Social Insects

- What do we mean by the term “social insect”?
- How many times has advanced social behavior (eusociality) evolved?
- What are the underlying preconditions for the evolution of eusociality and why is it so common in the Hymenoptera?
- What are the advantages of eusociality?
- How are insect colonies organized?

The 5 Kinds of Social Groups

- **Solitary**: adults live independent of one another and do not provide parental care to their young (most insects).
- **Subsocial**: adults care for their own young for some period of time (e.g., earwings, wood roaches, pentatomid bugs).
- **Communal**: adults use the same composite nest without cooperation in brood care (e.g., digger bees).
- **Quasisocial**: adults use the same nest and also show cooperative brood care (e.g., Euglossine bees).
- **Semisocial**: adults nest together, practice cooperative brood care with some reproductive division of labor (e.g., Halictid bees).
- **Eusocial**: overlapping generations of adults nest together, practice cooperative brood care with sterile, non-reproductive workers or helpers (e.g., honeybees, ants, social wasps).

How many times has eusociality evolved?

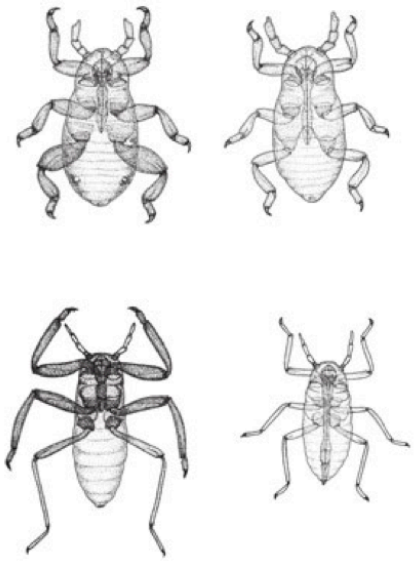
Insect order	Common Names	Number of Lineages
Hymenoptera	Ants, wasps, bees, sawflies	11
Isoptera	Termites	1
Homoptera	Gall-forming aphids	1
Coleoptera	Bark-nesting weavils	1
Thysanoptera	Gall-forming thrips	1
Non-insects	Snapping shrimps and naked mole rats	2
Total		17

Non-insect Eusocial Species

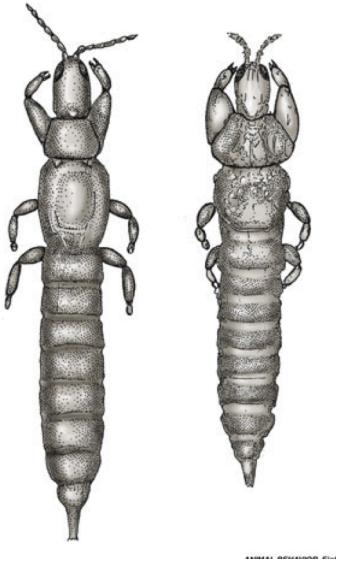
Eusocial mole rats. Two species, the naked mole rat (*Heterocephalus glaber*) and the Damaraland mole rat (*Fukomys damarensis*). Both species occur in Africa. Colonies consist of a single breeding pair and their non-reproductive offspring.

Eusocial snapping shrimp. Five species in the genus *Synalpheus*. All species live in association with sponges. Species occur in the western Atlantic Ocean. Colonies consist of one breeding female and her non-reproductive offspring, who defend, forage, and takes care of the colony.

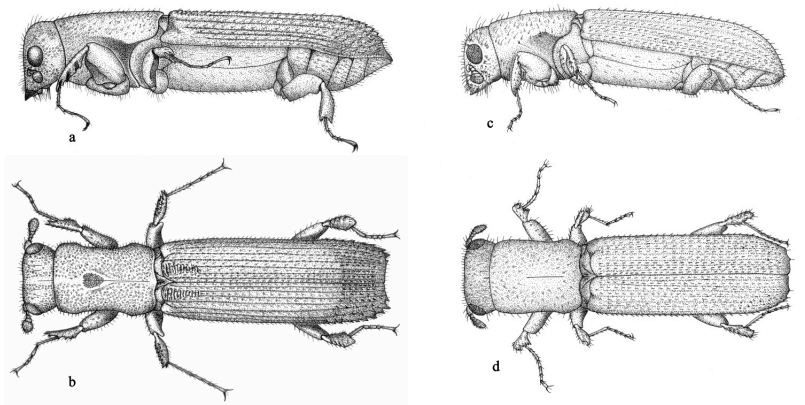
Eusocial Aphids, Thrips & Weevils



Social aphids live in dense clonal groups within galls on their host plants. In galls, specialized nymphal soldiers are produced that defend the clone from enemies.

