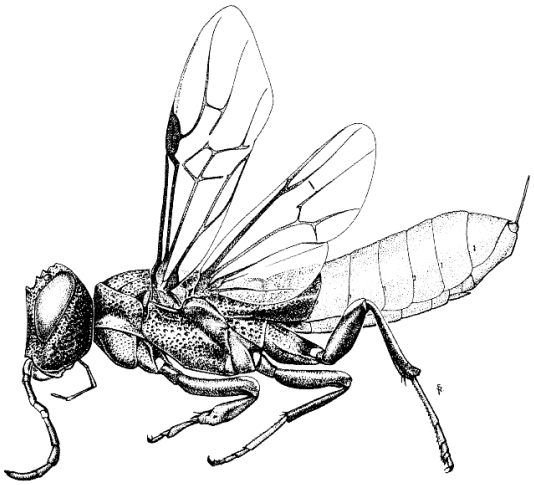
1.1 Non-apocritan Hymenoptera ("Symphyta")

Diagnostic characters: Body in dorsal view with very little or no constriction near its middle between abdominal segments 1 and 2 (*i.e.*, "wasp waist" absent; Figure 1a); cenchrus usually present (arrows in Figure 1a); fore tibia with two apical spurs; never less than 3 mm in length; first abdominal tergite usually divided medially.

Natural history: Non-apocritans, known commonly as "sawflies", are generally phytophagous as larvae. One important exception is the family Orussidae (Figure 1b; not covered in lab), which are parasitoids. Orussidae is understood to be sister to the megadiverse lineage called Apocrita.



(a) Symphytan dorsal habitus (Goulet *et al.*, 1993, pg. 42)



(b) Orussidae habitus (Goulet *et al.*, 1993, Fig. 24)

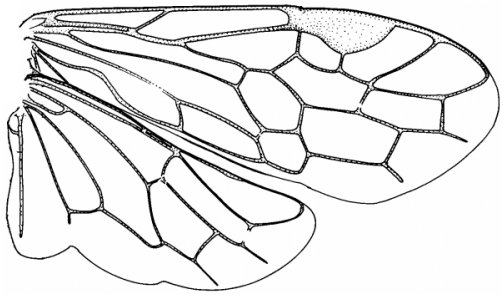
Figure 1

1.1.1 Xyelidae

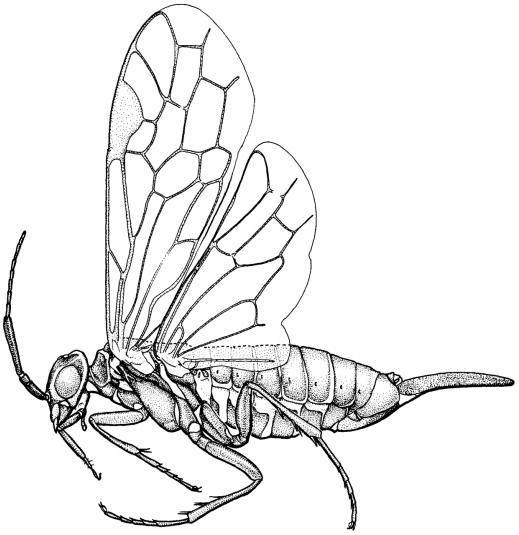
Diagnostic characters: Antennae with less than 10 flagellomeres; proximal-most flagellomere much longer than following flagellomeres; maxillary palp leg-like (Figure 2).

Natural history: Larvae develop inside pollen-producing cones of pine trees (*Pinus* spp.), while adults can be found very early in the spring, feeding on pine and other tree pollen. The oldest hymenopteran fossils (Triassic) look almost like extant xyelids. There are approximately 50 spp.

Question 10-1: Xyleids appear to be sister to all other Hymenoptera, and they exhibit numerous plesiomorphic character states. Can you find any? What is the function of those modified maxillary palps?



(a) Wings (Goulet *et al.*, 1993, modified from Fig. 32)



(b) Habitus (Goulet *et al.*, 1993, Fig. 32)

Figure 2: Xyelidae

1.1.2 Argidae (argid sawflies)

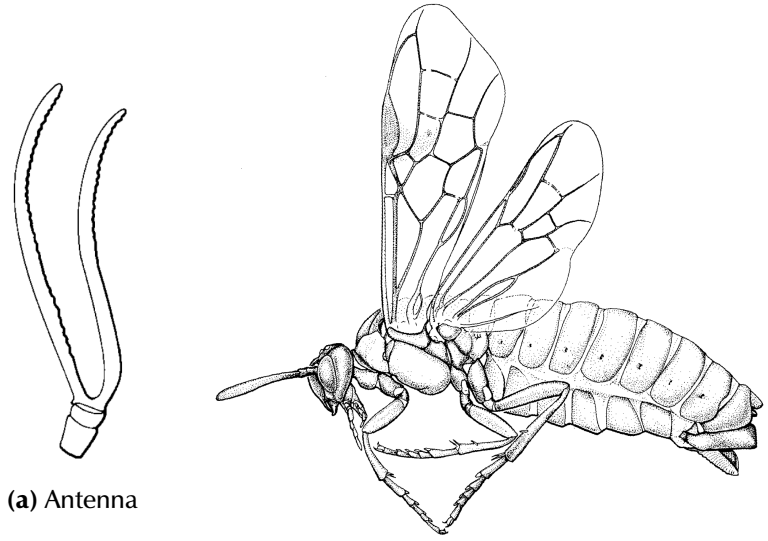
Diagnostic characters: Antenna with 1 flagellomere, sometimes U-shaped (Figure 3a); mesonotum not divided by straight transverse groove; fore wing 2r vein absent.

Natural history: Typically foliage feeders, this taxon is much more diverse in the tropics (>800 spp.) than in North America (~70 spp.)

1.1.3 Diprionidae (conifer sawflies)

Diagnostic characters: Antenna with ~20 flagellomeres, comb-like in males and saw-like in females; fore wing with less than 2 marginal cells; abdominal tergum 1 separated from metapleuron in both sexes.

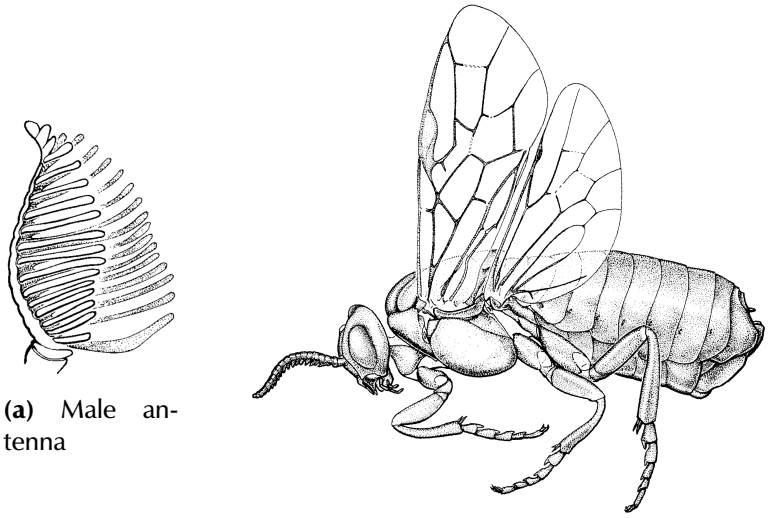
Natural history: Larvae develop as folivores on pines. Some species are considered pests. Larvae often feed gregariously, regurgitating pine resin when disturbed. Almost 100 species have been described.



(a) Antenna

(b) Habitus

Figure 3: Argidae (Goulet *et al.*, 1993, pg. 106 (a) and Fig. 26 (b))



(a) Male antenna

(b) Habitus, male (left) and female (right)

Figure 4: Diprionidae (Goulet *et al.*, 1993, pg. 108 (a) and Fig. 29 (b))

1.1.4 Tenthredinidae (common sawflies)

Diagnostic characters: Antenna with 3–7 flagellomeres (Figure 5); abdominal tergum 1 clearly separated from metapleuron.

Natural history: Larvae are diversely phytophagous, developing as folivores, borers, gallers, and even leaf miners. There are more than 7,000 described spp.

The next family represents a transition in life history, from larvae feeding mostly on leaves to larvae feeding inside wood.

