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Isoptera
(Termites)

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The ordinal name Isoptera is of Greek origin and refers to the two pairs of straight and very similar wings that termites have as reproductive adults. Termites are small and white to tan or sometimes black. They are sometimes called "white ants" and can be confused with true ants (Hymenoptera). However, a closer look reveals two easily observed, distinguishing features: termites have straight antennae and a broad waist between the thorax and the abdomen, whereas ants have elbowed antennae and a narrow waist. For reproductive forms, termites have four equally sized wings, whereas ants have two pairs of dissimilarly sized wings.

IMPORTANT FAMILIES OF TERMITES

The earliest known fossil termites date to the Cretaceous, about 130 mya. There are >2600 species of termites worldwide. Undoubtedly, more will be recognized with improved methods of discerning cryptic species and after intensive collecting of tropical and remote regions. It has been known for decades that termites are closely related to cockroaches. However, the latest molecular results, albeit controversial, suggest all termite species diversity can be accommodated as a single family within cockroaches (order, Blattodea). The greatest continental termite diversity is in Africa, where there are over 1000 species. Polar continents have none, and North America with 50 species and Europe with 10 species are intermediate in termite diversity.

Development is incomplete metamorphosis containing castes that include nymph, worker, pseudergate, soldier, and several types of reproductives (Figs. 1–3). Nymphs hatch from eggs and molt at least three times before becoming functional workers. Workers are wingless, do not lay eggs, and, except for the family Hodotermitidae, are blind. Worker and pseudergate castes are the most numerous in a colony and conduct all major foraging and nest-building activities. Soldiers defend colonies with fearsome mandibles and/or chemical squirts from a nasus, a frontal projection from their heads. Soldiers, cannot feed themselves. Reproductives consist of a royal pair, the original colony founders, but supplementary and replacement reproductives (neotenics) can be generated from workers, nymphs, or other immatures dependent on pheromonal cues from the queen and environmental factors.

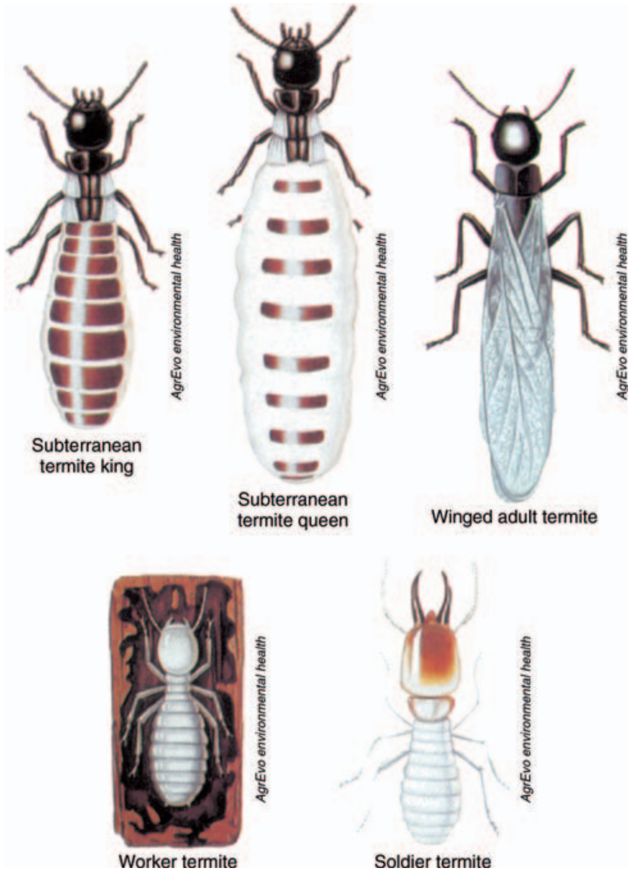

FIGURE 1 Castes for Isoptera. A lower termite group, *Reticulitermes,* is represented. A large queen is depicted in the center. A king is to the left of the queen. A worker and soldier are below. (Adapted, with permission from Aventis Environmental Science, from *The Mallis Handbook of Pest Control,* 1997.)

Termite families traditionally were categorized as lower or higher. However, this categorization may change soon as newer classification systems are adopted. Lower termites (families Mastotermitidae, Kalotermitidae, Termopsidae, Hodotermitidae, Rhinotermitidae, and Serritermitidae) have symbiotic intestinal protozoa and bacteria. Higher termites (Termitidae) have intestinal bacteria only.

Classically, termite identification at the family and genus level was determined using reproductive adults or soldiers or, in some groups, workers. Today, molecular techniques are gaining importance in the identification process. However, methodological and acceptance hurtles still remain and models that incorporate multiple genes, analyses of sequence codes, representative samples, as well as correlations with traditional and other methods of identification are still needed. All living termites can be divided into seven families as follows.

