

Primer

Termites

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Termites (Isoptera) are plagued by bad press. They destroy the livelihood of tropical farmers, literally eat their way through our homes, and even threaten our cultural heritage, including assaults on the Statue of Liberty in New York, the ancient books of the Vatican, or the historical city of Isfahan in Iran. One estimate from 2005 put the annual damage at about US\$ 50 billion worldwide, with the US alone investing more than US\$ 11 billion in termite control in 1994. As is so often the case, however, the termites' disrepute is the result of the actions of just a few, and the great majority of the over 2,600 described species are dwellers of the dark, whose pivotal role in ecosystem function often goes unnoticed. Termites are evolutionarily and ecologically very successful insects that share a common ancestry with cockroaches. Living in complex societies and being able to digest wood with the aid of a diverse symbiotic gut fauna seems to be the basis for this success story.

Termites: Social cockroaches

Termite societies, like those of eusocial Hymenoptera (ants and some bees and wasps), are generally large, extended families with a characteristic reproductive division of labor. Only a few individuals within a colony reproduce (in termites, generally one king and one queen; **Figure 1**), while the large majority of individuals forgo their own reproduction, at least temporarily (in termites, these are the workers and soldiers; **Figure 1**). However, the apparent similarity between the social organization of termites and Hymenoptera, and especially the ants, is rather superficial. Both groups of social insects evolved complex societies independently and their different ancestries provided them with different life

history pre-adaptations for social evolution.

Termites are believed to be the earliest-evolving social insects, with their complex societies dating back to the Cretaceous (130 millions years ago) when they scuttled under the feet of dinosaurs. The oldest termite fossils show that they were clearly already social and strikingly similar to the modern basal species and that they had already diversified, suggesting an origin in the upper Jurassic. Unlike the eusocial Hymenoptera, which are all basically wasps, termites find their

roots alongside the cockroaches (Blattodea) and mantids (Mantodea), which together form a natural assemblage known as the Dictyoptera. Although the relative positions of these lineages is somewhat debated, the weight of evidence from molecular markers and morphological traits strongly suggests that the termites are nested within the Blattodea; most likely the sister group of the Cryptoceridae (woodroaches). Thus, the termites in fact arose in a single 'social cockroach' species that diversified into a number of termite families. The monophyly of

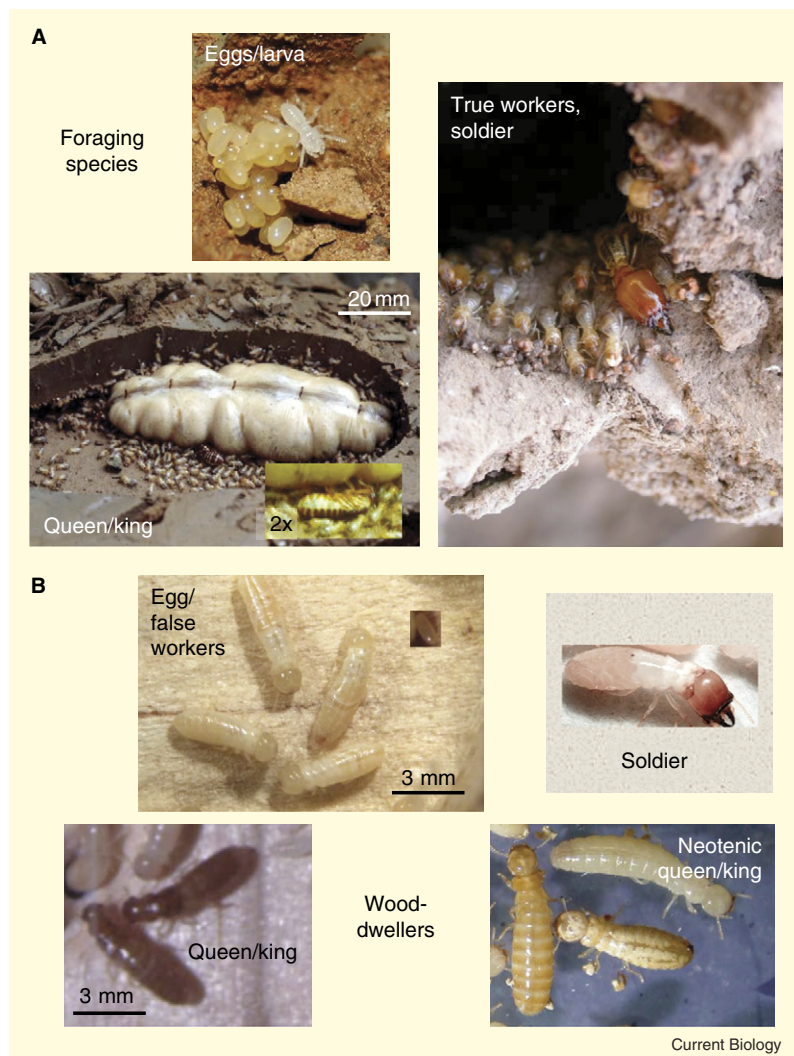


Figure 1. Termite castes and life types.