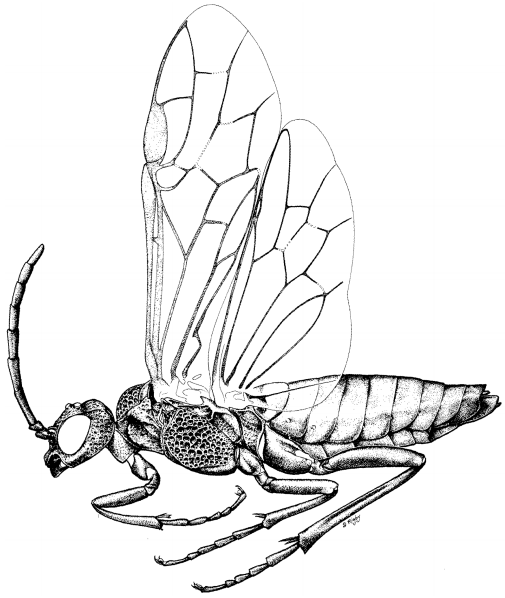


Figure 5: Tenthredinidae, lateral habitus (Goulet *et al.*, 1993, Fig. 31)

Question 10-2: Can you see evidence of this transition in the external morphology of these hymenopterans? Compare Siricidae Tenthredinidae or Argidae, for example, and describe or illustrate a few differences.

1.1.5 Siricidae (horntails)

Diagnostic characters: Antenna with >20 flagellomeres; pronotum with a large dorsal (horizontal) surface (Figure 6a); fore tibia with one apical spur; posterior-most tergum in females and sternum in males with apical projection (Figure 6b)

Natural history: There are ~150 described species. Female siricids have pockets ("mycangia"; we'll see this word again when we cover Coleoptera) at the base of their ovipositors that contain fungi.

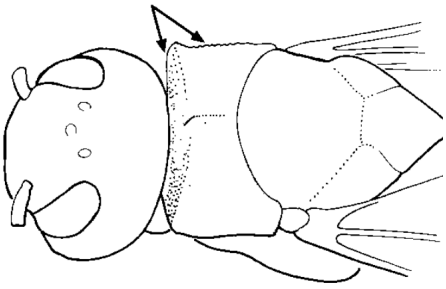
Question 10-3: What do you think is the role of the symbiotic fungi found in siricids?

1.2 Apocrita

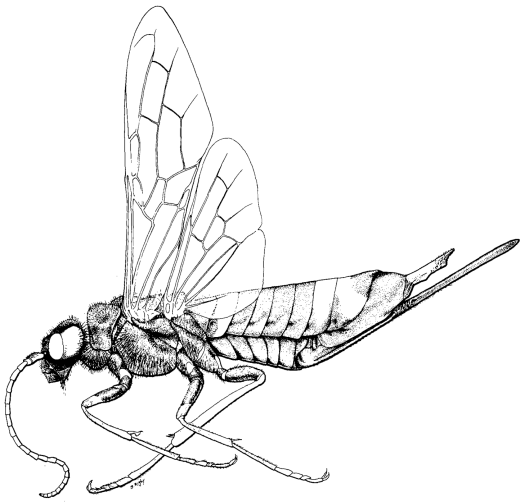
The remaining hymenopterans comprise the megadiverse Apocrita, a lineage characterized in part, at least ancestrally, by developing as parasitoids of other insects. In dorsal view, the body has a distinct constriction near its middle (*i.e.*, "wasp waist" present); note that the middle tagma is referred to as the "mesosoma" and the posteriormost tagma is the "metasoma".

1.2.1 Evaniidae (ensign or hatchet wasps)

Diagnostic characters: Antenna with 13 antennomeres (one neotropical genus has 10); pterostigma relatively small; mesosoma relatively stout; hind wing with jugal lobe; metasoma arising dorsally on mesosoma, distance between propodeal foramen and metacoxal cavity much larger than width of either



(a) Siricidae, dorsal head and thorax (Goulet *et al.*, 1993, pg. 70)



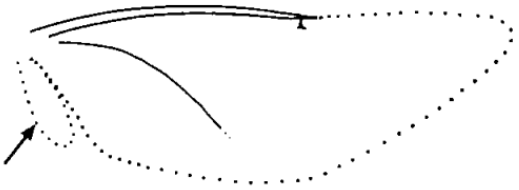
(b) Habitus (Goulet *et al.*, 1993, Fig. 25)

Figure 6: Siricidae

opening; metasoma hatchet-shaped; petiole tubular.

Natural history: These wasps develop as solitary predators of cockroach eggs, inside the ootheca. Approximately 550 species have been described, but only a handful occur in North America.

(a) Lateral habitus Photo (CC BY 2.0) by Mullins *et al.* (2012)



(b) Hind wing (Goulet *et al.*, 1993, pg. 510)

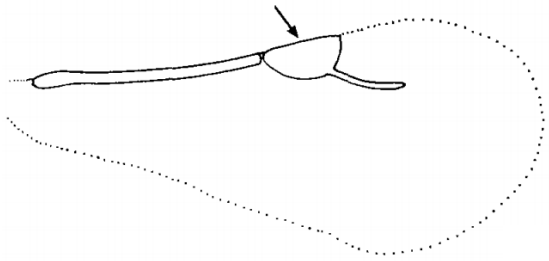
Figure 7: Evaniidae

1.2.2 Megaspilidae

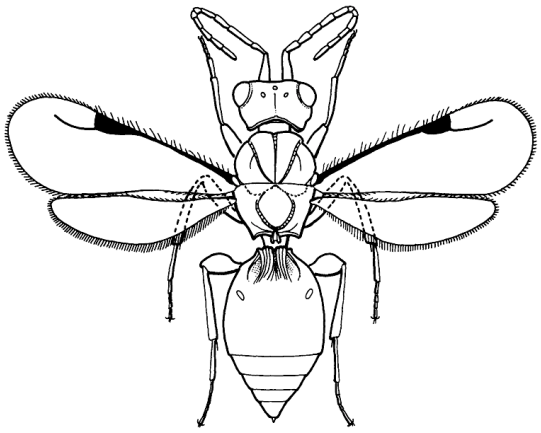
Diagnostic characters: Antenna with 12 antennomeres (Figure 8b); fore wing with no cells enclosed by tubular veins (Figure 8a)and only 1 proximal tubular vein on anterior margin; pterostigma distinct; protibia with two apical spurs; pronotum adjacent to tegula in lateral view (compare to Chalcidoidea).

Natural history: Parasitoids of many kinds of insects, including other parasitoid Hymenoptera (*i.e.*,

some megaspilids are hyperparasitoids). These wasps are relatively easy to collect, and there are just over 300 species known worldwide.



(a) Fore wing (Goulet *et al.*, 1993, pg. 566)



(b) Dorsal habitus (Goulet *et al.*, 1993, Fig. 209)

Figure 8: Megaspilidae

1.2.3 Braconidae

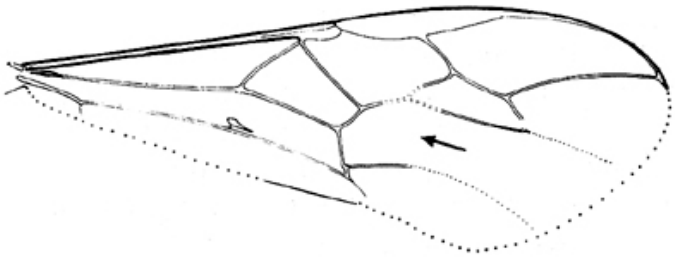
Diagnostic characters: Antenna usually with 16 or more antennomeres (Figure 9a); fore wing C + Sc + R fused (*i.e.*, anterior margin of wing with relatively thick wing vein); pterostigma usually present; one recurrent vein or none (Figure 9b arrow); no "horse head" cell (compare with Ichneumonidae); first and second metasomal segments often fused and immobile dorsally.

Natural history: These parasitoid wasps are extraordinarily diverse, with almost 20,000 described species. Many of them, especially the subfamily Microgastrinae, coevolved with viruses (polydnaviruses), which help them overcome the ho hosts' immune response.