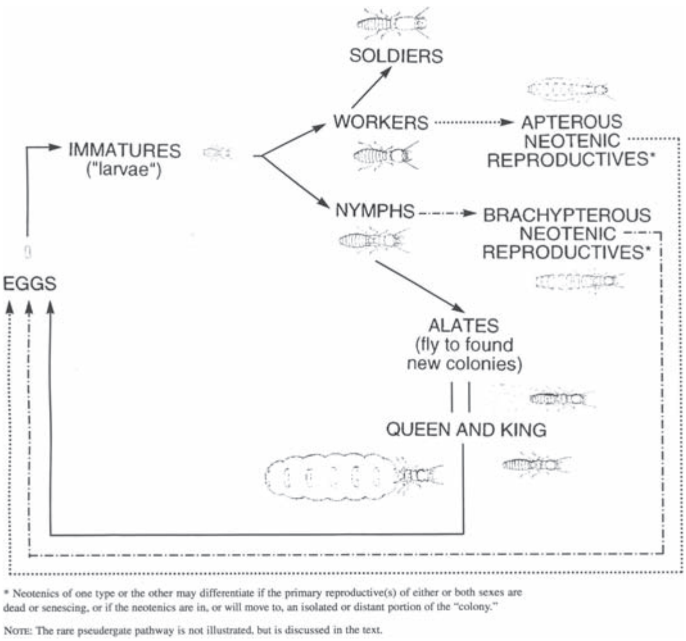

FIGURE 2 Life cycle of the termite. Lower termite family depicted. (Adapted, with permission from FMC Corp., from *The Mallis Handbook of Pest Control,* 1997.) Neotenics of one type or the other may differentiate if the primary reproductive(s) of either or both sexes are dead or senescing, or if the neotenics are in, or will move to, an isolated or distant portion of the "colony".

FIGURE 3 Castes of the Formosan subterranean termite, *Coptotermes formosanus* (Isoptera: Rhinotermitidae). In the center is a queen with large physogastric abdomen containing eggs. A king with a physogastric abdomen lies next to the queen. Soldiers have brown tear-shaped heads with sickle mandibles. A worker is also shown. (Photograph courtesy of Dr Minoru Tamashiro, University of Hawaii.)

Mastotermitidae

This family contains the most primitive living termite, *Mastotermes darwiniensis* (Fig. 4), now limited to Northern Australia and Papua New Guinea. In appearance, these termites are light brown, robust, and about 8–10 mm in length. This family is recognized by the presence of an anal lobe in the hind wing of the reproductive adults and five-segmented tarsi. The hind wings are very similar to those of some cockroaches. Like cockroaches, reproductive females also lay egg cases containing up to 24 eggs arranged in two regular rows. Although egg masses contain few eggs, *Mastotermes* has many neotenic reproductives (no primary queen has ever been found in the field), and colonies can reach a population size of millions. Soldiers have powerful mandibles and excrete a toxic brown substance from their buccal cavity that repels intruders.

FIGURE 4 *Mastotermes darwiniensis,* the most primitive termite from Darwin, Australia. Tertiary-era fossils contain species from this family. Reproductive adults are in the center. Soldiers have large heads and mandibles. Smaller termites are workers. (Photograph courtesy of Dr Barbara Thorne, University of Maryland.)

Kalotermitidae

Members of this family are commonly called "dry-wood termites" for their habit of nesting in wood above the soil level, although exceptions occur. Some dry-wood termites have subterranean habits, whereas others prefer rotten and damp wood. Dry-wood termites are brownish and are considered medium-sized termites, 10–13 mm in length. This family is recognizable by the presence of ocelli and two-segmented cerci in the alate form. There are more than 400 species worldwide. Dry-wood termites are common on most continents. Colonies are moderate in size and contain several thousand individuals, most of which function as workers. The queen lays about a dozen or so eggs per day.

Termopsidae

The damp-wood termites nest in wet and rotting wood, especially fallen logs and stumps in forests. Damp-wood termites were formerly grouped within harvester termites (Hodotermitidae), but now are considered a separate family. Damp-wood termites are among the largest termites, some reaching almost 25 mm in length. Most individuals retain marked developmental plasticity. There are about 20 species and they are limited to forests in the Americas, Eurasia, Africa, and Australia. Egg production per queen is relatively low (≤30 per day) and colony size is moderate, up to approximately 10,000.

Hodotermitidae

Members of this grass-harvesting family of 15 species are similar in appearance to damp-wood termites and are quite large (>15 mm in length). Reproductive adults lack ocelli and their cerci have three to eight segments. Modern species are savanna grass feeders and occur in Africa, the Middle East, and India. Queen egg production and colony size are similar to those of damp-wood termites.