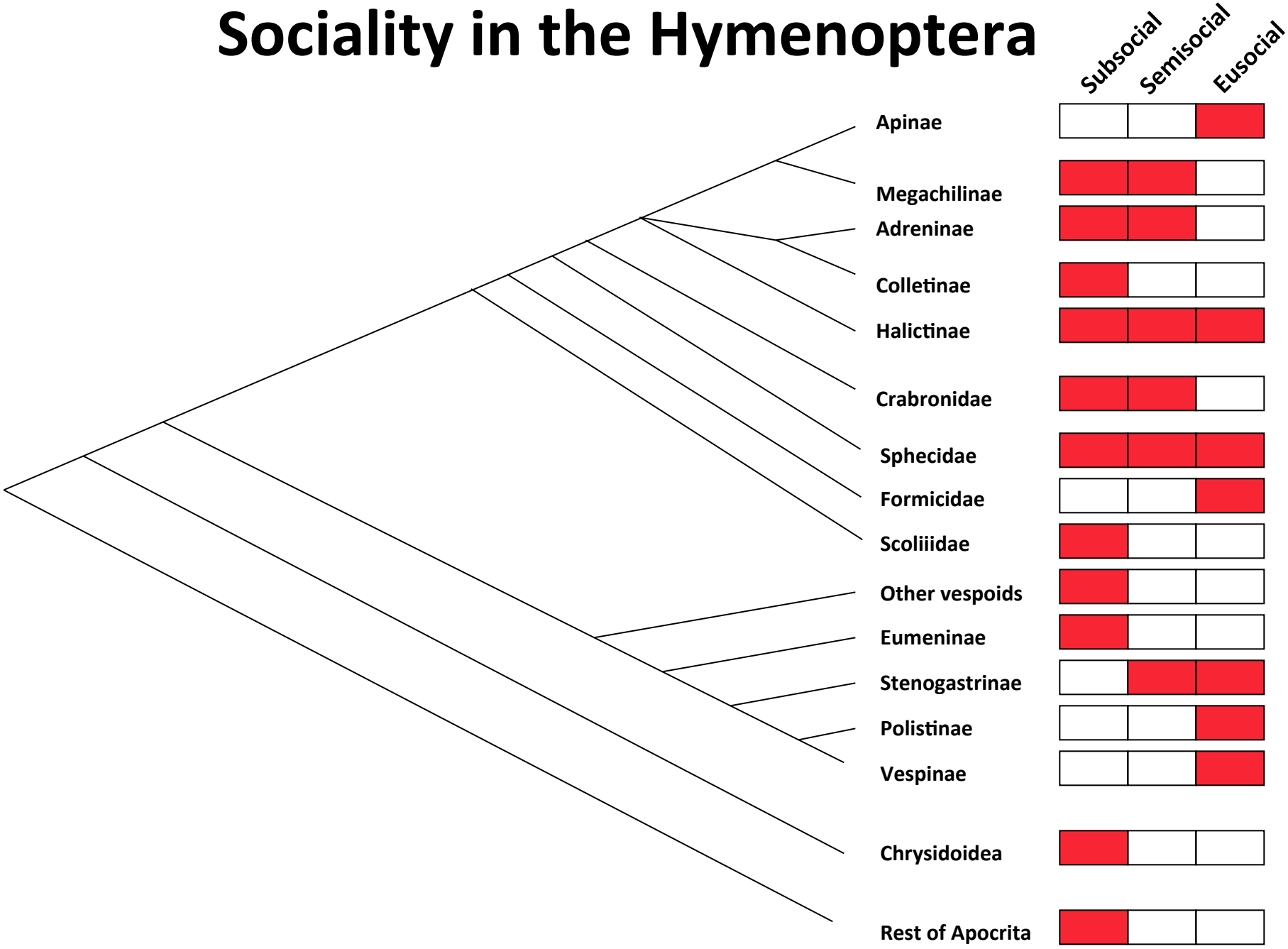


Social thrips live in colonies within galls on their host plants. Specialized soldiers are produced in the galls that defend the colony from enemies. These thrips species are haplodiploid.



