**Aims and Objectives**

**Aims**
1. To provide a systematic overview of eusocial insects emphasizing the multiple origins of eusociality.
2. To provide additional basic information on the different groups of social insects.

**Objectives**
1. To learn about the multiple origins of eusociality, and how this leads to the conclusion that many social traits have convergently evolved.
2. To have a basic awareness and knowledge of the different lineages of social insects, their relationship to each other and their main taxa.

Should this lecture be first? It will make more sense now that you have some information on social insect biology and diversity.

**The Big Picture**

Eusociality has evolved many times in insects
Many eusocial species are of the same eusocial lineage
  - any two ant species
  - any two termite species
  - any two eusocial Vespinae wasps
  - honey bees, bumble bees, stingless bees
Many eusocial species are NOT of the same eusocial lineage
  - any ant or termite and anything else
  - a honey bee and a wasp
  - an Augochlorini and a Halictini Halictinae bee
  - a Vespinae wasp & the one eusocial Sphecidae wasp

**Possible Phylogenies of Eusociality**

**Example Phylogenies 1 & 2**
- 1. No eusocial origin; no species eusocial: examples include moths+ butterflies (Lepidoptera)
- 2. One eusocial origin; all species eusocial: examples are termites (Isoptera) and ants (Formicidae)

**Example Phylogenies 3 & 4**
- 3. One eusocial origin; one eusocial species: examples include the wasp Microstigmus comes within Sphecidae wasps
- 4. One eusocial origin; a few eusocial species: examples are the eusocial thrips, Anthophoridae bees

**Example Phylogenies 5 & 6**
- 5. One eusocial origin, most species in taxon eusocial: examples include eusocial bees within the Apidae
- 6. Several eusocial origins within a taxon; examples include the Halictinae bees with 3 origins

**Example Phylogenies 7**
- 7. One eusocial origin with one reversion; example is within Halictinae (Augochlorini) bees.
**Systematic Distribution of Eusociality in the Insecta**

Eusocial insects have long been known in the insect orders Isoptera (termites) and Hymenoptera (bees, wasps, and ants). Eusociality has recently been discovered in Hemiptera (in gall-living aphids), in Thysanoptera (in gall-living thrips), & Coleoptera (one bark beetle). Unlike ants, bees, wasps, and termites, none is of major ecological importance. Insect eusociality is, therefore, widely distributed in the insects as a whole, occurring in both hemimetabolous and holometabolous (Hymenoptera, Coleoptera) orders. The order Isoptera is entirely eusocial. However, recent research indicates that, phylogenetically, termites should be regarded as a family of cockroaches (order Blattaria).

**Distribution of Eusociality in Insecta**

Eusocial insects have long been known in the insect orders Isoptera (termites) and Hymenoptera (bees, wasps, and ants). Eusociality has recently been discovered in Hemiptera (in gall-living aphids), in Thysanoptera (in gall-living thrips), & Coleoptera (one bark beetle). Unlike ants, bees, wasps, and termites, none is of major ecological importance. Insect eusociality is, therefore, widely distributed in the insects as a whole, occurring in both hemimetabolous and holometabolous (Hymenoptera, Coleoptera) orders. The order Isoptera is entirely eusocial. However, recent research indicates that, phylogenetically, termites should be regarded as a family of cockroaches (order Blattaria).

**Abstract from Inward et al.**

Inward, D., Beccaloni, G., Eggleton, P. 2007. Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. Biology Letters 3: 331-335. Termites are instantly recognizable mound-builders and house-eaters: their complex social lifestyles have made them incredibly successful throughout the tropics. Although known as ‘white ants’, they are not ants and their relationships with other insects remain unclear. Our molecular phylogenetic analyses, the most comprehensive yet attempted, show that termites are social cockroaches, no longer meriting being classified as a separate order (Isoptera) from the cockroaches (Blattodea). Instead, we propose that they should be treated as a family (Termitidae) of cockroaches. It is surprising to find that a group of wood-feeding cockroaches has evolved full sociality, as other ecologically dominant fully social insects (e.g. ants, social bees and social wasps) have evolved from solitary predatory wasps.
Hymenoptera

Hymenoptera Systematics

- Sympyta: sawflies & woodwasps
  - 7000 species; no eusocial species

- Apocrita: parasitic wasps
  - 55,000 species; no eusocial species

- Aculeata: parasitic wasps, solitary wasps, bees, ants, eusocial wasps
  - 54,000 species; many eusocial species
  - c. 10 origins of eusociality

Hymenoptera are divided into suborders Sympyta, Apocrita, Aculeata. All eusocial species are in Aculeata. Aculeata are defined by a shared derived characteristic (synapomorphy): non-use of the ovipositor to lay eggs. It still functions to sting.