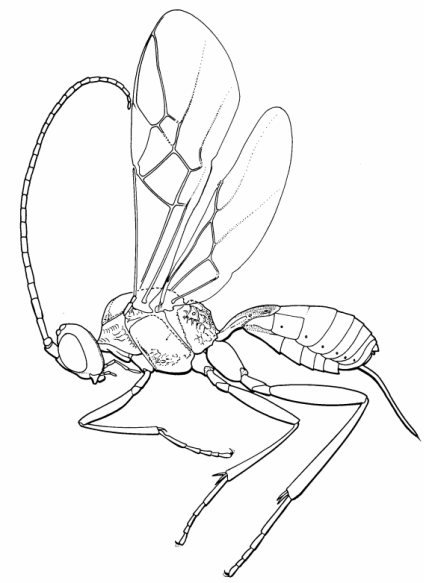
1.2.4 Ichneumonidae (ichneumon wasps)

Diagnostic characters: Antenna usually with 16 or more antennomeres; fore wing C + Sc + R fused (*i.e.*, anterior margin of wing with relatively thick wing vein); pterostigma usually present; two recurrent veins present (Figure 10a arrow); "horse head cell" present (often not quite horse-like); first and second metasomal segments not fused.

Natural history: One of the most diverse families of insects, with at least 24,000 named species and many, many more remaining to be described. Like their sister family, Braconidae, some species inject polydnaviruses into the hosts, along with the egg(s), to combat the hosts' immune responses. These wasps are parasitoids of many kinds of arthropods but mostly other insects.

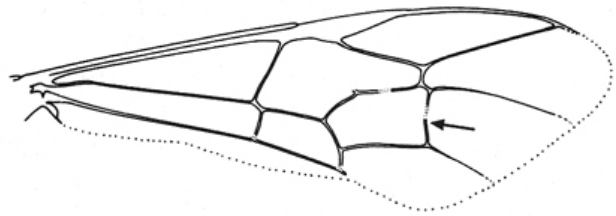


(a) Fore wing (Goulet *et al.*, 1993, pg. 359)



(b) Lateral habitus (Goulet *et al.*, 1993, Fig. 138)

Figure 9: Braconidae



(a) Fore wing (Goulet *et al.*, 1993, pg. 359)

(b) Lateral habitus (Goulet *et al.*, 1993, Fig. 159)

Figure 10: Ichneumonidae

1.2.5 Pelecinidae

Diagnostic characters: relatively large (20–70 mm long); fore wing with one cell enclosed by tubular veins; petiole tubular, female abdominal segments elongate, tubular (Figure 11).

Natural history: There is only one extant species, whose distribution spans from Canada to Argentina. Females use their extended metasomas to probe soil for hosts, which are larval scarab beetles (*Phyllophaga* spp.)

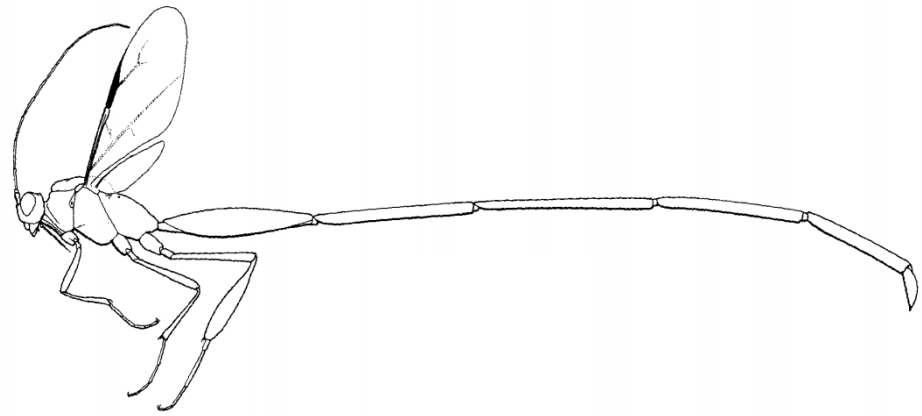


Figure 11: Pelecinidae, female habitus. (Goulet *et al.*, 1993, Fig. 198)

1.2.6 Diapriidae

Diagnostic characters: Antenna elbowed; antennal shelf present, articulation dorsally distant from clypeus; antenna with 11–15 antennomeres; fore wing venation variable (sometimes lacking wing cells); usually black or brown, often shiny and smooth in parts; petiole tubular.

Natural history: Approximately 2,500 species have been described from around the world. These wasps are very frequently collected in yellow pans and leaf litter samples, and most species are understood to be parasitoids of larval dipterans.

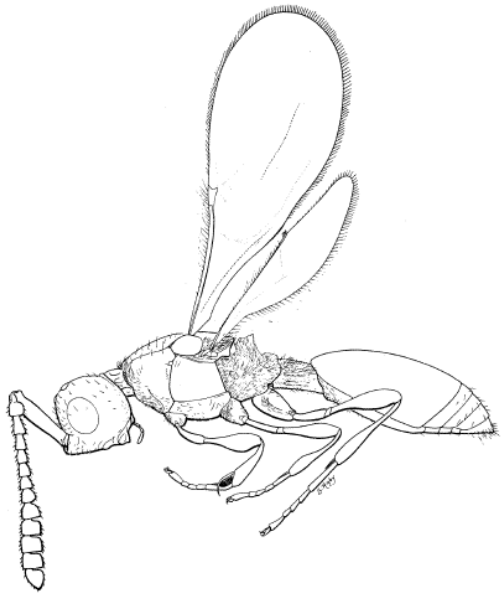


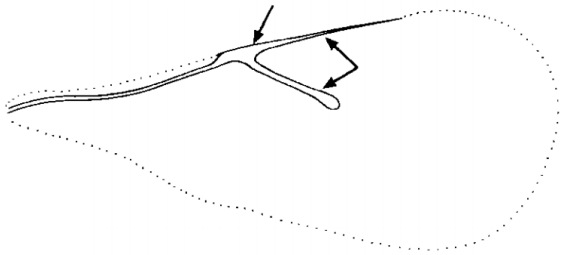
Figure 12: Diapriidae habitus (Goulet *et al.*, 1993, Fig. 206)

1.2.7 Scelionidae

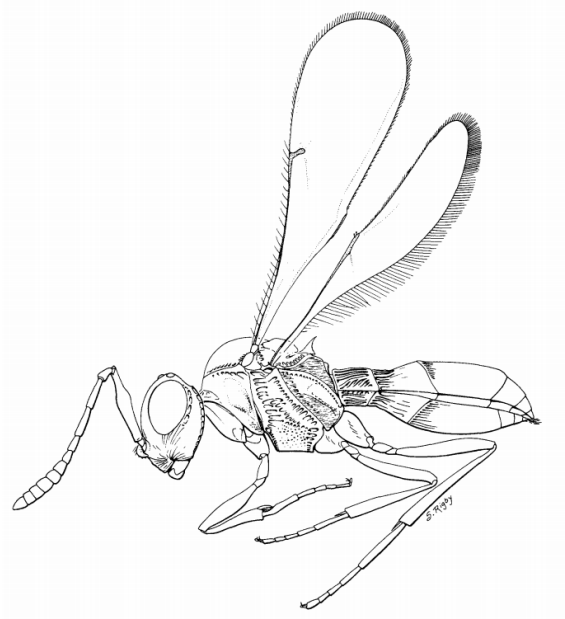
Diagnostic characters: Antenna elbowed; antennal shelf absent; antennal sockets usually close to clypeus; fore wing with 3 veins, pterostigma absent (Figure 13a); fore wing without proximal tubular vein on anterior margin; antenna usually with 11–12 antennomeres; small to very small, usually black or brown; pronotum adjacent to tegula; petiole not tubular; abdomen often flat, with sharp lateral edges.

Natural history: More than 3,000 species have been described from around the world. These wasps are parasitoids of insect eggs, and several species have been recruited for biocontrol.

Question 10-4: What do you notice about scelionid body shapes? What do you think is their biological significance?