Austroplatypus incompertus is a species of ambrosia beetle belonging to the weevil family. They are native to Australia. It forms colonies in the heartwood of *Eucalyptus* trees. Colonies contain a single fertilized female who is protected and taken care of by a small number of unfertilized females who also do much of the work.

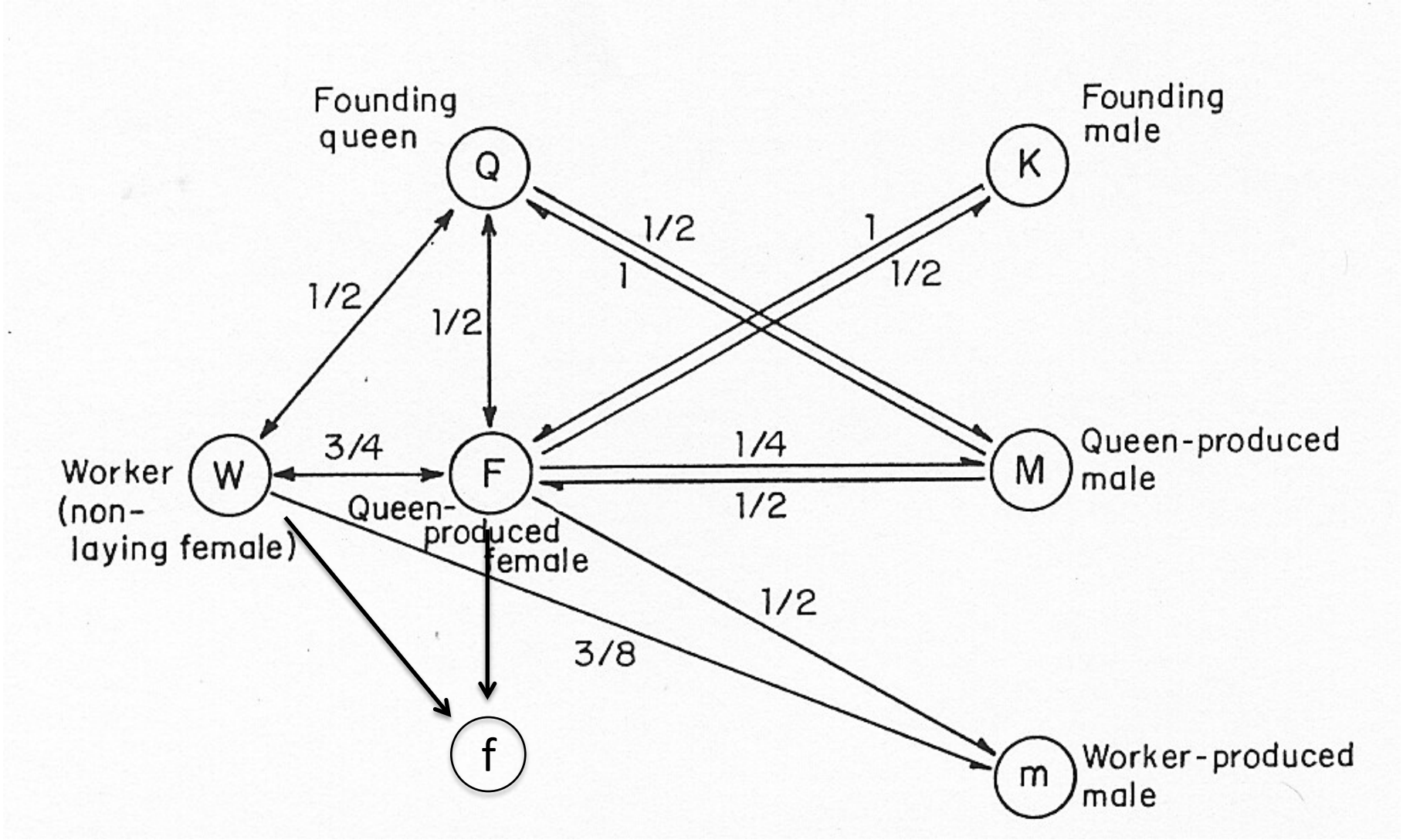
Sociality in the Hymenoptera



Why has eusociality evolved so many times in the Hymenoptera?

