

The Termites

Termites are almost literally social cockroaches. Detailed similarities exist in anatomy between the most primitive termite family, the Mastotermitidae, and the relatively primitive wood-eating cockroaches constituting the family Cryptocercidae. Even the intestinal microorganisms that digest cellulose are similar. Of the 25 species of hypermastigote and polymastigote flagellate protozoans found in the gut of the cockroach *Cryptocercus punctulatus*, all belong to families also found in the more primitive termites. Even one genus, *Trichonympha*, is shared. These intestinal protozoans can be successfully "transfaunated" from cockroach to termite and vice versa. It is of course too much to hope that any of the living cockroaches are really the ancestors of the termites. All known cockroaches have horny fore wings; the clear, membranous wings of the termites are more primitive. Other differences indicate that the two groups of insects originated from a common, cockroachlike ancestor. But they are not cardinal distinctions, and some entomologists have gone so far as to place termites in the same order (Dictyoptera) as the cockroaches and mantids.

Because the termites have climbed the heights of eusociality from a base extremely remote in evolution from the Hymenoptera, it is of great interest to know whether their social organization differs from hymenopteran organization in any fundamental way. Although value judgments of the degree of convergence of two radically differing stocks are difficult to make, much less to justify quantitatively, I believe the following assessment can reasonably be made. The termites have adopted mechanisms that are mostly but not entirely similar to those in the ants and other social Hymenoptera. Also, the level of complexity of termite societies is approximately the same as that in the more advanced hymenopteran societies. In Table 20-6, I have listed the principal known similarities and dissimilarities of the two kinds of societies. This simplified accounting does not overlook the fact, which was stressed earlier, that a great deal of important variation also occurs within the social Hymenoptera. Surely the similarities are remarkable in themselves. They seem to tell us that there are constraints in the machinery of the insect brain that limit not only the options of social organization but also the upper limit that the degree of organization can attain. These limits appear to have been reached between 50 and 100 million years ago in both the termites and the social Hymenoptera.

The most primitive living termite and sole surviving member of the Mastotermitidae, *Mastotermes darwiniensis*, is found over most of the northern half of Australia. In some ways it acts very strangely for a Mesozoic relic. It is the most destructive termite species in Australia and the most destructive insect of any kind in the northern part of the continent. The colonies, which nest in the soil, are immense, the largest containing over a million individuals. The diet of *M. darwiniensis* is the most catholic of any known termite; one might even say it resembles that of the cockroach. Workers have been observed attacking poles, fences, wooden buildings, living trees, crop plants, wool, horn, ivory, vegetables, hay, leather, rubber, sugar, human and animal excrement, and the plastic lining of electric cables. Unattended homesteads in the outback have been reduced to dust in only two or three years—house, fences, and all. Colonies of *M. darwiniensis* occupy many kinds of nest sites through a wide range of habitats, and they are able to excavate rapidly in both soil and wood. Their subterranean nests, which are often fragmented and connected by covered passageways constructed on the surface of the ground, are difficult to detect. The galleries run outward for as much as 100 meters or more from the nest. Most are shallow, extending no more than 40 centimeters below the surface. One gallery system, however, was uncovered by quarrying operations at a depth of 4 meters.

Considering its phylogenetic position and economic importance, surprisingly little is known concerning the biology of *Mastotermes*, including the most basic facts of the life cycle. One curious fact is that the primary reproductives are rare. Multiple supplementary reproductives appear to be the rule, and colony multiplication often occurs by budding. When groups of nymphs are detached from the main colony, some are able to develop into reproductive castes. Eggs are laid in packets of about 20 each, in a form resembling the oothecae of cockroaches. Nuptial flights occur regularly, but their relative contribution to the formation of new colonies is unknown.

The Kalotermitidae, known as the dry wood termites, are anatomically relatively primitive although still considerably advanced over the Mastotermitidae. Their sociobiology is a mosaic of elementary and advanced traits. The colonies, which rarely contain more than a few hundred individuals, live in ill-defined galleries inside the wood on which they feed. The termites rely on an intestinal flagellate fauna to digest the wood and do not utilize symbiotic fungi or store food. When the primary queens and males are lost, they are quickly replaced by secondary "neotenic" that transform in one molt from a labile, workerlike caste called pseudergates. When present, the primary reproductives prevent the transformation of pseudergates by means of inhibitory pheromones passed out of their anuses. Soldier inhibition also occurs, but the physiological basis is not yet known. The exchange of oral and anal liquids, as well as integumentary exudates, occurs very frequently among all members of the colony. Anal exchange is essential to the transmission of flagellates to young nymphs and newly molted individuals of all ages.

