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Subterranean Termites (Rhinotermitidae)

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Phylogeny and classification

The worldwide family Rhinotermitidae, or subterranean termites, comprises 15 genera and more than 300 species. They occupy an intermediate position between the so-called “lower” and “higher” termites and so are often referred to as “intermediate” termites (1).

The Rhinotermitidae appears to be paraphyletic, with most researchers placing the clade with *Coptotermes* and *Heterotermes* as a sister group to the Termitidae. Some researchers regard the Serritermitidae as paraphyletic within the Rhinotermitidae-Termitidae clade, while others place it as a basal group of Rhinotermitidae, near other basal groups such as *Rhinotermes*, *Prorhinotermes*, and *Schedorhinotermes*. Other researchers feel that Serritermitidae lies at the crossroads of worker caste evolution in termites, between the lower termites and the Rhinotermitidae+Termitidae clade. The most basal rhinotermitid taxa, such as *Rhinotermes*, diverged from the other lower termites less than 100 MA ago. The latest literature reviews indicate that the well-known, more derived genera *Reticulitermes* and *Coptotermes*+*Heterotermes* consistently form two distinct clades in a monophyletic branch within the family (2). These three genera account for more than half the species in Rhinotermitidae (184 of 305) and are the best studied within the family.

The native ranges of these three genera (*Reticulitermes*, *Coptotermes* and *Heterotermes*) are all broad but fairly distinct. *Coptotermes* and *Heterotermes* are largely pantropical, although *Heterotermes* does not occur in Africa. *Coptotermes* is absent from the Nearctic and Palearctic regions. *Reticulitermes* naturally occurs exclusively within temperate areas. The *Coptotermes*+*Heterotermes* clade and *Reticulitermes* separated about 60 MA, according to various researchers. However, based on historical biogeography, modern *Reticulitermes* species resulted from cladogenesis and are highly taxonomically distinct. More ancient fossils of the different genera have been found in Europe, and they geologically date back to around 38 MYA. In a recent molecular phylogeny for *Coptotermes*, created using the complete mitochondrial genome, the genus is composed of numerous poorly supported branches. This result is partly due to the high level of synonymy in the present nomenclature and does not help clearly differentiate the species. However, speciation patterns were relatively clear in Australia, where this clade is the best defined. Consequently, this genus should be revised to deal with the high levels of synonymy in some locations (3).

Subterranean termites are especially notable because they represent the transition from the less derived, one-piece-type termites (lower termites) to the more derived, separate-type termites (higher termites), which forage for food outside of the nest and form large populous colonies. This transition in termites is accompanied by an increase in the complexity of social interactions, which means well-developed communication is a major evolutionary transition in this group (1).

Coptotermes and *Reticulitermes* are the most notable of these intermediate termites as they form the largest colonies. The vast majority of subterranean termites are intermediate-type nesters, although *Prorhinotermes* are single-piece nesters and Australian *Coptotermes* are separate-piece nesters with the latter group forming mounds that are completely separate from their food source (Fig 1).

Development and caste differentiation

Subterranean termites also display a remarkable degree of developmental flexibility and reproductive complexity, indicating that these traits are key in termite eusociality. As noted above, Rhinotermitidae forms a clade with Termitidae — one of their synapomorphic characters is the presence of true workers, although some of the more basal genera (*Prorhinotermes* and *Termitogeton*) do not have true workers. In caste development in Rhinotermitidae, undifferentiated larvae follow one of two lines. In the apterous line, larvae become true workers or soldiers, or they become workers that transition into ergatoid neotenics (secondary reproductives). In the nymphal line, larvae become nymphs and then either alates (primary reproductives) or brachypterous neotenics (secondary reproductives) (Fig. 2).

Several differentially expressed genes must be involved in this polyphenism, as seen in the Japanese subterranean termite, *R. speratus*. The social environment (e.g., presence of soldiers) and endocrine factors (e.g., juvenile hormone III) influence gene expression and caste differentiation in *R. flavipes*, and several dozen genes may be significantly involved. In antioxidant defense in *C. formosanus* (which is particularly useful against pathogens), castes differentially express 17 genes: winged imagoes have the highest degree of upregulation and the most resistant cuticles, while the opposite is true of soldiers. However, it has been shown in *R. speratus* that the oldest soldiers take more risks, in particular with regards to predators, so temporal polyethism in addition to caste polyphenism contributes to task specialization.

Certain volatile pheromones have also been found to regulate caste differentiation — suppressing the differentiation of new female neotenics in particular — and to attract workers to eggs (4). A novel study on post-mortem signaling in *R. flavipes* has shown that termites can distinguish between early and late death cues, which elicit different behaviors that preserve colony health.

An important feature of the biology of Rhinotermitidae as well as all lower termites involves the gut microbiome. There a number of flagellate protists, bacteria and Archaea in the paunch, an enlarged section of the hindgut, that are essential for lignocellulose digestion. Studies of the bacteria show significant horizontal transfer among species (e.g., between *Reticulitermes* species and termitid species such as *Cubitermes*), likely during aggressive encounters or feeding. It seems probable that both horizontal and vertical transmission of bacteria and other symbionts must have played an important role in termite evolution.

Reproduction and colony life cycle

As noted above, there are two types of reproductives in Rhinotermitidae: alates and neotenic. This is one of the family's unique traits. In *Reticulitermes* in particular, neotenic play a crucial role in colony growth and development. The typical life cycle of subterranean termites begins with a mating flight in which alates fly usually in synchronous swarms. The season and time of day of swarms varies with the species. Male and female alates will land and males will pair with a female, sometimes with the aid of a sex pheromone released by the female. The male and female will then form a tandem pair with the male trailing the female. The pair will find a suitable nest site, usually in a log or under a stone, mate and lay eggs. The first instars will be nourished by the primary reproductives from body reserves accumulated before leaving their natal nest. The first batch of eggs typically produces 20-30 workers and at least one soldier.

