Order **HYMENOPTERA**
Francesco Fiume

The taxonomy of the *Hymenoptera* is:

Clade *Natura* Brands 1989
Clade *Mundus* Plinius
Superdomain *Biota*
Domain *Eukaryota* (Chatton 1925) Whittaker et Margulis 1978
Clade *Amorpha* Adl 2005
Clade *Opisthokonta* (Cavalier Smith 1987) Adl 2005
Clade *Holozoa* Lang et al. 2002
Kingdom *Animalia* Linnaeus 1758
Clade *Epitheliozoa* Ax 1996
Subkingdom *Eumetazoa* Bütschli 1910
Clade *Bilateria* Hatschek 1888
Clade *Eubilateria* Ax 1987
Clade *Protostomia* Grobben 1908
Clade *Ecdysozoa* Aguinaldo et al. 1997
Superphylum *Panarthropoda* Nielsen 1995
Phylum *Arthropoda* von Siebold 1848
Clade *Euarthropoda* Lankester 1904
Clade *Mandibulata* Snodgrass 1938
Clade *Crustaceomorpha* Chernyshev 1960
Clade *Labrophora* Siveter, Waloszek et Williams 2003
Subphylum *Pancrustacea* Zrzavý et al. 1997
Clade *Altocrustacea* Regier et al. 2010
Clade *Miracrustacea* Regier et al. 2010
Superclass *Hexapoda* Latreille 1825
Class *Insecta* Linnaeus 1758
Subclass *Dicondylia* Hennig 1953
Infraclasse *Pterygota*

*Metapterygota*
*Neoptera*
*Eumetabola*

*Holometabola*
Superorder *Hymenopterida* Linnaeus 1758
Order *Hymenoptera* Linnaeus 1758.

*Hymen-optera*: “membrane-wing”; thus, another plausible etymology involves *Hymen*, the Ancient Greek god of marriage, as these insects have “married wings” in flight.
The order is divided into two suborders, the *Symphyta* and *Apocrita*. The *Symphyta* are the more primitive suborder and can be distinguished from the *Apocrita* by an abdomen broadly joined to the thorax. In the Apocrita the abdomen has become subdivided into a thorax-associated, terminal *propodeum*, a slender, connecting “petiole” (the “thread-waist”) and the remainder of the segments, termed the *gaster*.
The *Apocrita* can be further subdivided into two major groups, the *Parasitica* and the *Aculeata*, reflecting the two most prevalent life histories found in the order. The *Parasitica* are characterized by a parasitoid lifestyle.
The life histories found within this group are often unorthodox if not just plain bizarre. The
Parasitica are an extremely diverse group, often overlooked due to their generally small size. In fact, over half of all Hymenoptera species are parasitoid wasps. Much of this diversity is based on the specializations on a single or a small number of related host species by each parasitoid and the number of potential host species to be found within the insect world. The Aculeata are defined by a predatory existence, for which the ovipositor has evolved into a prey-paralyzing device. In the most existing species of Aculeates and especially the social species, the sting is also used defensively, a relatively recent evolutionary adaptation. An exception to the predatory rule is found in the Apoidea which have become specialized to utilize pollen, rather than meat, as a protein source. Eusociality has arisen multiple times within the Aculeate Hymenoptera. Some of the most abundant and familiar insects, such as the honey bees and the ants, are found here although most Hymenoptera, even among the aculeates, are solitary. Haplodiploidy may have played a role in the development of hymenopteran societies by increasing the genetic similarity of siblings, thus fostering altruism.

The Hymenoptera are often considered a “beneficial” order because of the importance of pollination, for which many species are adapted, especially the bees, and also for biological control provided by parasitic species. However, there are pest hymenopterans, including Africanized honey bees (medical and nuisance pests), other stinging wasps and bees (nuisance pests), carpenter bees (structural pests), parasitoids of other beneficial insects, and some silvicultural and agricultural pests, chiefly sawflies (foliavors and gall makers) and siricids (borers).