Symphyta: Sawflies & Wood Wasps

- Hymenoptera: Sympyta. Sawflies (left) & wood wasps (right). 6000 species. Important herbivorous insects. Some are pests of forestry & agriculture. Sawfly larvae look superficially like a moth larva, but have more prolegs. Adults look like wasps but do not have a wasp waist.

Social Groups of Sawfly Larvae

- None of the Sympyta are eusocial. However, many sawflies have larvae that aggregate for mutualistic defence. Aggregation is simple as the mother will often lay a batch of eggs on the host plant. In some species the larvae regurgitate plant resins and wave their heads in unison. Above is an amazing group of sawfly larvae seen by F. Ratnieks in São Paulo State, Brazil in January 2006. They formed a single coordinated “caterpillar” 12cm long and were crossing a dirt road. How do they coordinate their actions and go in a consistent direction?

Apocrita: Ichneumon & Chalcid Wasps

- Above: Ichneumonidae wasps. Below: Chalcidoidea wasps; left: fig wasps; right: Nasonia vitripennis ovipositing on fly pupa.

Apocrita

- The Apocrita, sometimes called the Parasitica, are a diverse group (55,000 species) of parasitoid wasps. They lay eggs in or near the body of the host (which may be in immature or mature form). The larvae develop in or on the host and kill it.

- They are extremely important organisms as they kill other insects, including pest insects. There are many families including the Ichneumonidae. Nasonia vitripennis and fig wasps are parasitic wasps (Apocrita: Chalcidoidea).

- No species are eusocial. However, in a few species in which many sibling larvae develop in a single host, some larvae develop into “sterile defenders” which kill competing parasitic wasp larvae of their own or other species in the same host. In a sense this is reproductive division of labour, and is similar to what occurs in eusocial aphids. Examples like this show how difficult it is to define eusociality.

Aculeata
**Some Non-Eusocial Aculeate Wasps**

- Chrysididae (jewel wasps). Parasitic wasps. Female lays eggs in the nests of ground nesting bees & wasps.
- Vespidae: Eumeninae (potter wasps). Subsocial wasps. Female builds a mud nest and feeds the brood on insect prey. Some Vespidae and Apoidea are predators or herbivores (Apoidea: bees; Vespoida: some ants).
- Pompilidae (spider killers). Subsocial wasps. Female builds a nest in ground and feeds brood on insect prey.

**Eusocial Wasps: Vespidae**

- Euparaginae (honey wasps)
- Eumeninae (hover wasps)
- Polistinae (paper wasps)

This phylogeny of the 6 subfamilies of Vespidae wasps (Carpenter 1982) is based on a wide range of morphological and other characters. All species in the three subfamilies marked with an asterisk are eusocial or social parasites. The most parsimonious interpretation, therefore, is that eusociality evolved just once, in their common ancestor.

**Hymenoptera Aculeata: Wasps**

**Aculeata Phylogeny**

Chrysidioidea (= Bethylloidea)
- Vespidoidea eusocial taxa: ants, Vespidae wasps
- Apoidea (= Sphecoida)
- Chrysididae
- Sphecidae
- Vespidae

Aculeata are divided into the superfamilies Chrysidioidea, Vespidoidea, Apoidea. There are eusocial species in Vespidoidea and Apoidea. All Chrysidioidea and some Vespidoidea are parasitoids. Some non-eusocial Aculeata wasps are in Vespidoidea and Apoidea. They are in the two ant families (Formicidae) and have eusocial species. The Formicidae are all eusocial. In the others, some species are eusocial.

