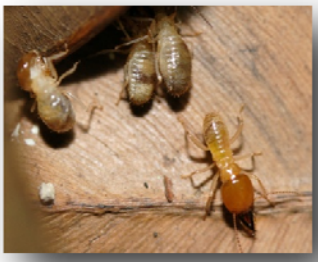
Termites

The **termites** are a group of social insects. As truly social animals, they are termed *eusocial* along with the ants and some bees and wasps which are all placed in the separate order Hymenoptera. Termites mostly feed on dead plant material, generally in the form of wood, leaf litter, soil, or animal dung, and about 10% of the estimated 4,000 species (about 2,600 taxonomically known) are economically significant as pests that can cause serious structural damage to buildings, crops or plantation forests. Termites are major detrivores, particularly in the subtropical and tropical regions, and their recycling of wood and other plant matter is of considerable ecological importance.

As eusocial insects, termites live in colonies that, at maturity, number from several hundred to several million individuals. They are a prime example of decentralised, self-organised systems using swarm intelligence and use this cooperation to exploit food sources and environments that could not be available to any single insect acting alone. A typical colony contains nymphs (semi-mature young), workers, soldiers, and reproductive individuals of both genders, sometimes containing several egg-laying queens. Termites are sometimes called "white ants", though they are unrelated to true ants.

Reproductives



A female that has flown, mated, and is producing eggs, is called a "queen". Similarly, a male that has flown, mated, and remains in proximity to a queen, is termed a "king". These anthropocentric terms have caused great misunderstanding of colony dynamics. Research using genetic techniques to determine relatedness of colony members is showing that the idea that colonies are only ever headed by a monogamous royal pair is wrong. Multiple pairs of reproductives within a colony are not uncommon. In the family's Rhinotermitidae and Termitidae, and possibly others, sperm competition does not seem to occur (male genitalia are very simple and the sperm are anucleate), suggesting that only one male (king) generally mates within the colony.

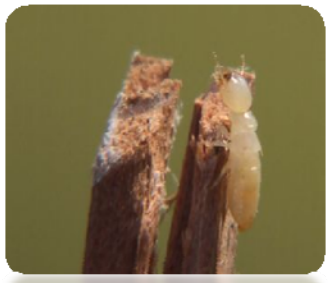
At maturity, a primary queen has a great capacity to lay eggs. In physogastric species, the queen adds an extra set of ovaries with each moult, resulting in a greatly distended abdomen and increased fecundity, often reported to reach a production of more than two thousand eggs a day. The distended abdomen increases the queen's body length to several times more than before mating and reduces her ability to move freely, though attendant workers provide assistance. The queen is widely believed to be a primary source of pheromones useful in colony integration, and these are thought to be spread through shared feeding (trophallaxis).

The king grows only slightly larger after initial mating and continues to mate with the queen for life. This is very different from ant colonies, in which a queen mates once with the male(s) and stores the gametes for life, and the male ants die shortly after mating.

The winged (or 'alate') caste, also referred to as the reproductive caste, are generally the only termites with well-developed eyes (although workers of some harvesting species do have well-developed compound eyes, and, in other species, soldiers with eyes occasionally appear). Termites on the path to becoming alates (going through incomplete metamorphosis) form a sub-caste in certain species of termites, functioning as workers ('pseudergates') and also as potential supplementary reproductives. Supplementary have the ability to replace a dead primary reproductive and, at least in some species, several are recruited once a primary queen is lost.

In areas with a distinct dry season, the alates leave the nest in large swarms after the first good soaking rain of the rainy season. In other regions, flights may occur throughout the year or more commonly in the spring and autumn. Termites are relatively poor fliers and are readily blown downwind in wind speeds of less than 2 km/h, shedding their wings soon after landing at an acceptable site, where they mate and attempt to form a nest in damp timber or earth.

Workers



Worker termites undertake the labors of foraging, food storage, brood, nest maintenance, and some of the defense effort in certain species. Workers are the main caste in the colony for the digestion of cellulose in food and are the most likely to be found in infested wood. This is achieved in one of two ways. In all termite families except the Termitidae, there are flagellate protists in the gut that assist in cellulose digestion. However, in the Termitidae, which account for approximately 60% of all termite species, the flagellates have been lost and this digestive role is taken up, in part, by a consortium of prokaryotic organisms. This simple story, which has been in entomology textbooks for decades, is complicated by the finding that all studied termites can produce their own cellulose enzymes, and therefore can digest wood in the absence of their symbiotic microbes. Our knowledge of the relationships between the microbial and termite parts of their digestion is still rudimentary. What is true in all termite species, however, is that the workers feed the other members of the colony with substances derived from the digestion of plant material, either from the mouth or anus. This process of feeding of one colony member by another is known as trophallaxis and is one of the keys to the success of the group. It frees the parents from feeding all but the first generation of offspring, allowing for the group to grow much larger and ensuring that the necessary gut symbionts are transferred from one generation to another. Some termite species do not have a true worker caste, instead relying on nymphs that perform the same work without molting into a separate caste.