It is a curious fact that most kalotermitids, as well as most other relatively primitive termite groups, are concentrated in the temperate zones. The tropics, constituting the true headquarters of the world fauna, are dominated by the "higher" termites of the family Termitidae. The majority of the termitids are soil dwellers and are responsible for most of the elaborately structured mounds that are such a conspicuous feature of the tropical landscape. Various of their species have specialized on

virtually every conceivable cellulose source. To reach this food, workers extend galleries through the soil, or construct covered trailways over the surface of the ground, or even march in columns along exposed odor trails.

As an example of a relatively unspecialized termitid, we can take *Amitermes hastatus*, which has been studied in detail by Skaife (1954a,b; 1955). The species occurs in South Africa, in the mountains of the southwest Cape at elevations from about 100 to 1,000 meters above sea level. It nests in the sandy soil of the natural veld, throwing up conspicuous hemispherical or conical mounds constructed of a black mixture of soil and excrement. In the late summer months of February and March large numbers of white nymphs with wing pads are to be found in the larger nests. By the end of March, or April at the latest, these individuals have transformed into winged reproductives. For several weeks the alates wander slowly through the nest. Then, soon after the onset of the autumn rains, the nuptial flight occurs. One day between 11 o'clock in the morning and 4 o'clock in the afternoon, immediately after a ground-soaking rain and with the temperature rising, the exodus begins. The workers first excavate large numbers of tightly grouped exit holes, each about 2 millimeters in diameter, giving the apex of the mound the appearance of a coarse sieve. True to the pattern of most termite species, this is the only time the workers breach the walls of their nest and expose themselves to the outside air. Workers, soldiers, and alates boil out of the holes in a state of intense excitement, the alates fly off almost immediately, and within three or four minutes the termites retreat back down into the nest, plugging the exit holes after them. Most, but not all, of the alates leave in this first flight. A few remain behind to participate in later departures. The alates are feeble flyers; many do not travel more than 50 or 60 meters from the nest before alighting. As soon as they land they break off their wings at the basal fracture line by swiftly pressing the wing tips to the ground. The subsequent pairing and nest-founding behavior follows the same basic sequence as in *Kaloterme*s. The construction of the initial nest chamber is conducted principally by the queen; sometimes the king does not assist at all. The pair remain in the incipient nest through the winter and apparently do not copulate until the arrival of warmer weather. In the spring months of October and November the queen lays the first five or six eggs. The individuals of the first brood develop into stunted worker. Soldiers make their appearance in later broods, and finally after four years alate reproductives are produced. The growth of a typical nest is displayed in Figure 20-10. Skaife has estimated the age of some mounds of *Amitermes hastatus* to be greater than 15 years, but judging strictly from the size of the mounds, he did not believe any to be more than 25 years old. This mortal state of individual colonies, if true, is an unexpected feature, because presumably the colonies are capable of producing secondary reproductives when the queen dies. When the primary queen does

fail, the workers put her to death, apparently by licking her abrasively. As Skaife describes it, "She is surrounded by a crowd of workers, all with their mouthparts applied to her skin, and this goes on for three or four days, her body slowly shrinking until no more than the shrivelled skin is left."

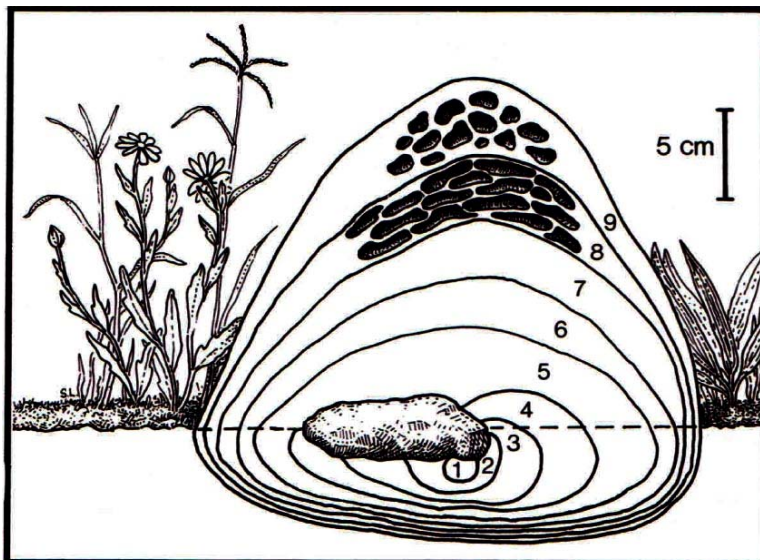


Figure 20-10 The growth of a typical mound or the south African termitid *Amitermes hastatus*, over a period of nine years. Each successive year's growth is indicated by a number. Representative outer and inner cells are shown at the top of the mound. There is no royal cell. (Based on Skaife, 1954a.)