**Aculeata Phylogeny**

The aculeate phylogeny on the previous slide, from Hölldobler & Wilson 1996, presents an overview showing superfamilies and families. The synapomorphy (shared derived character) showing that Aculeata are a monophyletic group is the use of the ovipositor solely as a sting. It is not used for laying eggs. Eggs exit the female at the base on the sting. The families with eusocial taxa are placed in boxes. Three bee families (Apidae, Anthophoridae, Halictidae), two wasp families (Vespidae, Sphecidae), and one ant family (Formicidae) have eusocial species. The Formicidae are all eusocial. In the others, some species are eusocial.

The phylogeny shows that bees and ants are modified wasps, and that the Sphecidae are more closely related (share a more recent common ancestor) to bees that to Vespidae wasps. The most recent common ancestor of an ant and a bee was a non-eusocial wasp. Some of the taxon names and levels used by H&W are different to those often used. For example, the Vespidae, Masaridae, and Eumenidae are given family rank. But they are usually considered to belong to one family, the Vespidae, with Masarinae (honey wasps) and Eumeninae (potter wasps) given subfamily rank. What is referred to by H&W as Sphecoidae is now usually called Apoidea.

**Why Are Only Aculeata Eusocial?**

There are approximately 9 origins of eusociality in the Hymenoptera. All are in the Aculeata. However, the Aculeata are only 46% of hymenopteran species. Why is eusociality concentrated in this group?

The reason is almost certainly that subsocial behaviour in Hymenoptera only occurs in Aculeata. Many species build nests to rear their brood. The mother provisions the nest with prey or nectar & pollen. The nest can be reused and is a location where kin are present and can be helped. These features preadapt subsocial bees & wasps to eusociality. Another explanation for multiple origins of eusociality in Hymenoptera is haplodiploidy, which causes higher relatedness, 0.75, among sisters. However, all Hymenoptera are haplodiploid. If haplodiploidy alone were the cause, then eusociality should be found throughout the order. The haplodiploid hypothesis is no longer thought to be important in explaining why there are so many origins of eusociality in Hymenoptera. Although relatedness among full sisters is greater than in diploids (0.75 v 0.5), relatedness of sisters to brothers is lower (0.25 v 0.5). Thus, a daughter helping her mother is rearing siblings with an average relatedness of 0.5, the same as in diploids rearing full siblings.

- **Species**
  - **Chrysididae** (jewel wasps). Parasitic wasps. Female lays eggs in the nests of ground nesting bees & wasps.
  - **Vespidae**: Eumeninae (potter wasps). Subsocial wasps. Female builds a mud nest and feeds the brood on insect prey. Some Vespidae and Apoidea are predators or herbivores (Apoidea: bees; Vespoida: some ants).
  - **Mutillidae** (velvet ants). Parasitic wasps. Female lays eggs in the nests of ground nesting bees & wasps. Females are wingless and look superficially like ants. Hairy. Painful sting.
  - **Pompilidae** (spider killers). Subsocial wasps. Female builds a nest in ground and feeds brood on insect prey.

**Aculeata Phylogeny**

- **Eumeninae** is a possible precursor to eusociality.
- Vespidae are eusocial so the nest building and maternal care in Eumeninae is a possible precursor to eusociality.
- Relatedness of 0.5, the same as in diploids rearing full siblings.
- Although relatedness among full sisters is greater that in diploids (0.75 v 0.5), relatedness of sisters to brothers is lower (0.25 v 0.5). Thus, a daughter helping her mother is rearing siblings with an average relatedness of 0.5, the same as in diploids rearing full siblings.

- **Eusociality** evolved just once, in their common ancestor.
Eusocial Wasps: Vespidae (Hines et al.)

The Vespidae phylogeny on the previous slide has been called into question by more recent work by Hines et al. (2007). They suggest that the hover wasps are only distantly related to the other Vespidae. If so, this implies that eusociality evolved independently in the Stenogastrinae and in the Polistinae + Vespinae.