(A) Castes in foraging termite species, here the fungus-growing termite *Macrotermes bellicosus*. Eggs develop into larva that either become (true) workers, soldiers or reproductives. (B) Caste in wood-dwelling termite species, here the drywood termite *Cryptotermes secundus*. Eggs develop via larvae into totipotent (false) workers, which have the capability to become soldiers, or two forms of reproductives: neotenic reproductives, which breed within the natal nest when the current reproductives die, or winged sexuals (primary reproductives), which disperse and found a new nest. (Photo: S. Reichmann, V. Salewski, and J. Korb.)

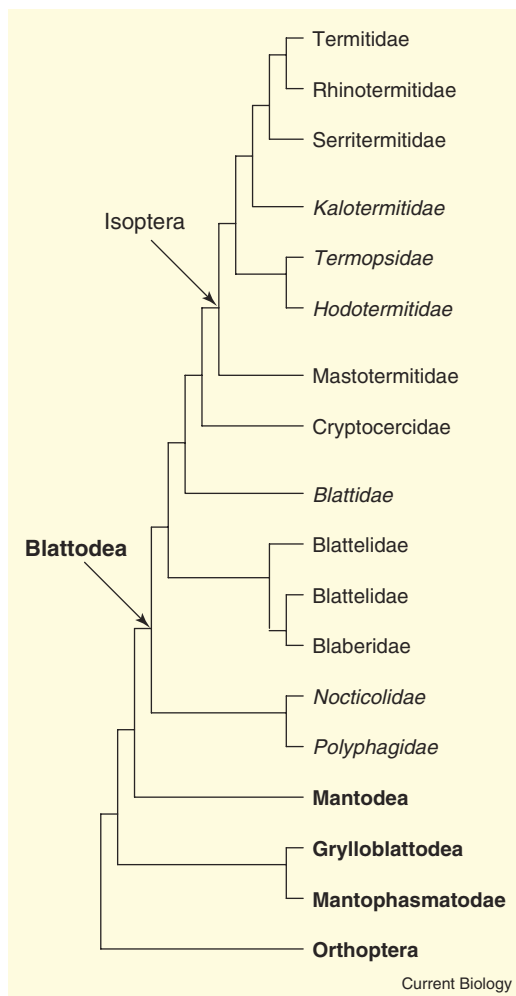


Figure 2. Phylogenetic tree. From phylogenetic analysis of molecular and morphological traits, the Isoptera (termites) are now placed within the Blattodea (cockroaches). Bold, orders; italics, unresolved positions.

some of these ‘traditional’ families is questionable, with their relative positions sometimes unresolved, but the single origin to the termite does not seem to be in doubt and they form a monophyletic clade within the Blattodea (Figure 2). Social Hymenoptera, by contrast, evolved complex societies at least eleven times independently from different ancestors within the Hymenoptera, with ants evolving from predatory wasps.

The distinct heritage of the social Hymenoptera and termites is evident from their divergent biology and social organization. Termites are hemimetabolous insects, which have multiple immature stages that gradually develop into adults, while Hymenoptera are holometabolous insects and have a single larval stage, which develops via a pupae directly into adulthood, as a caterpillar to a butterfly. Moreover, their genetics are

different. Termites are diploid just like us, with both sexes carrying two copies of each chromosome, while the Hymenoptera exhibit haplodiploidy, where females develop from fertilized eggs and are diploid, while males develop from unfertilized eggs and are haploid. These differences between both groups have important consequences: first, the older immature stages in termites are relatively independent, while the helpless Hymenopteran brood need to be cared by adults. Second, in termites the relatedness among full siblings and among parents and their offspring are generally symmetrical, whereas in Hymenoptera full sisters are more closely related to each other than parents are to their offspring or than sisters are to their brothers. All else being equal, this selects for sister-directed altruistic helping of female adults in Hymenoptera, while in termites

no sex bias should be observed and helping could be performed by immatures. Indeed, termite colonies contain both sexes and the non-reproducing individuals within a colony are mostly formed by arrested stages of immatures — child labor is common in termites. This contrasts with social Hymenopteran colonies, which consist mainly of female adult workers. In addition to the workers, a unique sterile soldier caste exists in termites, which has exclusively defensive functions.