- Hymenoptera are haplodiploid (males are haploid, females are diploid).
- Modification of the ovipositor into a hunting and defensive weapon, the sting.
- Maternal defense and feeding of young in a protected cavity, the nest.
- Low success of young adults or solitary pairs that attempt to reproduce (but that's true for lots of insects).

Haplodiploidy gives rise to asymmetries in relatedness in families



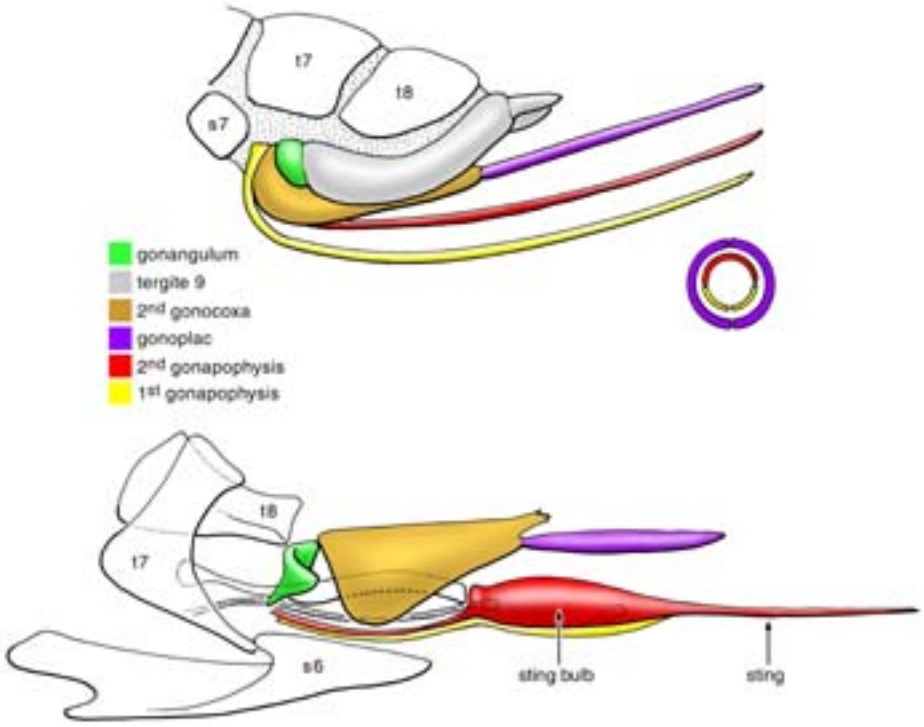
Consequences of Asymmetries in Relatedness

- Daughters of queens should favor raising reproductive sisters rather than reproductive daughters.
- A queen and her daughter workers should conflict over the preferred sex-ratio of reproductives (queens favoring a 50:50 male:female ratio and daughter workers favoring a 1:3 male:female ratio).
- Colonies of the Halictid bee *Augochlorella striata* with a queen present produce more female bias sex ratios than colonies composed of sisters.
- Colony sex ratios of many ant species are female bias, but this is not always the case.