Termite workers are generally blind due to undeveloped eyes. Despite this limitation, they are able to create elaborate nests and tunnel systems using a combination of soil, chewed wood/cellulose, saliva, and feces. Some species have been known to create such durable walls that industrial machinery has been damaged in an attempt to break their tall mounds. Some African and Australian species have mounds more than 4 meters high. The nest is created and maintained by workers with many distinct features such as housing the brood, water collection through condensation, reproductive chambers, and tunnel networks that effectively provide air conditioning and control the CO_2/O_2 balance. A few species even practice agriculture, with elaborate fungal gardens which are fed on collected plant matter, providing a nutritious mycelium on which the colony then feeds.

Soldiers

The soldier caste has anatomical and behavioral specializations, providing strength and armor which are primarily useful against ant attack. The proportion of soldiers within a colony varies both within and among species. Many soldiers have jaws so enlarged that they cannot feed themselves, but instead, like juveniles, are fed by workers. The pan-tropical sub-family Nasutitermitinae (*The South American species of which are under review and are likely to deserve a separate taxon*) have soldiers with the ability to exude noxious liquids through either a horn-like nozzle (nasus) or simple hole in the head (fontanelle). Fontanelles which exude defensive secretions are also a feature of the family Rhinotermitidae. Many species are readily identified using the characteristics of the soldiers' heads, mandibles, or nasus. Among the drywood termites, a soldier's globular ("phragmotic") head can be used to block their narrow tunnels. Termite soldiers are usually blind, but in some families, soldiers developing from the reproductive line may have at least partly functional eyes.

It's generally accepted that the specialization of the soldier caste is principally a defense against predation by ants. The wide range of jaw types and phragmotic heads provides methods which effectively block narrow termite tunnels against ant entry. A tunnel-blocking soldier can rebuff attacks from many ants. Usually more soldiers stand by behind the initial soldier so once the first one falls another soldier will take the place. In cases where the intrusion is coming from a breach that is larger than the soldier's head, defense requires special formations where soldiers form a phalanx-like formation around the breach and blindly bite at intruders or shoot toxic glue from the nasus. This formation involves self-sacrifice because once the workers have repaired the breach during fighting, no return is provided, thus causing the death of all the defenders.

Termites undergo incomplete metamorphosis, with their freshly hatched young taking the form of tiny termites that grow without significant morphological changes (other than wings and soldier specializations). Some species of termite have dimorphic soldiers (up to three times the size of smaller soldiers). Though their value is unknown, speculation is that they may function as an elite class that defends only the inner tunnels of the mound. Evidence for this is that, even when provoked, these large soldiers do not defend themselves but retreat deeper into the mound. On the other hand, dimorphic soldiers are common in some Australian species of

Schedorhinotermes that neither build mounds nor appear to maintain complex nest structures. Some termite taxa are without soldiers; perhaps the best known of these are the Apicotermitinae.

Diet

Termites are generally grouped according to their feeding behavior. Thus, the commonly used general groupings are subterranean, soil-feeding, drywood, dampwood, and grass-eating. Of these, subterranean and drywoods are primarily responsible for damage to human-made structures.

All termites eat cellulose in its various forms as plant fiber. Cellulose is a rich energy source (as demonstrated by the amount of energy released when wood is burned), but remains difficult to digest. Termites rely primarily upon symbiotic protozoa (metamonads) such as *Trichonympha*, and other microbes in their gut to digest the cellulose for them and absorb the end products for their own use. Gut protozoa, such as *Trichonympha*, in turn rely on symbiotic bacteria embedded on their surfaces to produce some of the necessary digestive enzymes. This relationship is one of the finest examples of mutualism among animals. Most so called "higher termites", especially in the Family Termitidae, can produce their own cellulose enzymes. However, they still retain a rich gut fauna and primarily rely upon the bacteria. Due to closely related bacterial species, it is strongly presumed that the termites' gut flora are descended from the gut flora of the ancestral wood-eating cockroaches, like those of the genus *Cryptocercus*.

Some species of termite practice fungi culture. They maintain a 'garden' of specialized fungi of genus *Termitomyces*, which are nourished by the excrement of the insects. When the fungi are eaten, their spores pass undamaged through the intestines of the termites to complete the cycle by germinating in the fresh fecal pellets. They are also well known for eating smaller insects in a last resort environment.