Wood-dwellers and foragers

Based on their ecology and particularly nesting and feeding habits, termites can be grouped into two life types. The first are the one-piece nesting termites: Termopsidae, Kalotermitidae and *Protermitidae* within the Rhinotermitidae, hereafter referred to as wood-dwellers (Figure 1). These species live in their food and spend their entire colony life in a single piece of wood which serves as both food source and shelter. Thus, there is no need for costly foraging, food is easily accessible to all colony members and it is a bonanza type food source, whose availability will decline predictably. The second are the multiple-pieces nesting termites: Mastotermitidae, most Rhinotermitidae, Serritermitidae, Termitidae, hereafter referred to as foraging species (Figure 1). These species live in a well-defined nest that is more or less separated from the foraging grounds. To get access to food, individuals sooner or later have to forage outside the nest with the advantage that the colony’s longevity is less limited by food availability than in wood-dwelling species.

This ecological classification is also reflected in the social organization of the colonies. Wood-dwelling species have a flexible development in which ‘workers’ are totipotent and can explore all caste options. They build the platform from which three permanent castes develop: sterile soldiers; winged sexuals that leave the nest and found new colonies; or neotenic replacement reproductives that inherit the

natal breeding position when the same-sex reproductive of the colony dies or becomes unhealthy. These 'workers' have also been called pseudergates, helpers or false workers (the latter in contrast to the true workers of the multiple-pieces nesting termites). The flexibility in development in wood-dwelling termites is achieved through a unique combination of progressive, stationary and regressive molts, reflected, respectively, by an increase, no change or a decrease in morphometric size and wing development.

In contrast, the true workers of foraging termite species have a more restricted development. Their capability for regressive molts is increasingly reduced, as within the Rhinotermitidae, or absent, as in the Termitidae. In these species, there is an early separation into two developmental pathways. In the apterous line, individuals are unable to develop wings and cannot disperse as winged sexuals. They become the workers and the soldiers of a colony, although in some species they can still reproduce as neotenic reproductives in the natal nest. In the nymphal line, individuals will gradually develop wings via several instars to become alates that found new colonies. The separation of individuals into both pathways can already be determined in the egg stage and it seems to be influenced by season.

True and false workers

Corresponding to the separation into wood-dwelling and foraging termite species, recent results also suggest that the ultimate cause of individuals staying as workers in the nest might differ between both groups. Like workers in most social Hymenoptera, especially ants, the true workers of the foraging termite species are altruistic individuals that stay in the nest and gain indirect fitness by raising siblings. But the totipotent false workers of the wood-dwelling termites appear to be less engaged in altruistic helping than is generally assumed. In the drywood termite *Cryptotermes secundus*, false workers do not take care of eggs

or young; the 'developmental decision' of false workers to stay in the nest or leave the nest as winged sexuals is not influenced by the amount of brood in the nest; and added surplus brood develop even though false workers leave the nest. This seems possible because termites have a hemimetabolic mode of development and, in wood-dwelling termites, food is easily accessible to all nestmates as they nest inside their food. Thus, there is a low incentive for brood care. This, however, all changes with the transition to the foraging termite species.

An explanation for why individuals in the wood-dwelling termites nevertheless delay maturity and stay as 'false workers' in the nest might be their opportunity to inherit the natal breeding position as neotenic reproductives when a current reproductive dies. Philopatric reproduction presents an alternative breeding tactic that avoids costly dispersal. At the same time, staying in the nest is not selected against by local resource competition with relatives, as the nest constitutes a bonanza food resource, generally for longer than the lifetime of the founding reproductives. As these traits are particular to wood-dwelling termites, the explanation that false workers do not mainly stay for kin's sake, but to gain direct fitness benefits, might apply generally. In having false workers, wood-dwelling termites might be more similar to those cooperatively breeding vertebrates, where individuals stay as hopeful reproductives, than to most social Hymenoptera and foraging termite species where the workers stay to raise siblings.

Who came first?