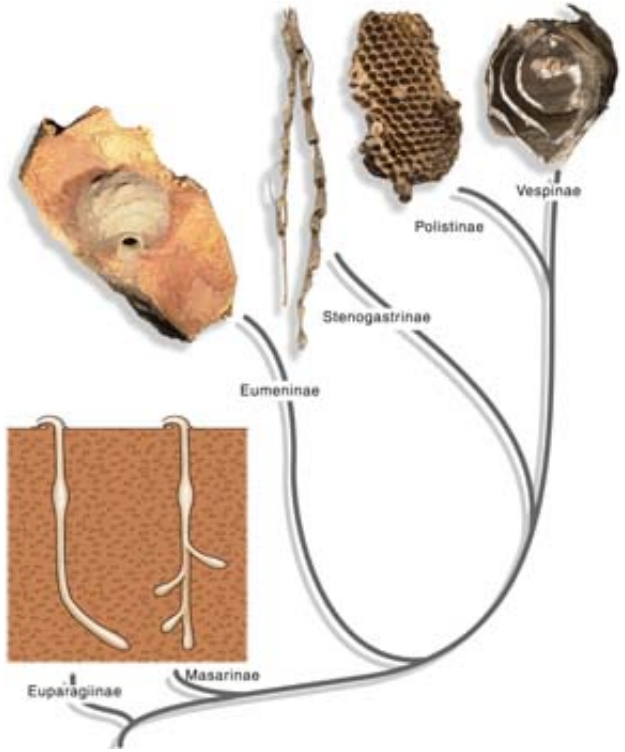
Haplodiploidy is not necessary or sufficient for the evolution of eusociality

- Multiple mating by the queen reduces asymmetries in relatedness.
- Multiple queens in a nest reduce asymmetries in relatedness.
- Queens in some species enforce sex ratio of reproductives which prevent workers from capitalizing on relatedness asymmetries.
- Not all haplodiploid species are eusocial. Not all eusocial species are haplodiploid.

Other Preconditions Required for the Evolution of Eusociality



A defining feature of the Aculeata is the sting, which is an ovipositor modified to inject venom by where eggs pass through an opening at the base of the sting.



Evolution of nest types in the family Vespidae. Many Aculeate rear their young in nests.

What are the adaptive values of eusociality?

- **Parallel tasks**: different individuals can perform different functions simultaneously.
- **Group response:** large numbers of individuals accomplishing difficult tasks.
- **Homeostasis through specialization**: maintaining optimal conditions through division of labor.

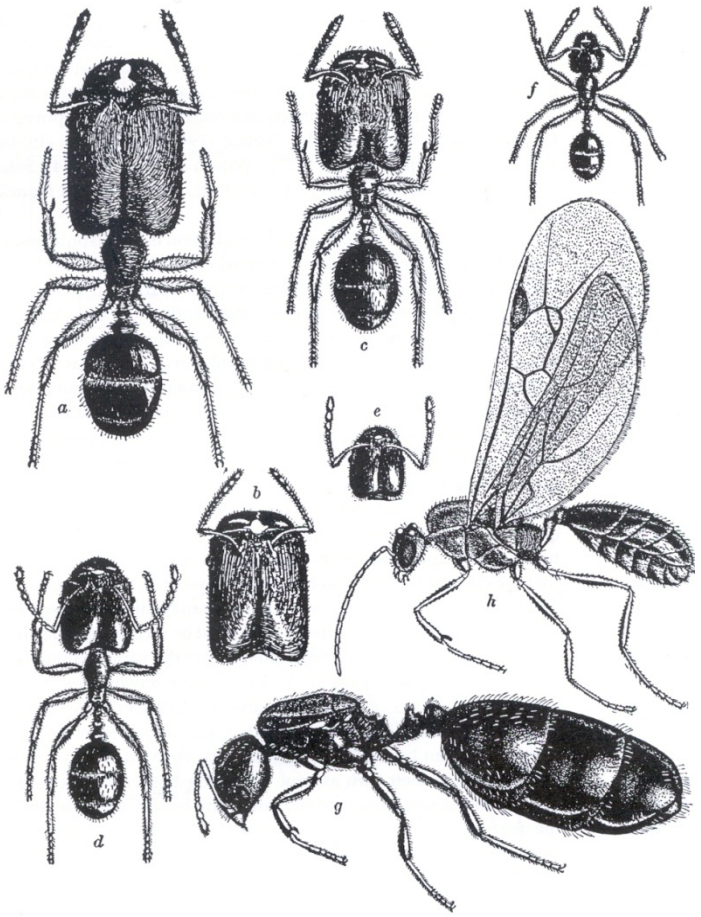
<u>Examples:</u>

Savings in energy (especially in nest-building).
Increased security (defensive ability).
Greater food-gathering potential.
Maintenance of constant interior (nest) environment.
More efficient performance of various behaviors by the colony, ability to “multi-task”.