(a) Fore wing (Goulet *et al.*, 1993, pg. 560)



(b) Lateral habitus (Goulet *et al.*, 1993, Fig. 207)

Figure 13: Scelionidae

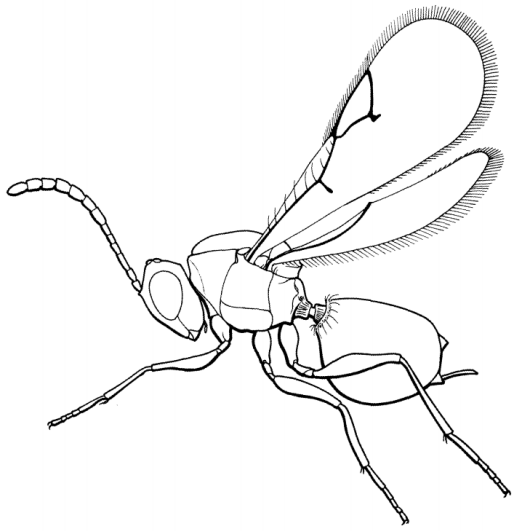
Cynipoidea The next two families are classified in Cynipoidea, which share the following characteristics:

- distinctive wing venation: no proximal vein along anterior margin, with well developed marginal cell (R1), no pterostigma
- antenna with 11–16 antennomeres, not elbowed (*i.e.*, not geniculate)
- abdomen laterally flattened

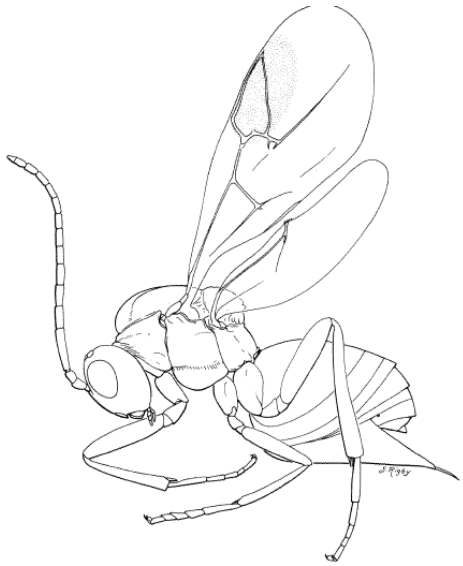
1.2.8 Figitidae

Diagnostic characters: Fore wing with cell RI 3–4 times as long as wide; hind leg with tarsomere 1 not longer than remaining tarsomeres combined; petiole of metasoma usually elongate, longer than wide; scutellum usually elaborate, with keel or oval elevation; if scutellum not elaborate, then 3 abdominal tergites visible or head wider than mesosoma.

Natural history: There are ~1,400 described species, the vast majority of which are parasitoids of Diptera larvae. Some species are hyperparasitoids on Sternorrhyncha.



(a) Figitidae habitus (Goulet *et al.*, 1993, Fig. 195)



(b) Cynipidae habitus (Goulet *et al.*, 1993, Fig. 197)

Figure 14: Cynipoidea

1.2.9 Cynipidae (gall wasps)

Diagnostic characters: fore wing with cell RI 3–4 times as long as wide; hind leg with tarsomere 1 not longer than remaining tarsomeres combined; petiole of metasoma hidden or wider than long (Figure 14b); scutellum rounded, not elaborate; >3 abdominal tergites visible, head always wider than mesosoma.

Natural history: Most of the ~1,300 species are gall-makers on plants or inquilines inside the galls of other insects. Many of these wasps are associated with oaks (*Quercus* spp.).

Question 10-5: Based on what you know about plants, which may be very little, how do you think gall wasps can induce galls and facilitate predictable extended phenotypes?

Chalcidoidea The next families are classified in the super diverse taxon Chalcidoidea. We'll look at five families, but keep in mind there are more than 20 chalcidoid families worldwide, many of which

are quite common in Pennsylvania. They all share the following characteristics, the combination of which separates chalcidoids from other apocritans:

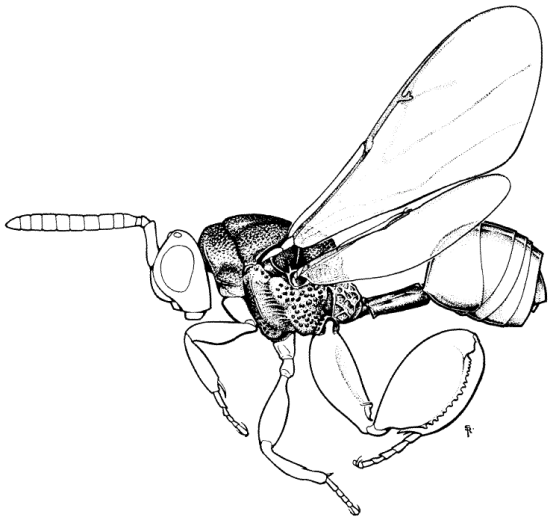
- antenna geniculate, with "ring segments' (*i.e.*, short, ring-like sclerites at the base of the flagellum)
- pronotum not reaching tegula (*i.e.*, a sclerite (prepectus) is present between the pronotum and tegula)
- fore wing with 3 veins, similar to Scelionidae

1.2.10 Chalcididae (chalcidid wasps)

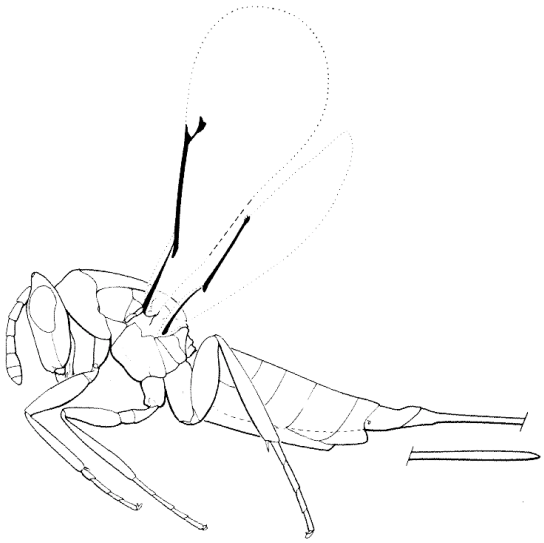
Diagnostic characters: Tarsi 5-segmented; hind femora greatly swollen and often toothed, hind tibiae curved to fit femora (Figure 15a); hind coxae much larger than front coxae (Figure 15a); fairly large (for chalcidoids!); very rarely (if ever) metallic in color.

Natural history: Almost 1,500 species are known worldwide. Most are parasitoids of Lepidoptera (especially the pupa) or late instar Diptera.

Question 10-6: What do you think is/are the function(s) of the hind femora in Chalcididae? What makes them so large?



(a) Chalcididae lateral habitus (Goulet *et al.*, 1993, Fig. 212)



(b) Eulophidae habitus (Goulet *et al.*, 1993, Fig. 228)

Figure 15: Chalcidoidea

1.2.11 Eulophidae (eulophid wasps)

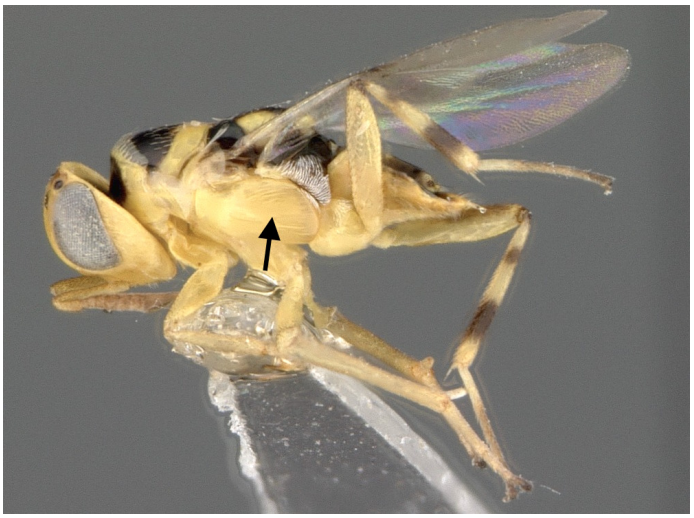
Diagnostic characters: Antennal funicle with 4 or fewer antennomeres; tarsi 4-segmented (Figure 15b); apical spur of front tibiae short and straight; small, often black, brown, or blue.

Natural history: More than 4,300 species have been described, and they are biologically quite diverse. Most species develop as parasitoids of other insects, especially Holometabola, but some species are gall-makers.

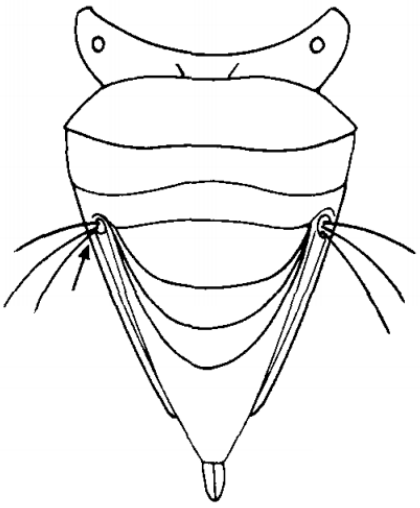
1.2.12 Encyrtidae

Diagnostic characters: mesopleuron strongly convex, without grooves (Figure 16a); tarsi usually 5-segmented; if tarsi 4-segmented, funicle with 5+ antennomeres; apical spur of middle tibiae large; usually rather stout-bodied and very small; cerci distinctly anterior to apical abdominal margin (Figure 16b).

