Farming symbiosis between *Termitomyces* and Macrotermitinae

The basidiomycete genus *Termitomyces* is a well-known genus that forms edible mushrooms in the wild, mostly in Asia and tropical Africa. They are especially known for their symbiosis with fungus-farming termites in the subfamily Macrotermitinae. The symbiosis originated once in Macrotermitinae around 30 million years ago in Africa.¹² The farming-like mutualistic symbiosis is based on the exchange of especially food and shelter.

Within special structures of the termite nests called fungus combs (Fig.1), *Termitomyces* fungi are ensured continuous food supply from the termites of partly digested plant material¹. The plant biomass is further decomposed by the fungi and ingested by termites together with so-called nodules.¹ Nodules are structures on the combs made by fungal mycelium, storing gut-resistant asexual spores that are dispersed in feces, as they serve as an important nitrogen-rich food source for the termites, especially for the queen and developing larvae.^{3,4}

The fungus combs are built of these fecal droplets from young termites that consist of organic matter and nodules. The feces droplets form small units called mylosperes that fuse together forming the solid spongelike comb-structures. The structure of the combs varies among species and even among termite colonies within the same species. Older comb structures are eventually consumed by old termites.⁴

The fungal growth is thus promoted by the dispersal of the asexual spores.³ The fungi are also ensured a competition-free growing environment within the combs due to termite workers cleaning the fungi-growing area, which prevents the growth of pathogenic fungi, and due to



Fig. 1. (A-B) Fungus combs with white nodules. (E) Fruiting bodies of *Termitomyces* sp. emerging from termite nest.^{2,4}

microenvironmental conditions that favor the growth of *Temitomyces* while inhibiting the growth of other fungi.⁴

During sexual reproduction, the fungi form fruiting bodies. The fruiting bodies emerge from the

soil to the environment above the termite nests. The basidiospores are dispersed to the surrounding environment, collected by foraging working termites, and spread to fungus-free termite colonies. Research suggests that termites within the nests suppress the formation of fruiting bodies since the fruiting-body formation takes up resources that could have been used for growth within the colony.³

Most *Termitomyces* are edible and considered to have great nutritional value, as they are a source of protein, fibers, and carbohydrates, as well as beneficial minerals and amino acids.⁵ *Termitomyces* fungi are consumed throughout all of Asia e.g. in India, China, Nepal, and Thailand. In West Africa and Zambia, the edible *Termitomyces titanicus*, the largest edible mushroom in the world, is an important food source to local people, while in Tanzania, the high market value of fungi within *Termitomyces* have contributed to the socio-economic development of the country.⁵ Studies suggest several health benefits of polysaccharides of *Termitomyces* such as antioxidant activity, and improvement of cellular and humoral immune function. Polysaccharides of *Termitomyces* also seem to exert anti-tumor activity against cancer cells, although little research has been performed.^{5,6}

Literature

- 1. Schmidt, S., Kildgaard, S., Guo, H., Beemelmanns, C. & Poulsen, M. The chemical ecology of the fungus-farming termite symbiosis. *Natural Product Reports* vol. 39 231–248 Preprint at https://doi.org/10.1039/d1np00022e (2022).
- 2. Poulsen, M. Towards an integrated understanding of the consequences of fungus domestication on the fungus-growing termite gut microbiota. *Environmental Microbiology* vol. 17 2562–2572 Preprint at https://doi.org/10.1111/1462-2920.12765 (2015).
- 3. Vreeburg, S. M. E. *et al.* Asexual and sexual reproduction are two separate developmental pathways in a Termitomyces species. *Biol Lett* **16**, (2020).
- 4. Vesala, Risto., A. Laura., R. J. Termitomyces fungus combs formation, structure, and functional aspects. in *Microbial Symbionts: Functions and Molecular Interactions on Host* (ed. Dharumadurai, D.) 659–677 (Academic press, 2023).
- 5. Paloi, S. *et al.* Termite Mushrooms (Termitomyces), a Potential Source of Nutrients and Bioactive Compounds Exhibiting Human Health Benefits: A Review. *Journal of Fungi* vol. 9 Preprint at https://doi.org/10.3390/jof9010112 (2023).
- Liu, J. *et al.* Isolation, Structural Properties, and Bioactivities of Polysaccharides from Mushrooms Termitomyces: A Review. *Journal of Agricultural and Food Chemistry* vol. 70 21–33 Preprint at https://doi.org/10.1021/acs.jafc.1c06443 (2022).