An interesting question arising from these results is whether the false workers of the wood-dwelling termite species, or the true workers of the foraging termite species, reflect the ancestral state in termites' evolution — whether altruistic helping only evolved secondarily after family groups had formed for 'selfish', directly selected fitness benefits. Generally,

the wood-nesting life type has been regarded as ancestral in termite evolution, although recently there has been some debate about this. So far, phylogenetic analyses cannot answer the question. It is as parsimonious to assume a basal evolution of true workers and subsequent evolution of false workers, as to assume a basal condition of false workers and subsequent evolution of true workers. Yet, other recent results leave less doubt about the basal position of false workers, and thus of the one-piece nesting lifestyle. First, developmental studies have shown that the true workers of different termite families evolved at least twice. Second, the close phylogenetic relationship of termites with the woodroaches that have a wood-living lifestyle similar to the wood-dwelling termites suggest that it is ancestral, probably inherited from the common ancestor. But there is no firm evidence that false workers evolved from true workers.

Current knowledge thus suggests that, although the societies of social Hymenoptera and termites look strikingly similar, the main selective forces during their evolution might have been different, because of their different ancestry and life history. In the holometabolic social Hymenoptera, which have progressive food provisioning, brood care is an essential determinant of the reproductive success of individuals. Hence, altruistic helping in raising siblings can considerably increase the indirect fitness of an individual. In wood-nesting hemimetabolous termites, intensive brood care is less essential, but the wooden nest presents a safe haven where individuals can inherit the natal breeding position, which thus selects for delayed dispersal. As family groups form, altruistic defense by soldiers is selected, while, with the transition to forage outside the nest, brood care becomes more important.

Ecosystem engineers

Nowadays, more than 80% of termites belong to foraging species with true workers, and these are ecologically the most

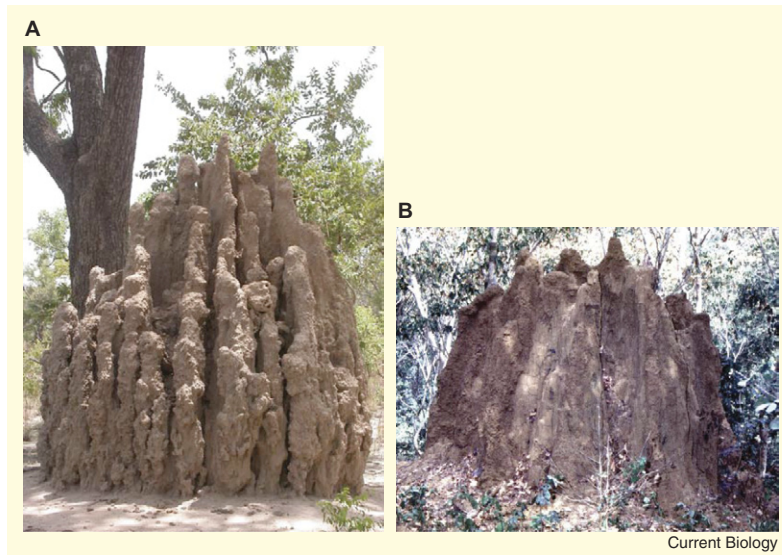


Figure 3. Termites adapt the architecture of their mounds to ambient conditions. The photographs show two *Macrotermes bellicosus* mounds in neighboring habitats in the Comoé Nationalpark (Côte d'Ivoire, Western Africa). (A) A cathedral-shaped mound with thin walls and many ridges from the savanna, (B) A dome-shaped mound with thick walls and low surface complexity from the forest. Both photos have the same scale. (Photo: J. Korb.)

dominant species, while wood-dwelling species are often restricted to islands, coastal habitats or human buildings. Their social life makes termites pivotal components of subtropical and tropical ecosystems, where they can make up to 95% of the soil insect biomass. They are important in nutrient recycling, habitat creation and soil formation. Their soil-dwelling activity changes soil properties and structure, affecting, for example, the flow of water through the soil and creating habitat heterogeneity fundamental for species diversity. Thus, termites qualify as true ecosystem engineers.

The greatest diversity of termite species is found in wet lowland tropical forests, where especially inconspicuous soil feeders are essential for the transformation of organic material into humus. In drier savanna ecosystems, soil-feeding termite species are largely replaced by leaf-litter feeders, which sometimes build massive fortress-style nests that can stand 8 meters tall. These mounds not only protect the termites, but also form a microhabitat for myriad other organisms, such as ants, specialized beetles or fungi. And, once the termites die, even more creatures move in, ranging

from other arthropods, such as millipedes, spiders and ants, to small rodents and reptiles. This unique biotia includes several species who appear to only survive on dead termite mounds. Some woody plants can only establish successfully on dead termite mounds, which provide protection against annual flooding and fires. In time, these develop into dense woody thickets, forming a patch of unique biodiversity in the surrounding savanna. These thickets are thought to be the starting point for the development of island forests (îlot forestier) that are interspersed into West African savannas.