Evolution
Hymenoptera originated in the Triassic, with the oldest fossils belonging to the family Xyelidae (xyelid sawflies). Social hymenopterans appeared during the Cretaceous (Hoell et al. 1998). The evolution of this group has been intensively studied by Alex Rasnitsyn, Michael S. Engel, G. Dlussky, and others. The Xyelidae are a small family of sawflies known from fewer than 50 extant species in five genera, but with an extensive fossil record; they are the oldest fossil Hymenoptera, dating back to the Triassic, between 245 and 208 million years ago. Most species occur in the Northern Hemisphere, especially in boreal regions, though there are a few neotropical species. Most are associated with conifers (Pinus and Abies), where the larvae feed on pollen or within buds, though larvae of a few species feed on the leaves of deciduous trees. This clade has been studied by examining the mitochondrial DNA (Mao et al., 2015). Although this study was unable to resolve all the ambiguities in this clade, some relationships could be established. The Aculeata, Ichneumonomorpha, and Proctotrupomorpha were monophyletic. The Megalyroidea and Trigonalyoidea are sister clades as are the Chalcidoidea+Diaprioidea. The Cynipoidea was generally recovered as the sister group to Chalcidoidea and Diaprioidea which are each other's closest relations.

Anatomy
Hymenopterans range in size from very small to large insects, and usually have two pairs of wings. Their mouthparts are adapted for chewing, with well-developed mandibles (ectognathous mouthparts). Many species have further developed the mouthparts into a lengthy proboscis, with which they can drink liquids, such as nectar. They have large compound eyes, and typically three simple eyes. The forward margin of the hind wing bears a number of hooked bristles, or "hamuli", which lock onto the fore wing, keeping them held together. The smaller species may have only two or three hamuli on each side, but the largest wasps may have a considerable number, keeping the wings gripped together especially tightly. Hymenopteran wings have relatively few veins compared with many other insects, especially in the smaller species. In the more ancestral hymenopterans, the ovipositor is blade-like, and has evolved for slicing plant tissues. In the majority, however, it is modified for piercing, and, in some cases, is several times the length of the body. In some species, the ovipositor has become modified as a stinger, and the eggs
are laid from the base of the structure, rather than from the tip, which is used only to inject venom. The sting is typically used to immobilize prey, but in some wasps and bees may be used in defense (Hoell et al., 1998).

The larvae of the more ancestral hymenopterans resemble caterpillars in appearance, and like them, typically feed on leaves. They have large chewing mandibles, three pairs of thoracic limbs, and, in most cases, a number of abdominal prolegs. Unlike caterpillars, however, the prolegs have no grasping spines, and the antennae are reduced to mere stubs.

The larvae of other hymenopterans, however, more closely resemble maggots, and are adapted to life in a protected environment. This may be the body of a host organism, or a cell in a nest, where the adults will care for the larva. Such larvae have soft bodies with no limbs. They are also unable to defecate until they reach adulthood due to having an incomplete digestive tract, presumably to avoid contaminating their environment (Hoell et al., 1998).

Reproduction

Sex determination. Among most or all hymenopterans, sex is determined by the number of chromosomes an individual possesses (David et al., 2004). Fertilized eggs get two sets of chromosomes (one from each parent’s respective gametes), so develop into diploid females, while unfertilized eggs only contain one set (from the mother), so develop into haploid males; the act of fertilization is under the voluntary control of the egg-laying female ((Hoell et al., 1998)). This phenomenon is called haplodiploidy.

However, the actual genetic mechanisms of haplodiploid sex determination may be more complex than simple chromosome number. In many Hymenoptera, sex is actually determined by a single gene locus with many alleles (David et al., 2004). In these species, haploids are male and diploids heterozygous at the sex locus are female, but occasionally a diploid will be homozygous at the sex locus and develop as a male, instead. This is especially likely to occur in an individual whose parents were siblings or other close relatives. Diploid males are known to be produced by inbreeding in many ant, bee, and wasp species. Diploid biparental males are usually sterile but a few species that have fertile diploid males are known (Elias et al., 2009).

One consequence of haplodiploidy is that females on average actually have more genes in common with their sisters than they do with their own daughters. Because of this, cooperation among kindred females may be unusually advantageous, and has been hypothesized to contribute to the multiple origins of eusociality within this order ((Hoell et al., 1998). In many colonies of bees, ants, and wasps, worker females will remove eggs laid by other workers due to increased relatedness to direct siblings, a phenomenon known as worker policing (Davies et al., 2012).