Natural history: There are ~3,700 described species worldwide. Like other chalcidoids, this lineage is biologically diverse. Most species are parasitoids of insect eggs or of sternorrhynchans, and many are important biological control agents.



(a) Habitus. Photo CC0 by Michael Gates `http://morphbank.net/?id=228742`



(b) Metasoma in dorsal view (Goulet *et al.*, 1993, pg. 581)

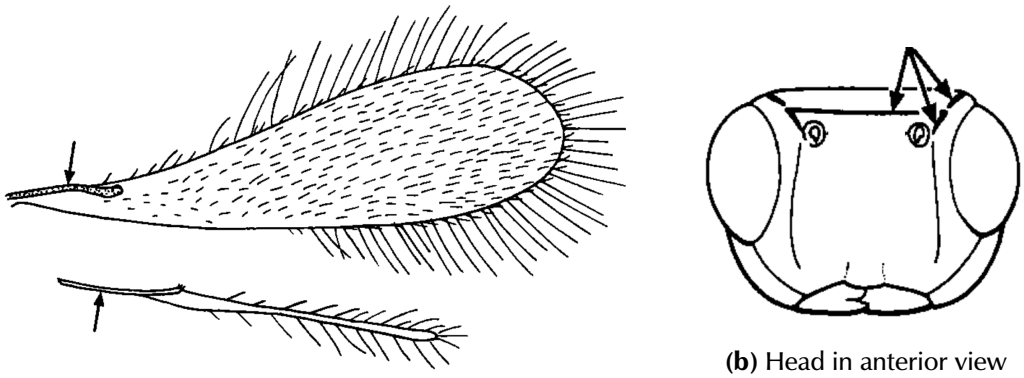
Figure 16: Encyrtidae

1.2.13 Mymaridae (fairyflies)

Diagnostic characters: Body typically very small (these wasps are parasitoids of insect eggs); head with H-shaped complex bar-like structures on face (trabeculae); wings fringed; hind wing stalked proximally.

Natural history: There are >1,400 known species, all of which are (probably) parasitoids of insect eggs. This family includes the smallest known insect (*Dicopomorpha echmepterygis* Mockford, 1997) and the smallest known flying insect (*Kikiki huna* Huber & Noyes 2013). The facial trabeculae likely correspond to an egg-bursting structure that facilitates eclosion and escape from the host remains.

Aculeata In Aculeata, the egg does not enter the ovipositor assembly prior to deposition but rather leaves the metasoma anterior to the ovipositor. The ovipositor functions only to inject venom gland



(a) Wings

(b) Head in anterior view

Figure 17: Mymaridae (Goulet *et al.*, 1993, pg. 87)

products (*i.e.*, venom). Besides the structure of the ovipositor, the monophyly of Aculeata is supported mostly by indistinct internal characters (*e.g.*, the shape, pattern and presence/absence of thoracic muscles). The only distinct synapomorphy of the infraorder is the presence of the supramesopleural sclerite (sms), that partially obscures the second thoracic spiracle. (Caveat: The sms is absent from a few Aculeata and *present* in some non-aculeates, like Evaniidae and Trigonalidae.)

Besides the above-mentioned synapomorphies, Aculeata can be superficially characterized by their well-developed wing venation (but see some "Chrysidoidea", e.g., Figure 18a), distinct wasp waist (unlike sawflies), well sclerotized metasomal sternites (unlike most Ichneumonoidea), having fewer than 11 flagellomeres (numerous Ichneumonoidea have more than 11 flagellomeres), and convex, almost bulbous metasoma.

Traditionally the infraorder is subdivided into three superfamilies: Chrysidoidea, Apoidea, and Vespoidea. Only the monophyly of Apoidea is supported in the latest phylogenetic analyses.

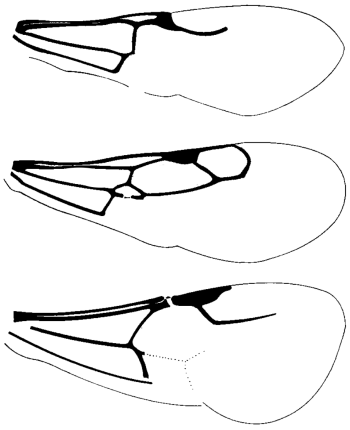
1.2.14 Bethylidae

Diagnostic characters: Body usually weakly sculptured and brown or black (not typically metallic); head usually prognathous (Figure 18a); antenna with 11 (rarely 10 or 8) flagellomeres; pronotum with anterior flange, propleuron thus concealed in dorsal view; distal venation of wing reduced; metasoma with 6 or 7 exposed terga.

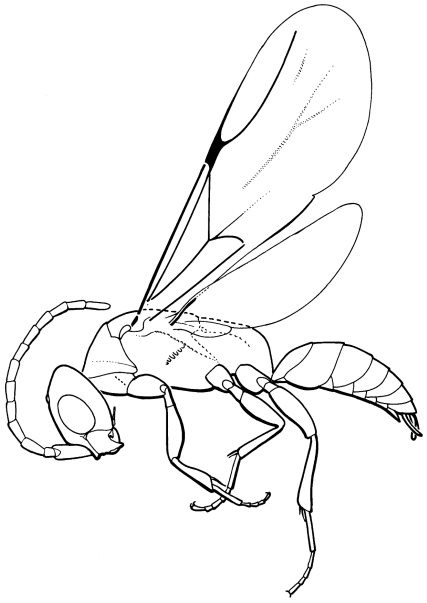
Natural history: This taxon includes >2,200 species, many of which are known to develop as parasitoids of holometabolous insects in concealed environments (e.g., wood-boring Coleoptera).

1.2.15 Chrysididae (cuckoo wasps)

Diagnostic characters: Head typically hypognathous; antenna with 11 flagellomeres; pronotum with anterior flange, such that propleuron is concealed in dorsal view; pronotum with posterolateral apex usually well separated from tegula; metasoma usually with 5 or fewer exposed terga and strongly concave ventrally (Figure 19a); usually strongly sculptured and metallic.



(a) Fore wings (Goulet *et al.*, 1993, pg. 134)

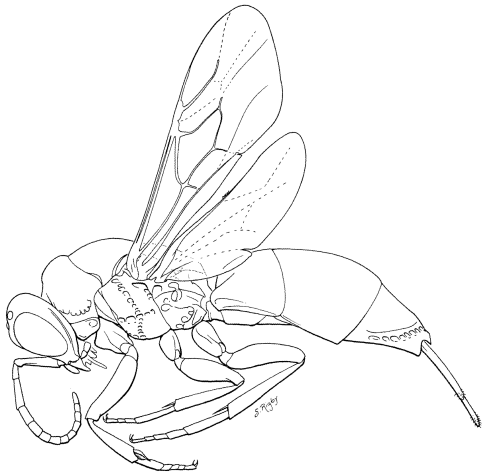


(b) Habitus (Goulet *et al.*, 1993, Fig. 37)

Figure 18: Bethylidae

Natural history: Of the >3,000 known species, the majority are predicted to develop as cleptoparasites of other aculeates. That is, most chrysidids lay their eggs in the nests of bees and wasps, and the subsequent larvae develop on the provisions and eggs located therein. Other species develop as parasitoids, for example in phasmatodean eggs.