Colony Structure

Eusocial insects have reproductive and non-reproductive **castes**.

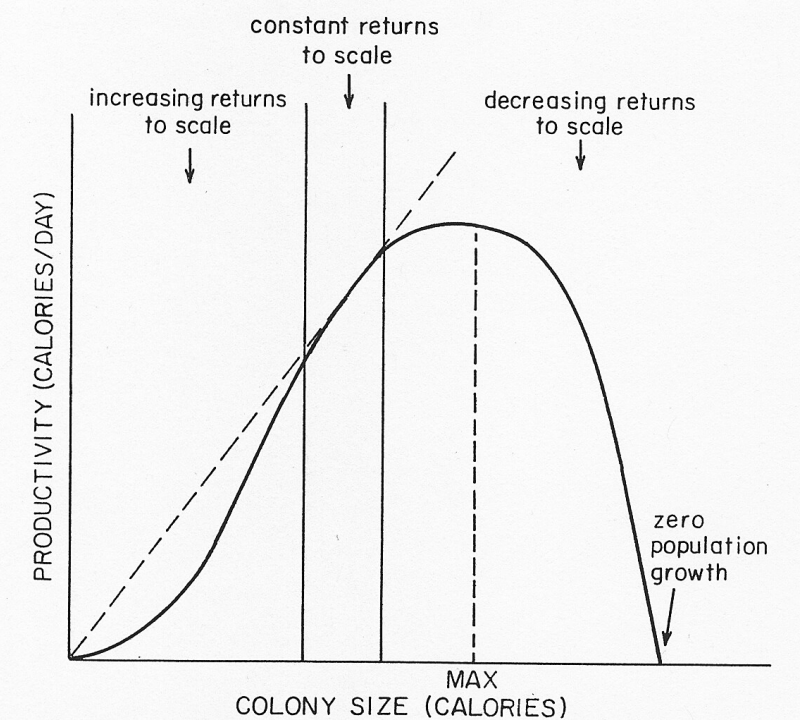
- **Queen.** The female reproductive caste in the colony.
- **Worker.** The female non-reproductive, laboring caste in the colony. The worker caste may be divided into several subcastes.
  - **Minor.** The smallest worker subcaste, responsible for most of the general tasks of the colony.
  - **Major.** The largest worker subcaste, usually specialized for defense, seed cracking or food storage.
- **Drone.** The male reproductive caste in the colony. Usually only present during the reproductive cycle and does not play an important role in the social life of the colony.

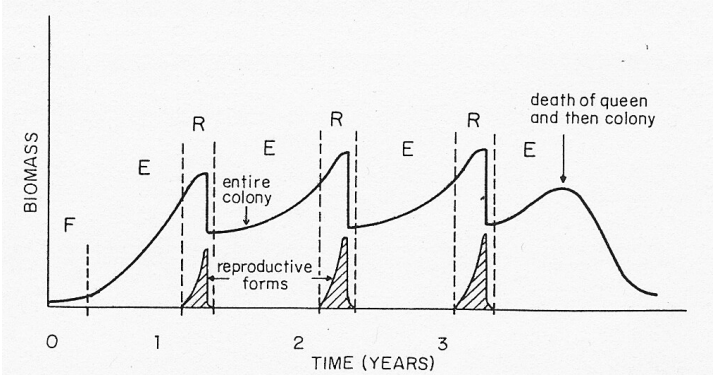


Pheidole tepicana

Three Stages of the Colony Cycle

- **Founding stage.** One or more queens begin a new colony, sometimes with a contingent of workers.
- **Egonomic stage.** The growth stage through addition of more workers. Returns to scale determined by resource production rates and contraints on the colony's social system.
- **Reproductive stage.** Stage at which reproductive castes are produced and released. Colonies may reach this stage only once or repeatedly during its lifetime.



