



Farming fungi termites show the way

It's been known for a long time that some termites perform intensive agriculture – they cultivate mushrooms inside their nests. **Duur Aanen** and **Wilhelm de Beer** describe new research, which suggests that termite agriculture had its beginning in the rain forests of central Africa and spread later to savannas and to Asia.



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Top: Close-up of a fragment of the fungus garden cultivated by a colony of the termite species *Macrotermes bellicosus*.
Photograph: Karen Machielsen

Above: A fragment of fungus garden.

Humans began to practise agriculture some 10 000 years ago, but cultivating your own food is not unique to people – a group of termites¹ found in tropical Africa and Asia has been growing a fungus for food inside their nests² for millions of years.

The cooperation between termites and fungi is an impressive example of 'mutualistic symbiosis', that is, of natural cooperation and coexistence between two different species that is of advantage to both.

In this case, the termites build nests that act like greenhouses, and go out in search of plant material with which to provision their fungal gardens. They offer their fungal symbionts finely broken down, usually dead, plant material, such as wood and dry grass, and the fungi grow on this substrate. In their turn, the fungi decompose carbon-rich complex plant materials, such as cellulose and lignin – which the termites do not have the enzymes to digest

directly – forming nitrogen-rich fungal biomass that provides the termites with most of their food.

A termite colony can consist of millions of sterile workers and soldiers, all descending from a single queen and a single king. Inside the termite nest, which can become very large, the fungus is grown on a fungus comb maintained by the workers. They constantly add new plant substrate, all the while consuming older fragments and asexual fruiting bodies (or nodules)³.

The evolution of the symbiosis

New research has been conducted, reconstructing the phylogenies (or evolutionary developments) of both partners in this symbiosis. It has shown that there was a single, dramatically innovative and irreversible transition to agriculture in this group of termites. In other words, the phylogenetic reconstructions show all fungus-growing termites descending from a single ancestor that 'invented' agriculture about

1. Termites used to be called 'white ants', even though they are not ants at all.

2. Ants are the other social insects, apart from termites, that, about 50 million years ago, learnt to cultivate fungi for food.

3. They eat the older fragments for food. The asexual fruiting bodies carry the spores of the fungus, which the termites redistribute to new parts of the substrate to speed up the cultivation process.



Above: Some of the different castes of *Macrotermes natalensis*: large soldiers, small soldiers, and workers. They are closing off holes in the side of a mound.

Right (from top down): The central fungal chamber inside a nest of *M. natalensis*, about 80 cm beneath the ground surface. The fungus garden is distributed over small chambers, carefully maintained by a large worker force.

The complete fungus garden of a medium-sized colony of *M. natalensis*, opened in a common effort by researchers in the grounds of the Plant Protection and Research Institute at Rietondale, Pretoria.

The above-ground portion (which serves mainly as an air-conditioner) of a mound of the termite *M. natalensis*, in an open stretch of savanna grassland.

Two Pierneef woodcut prints of termite mounds in Namibia. Courtesy of the Natural Cultural History Museum, Pretoria, both prints entitled "Miershoop S.W.A."



30 million years ago.

These termites domesticated only a single fungal lineage, represented by the extant genus *Termitomyces*, and, in the millions of years that the symbiosis has existed, they have not domesticated any other fungi. Furthermore, once the symbiosis had been established, neither of the two parties ever reverted to a non-symbiotic lifestyle. To this day, they continue to depend upon one another.

Colonizing success

The symbiosis between fungus-growing termites and their fungi has a big impact on most African and Asiatic ecosystems. Although fungus-growing termites are also found in tropical rain forests, they flourish in savanna ecosystems, where their ecological impact is greatest. **It has been estimated, for example, that fungus-growing termites are responsible for 90% of the decomposition of wood in some savanna areas in Kenya.**

The domesticated fungus, *Termitomyces*, is a so-called white-rot fungus. White-rot fungi are among the

few organisms that can degrade the plant material lignin, so they play an important role in the ecosystem's carbon cycle. The optimal conditions for white-rot degradation are humidity combined with a constant and high temperature. These conditions are met in rain forests, but not normally in savannas.

So how can white rot function in these environments? The answer is: through the extraordinary sophistication of termite farming.

Inside a termite nest in the savanna environment, the conditions are very similar to those in the tropical rain forest, and the termites have developed highly advanced and flexible ventilation techniques to maintain constant rain-forest conditions. Research in west Africa has shown, for instance, that outside temperatures can fluctuate by as much as 35 °C between winter nights and summer days, whereas within the termite nests, where the fungi are grown, the temperature always remains in the narrow range of 29–31 °C. >>





Top: Fruiting bodies of *Termitomyces reticulatus* between the inconspicuous mounds constructed by the termite *Odontotermes latericius*.