Abstract from Hines et al. 2007


Eusocial wasps of the family Vespidae are thought to have derived their social behavior from a common ancestor that had a rudimentary caste-containing social system. In support of this behavioral scenario, the leading phylogenetic hypothesis of Vespidae places the eusocial wasps (subfamilies Stenogastrinae, Polistinae, and Vespinae) as a derived monophyletic clade, thus implying a single origin of eusocial behavior. This perspective has shaped the investigation and interpretation of vespid social evolution for more than two decades. Here we report a phylogeny of Vespidae based on data from four nuclear gene fragments (18S and 28S ribosomal DNA, abdominal-A and RNA polymerase II) and representatives from all six extant subfamilies. In contrast to the current phylogenetic perspective, our results indicate two independent origins of vespid eusociality, once in the clade Polistinae+Vespinae and once in the Stenogastrinae. The stenogastrines appear as an early diverging clade distantly related to the vespines and polistines and thus evolved their distinctive form of social behavior from a different ancestor than that of Polistinae-Vespinae. These results support earlier views based on life history and behavior and have important implications for interpreting transitional stages in vespid social evolution.

Aculeata: Wasps

The Aculeata are all wasps, in the sense that bees and ants are modified wasps. Leaving bees and ants aside, there are a large range of wasp families in the Aculeata. It is not necessary to know them in detail. We will concentrate on the eusocial ones.

The first thing to note is that the two eusocial wasp lineages are in widely separate families, the Sphecidae and the Vespidae. There is just one eusocial sphecid, found in Costa Rica. 99.9% of the eusocial wasps including all the familiar eusocial wasps are in the Vespidae.

The sister group of the eusocial Vespidae are the potter wasps, Eumeninae. These are eusocial. The Vespidae and Eumeninae have the same social organization as the sphecids. They build small nest nests which are provisioned with insect prey that have been paralyzed with venom. The fact that the sister group of the eusocial clade has nest building females is evidence that eusociality has arisen from subsociality.

The other slides show more detailed phylogenies of the Vespidae, and the Vespinae. The phylogeny of the Vespidae, Carpenter 1982, indicates a single origin of eusociality. However, a more recent phylogeny, Hines et al. 2007 indicates two origins. The phylogeny of the Vespinae shows the relationship of the four genera. From this we can infer various things, including that low relatedness caused by multiple mating is derived.

Phylogeny of Bees

This phylogeny of the bees, taken from Grimaldi & Engel 2005, is more detailed than our needs. Do not try to learn the names. You can take the following main points:

1. Eusociality (yellow, red) has evolved within three groups here called (Corbiculate Apines = Apidae), Halictinae, and Xylocopinae.
2. Eusociality in Apidae evolved c. 80 million years ago in the late Cretaceous. (They are probably in error in giving eusocial a similarly age in Halictinae & Xylocopinae.)

Hymenoptera Aculeata: Bees

Hymenoptera Aculeata: Bees

Apidae: Four Subfamilies

- Xylocopinae
- Euglossinae
- Bombinae
- Apinae

Apidae Phylogeny

Despite being the best studied group of eusocial insects, the phylogeny of the Apidae bees is not yet known for sure. Phylogenies constructed with molecular versus morphological data (e.g., see previous slide of Grimaldi & Engel) do not give the same result. The phylogeny above is probably the correct one.

Reversions Within Halictus

This detailed phylogeny of *Halictus* shows that within this eusocial lineage, there have been 4-6 reversions to subsocial (= solitary) nesting. That is, eusociality has been lost many times. In some cases there is insufficient data on nesting to know if nests are eusocial or subsocial. In some cases nests may be both (= polymorphic).

(Danforth 2002, Figure 2)

Lessons From Halictidae Bees

Until recently it was thought that eusociality had evolved 6 or more times in Halictidae bees (sweat bees). But detailed phylogenies, constructed using DNA base pair sequences as characters, have shown that eusociality only evolved 3 times, but has been lost more than 10 times with reversions to solitary nesting (and also to social parasitism).

The phylogeny of the Halictidae also shows that the sister groups of the eusocial clades have subsocial nesting, similar to the situation in Vespidae wasps. In addition, both groups have overwintering females. So it seems that eusociality in these groups has arisen from subsocial species in which overwintered females establish a nest in the spring.

The Halictidae bees and the Vespidae wasps are among the best groups of eusocial insects in which to investigate the origin of eusociality. This is because there are both eusocial and non-eusocial species. Ants and termites, for example, have only eusocial species.