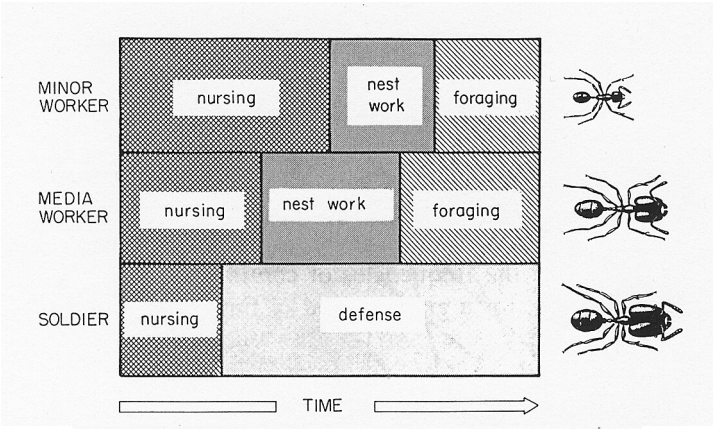


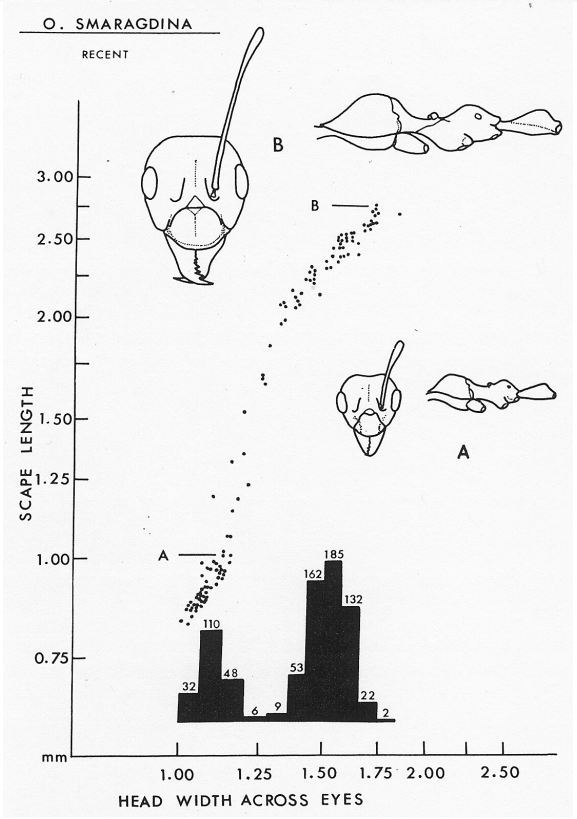
Division of Labor in Colonies

- **Polyethism** is division of labor among members of a colony. **Caste polyethism** refers to division of labor among the physical types within the colony. **Temporal polyethism** refers to changes in behavioral specialization as an individual ages.

- Workers perform their tasks in **parallel** with many ants performing the same task at the same time. Parallel processing increases the **reliability** of the system and favors the division of labor and evolution of specialization.

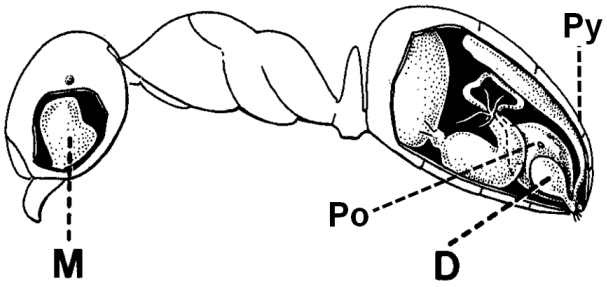
- Physical castes in ants are based on three factors: 1) increased size variation among workers, 2) bimodal or trimodal size distributions, 3) **allometric growth** over this increased size range.





