Self-organized Linear and Helicoidal Ramps
in Insect Nests

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Abstract—**The nests built by termites of the genus *Apicotermes* present a regular succession of floors interconnected by vertical passages. By scanning these nests with X-ray tomography we observed that two different configurations of vertical passages coexist: ramps and helices. Based on our current knowledge of the mechanisms of nest building behaviour in different groups of social insects we formulate hypotheses about the mechanisms that could lead to the formation of these structures. In particular, we show that a 3D model of nest building in *Lasius niger* ants (Khuong et al, 2016) is capable of producing layered structures with vertical helices similar to the structures built by *Apicotermes* by simply running it with parameters different from those empirically measured for ants. It is possible that similar self-organised building mechanisms underlie the construction of the different nest structures produced by different groups of social insects.**

Keywords: organization; social insect nests; termites; stigmergy; helicoidal structures

I. Introduction

The nests of social insects are among the most complex structures built by animal groups [1]. Ants and termites build a large variety of structures, from simple excavated chambers to complex constructed mounds up to 10 m in height and containing specific areas for reproduction, brood rearing, fungus cultures, nest ventilation [2-3].

The complexity of these nests is even more striking if we consider that these structures are not built by animals with putatively higher 'intelligence' such as primates, but by insects with limited cognitive capacities and whose individual behaviour is highly stochastic. This apparent discrepancy between individual capabilities and the complexity of the built structures indicates that nest building in social insects is a self-organized process whereby ordered structures are produced by the actions and interactions of multiple individuals exhibiting simple behaviours [4-5]. Understanding the mechanisms of this self-organized process could enable us to mimic insect behaviour in order to design and build artificial systems capable of making similarly complex structures with limited resources [6-7].

We already know that the coordination of nest building behaviour in social insects is mainly mediated by interactions with the building substrate: worker insects respond to the local configuration of the growing nest by performing specific actions. For instance, if an insect encounters an agglomerate of building pellets forming a heap it might be induced to deposit new pellets on top of the heap to form a pillar; encountering a pillar that has reached a critical height might induce the deposition of pellets on its sides to form a roof and so on. Every time an insect performs one such building action, it modifies the growing structure in such a way to produce new stimuli, which will trigger new building responses by the same worker or by other members of the colony. This mechanism, first described by the French biologist Pierre-Paul Grassé in 1959 [8] is known under the name of stigmergy. The whole sequence of stimuli and behavioural responses leads to an almost perfect collective construction that may give the impression that the whole colony is following a well-defined plan (see [9] for a historical review).

While stigmergic interactions are likely to be widespread in social insects, direct and detailed empirical characterizations and quantifications in the context of nest building behaviour are relatively scarce. This may be in part due to the difficulty to visualise and quantify insect behaviour inside three-dimensional structures.

Bruinsma [10] studied the construction of the royal chamber by the fungus growing termite *Macrotermes subhyalinus*. The behaviour of worker termites is modulated by at least three distinct pheromones - the stigmergic stimuli used in this particular system. The first stimulus is a building pheromone that diffuses from the queen, creating a gradient around its body; the gradient of pheromone concentration acts then as a chemical template, which stimulates the workers to deposit their pellets at a certain value of concentration along this gradient, that is, at a certain distance from the queen. In addition, workers add a cement pheromone to the building material, which induces other workers to deposit their pellets at the same location as recently deposited ones, so leading to the formation of pillars at the right distance from the queen. Finally, termites mark

their paths leading to the building site with trail pheromones. These latter provide a long-range guidance for workers to the building site and might ensure the persistence of a single chamber entrance.

A simulation model by Ladley and Bullock [11] showed that these three pheromones can indeed lead to the construction of a chamber, but the parameters and functional relationships were only qualitatively inspired from Bruinsma's experiments. Bruinsma's work also inspired simulation studies beyond royal chamber construction: Bonabeau et al [12] showed that this volatile cement pheromone leads to regularly spaced pillars in 2D space.