Secondary and tertiary queens do appear in the presence of the queen—at least sometimes (see Figure 20-11). Skaife, however, was unable to rear them in queenless colonies kept in artificial nests, and he found that only about 20 percent of the natural mounds contained them. Clearly, then, either the supplementary reproductives are rare, or appear only under special conditions, or the colonies that possess them are relatively short-lived.

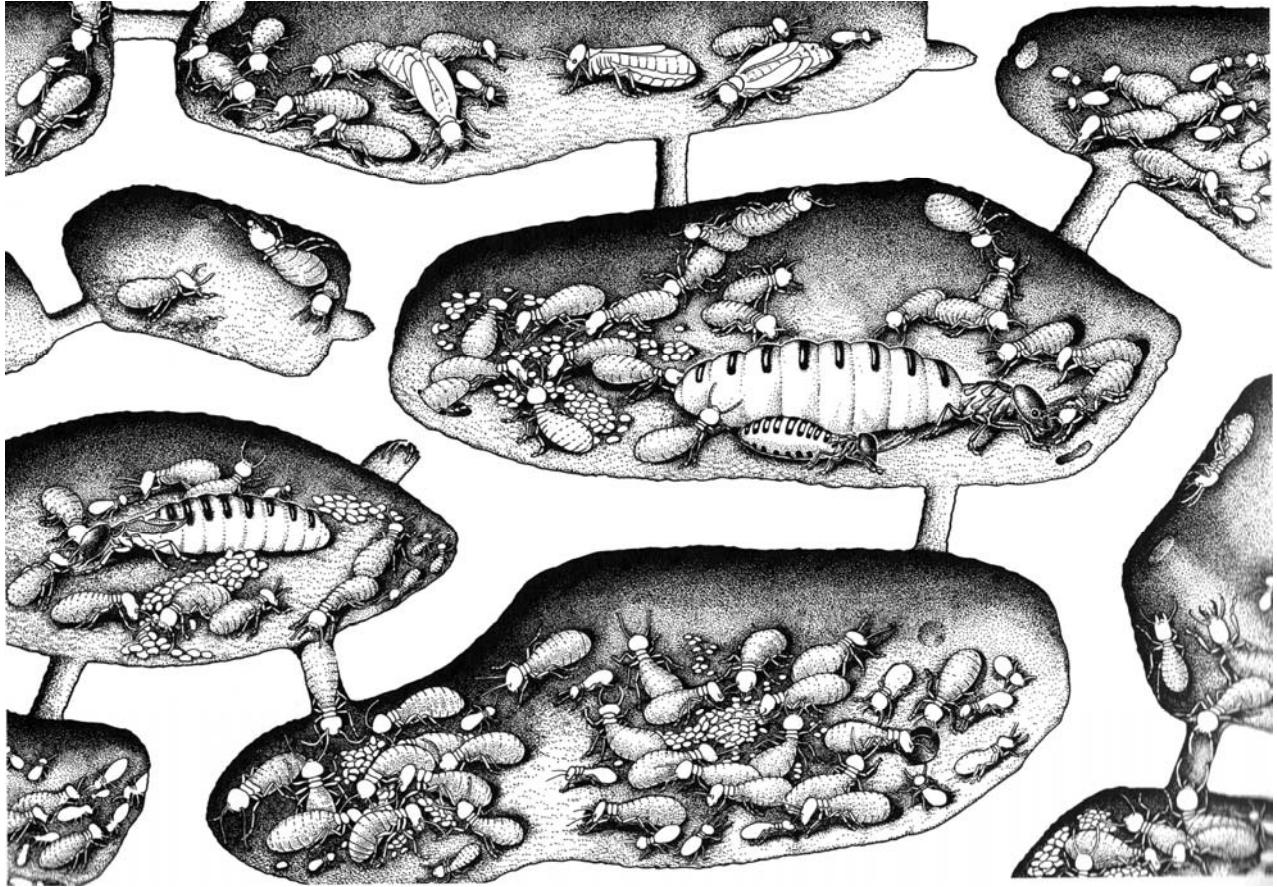


Figure 20-11 The interior of a typical nest of the higher termite *Amitermes hastatus* of South Africa. The primary queen and much smaller primary male sit side by side in the middle cell. To the lower left can be seen a secondary queen, who is also functional in this case. In the chamber at the top are reproductive nymphs, characterized by their partially developed wings. Workers attend the queens and are especially attracted by their heads, to which they offer regurgitated food at frequent intervals. Other workers care for the numerous eggs. A soldier and presoldier (nymphal soldier stage) are seen in the lower right chamber, while worker larvae in various stages of development are found scattered through most of the chambers. (Drawing by Sarah Landry; from Wilson, 1971a.)

Texten är ett utdrag från: E.O. Wilson, *Sociobiology*, 1975.