Rhinotermitidae

Commonly called subterranean termites, this family typically requires its nest to contact the soil. However, exceptions occur (genera *Coptotermes* and *Recticulitermes*). Most species in this family are recognizable by their reproductive adults and a flat pronotum behind the head of soldiers. The soldiers of some species produce a defensive fluid from a fontanelle gland that is located on their head. Workers and soldiers are small (<5 mm) and are very pale white in color. More than 300 species are recognized. They occur on most continents except in polar and near-polar regions and are serious pests of structures. Queens of some species can produce more than 100 eggs per day, and colonies can number from the tens of thousands to the millions. Some mound-builders and aerial-nesters are found in this family. Aerial-nesting species still maintain contact to the soil for water by runways constructed from soil and saliva.

Serritermitidae

This family is very similar in appearance and closely related to subterranean termites (Rhinotermitidae). It also requires its nest to contact the soil. A single species occurs in South America. Soldiers have serrated teeth along the entire inner margin of the mandibles.

Termitidae

This family contains builders of the great mounds (up to 8 m high) that occur in the tropics, mainly in Asia, Africa, Australia, and South America. There are a few species in North America and none occur in Europe. More than 1800 species have been described, many from Africa. Termitids are distinguished by two prominent teeth on the left mandible of reproductive adults and a saddle-shaped pronotum. The Termitidae have a true worker caste. Workers are very small (<5 mm) and pale or dark in color. Many species have nasute soldiers—these eject anoxious fluid from a horn-shaped nozzle on their heads. Members of this family are some of the most prolific producers of eggs in the animal kingdom. A queen can produce more than 10 million eggs in a single year.

TERMITE BIOLOGY AND ECOLOGY

Termites live in colonies that are social and can be long-lived. Colonies are composed of castes that conduct all tasks for survival (Figs. 1and 3). Some termite queens are larger than the length of a human thumb and can lay more than 1000 eggs per day. The king is also long-lived and mates intermittently to provide sperm to the queen. Some of the longest living insects are termites: some termite mounds and their queens are thought to be more than 70 years old and Aborigine folklore claims some mounds in Australia are over 200 years old. There are no methods to age a queen.

Termites are herbivores, fungivores (i.e., plant or fungus feeders), and humivores (soil feeders). They feed on cellulose, directly from plants, dead or alive, or indirectly from fungus arising from decaying plant material within mounds. Plants are made of cellulose, a polysaccharide that is composed of glucose units. The traditional view is that termites rely on intestinal gut microorganisms for cellulose digestion. However, there is growing molecular evidence that termites also use their own enzymes for cellulose digestion.

Before mating and starting new colonies, new kings and queens, called alates or swarmers, depart the colony and fly (Fig. 2). They mate after landing on the ground. Swarming behavior varies considerably among termite families and species, but occurs most frequently during the rainy season. However, dry-wood termites can swarm during hot days or sometimes on summer evenings. A mated king and queen lose their wings and find a suitable nesting site near or in wood where they construct a small chamber that they enter and seal. The queen soon begins laying eggs, and both the king and the queen feed the young predigested food until they are capable of feeding themselves. Once workers and nymphs are produced, the king and queen are fed by the workers and cease feeding on wood. The exchange of food among colony members is called trophallaxis. Social insects exchange food in two ways, stomodeal and proctodeal trophallaxis. Termites use the latter method for food and symbiont exchange, mouth to anus. Symbionts are protozoa and bacteria that occur in the hindgut of termites. These microbes help digest cellulose, the major food source for termites.

The reproductive adults have functional eyes, needed for flight and initial finding of nest sites. The blind workers and soldiers live deep in nests, soil, or mounds and do not require vision. They already are in contact with or close to their food source.

Termites can also communicate through chemical, acoustical, and tactile signals. Two termite trail pheromones, (*Z*,*Z*,*E*)-(3,6,8)-dodecatrienol and (*E*)-6-cembrene, have been identified. These messages are produced in a sternal gland on the underside of the termite's abdomen. However, other chemical signals, such as those used for alarm and colony recognition, are produced from other glands located throughout their body. Many termite behaviors (e.g., trail following, alarm, and sexual communication) are mediated by pheromones. Soldiers also produce chemicals that are important for colony defense. Colony recognition and colony spacing are thought to be regulated by cuticular hydrocarbons. These waxy compounds are produced over the exterior cuticle of termites and spread throughout the colony. Termites can also communicate danger by "head-banging" of soldiers, in which they tap their heads in galleries to alert their nestmates.