Middle: In many species of fungus grown by termites, the fungus regularly reproduces sexually via the formation of mushrooms. Here the mushrooms of *T. reticulatus* are growing straight out of the underground fungus gardens of the termite *Odontotermes badius*.

Below: A fruiting body of *Termitomyces sagittiformis*. In the centre of the cap can be seen the hardened umbo (or small hump), which had bored upwards through the surface of the ground.

Warning: Do not pick or eat any mushrooms that have not been identified by an expert or by a person who knows mushrooms well. Certain white-gilled mushrooms that look similar to *Termitomyces* are in fact poisonous to humans.

- ▷ The air-conditioning techniques that the termites use depend on an air-flow design that keeps the conditions right for growing the fungus. In Namibia and northern South Africa, we have observed, for instance, that the tall, conical mounds built by some fungus-growing termite species point north, at an angle that reduces as far as possible the absorption of heat from the sun⁴.

From rain forest to savanna

The termites' efforts to maintain a 'rain forest' climate inside their nests can be explained by the new findings, which indicate that termite agriculture originated in Africa's rain forests.

Based on the distribution of the habitats and the areas where extant species of fungus-growing termites are found, phylogenetic trees were developed for the termites and the fungi so as to reconstruct their original habitat and geography. (This research involves comparing the DNA from fungi and termites to establish genetic relationships, and using the information to extrapolate back into the past.)

The rain-forest origin of fungus-growing termites is a remarkable finding, since extant species of fungus-growing termites are mainly found in savanna ecosystems, where their success has been both ecological (with respect to their relative share of the processes of ecosystem decomposition) and evolutionary (with respect to the high number of species that has evolved)⁵.

We believe that what enabled both partners to colonize the savannas were the agricultural habits and

innovations of the termites, and their need to maintain the symbiotic relationship between the fungi and the termites outside the rain forest.

To survive in their new, very different savanna environment, the termites had to make sure that they could feed themselves by cultivating their fungi. This meant creating nests with special 'greenhouse' rain-forest conditions in which they could grow their crops, enabling the termites as well as the fungi to spread beyond the rain-forest regions.

Today, both the agricultural termites and their crops succeed better in the savanna environment than do their closest non-agricultural relatives, which still flourish best in rain forests.

Out of Africa

Apart from their agricultural life style, fungus-growing termites are similar to humans in yet another way. Analyses of mitochondrial DNA in humans – which is transmitted only via the female line – have shown that humanity's ancestral mother, the so-called 'mitochondrial Eve', lived in Africa. Similarly, analyses of the mitochondrial DNA of fungus-growing termites have shown that the 'mitochondrial termite Eve' was also African.

And, just as humans subsequently migrated out of Africa, so also did fungus-growing termites migrate, colonizing Asia at least four times and Madagascar once.

Partners and rivals

Nowadays many biologists consider the phenomenon of symbiosis as 'reciprocal exploitation' rather than as the kind of cooperation in which both partners are of assistance for each other's benefit.

Both partners clearly benefit from the association in the world of fungi and the termites that grow them, but their needs are not always the same. An example of a conflict of interest is the use of mutually maintained resources for reproduction. Although each is 100% dependent on the other inside a colony, their reproduction – in by far most of the species – occurs independently. This means that both sides – from their own perspective – would have an interest in limiting the other's reproduction.

Humans benefit too!

Humans have also benefited from the agricultural success of the fungus-growing termites, as the fungi that these insects grow for food produce above-ground fruit in the form of mushrooms that are safe for humans to eat.

4. If the conical mound were built vertically, a larger area of their northern surface would be exposed to the heat of the midday sun. Pointing northwards at an angle, towards the sun, the mounds are less exposed to heat on the northern side. This effect has to do with the fact that the termite mounds in Namibia and northern South Africa are far enough south of the equator for the angle to make a difference.

Here is how it works. When a tall object is located on the equator, its shadow falls directly beneath it at midday. When that object is located further south (in the southern hemisphere), its shadow at midday falls in a southerly direction – the further south it is moved, the longer its shadow becomes. (In the northern hemisphere, the midday shadow falls in a northerly direction.) The angle at which the termites build their mounds seems to be the one that provides the greatest protection to the northern surface of their nests. (You can illustrate this principle by holding a pencil directly underneath a light to see how the shadow falls – if you then move the pencil south, you will see its shadow change in length and point away from the source of light.)

5. In southern Africa, there are more than 40 fungus-growing termite species, but only about 7 or 8 morphologically distinct fungal species are cultivated by them.



The *Termitomyces* mushrooms grow from the underground fungus gardens (sometimes several metres deep) like closed umbrellas pushing up through the ground. Their toughened tips bore through soil that is often very hard and compacted, breaking through the surface. There the fruiting bodies open out to form a cap (pileus) with a diameter, in certain species, of up to one metre.