Thelytoky. Some hymenopterans take advantage of parthenogenesis, the creation of embryos without fertilisation. Thelytoky is a particular form of parthenogenesis in which female embryos are created (without fertilisation). The form of thelytoky in hymenopterans is a kind of automixis in which two haploid products (proto-eggs) from the same meiosis fuse to form a diploid zygote. This process tends to maintain heterozygosity in the passage of the genome from mother to daughter. It is found in several ant species including the desert ant Cataglyphis cursor (Pearcy et al., 2004), the clonal raider ant Cerapachys biroi (Oxley et al., 2014), the predaceous ant Platthyrea punctata (Kellner et al., 2011), and the electric ant (little fire ant) Wasmannia auropunctata (Rey et al., 2011). It also occurs in the Cape honey bee Apis mellifera capensis (Baudry et al., 2004).

Oocytes that undergo automixis with central fusion often have a reduced rate of crossover recombination, which helps to maintain heterozygosity and avoid inbreeding depression. Species that display central fusion with reduced recombination include the ants Platthyrea punctata ((Kellner et al., 2011) and Wasmannia auropunctata (Rey et al., 2011) and the honey bee Apis mellifera capensis.[14] In A. m. capensis, the recombination rate during meiosis is reduced more than 10-fold (Baudry et al., 2004). In Wasmannia auropunctata the reduction is 45-fold (Rey et al., 2011).
Single queen colonies of the narrow headed ant *Formica exsecta* illustrate the possible deleterious effects of increased homozygosity. In this ant, colonies with more homozygous queens age more rapidly. The result is reduced colony survival (Haag-Liautard *et al.*, 2009).

**Diet**

Different species of *Hymenoptera* show a wide range of feeding habits. The most primitive forms are typically herbivorous, feeding on leaves or pine needles. Stinging wasps are predators, and will provision their larvae with immobilised prey, while bees feed on nectar and pollen.

A number of species are parasitoid as larvae. The adults inject the eggs into a paralysed host, which they begin to consume after hatching. Some species are even hyperparasitoid, with the host itself being another parasitoid insect. Habits intermediate between those of the herbivorous and parasitoid forms are shown in some hymenopterans, which inhabit the galls or nests of other insects, stealing their food, and eventually killing and eating the occupant (Hoell *et al.*, 1998).

**Classification**

The *Hymenoptera* are divided into two groups (table 1), the *Symphyta* which have no waist, and the *Apocrita* which have a narrow waist (Aguiar *et al.*, 2013).

<table>
<thead>
<tr>
<th>TAXON</th>
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<td>COMMON NAME</td>
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**Table 1 – Classification of the Hymenoptera.**