Hymenoptera Aculeata: Bees

**Halictidae**

- **Halictidae Bees**
  - Outgroup: Rophitinae
  - Nomiinae: 0 eusocial origins
  - Nomioidinae: 0 eusocial origins
  - Halictinae: 3 eusocial origins

This phylogeny of the Halictidae is constructed from a sequence of 1800 base pairs of nuclear DNA using a bee from another family as an outgroup (Danforth 2002). Eusociality has evolved 3 times in the Halictidae, all three times within the Halictinae. (It is not necessary to learn the names of the other 3 subfamilies.) Danforth, B. N. 2002. Evolution of sociality in a primitively eusocial lineage of bees. PNAS 99: 286-290.

**Halictidae Bees**

- Outgroup: Rophitinae
- Nomiinae: 0 eusocial origins
- Nomioidinae: 0 eusocial origins
- Halictinae: 3 eusocial origins

This phylogeny of the Halictidae is constructed from a sequence of 1800 base pairs of nuclear DNA using a bee from another family as an outgroup (Danforth 2002). Eusociality has evolved 3 times in the Halictidae, all three times within the Halictinae. (It is not necessary to learn the names of the other 3 subfamilies.) Danforth, B. N. 2002. Evolution of sociality in a primitively eusocial lineage of bees. PNAS 99: 286-290.

**Halictidae Bees**

- Outgroup: Rophitinae
- Nomiinae: 0 eusocial origins
- Nomioidinae: 0 eusocial origins
- Halictinae: 3 eusocial origins

Three origins of eusociality in Halictinae:

1. **Rophitinae**
2. **Nomiinae**
3. **Nomioidinae**
4. **Halictinae**

**Halictidae Bees**

This phylogeny of the Halictidae is constructed from a sequence of 1800 base pairs of nuclear DNA using a bee from another family as an outgroup (Danforth 2002). Eusociality has evolved 3 times in the Halictidae, all three times within the Halictinae. This implies that swarm founding of nests evolved once in each group. This is not a surprising conclusion as the mechanisms of swarming are very different in the two groups, suggesting they evolved independently.

No eusocial origins

**Eusocial Halictinae Bee**

Lastoglossum zephyrum. A eusocial halictine bee species much studied by in the USA by Charles Michener & colleagues. The nest is below ground. Each larva develops on a provision mass of pollen and nectar in a cell. Mature nests are small, with just 6-20 females.

**Apidae Phylogeny**

Female Apidae bees share one well-known trait: the pollen basket (corbicula) on the female hind leg. This has been secondarily lost in parasitic bumble bees, and also in queen honey bees and stingless bees. You are familiar with the Bombinae (bumble bees) and Apinae (honey bees) which are common in Britain. The Meliponinae (stingless bees) are found worldwide in the tropics. There are probably 1000 species. Like honey bees they have large perennial colonies, and swarm-founded nests. The orchid bees (Euglossinae) are found only in the American tropics. There are probably 1000 species. Like honey bees they have large perennial colonies, and swarm-founded nests. The meliponine bees (Meliponinae) are found worldwide in the tropics. There are probably 1000 species. Like honey bees they have large perennial colonies, and swarm-founded nests. The orchid bees (Euglossinae) are found only in the American tropics. There are probably 1000 species. Like honey bees they have large perennial colonies, and swarm-founded nests. The meliponine bees (Meliponinae) are found worldwide in the tropics.

**Hymenoptera Aculeata: Bees**

- **Halictidae**
- **Euglossinae**
- **Apidae** (honey bees)
- **Meliponinae** (stingless bees)
- **Bombini** (bumble bees)

**Eusocial Halictinae Bee**

This detailed phylogeny of the Halictinae shows that eusociality probably evolved once. However, it also shows that the Apinae and the Meliponinae are not sister groups. This implies that swarm founding of nests evolved once in each group. It is not a surprising conclusion as the mechanisms of swarming are very different in the two groups, suggesting they evolved independently.

Note: some authors refer to the Apidae as the Apinae, in which case all the subfamilies are referred to as tribes (e.g., Apini, Bombini etc.). A name which is sometimes used to refer to all 4 Apidae subfamilies is the “corbiculate bees”, meaning the lineage of bees with a pollen basket. These authors include some other bees in the Apidae.