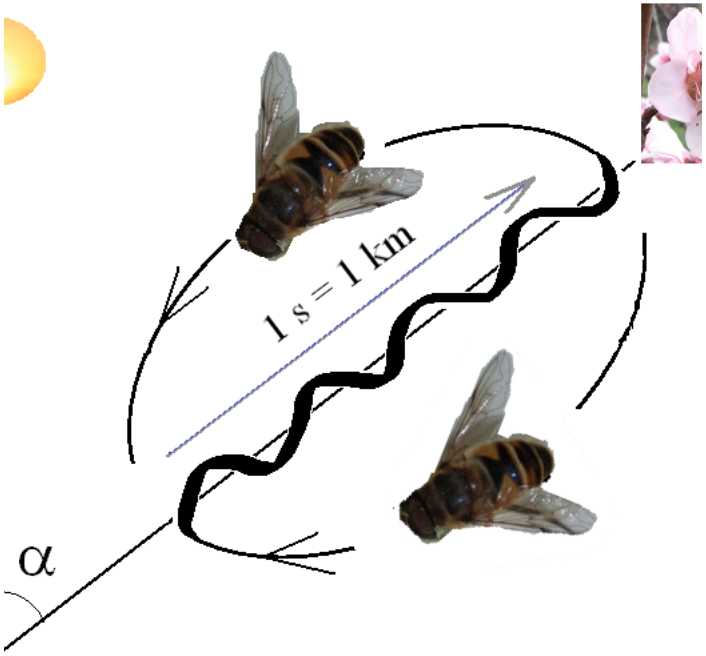
Coordinating Colony Members

Chemical communication through the use of social **pheromones**. Pheromones are chemical blends produced in a variety of exocrine glands. They serve as signals for alarm, nestmate recruitment and physiological regulation.



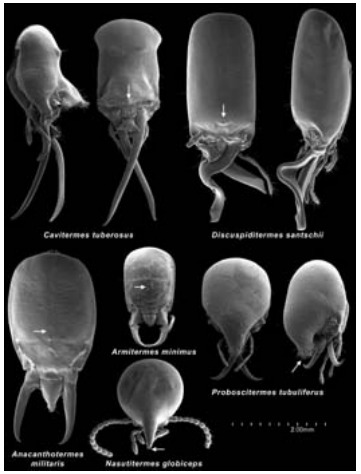
Anatomical location of the 4 major exocrine glands of ants. M = mandibular gland; D = Dufour's gland; Po = poison gland or sac; Py = pygidial gland. Modified from Hölldobler & Wilson (1990).

Symbolic communication through worker movement. The **waggle dance** in honey bees is performed by a newly returned forager and tells the direction and distance of a flower source. Other forms of symbolic communication include shakes, trembles and rushing movements, all of which have specific meanings.



Termite societies are different from ant, bee and wasps societies

- All species of termites are diploid in both sexes. There are no asymmetries in relatedness.
- Both males and females function as sterile workers in termite colonies.
- Both immature and adult stages contribute to the colony work force in termites.
- Termite colonies often have supplementary reproductives, hymenopteran colonies do not.



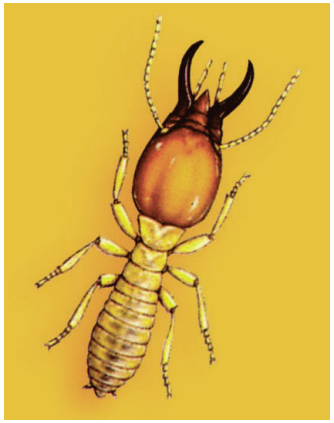
Above: termite colony with various castes.

Left: specialized heads of termite soldiers.

Why are termites eusocial?

Features of termite eusociality

- No asymmetries in degrees of relatedness.
- Both males and females function as sterile workers.



Hypotheses for termite eusociality

- Intergenerational dependence on endosymbionts.
- Large fraction of the genome propagated as a sex-linked complex, functionally equivalent to haplodiploidy.
- Presence of secondary reproductives suggest termite colonies are highly inbred, which favors eusociality.

photos: BugGuide.net, Google

Summary

- Eusociality occurs in several insect and non-insect groups, but has evolved repeatedly only in the Hymenoptera.
- Haplodiploid sex determination in Hymenoptera may play a role in the evolution of eusociality, but it is neither necessary nor sufficient for its evolution.
- Evolution of the sting and maternal feeding and defense of young in a nest in the Hymenoptera are probably more important preconditions for the evolution of eusociality.
- Eusocial species in the Hymenoptera may have very complex societies with thousands to millions of members.
- Eusociality in other groups appears to be associated with resources that require cooperation to successfully harvest and protected areas where immatures can develop. Colonies tend to be small and dispersed.