Termites play a major role in recycling wood and plant material, but their tunneling effort also ensures that soils are porous, aerated, and enriched in minerals and nutrients, all of which improve plant growth. For example, termite activity in the desert areas of West and North Africa helps to reclaim soils damaged by overgrazing. Termites are an important food source for many other animals, including reptiles, birds, and mammals. Termite mounds and trees hollowed out by termites provide shelter and breeding sites for birds, mammals, and other insects.

Termites also contribute to atmospheric gases. The most abundant gases produced are carbon dioxide and methane. Both are greenhouse gases, but they are not produced in sufficient quantities to have negative effects on the atmosphere.

The quest for alternative fuels now includes termites. The gut fauna of termites is being mined for molecular sequences that could lead to the efficient conversion of plant sugars into ethanol; the planned future source of power for motorized vehicular transportation.

TERMITES AS PESTS

Some termites are destructive feeders and consume homes, other wooden structures, and agricultural crops. In some regions of the world, tunneling by termites damages dams, which then results in flooding. Worldwide, several billion dollars is spent annually for the control and repair of damage caused by termites. In the United States alone, over $1,000 million is spent yearly on termite control and damage repairs. Globally, subterranean termites (Rhinotermitidae: genera *Reticulitermes, Coptotermes, Heterotermes,* and *Psammotermes*) are the most responsible for the control and damage costs. Dry-wood termites

(Kalotermitidae: genera *Incisitermes* and *Cryptotermes*) have lesser importance as structural pests and are more prevalent in coastal, arid, or semiarid regions. Termites as agricultural pests are confined primarily to Asia, Africa, South America, and Australia. The major pest species belong to the genera *Microtermes, Macrotermes,* and *Odontotermes* (Termitidae) in Africa and Indo-Malaysia. *Mastotermes* (Mastotermitidae) is an important pest in Australia, whereas *Cornitermes* and *Procornitermes* (Termitidae) are important pests in South America. Damage varies from superficial to killing the plant. Healthy plants can tolerate some termite damage with reduced yields. In general, exotic plants and stressed plants are most prone to termite attack.

TERMITE CONTROL/MANAGEMENT

Before termites in structures can be treated, the extent of the infestation must be assessed. Visual searching and probing of wood are the dominant means of inspection. However, the efficacy of visual searches is questionable, because structures have inaccessible areas. The list is growing for nonvisual detection methods used, including carbon dioxide gas detectors, infrared, microwave, acoustic emission devices, and X-ray, but each of these technologies has some limitations. For subterranean termites, wood-baited monitoring stations can identify the presence and delimit the extent of colonies. Some species of subterranean termite have colonies as large as several million individuals, and these forage over an area of more than 10,000 m^2. Other termite species have much smaller colonies and forage within areas of only a few square meters. There is considerable debate about the methods and accuracy in reporting termite numbers and foraging behavior.

Termite control is most regulated in North America, Europe, and Australia. However, in many countries controlling termites is achieved by the hand removal of queens and nests, flooding nests, or drenching them with used motor oil. Soil drenches with liquid termiticides injected into the soil beneath the structures to protect foundations and structural wood is the dominant control tactic for subterranean termites for several continents. Chlorinated hydrocarbon insecticides, such as chlordane, have been used extensively for subterranean termite control because of their long persistence, $>$30 years in the soil. Because of persistence and suspicions of health-related problems, chlordane has been removed from many markets. Chloronicotinyls and phenyl pyrazoles are new compounds marketed for termite control. Also increasingly being marketed are "green" products (plant natural compounds). The use of toxic baits (e.g., containing chitin and metabolic inhibitors) and physical barriers (sand and stainless steel mesh) for controlling subterranean termites are also gaining acceptance. Techniques to prevent infestations of subterranean termites include using wood pressure-treated with oil and water-soluble chemicals. Care must be taken for both remedial and preventative control methods, because reinvasion, budding, and over-looked incipient colonies are frequent. Future innovations for control include use of molecularly altered products and microbes directed against termite colonies.

Surveys of pest control firms in the United States reveal that poor building practices, particularly wood in contact with soil and cracks in concrete foundations, lead to many of the subterranean termite infestations. Experimental efforts have been made to control soil-dwelling termites using biological control agents, such as argentine ants and nematodes. However, these methods have not yet been proven effective.

Dry-wood termite colonies are usually above soil level in structures, small, and difficult to detect. Treatments include whole-structure applications of fumigants (such as sulfuryl fluoride) and heat. Chemicals (including green products), heat, freezing, microwaves, and electricity are used for localized or spot treatments of dry-wood termites. Portable detection equipment is now commercially available to enhance localized and spot treatments.

See Also the Following Articles

Blattodea ■ *Caste* ■ *Sociality* ■ *Urban Habitats*

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