(a) Habitus. Photo CC0 by James Marchment `https://flic.kr/p/DciZEn`



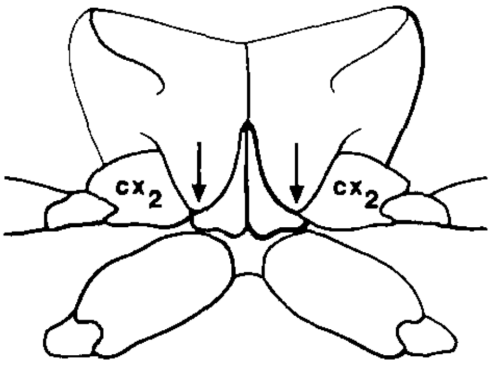
(b) Habitus (Goulet *et al.*, 1993, Fig. 42)

Figure 19: Chrysididae

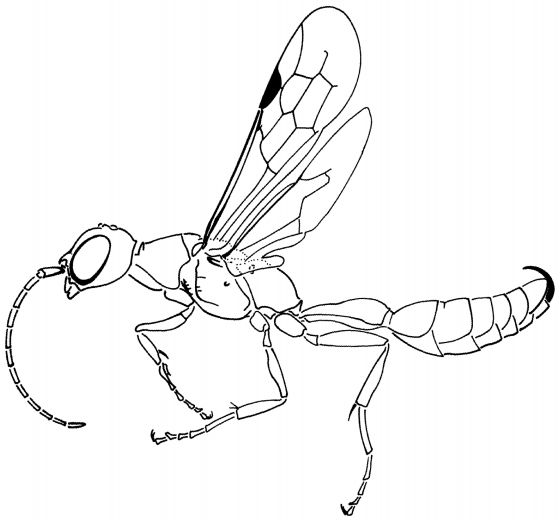
1.2.16 Tiphiidae

Diagnostic characters: eye not usually "notched"; mesosternum with laminate expansions on each side of midline covering bases of contiguous mesocoxae (Figure 20a), the expansions rarely reduced to small teeth; hind wing with deeply separated (jugal) lobe (Figure 20b); female usually with mesotibia and metatibia stout and spiny; metasomal segment 1 without a true node (like we see in Formicidae), although sometimes approaching it; male metasomal sternum 8 (hypopygium) usually forming a single upcurved hook (Figure 20b), the hypopygium sometimes simple or with 2–5 spines, and usually entirely exposed.

Natural history: More than 1,500 species of tiphiids have been described worldwide, and rearing records indicate that a majority are parasitoids of Coleoptera, especially Scarabaeidae.



(a) Mesosoma in venral view (Goulet *et al.*, 1993, pg. 163); cx2 = mesocoxa



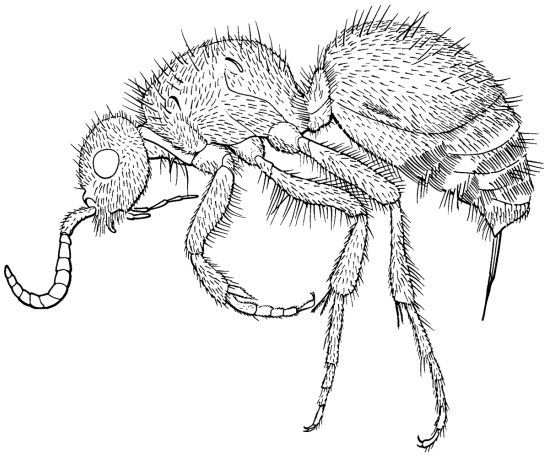
(b) Habitus (Goulet *et al.*, 1993, Fig. 49)

Figure 20: Tiphiidae

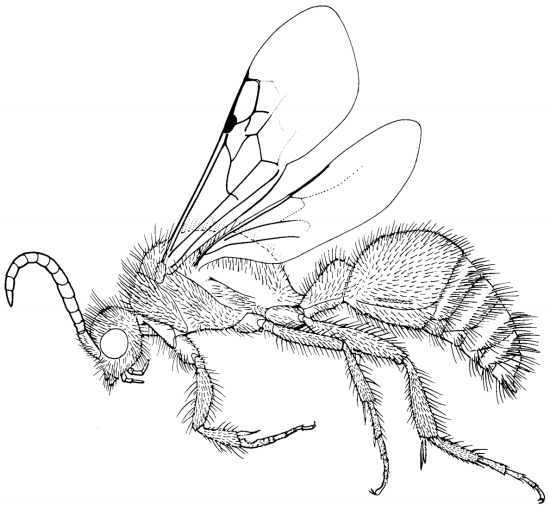
1.2.17 Mutillidae (velvet ants)

Diagnostic characters: metasomal segment 1 without a true node; metasomal segment 2 usually with longitudinal felt line or with felted pit on tergum and/or sternum (but sometimes without); female almost always apterous (Figure 21a); apterous forms with pronotum usually fused to mesothorax and mesonotum to metanotum-propodeum complex; usually very furry and often colorful or brownish and quite "bristly"; body often very hard and difficult to pin.

Question 10-7: What can you hypothesize about their natural history, given your observations of their phenotypes? Why are velvet ants typically brightly colored?



(a) Female habitus (Goulet *et al.*, 1993, Fig. 63)



(b) Male habitus (Goulet *et al.*, 1993, Fig. 64)

Figure 21: Mutillidae

1.2.18 Formicidae (ants)

Diagnostic characters: Metapleural gland present (in most species), its opening usually distinct; posterior (inner) spur of metatibia modified as a calcar; reproductive forms usually macropterous (Figure 22b), sterile female apterous; apterous form with with pronotum usually freely articulating but sometimes fused with mesothorax; mesonotum and metathorax-propodeum complex usually fused (Figure 22a; metasoma petiolate; metasomal segment 1 usually strongly constricted at each end, forming a true node; metasomal sternum 1 separated from sternum 2 by a deep constriction.

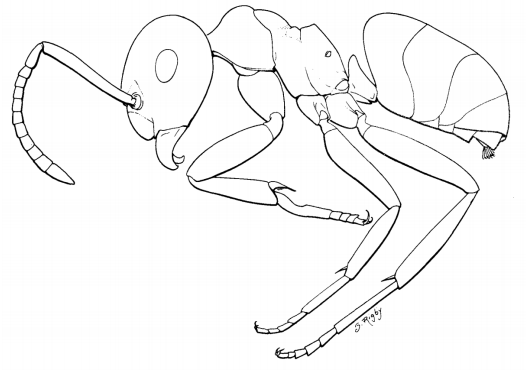
Natural history: Highly eusocial insects, with a wide array of life history strategies (small *vs*. large colonies, diet specializations, *etc*.) There are ~15,000 species known worldwide.

Question 10-8: Do you see any morphological evidence that ants are highly eusocial? Remember the three main conditions of eusociality ...

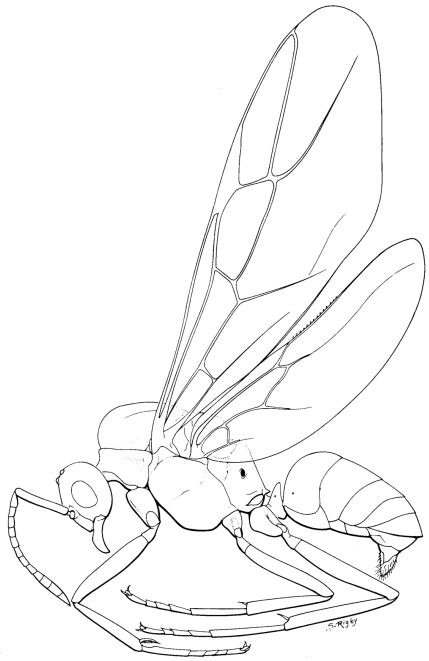
1.2.19 Pompilidae (spider wasps)

Diagnostic characters: Antennal segments distinctly separated and often curled in dead specimens; pronotum with posterolateral apex rounded anterior to tegula; mesopleuron usually with oblique sulcus (Figure 23a); mesosoma usually laterally flattened (*i.e.*, mesosoma higher than wide in anterior or posterior view); hind wing without distinct claval lobe but with distinct jugal lobe (Figure 23b); legs usually conspicuously elongate, spiny.

Natural history: Larvae develop as parasitoids of spiders or as cleptoparasites of other pompilids. The spiders are usually paralyzed and brought to a nest (*e.g.*, a mud pot or a burrow in the soil), prior to



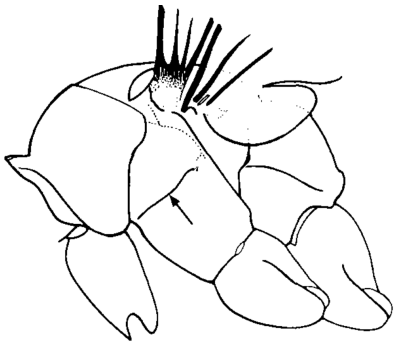
(a) Female habitus (Goulet *et al.*, 1993, Fig. 91)



(b) Male habitus (Goulet *et al.*, 1993, Fig. 92)

Figure 22: Formicidae

oviposition. At least 4,200 species are known worldwide.