<table>
<thead>
<tr>
<th>Suborder SYMPHYTA</th>
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<tbody>
<tr>
<td>Tenthredinidae</td>
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<td>Cimbicidae</td>
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<td>Siricidae</td>
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<table>
<thead>
<tr>
<th>Suborder APOCRITA</th>
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<tbody>
<tr>
<td>Division PARASITICA</td>
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<tr>
<td>Superfamily Ceraphronoidea</td>
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<tr>
<td>Superfamily Chalcidoidea</td>
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<tr>
<td>Superfamily Cynipoidea</td>
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<tr>
<td>Cynipidae</td>
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<tr>
<td>Superfamily Diaprioidea</td>
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<tr>
<td>Superfamily Evanioidae</td>
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<tr>
<td>Superfamily Ichneumonoidea</td>
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<tr>
<td>Braconidae</td>
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<tr>
<td>Ichneumonidae</td>
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<tr>
<td>Eoichneumonidae</td>
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<tr>
<td>Praeichneumonidae</td>
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<tr>
<td>Superfamily Megalyroidea</td>
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<td>Superfamily Mimarommatoidae</td>
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<td>Superfamily Platygastroidea</td>
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<td>Superfamily Pompiloidea</td>
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<tr>
<td>Superfamily Proctotrupoidea</td>
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<td>Superfamily Serphitoidea</td>
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<td>Superfamily Stephanoidea</td>
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<td>Superfamily Trigonaloidea</td>
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<tr>
<td>Superfamily Trigonalyoidea</td>
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<tr>
<td>Division ACULEATA</td>
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<tr>
<td>Superfamily Chrysidoidae</td>
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<tr>
<td>Bethylidae</td>
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<td>Chrysididae</td>
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<tr>
<td>Cleptidae</td>
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<td>Dryinidae</td>
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Ceraphronoids, chalcidoids, chalcid wasps, cynipoids, gall wasps, parasitic wasps, parasitic hymenoptera, braconid wasps, ichneumon wasps, eoichneumon wasps, praenichneumon wasps, bethylid wasps, chrysidid or jewel wasps, dryinid wasps.
Embolemidae  embolemid wasps
Loboscelidiidae  loboscelidiid wasps
Plumalexiidae  plumarid wasps
Plumaiidae  sclerogibbid wasps
Sclerogibbidae  sclerogibbid wasps
Scolebythidae  scolebythid wasps
Superfamily Vespoidea  scolioid wasps and ants
Anthoboscidae  bradynobaenid wasps
Armaniidae  mason wasps
Brachycistidae  cow ants, velvet ants
Eumenidae  myrmosid wasps
Falstiformicidae  spider wasps, pompilid wasps
Limnetidae  pollen wasps
Masaridae  pollen wasps
Methochidae  cow ants, velvet ants
Mutillidae  myrmosid wasps
Pompilidae  spider wasps, pompilid wasps
Psammocharidae  rhopalosomatidae wasps
Rhopalosomatidae  club-horned wasps
Sapygidae  scoliid wasps
Scoliidae  scolioid wasps
Sphecomyrmidae  social wasps, yellowjackets, hornets
Vespidae  solitary bees
Superfamily Apoidea: 2 groups and 10 families
Group Apiformes  solitary bees
Andrenidae  mining bees
Colletidae  plasterer bees, cellophane bees, whitefaced bees
Halictidae  sweat bees
Megachilidae  leafcutter bees, mason bees, carder bees
Melittidae  melittid bees
Stenotritidae  stenotritis
Group Spheciformes  sphecoloid wasps
Ampulicidae  amputlicid wasps
Crabronidae  crabronid wasps
Heterogynaidae  heterogynaid wasps
Sphecidae  thread-walsted wasps, mud daubers
Angarosphecidae  social and orchid bees, stingless bees
Anthophoridae  social and orchid bees, stingless bees
Apidae  social and orchid bees, stingless bees
Baissodidae  social and orchid bees, stingless bees
Charipidae  social and orchid bees, stingless bees
Dasypodaidae  social and orchid bees, stingless bees
Meganomiidae  social and orchid bees, stingless bees
Melittosphecidae  social and orchid bees, stingless bees
Oxaecidae  social and orchid bees, stingless bees
Paleomelittidae  social and orchid bees, stingless bees

Symphyta. The suborder Symphyta includes the sawflies, horntails, and parasitic wood wasps. The group may be paraphyletic, as it has been suggested that the family Orussidae may be the group from which the Apocrita arose. They have an unconstricted junction between the thorax and
abdomen. The larvae are herbivorous, free-living eruciforms, with three pairs of true legs, prolegs (on every segment, unlike Lepidoptera) and ocelli. The prolegs do not have crochet hooks at the ends unlike the larvae of the Lepidoptera. **Apocrita.** The wasps, bees, and ants together make up the suborder Apocrita, characterized by a constriction between the first and second abdominal segments called a wasp-waist (petiole), also involving the fusion of the first abdominal segment to the thorax. Also, the larvae of all Apocrita lack legs, prolegs, or ocelli. The hindgut of the larvae also remains closed during development, with feces being stored inside the body, with the exception of some bee larvae where the larval anus has reappeared through developmental reversion. In general, the anus only opens at the completion of larval growth (Hunt, 2007).

**References**


31. Sharkey, Michael J.; Carpenter, James M.; Vilhelmsen, Lars; Heraty, John; Liljeblad, Johan; Dowling, Ashley P.G.; Schulmeister, Susanne; Murray, Debra; Deans, Andrew R.; Ronquist, Fredrik; Krogmann, Lars; Wheeler, Ward C. (February 2012). "Phylogenetic relationships among superfamilies of Hymenoptera". Cladistics. 28 (1): 80–112.

32. Song, Sheng-Nan; Tang, Pu; Wei, Shu-Jun; Chen, Xue-Xin (16 February 2016). "Comparative and phylogenetic analysis of the mitochondrial genomes in basal hymenopterans". Scientific Reports. 6: 20972.