Once the first offspring reach the third instar, they begin to forage and start to feed the reproductives and take over care of the young. The colony then grows, reaching maturity after several years, at which time it will produce new alates. At some point in the colony lifecycle, the king and/or queen may die and be replaced by neotenic reproductives of the corresponding sex, usually of the brachypterous form but sometimes of the ergatoid form (5). When neotenic are present, females usually outnumber males by about 2:1. Neotenic inbreed within the nest leading to inbred colonies.

Occasionally, colonies can fuse resulting in genetically complex groups. Ecological conditions may play a role in shaping colony breeding structure. Three species of *Reticulitermes* (*R. speratus*, *R. virginicus* and *R. lucifugus*) have been shown to have a breeding system called asexual queen succession (AQS). Under AQS, the primary queen is replaced by parthenogenetically produced daughter queens that develop into brachypterous neotenic. There can be hundreds of asexual neotenic who mate with the primary king (or sometimes a single brachypterous king) to produce workers and alates through sexual reproduction. Species with AQS tend to have a female biased sex ratio due to the higher reproductive value of females in this system. Since the discovery of AQS in subterranean termites, it has also been found in at least four species of higher termites and may be widespread throughout the Isoptera. In *R. speratus* and other related species, parental phenotypes (worker-derived or nymph-derived reproductives) influence the caste fate of the offspring. For example, female offspring of nymph-derived queens and worker-derived males develop exclusively into nymphs, as do parthenogenetically produced daughters. In contrast, female offspring of worker-derived queens and nymph-derived males develop exclusively into workers. This parental effect is not due to genetic inheritance but due to genomic imprinting. Dispersal takes place primarily through mating flights. However human mediated dispersal can be important in both *Reticulitermes* and *Coptotermes*.

Chemical communication

As mentioned above, communication — and, more specifically, chemical communication — is a key component of the complex social interactions seen in the Rhinotermitidae. Indeed, in termites, chemical communication is essential in every facet of colony life and this is especially true for the Rhinotermitidae. Contact semiochemicals, such as the complex mixtures making up cuticular

hydrocarbon (CHC) signatures, are significantly involved in species, colony, caste, and sex recognition in many rhinotermitid genera and species, although the degree of involvement may vary. The first evidence for the role of CHCs in insect recognition processes was acquired experimentally in subterranean termites. In general, CHC signatures vary qualitatively among species and quantitatively within species. Curiously, some *Reticulitermes* species share similar cuticular chemical signatures, even though they are found in different parts of the world. These similarities have namely been observed in *R. flavipes* in eastern North America, *R. urbis* in the Balkans, *R. clypeatus* in the far western Mediterranean, and *R. speratus* in Japan. This pattern could be indicative of a shared common ancestor.

The social environment (e.g., the presence of predators) can also influence this signature. Sometimes, very few compounds—even just one or two—play a key role. For example a single C21 compound was found to act as a king and queen recognition pheromone in *R. flavipes* (6). Many glands, such as the sternal and tergal glands, or the frontal gland in soldiers, contain largely volatile compounds that serve various functions, including defense and trail marking. They are found across a range of genera, from the basal *Prorhinotermes* to the more derived *Reticulitermes*. These volatile compounds are mostly terpenoids but can also be small esters, alcohols, or other oxygen-bearing compounds. Additionally, different compound types—volatile, less volatile, and non-volatile—have multifaceted roles in caste regulation and/or reproduction. They have also been described in many species of Rhinotermitidae. Some pheromones can have multiple functions, as is the case for the volatile pheromones of *R. speratus*, which can inhibit neotenic differentiation, serve as egg attractants and reduce fecundity in nestmate queens.

Rhinotermitidae often utilize antimicrobial compounds for communication signals. For example, *Reticulitermes* and *Coptotermes* use egg surface compound lysozyme as the egg recognition pheromone, whose primary function is to protect eggs from pathogens. These aspects of chemical communication are the subject of much current research.

Pest status

Both native and invasive subterranean species are well-known structural pests in urban environments. Indeed, most of the research on Rhinotermitidae is due to that fact that members of this family are destructive pests. The majority of known termite invaders belong to the Rhinotermitidae genera *Coptotermes*, *Heterotermes*, and *Reticulitermes*, although there are also a few from the families Kalotermitidae and Termitidae. For example, *C. formosanus* is native to China but is found throughout Hawaii and parts of Japan and the mainland US, and *R. flavipes*, native to large parts of eastern and central North America, has been introduced into Europe and South America. Recent research has shown that *C. formosanus* is one of the costliest invasive species in the USA, but the whole *Coptotermes* genus has had serious economic impacts worldwide. Molecular genetics and chemical ecology have helped reveal the origins of termite invaders. For example, the *R. flavipes* population that has been present in Europe since the 17th century was discovered to have come from Louisiana (7). It seems likely that subterranean termite species will expand their ranges in the future, as a result of both global trade and climate change (8). Invasive species may also hybridize—a notable level of hybrid vigor has resulted from mating between two invasive

Coptotermes species in southern Florida. The cryptic nature of subterranean termite foraging and nesting habits as well as their reproductive flexibility (in addition to other adaptive peculiarities) have made them worldwide pests with significant ecological and economic impacts.

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Figures

1. Left: Primary couple of *Reticulitermes flavipes* with offspring; photo by Barbara L. Thorne. Right: Primary couple of *R. speratus* center) with several secondary queens (the right) and offspring; photo by Kenji Matsuura.



2. Workers and soldiers of *Coptotermes formosanus*. Photo by Thomas Chouenc.