(a) Mesosoma, with mesopleural sulcus (arrow) (Goulet *et al.*, 1993, pg. 170)

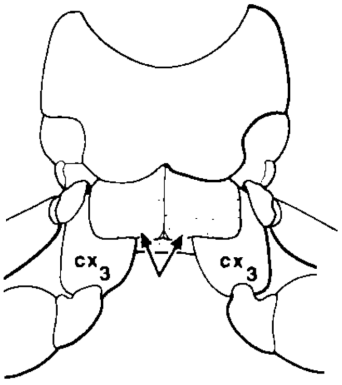
(b) Habitus (Goulet *et al.*, 1993, Fig. 71)

Figure 23: Pompilidae

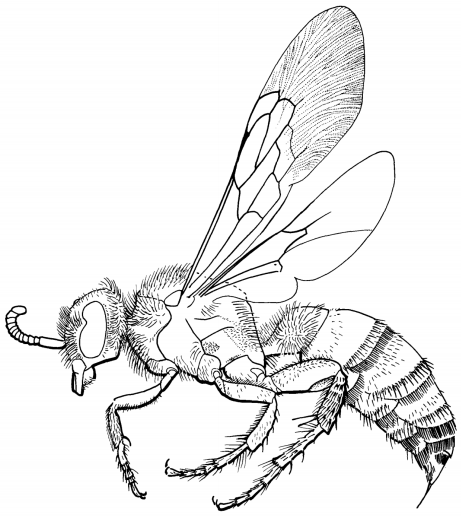
1.2.20 Scoliidae

Diagnostic characters: Eye with inner margin deeply emarginated ("notched"); pronotum with posterodorsal margin U-shaped; mesocoxae and metacoxa widely separated; wings with dense fine longitudinal wrinkles near apices (Figure 24a); hind wing without distinct claval lobe but with distinct jugal lobe; female usually with mesotibia and metatibia stout and spiny; metasomal sternum 1 separated from sternum 2 by a deep constriction.

Natural history: Based on rearing records, most of the ~300 described species are predicted to be ectoparasitoids of Coleoptera larvae, especially Scarabaeoidea.



(a) Mesosoma in ventral view (Goulet *et al.*, 1993, pg. 162); cx3 = metacoxa



(b) Habitus (Goulet *et al.*, 1993, Fig. 78)

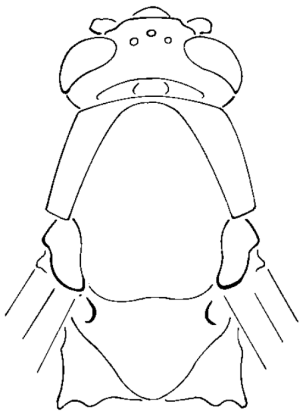
Figure 24: Scoliidae

1.2.21 Vespidae

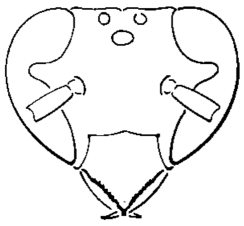
Diagnostic characters: Eye with inner margin deeply emarginated; pronotum posterodorsal margin V-shaped, and with pronotum posterolateral apex acute and strongly produced above anterior margin of tegula; fore wing almost always longitudinally folded when at rest; hind wing without distinct claval lobe, and usually with distinct jugal lobe; posterior (inner) spur of metatibia weakly modified as a calcar; metasomal sternum 1 separated from sternum 2 by a deep constriction.

Natural history: With about 4,000 described species, this family exhibits a wide range of behaviors. Many species (*e.g.*, Eumeninae) are solitary, while others are highly eusocial (*e.g.*, Vespinae).

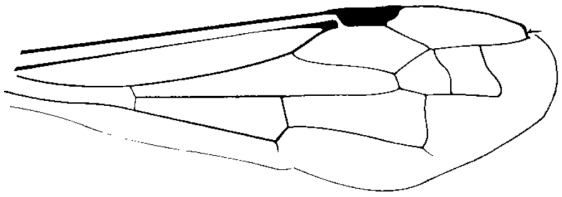
Question 10-9: Do you see any morphological evidence that these species are eusocial? Recall the question above for Formicidae.



(a) Dorsal head and mesosoma (Goulet *et al.*, 1993, pg. 215)



(b) Anterior head (Goulet *et al.*, 1993, pg. 214)



(c) Fore wing (Goulet *et al.*, 1993, pg. 214)

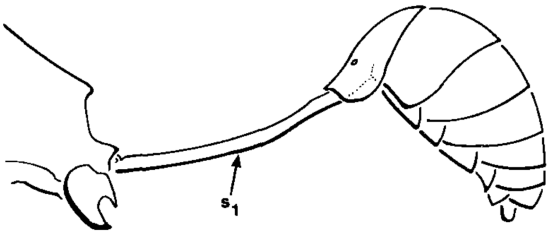
Figure 25: Vespidae

Apoidea Now we're looking at taxa classified in Apoidea. There are four families of "spheciform" wasps (we'll look at two), which are mostly predators of other insects, and seven to nine families of bees (Anthophila; we'll look at four bee families), which collect pollen.

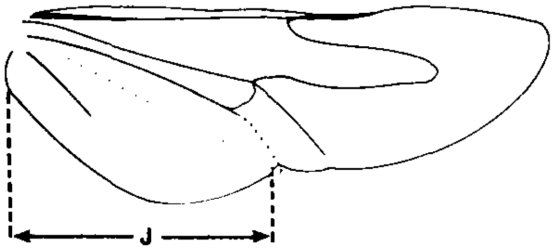
1.2.22 Sphecidae (thread-waisted, hunting wasps)

Diagnostic characters: Plumose, branched setae absent; hind leg basitarsus as wide as subsequent tarsomeres; metasoma petiolate (Figure 26a); first metasomal segment tube-like (sternum and tergum fused).

Natural history: Females construct nests from mud, use pre-existing cavities, or excavate nests from soil or sand. The nests are selectively provisioned with prey for the larvae to consume during their development. There are almost 800 described species, and they exhibit a range of behaviors from solitary to almost eusocial.



(a) Mesasoma; s1 = sternite 1



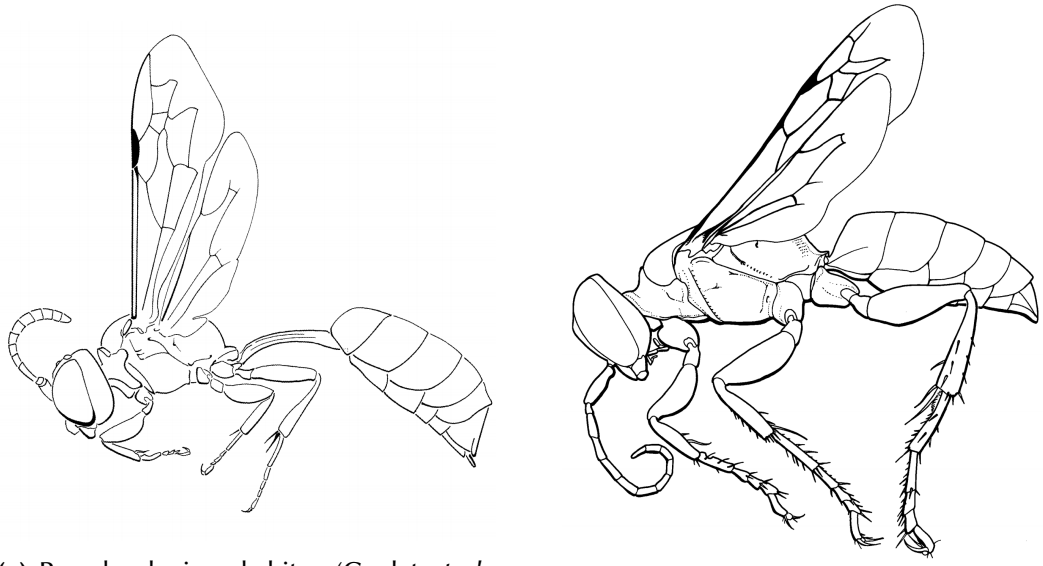
(b) Hind wing; J = jugal lobe

Figure 26: Sphecidae (Goulet *et al.*, 1993, pg. 281)

1.2.23 Crabronidae (hunting wasps, aphid wasps, beewolves, cicada killers, *etc*.)

Diagnostic characters: plumose, branched setae absent; hind leg basitarsus as wide as subsequent tarsomeres; tergum and sternum distinctly separated on metasomal segment 1; sometimes forming tube-like petiole; often determined through the process of elimination.

Natural history: This taxon is among the most diverse in Apoidea, with almost 9,000 described species. The limits of this family are still being debated, and it's likely that our concept of Crabronidae is polyphyletic. The nesting behaviors and prey specialization are highly variable.