The mechanisms involved in the coordination of building behaviour have also been studied experimentally in the context of simple 2D structures produced by ants and termites, either by digging the substrate [13-16] or piling up soil particles [17-19]. Only quite recently had the coordination mechanisms involved in 3D nest construction been studied. This was done by Khuong and collaborators, who studied the building of above-ground nests by the ants *Lasius niger* [20]. *L. niger* build relatively simple mounds, up to 20 cm high, that enclose a large number of twisting and bubble-like chambers. As in the case of *Macrotermes subhyalinus*, a cement pheromone added to the building material allowed the ants to identify the active building sites. In contrast, the mechanism for regulating the height of the chambers was implemented at the level of individual ants: ants deposited their pellets on top of the growing pillars as long as the height of the pillar was shorter than the length of the ants' own body, then they started to deposit building materials on the sides of the pillars. So, the ants' own body served as a template for determining the height of the roofs.

While these building mechanisms are extremely simple, Khuong and collaborators showed that they are sufficient to reproduce many of the observed features of real nests by implementing the rules of individual behaviour observed experimentally in an agent based model. One parameter of the model -the lifetime of the cement pheromone- controlled much of the final shape of the nest, determining in particular the spacing of the pillars and the rate at which the structure was continuously remodelled.

In all these examples, it was the description of social insect behaviour and of the nest architectures that this behaviour produces that triggered the research for the underlying mechanisms in the framework of self-organized constructions, gradually moving from qualitative behavioural descriptions that inspired the first simulation studies, to fully parameterized and experimentally validated quantitative models to ascertain that the postulated mechanisms were actually at work.

In the present manuscript we focus on *Apicotermes* nests, which provide a particular example of structures built by social insects which are characterised by a regular organisation in evenly spaced layers interconnected by vertical ramps. Our goal, starting from qualitative descriptions of these structures, is to infer the potential building mechanisms at the individual level that could lead to the formation of *Apicotermes*-like nest architectures.
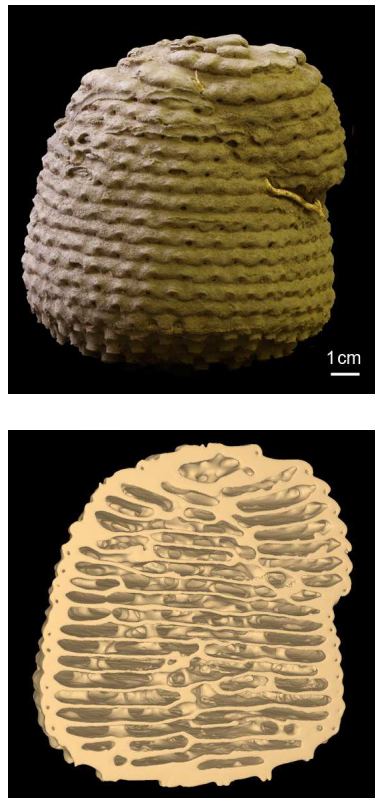

Figure 1. (top) Photo of an *Apicotermes lamani* nest, (bottom) virtual reconstruction of a nest half from X-ray tomography data. The termites access it through a tunnel on the top of the nest to arrive in a regularly layered structure.

We will first summarize some useful natural history facts of *Apicotermes*, then show for a particular nest (virtually reconstructed by non-destructive X-ray tomography) the ramps and helices that permit movement inside the nest, then discuss how helicoidal ramps can emerge and validate these suggestions through an individual based simulation model.

II. THE ARCHITECTURE OF *APICOTERMES* NESTS

Termites of the genus *Apicotermes* live mainly in the forests of Central and West Africa, extending sometimes to the surrounding savannah [21]. The life of this humivorous species is exclusively underground (including a cryptic nest 5 to 25 cm below ground that cannot be detected from above ground) which makes their study particularly difficult.

Across the whole range of forms of the nests built by ants and termites, the nests of *Apicotermes* represent one extreme because of the impressive regularity and symmetry of their features. The nests are built from fecal matter and they usually comprise several ovoid calies, similar to that shown in Fig. 1 (top). These calies are connected by tunnels and are separated by less than one meter from each other.