**Apidae Phylogeny**

- **Aculeata**
- **Hymenoptera**
- **Eusocial Halictinae Bee**

**Apidae Phylogeny**

- **Hymenoptera**
- **Aculeata**
- **Eusocial Halictinae Bee**

**Lessons From Halictidae Bees**

Until recently it was thought that eusociality had evolved 6 or more times in Halictidae bees (sweat bees). But detailed phylogenies, constructed using DNA base pair sequences as characters, have shown that eusociality only evolved 3 times, but has been lost more than 10 times with reversions to solitary nesting (and also to social parasitism).

The phylogeny of the Halictidae also shows that the sister groups of the eusocial clades have subsocial (= solitary) nests, rather than communal (many mothers) or communal (co-founding sisters) nests. Note: not all Halictini species were analysed. (modified from Danforth 2002, Figure 1)

**Reversions Within Halictus**

This detailed phylogeny of *Halictus* shows that within this eusocial lineage, there have been 4-6 reversions to subsocial (= solitary) nesting. That is, eusociality has been lost many times. In some cases there is insufficient data on nesting to know if nests are eusocial or subsocial. In some cases nests may be both (= polymorphic).

(Danforth 2002, Figure 2)
This phylogeny taken from Grimaldi & Engel 2005, is more detailed we need. Do not learn all the subfamily names. Take the following main points.

1. Ants evolved c. 120 million years ago in the Cretaceous.
2. Large colonies probably evolved many times given that large colonies occur in many subfamilies.

Doryline section: army ants
Formicinae: including wood ants Formica, Camponotus, Oecophylla weaver ants
Dolichoderinae: including Linepithema Argentine ants
Myrmicinae: including Atta leafcutter ants, Monomorium Pharaoh’s ants.

The Ants
Most diverse group of eusocial insects
Basically ground dwelling predatory wasps
Diet has diversified: seed gathering, fungus farming
Largest colonies and most complex symbiotic interactions of any of the social Hymenoptera (fungus farming, aphid farming, living within plants)
Loss of wings; but queens & males usually winged
Workers may show complex morphological castes
Social parasitism common: slavery, workerless parasites, parasitic founding of nest by queens

Leafcutter ant Atta laevigata
Termites Nasutitermes
Wasps Polybia
Silk weaving ant Camponotus sexs
Stingless bee Trigona spinipes
Fearless student Margaret Couvillon & Stingless bee Trigona spinipes
Big Nests at Fazenda Aretuzina

Fazenda Aretuzina is a small farm near the small town of São Simão, São Paulo State, Brazil. Formerly a coffee farm, it is now used for conservation and research. Social insects are by far the most numerous animals. Colonies are everywhere. The preceding slides show some of the most impressive nests.

Isoptera: Termitidae. *Nasutitermes* sp. Nest made of soil and organic matter in tree. Many covered trails can be seen leading away from the nest so that the termites can forage for organic matters all over the tree and in the surroundings. Estimated population 500,000.

Formicidae: Myrmicinae, *Atta laevigata*. Nest of leafcutter ants. Photo shows about one quarter of soil dump area above the nest. There are many holes for soil dumping and foraging. Estimated population 500,000 ants.


Insights from Phylogenies & Systematics

Use your “systematic” understanding of social insects to gain insights into social evolution. One place to start is convergent evolution. How often have various social traits evolved? Below are some examples. Can you think of a major social trait that evolved just once?

**Eusociality**

- c. 9 times in Hymenoptera, once in termites

**Fungus farming**

Twice: *Attini* ants, *Termitidae* termites

**Large colonies**

- c. 50,000 workers or more

**Morphologically distinct workers and queens**

- at least 4 times: *Termitidae* termites, *Ants*, *Apidae* bees, *Vespinae* wasps

**Large variation in morphology of workers**

- Only in ants and termites, but probably many times in ants

**Communication in foraging**

- Many times and in many ways (honey bee waggle dance, pheromones)

Handout: Further Information

The Big Picture

Why it is necessary to have a lecture on systematics, and some insights that come from social insect systematics.

Brief sketches of the eusocial Hymenoptera

Information about each taxon and its systematics.

Number of independent origins of eusociality

Some key taxon and common names to learn

If you learn the names in this list you will be well prepared to make sense of the taxa mentioned during the course.

British social insect diversity

Reference information. It is not necessary to memorize this. Look it over to understand what we have in Britain, what groups are absent etc.