(a) Pemphredoninae habitus (Goulet *et al.*, 1993, Fig. 99)

(b) Larrinae habitus (Goulet *et al.*, 1993, Fig. 102)

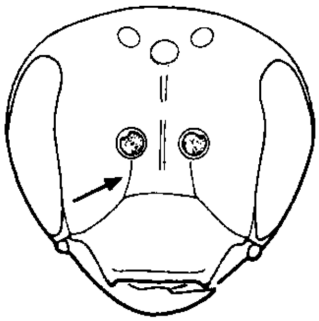
Figure 27: Crabronidae

Apoidea: Anthophila The remaining families comprise the bees. All have branched setae on their bodies (lost in some cleptoparasitic species) and usually have (in females) some kind of pollen-carrying structure on the hind legs or abdomen.

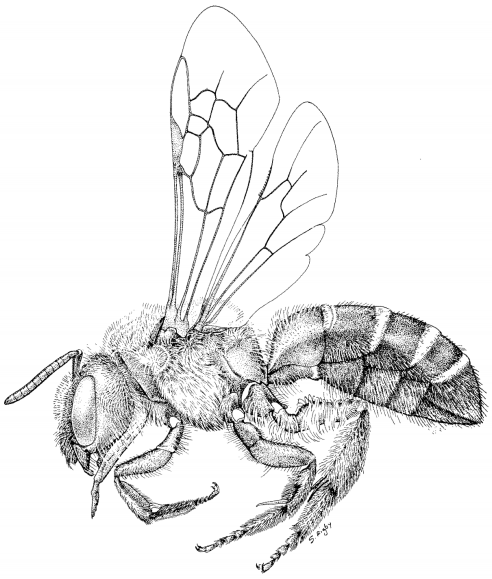
1.2.24 Halictidae (sweat bees)

Diagnostic characters: Hind leg basitarsus much wider than subsequent tarsomeres; face with one subantennal suture; proboscis short; jugal lobe of hind wing long; basal vein of fore wing strongly arched (Figure 28a); small to medium-sized, often metallic.

Natural history: Halictids generally nest in the soil or in rotting wood, and some species are facultatively eusocial. At least 2,000 species have been described.



(a) Face (Goulet *et al.*, 1993, pg. 315)



(b) Habitus (Goulet *et al.*, 1993, Fig. 118)

Figure 28: Halictidae

1.2.25 Andrenidae (mining bees)

Diagnostic characters: Proboscis short; face with two subantennal sutures (Fig. 29a, double arrow) and often with facial foveae (Fig. 29a, single arrow); jugal lobe of hind wing long; basal vein of fore wing not strongly arched; small to medium-sized, often (not always!) with hairier thorax than halictids.

Natural history: These bees typically nest in the soil. None is eusocial, as far as is known, but some species nest communally. There are ~2,100 described species.

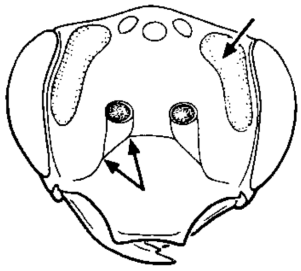
1.2.26 Megachilidae (mason, leafcutter bees, *etc*.)

Diagnostic characters: Proboscis rather long; jugal lobe of hind wing short; fore wing with two submarginal cells, usually equal in length; females with scopa (pollen carrier) on ventral surface of metasoma; variable in color and shape, but often stouter or "chunkier" than other bees.

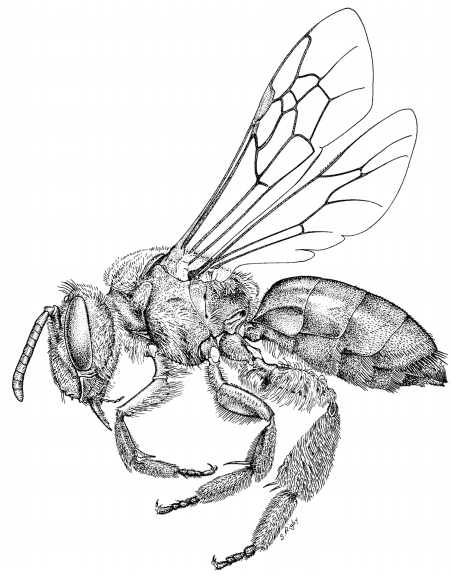
Natural history: These bees usually nest in cavities, fro example holes in wood, and have common names that reflect the materials they use to line nests: carder (plant or animal hairs), mason (resin or soil), or leaf cutter (leaves) bees. All known species are solitary or communal. There are more than 2,000 species worldwide.

1.2.27 Apidae (cuckoo, nomad, carpenter, bumble, honey bees, *etc*.)

Diagnostic characters: Tongue long, maxillary palps vestigial; jugal lobe of hind wing usually absent; fore wing with three submarginal cells; hind tibiae usually with a scopa used to carry pollen.

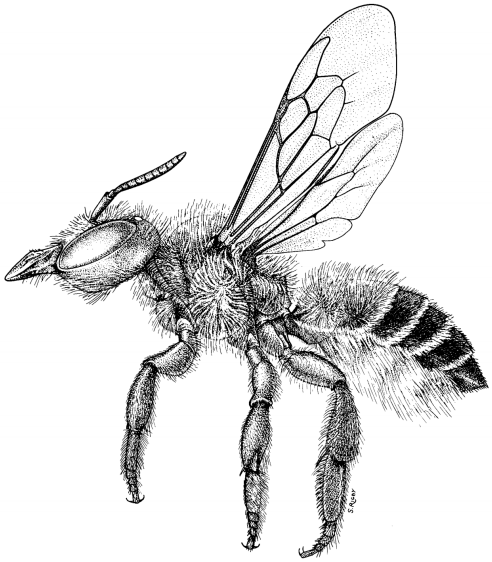


(a) Head in anterior view (Goulet *et al.*, 1993, pg. 313)

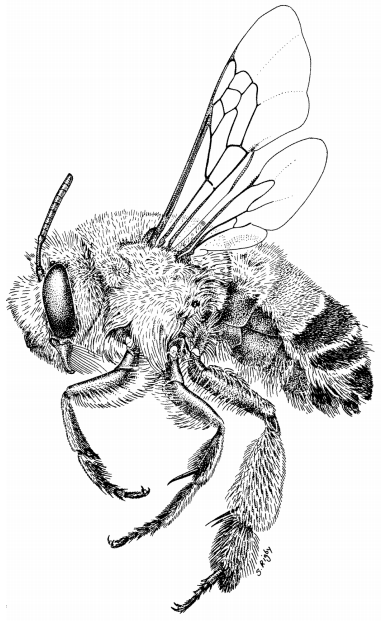


(b) Habitus (Goulet *et al.*, 1993, Fig. 116)

Figure 29: Andrenidae



(a) Habitus (Goulet *et al.*, 1993, Fig. 116)



(b) Habitus (Goulet *et al.*, 1993, Fig. 123)

Figure 30

Natural history: Apidae is by far the most diverse family of bees, with >5,700 species described worldwide. These bees range from solitary (e.g., carpenter bees) to primitively eusocial (bumble bees) to highly eusocial (honey and stingless bees).

As you have now seen, almost all bees are covered in plumose or branched setae and have special

structures for carrying pollen. (Note: There are some species of cleptoparasitic bees that lack these structures.) Take a close look at the setae. Are they uniform in size and shape? How many specialized structures can you find on the body that you hypothesize might be involved in pollen collection? Based on the morphology, can you envision how pollen collection works from a behavioral perspective?

Test yourself

Given what you read and discussed in lecture, what adaptations contributed to such a large radiation? How does this diversity look phylogenetically?

How do **idiobiont** parasitoids differ from **koinobiont**s?

Familiarize yourself with the following taxon names, which refer to organisms you are likely to encounter in the northeastern USA and/or which are phylogenetically relevant. Can you describe how these arthropods live (natural history) and roughly how diverse they are? Do you know how they're related to one another? If you had to choose a family to study from the taxa below which one would it be and why?

1. Apocrita
2. Aculeata
3. Orussidae

Epilogue

This handout is part of an open curriculum. Original files are available free for anyone to download, copy, modify, and improve at the Open Entomology GitHub repository (Open Entomology Project, 2016), which also provides a mechanism for reporting problems and other feedback:
`https://github.com/OpenEntomology/InsectBiodiversityEvolution/issues`

Acknowledgments

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