Agriculturalists

Amongst all the termites that typically decompose dead plant material with the aid of a diverse biota of symbiotic gut microbes, one group became agriculturalists. The appropriately named fungus-growing termites (Macrotermitinae) cultivate fungi of the genus *Termitomyces* inside their nests, in an obligate mutualism that seems to be the key for the termites' ecological success, especially in drier savanna ecosystems. Fungus-growing termites originated once, probably in the African rainforest, from where they

spread into Asia and Madagascar and into savannas.

The exact role of the cultivated fungus seems to differ between species, but its primary function is to break down complex chemical substances from plant material, such as lignin, and make them available for the termites. The termites reciprocate by providing the fungus with a haven of pre-processed food, and a competitor-free environment with optimal temperature and humidity conditions. This allows the fungus to grow all year and through dry periods, providing the termites with a year-round, nitrogen-rich food source. The result is a colony that can grow rapidly, largely independently of the season, and out-compete savanna termites that are limited by inappropriate food supply during the dry season. Correspondingly, on a large scale the relative importance of Macrotermitinae over other termites for decomposition processes increases with increasing aridity of an area.

Architects

The impressive ability of termites to regulate their nest environment as agriculturalists is also testament to their skills as architects. Living in large colonies and nesting in thermally inert materials, such as soil or wood, buffers environmental fluctuations. But this might not be sufficient, especially for fungus-growing termites. For an optimal growth, the fungus requires constant warm temperatures, high humidity and an efficient exchange of respiratory gases.

Fungus-growing termites often build mounds adapted to these sometimes conflicting demands. For instance, *Macrotermes bellicosus* constructs cathedral-shaped mounds with thin walls and many ridges in open savannas with rather optimal temperature conditions (Figure 3A), but dome-shaped mounds with thick walls and a low surface complexity in neighboring forests where the temperature is suboptimally low (Figure 3B). Yet reducing surface complexity in the forest comes with a cost. As the mounds do not have holes,



Figure 4. Termites during mound building.

(A) Termites are attracted to sites where other individuals just deposited soil particles which leads to the production of pillars. As termites gather at building sites, newly arriving individuals can only deposit their particles next to the pillars. This leads to the extension of pillars into walls (B). (C) A macroscopic picture of the construction. (Photo: V. Salewski, J. Korb).

gas exchange is reduced. The trade-off between gas exchange and thermoregulation that results from the restrictive requirements of the fungal symbiont seems to reduce the colonies' reproductive success, to limit *M. bellicosus* to open forest stands and, on a geographical scale, to explain its restriction to savanna habitats. A similar constraint does not exist for fungus-growing termites, which occur in forests probably because they cultivate different fungal symbionts. Thus, as selective regimes differ between areas, mound architecture can be adapted to various factors. In arid regions they seem to be adapted to conserve water, while the famous north-south elongated magnetic termite mounds in Australia (they are no fungus-growing termites) seem to be an adaptation to the seasonal flooding of their habitat.

How are termites able to construct such huge mounds adapted to local conditions? By analogy with our own societies, it is tempting to infer the existence of top-down design: a coordinating group member that organizes the construction process. The real answer, however, lies in self-organization — the emergence of higher-level patterns and collective action from simple low-level behaviors. Self-organization is seen regularly in our own societies in the form of crowd movements, queuing behavior and even 'Mexican' waves in sports stadiums. It is primarily through such processes that termites, and other social organisms, are able to produce complex high-level behaviors and patterns.

We cannot yet fully explain all the macroscopic features of termite mounds by self-organization, but several models

have been developed to account for the construction of soil pillars and walls, the building elements of mounds. In particular, it seems to be that termites are more likely to deposit soil particles where other individuals have just placed some particles, perhaps because of the build-up of some short-lived pheromone (Figure 4). Such positive feedback is a common feature of self-organization and, for the termites, it ensures that building focuses only in particular areas, which leads to the production of the central structural pillars. And, as termites gather at building sites, newly arriving individuals can only deposit their soil particles next to the pillar, which leads to the extension of pillars into walls. Understanding precisely how these walls become air-conditioned buildings, up to a thousand times larger than its constructors, requires further study. But the fact that it happens shows that termites are more than pest species. Their ecological importance and intriguing social life warrant a wider recognition beyond the perspective of a vermin exterminator.

Further reading

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