These *Termitomyces* fruiting bodies are a delicacy in many regions in sub-Saharan Africa. One of the best known species is *Termitomyces titanicus*, the world's largest edible mushroom, which is highly prized in countries such as Zambia and Tanzania. In northern Kwazulu-Natal, *T. umkowaani* mushrooms are often sold by the roadside in the rainy season when they fruit – the Zulu name is *ikboue*.

During the early 1990s, research was conducted at the University of Pretoria to determine the nutritional value of *Termitomyces* species. It was shown that *T. umkowaani* contains much higher levels of amino acids, such as methionine and cysteine, than are present in commercially cultivated mushrooms. This makes these mushrooms more nutritious than other

varieties and could serve as a good source of protein in the human diet.

In spite of the most modern and sophisticated agricultural technologies available, however, no human being to date has been able successfully to cultivate a *Termitomyces* mushroom in a way that is economically viable. We shall need to conduct much more research before we can understand fully the technologies that the first mushroom breeders have been applying with great success for millions of years. □

Research into the evolution and other aspects of the symbiosis between termites and fungi are ongoing under the guidance of geneticist Dr Duur Aanen from the University of Wageningen in the Netherlands. Collections in the field and initial laboratory work are conducted during extensive annual visits to South Africa, in collaboration with mycologist Wilhelm de Beer at the Forestry and Agricultural Research Institute at the University of Pretoria.

For further details, read: Duur K. Aanen and Paul Eggleton, "Fungus-growing termites originated in African rain forest", *Current Biology*, vol. 15 (2005), pp.851–855; Duur K. Aanen and Jacobus J. Boomsma, "Social-insect fungus farming", *Current Biology*, vol. 16 (2006), pp.R1014–R1016; Henrik Hjarvard de Fine Licht et al., "Presumptive horizontal symbiont transmission in the fungus-growing termite *Macrotermes natalensis*", *Molecular Ecology*, vol. 15 (2006), pp.3131–3138; Albert Eicker and Gideon C.A. van der Westhuizen, "Field Guide – Mushrooms of Southern Africa (Cape Town, Struik, 1996); Judith Korb, "Thermoregulation and ventilation of termite mounds", *Naturwissenschaften*, vol. 90 (2003), pp.212–219; Gideon C.A. van der Westhuizen, and Albert Eicker, "Species of *Termitomyces* occurring in South Africa", *Mycological Research*, vol. 94 (1990), pp.923–937; Wilhelm J. Botha and Albert Eicker, "Nutritional value of *Termitomyces* mycelial protein and growth of mycelium on natural substrates", *Mycological Research*, vol. 96 (1992), pp.350–354; and Eugene N. Marais, *The Soul of the White Ant* (Penguin, 1973).



Top left: Not all *Termitomyces* species produce large mushrooms: here is a cluster of smaller fruiting bodies of most probably *T. clypeatus*.

Top: A basket of *T. reticulatus* fruiting bodies, showing the long pseudorrhiza that grows from the underground fungal chamber all the way up to the soil surface, where the mushroom then opens.

Above: Sliced and butter-fried *T. reticulatus* served on toast: a meal fit for royalty! The hand-printed Zambian cloth in the background, with the artist's impression of a *Termitomyces* mushroom connected to the fungus comb, celebrates the interaction between the termites and their fungi.

Facts about termites

In the past, termites were often called 'white ants', even though they are no relation to true ants. They are, in fact, closely related to cockroaches, so some people view them as 'social cockroaches'.

There are about 2 600 species of termites, represented by 7 families and 281 genera. They are cosmopolitan insects, but are geographically limited to warm regions.

All termites are social. They live in large societies of closely related individuals. Reproduction in a termite society is normally limited to the so-called 'royal couple', consisting of a queen and a king, both of which live much longer than the other individuals in termite society – the workers and the soldiers. Workers and soldiers do not reproduce, but, instead, help their parents and brothers and sisters to reproduce.

Apart from their social behaviour, termites are well known for their symbiotic relationship with a variety of other organisms, which help them to digest the plant materials they consume. All termites have intestinal bacteria, and most also support protozoa in their guts.

Only a minority of termite species cultivate fungi. These fungus-growing termites belong to a single sub-family (*Macrotermittinae*) consisting of 11

genera and about 330 species. Fungus-growing termites are found only in Africa and Asia.



Above: A *Macrotermes natalensis* queen, taken out of the royal chamber.

Above right: An opened 'royal chamber' of a colony of *Macrotermes bellicosus*, where the queen (the bloated individual in the centre) lives with the king (indicated by the arrow). The small individuals are workers, all produced by the queen. She can be described as an 'egg battery' as she can lay up to 30 000 eggs per day.

Q Fact file