The external surface of a calie is characterised by the presence of regularly spaced pores, arranged in horizontal lines along all the surface of the nest (Fig. 1 top). The pores are connected to circular channels that run along all the
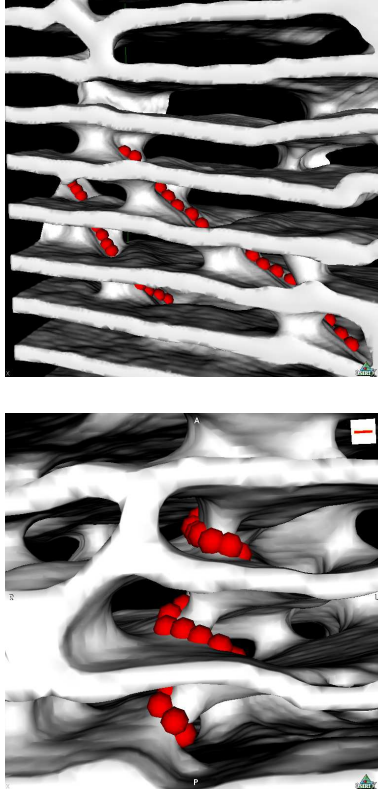
Figure 2. (top) Ramps (visualized by red dots) and (bottom) a helix found in the nest of Fig. 1.

perimeter of the nest whose position coincides with that of the different floors. In some species, the size of these openings is too small to allow the passage of termite workers. It is hypothesized that this particularly complex circuitry likely serves the gas exchange in the underground nest.

The interior of the calie comprises a series of regularly spaced chambers or levels (Fig. 1 bottom) separated by thin horizontal partitions. The movement between the levels is possible through inclined ramps or helices that connect several floors. At each level, there are several ramps creating different routes between two adjacent floors. (See https://www.youtube.com/watch?v=kfOs1MAblNM for a virtual flight through these structures.)

Within a given *Apicotermes* species nest architecture varies very little. This constancy of the architecture allowed Schmidt [22] to construct a phylogeny of the genus *Apicotermes* based solely on the characteristics of the nest structure (the nest is interpreted as an extended phenotype of the species). This phylogeny is consistent with the more conventionally established one on the basis of the insects' morphology [23].

Given the difficulty to observe directly the behaviour of *Apicotermes* during nest building we must infer the nest building mechanisms from the structure of the final nests. Our knowledge of the nest building behaviour of other social insect species will help us formulate hypotheses about how

the different structures observed in *Apicotermes* nests can be produced.

III.   DETECTING RAMPS AND HELICES IN *APICOTERMES* NESTS

Our observations are based on three complete *Apicotermes* nests originating from museum or private collections. For the present study we focus in particular on one *Apicotermes* nest. The nest is an *Apicotermes lamani* Sj. nest collected in 2008 around Pointe-Noire (Democratic Republic of the Congo). The nest was first digitized with X-ray computer tomography [24-25] and reconstructed to produce a series of dicom images. Each image represents a virtual slice across the nest, with a pixel resolution of ~0.3 mm and interslice distance of 0.3 mm (nearly isotropic voxels).

We used the dicom viewing software Osirix (V 3.7.1) to navigate through the slices and visually identify different types of structures. With the same software we subsequently produced three-dimensional surface renderings of selected structures for visualisation purposes.

Fig. 1 (bottom) shows one such visualization in which an *Apicotermes* nest is virtually opened with a vertical cut to show the internal structure. In the image the different layers composing the nest are clearly visible. One layer comprises in general one single large chamber spanning horizontally the entire nest. Several pillars are also visible in the image, probably supporting the floors of different layers and conferring stability to the entire structure. In this figure the vertical passages across layers are not directly visible, but these can be easily identified both in the series of two-dimensional tomographic slices and by navigating in the three-dimensional renderings (see https://www.youtube.com/watch?v=kfOs1MAblNM).

Fig. 2 shows a zoom on specific regions to illustrate the different structures that we classify as 'ramps' and 'helices'. In Fig. 2 (top) two ramps are visible (which we have marked with red dots). Each ramp spans multiple nest layers with a roughly straight progression. Fig. 2 (bottom) shows one helicoidal ramp twisting inside the nest for about four layers. Ramps and helices do not only differ in their straight or twisting horizontal progression as they climb across nest layers: ramps can be seen as a sequence of pillars, each associated with a 'trapdoor' that allows access to the upper layer. The layers remain otherwise separated and easily identifiable (Fig. 3 top). In the case of helices, the entire floor twists around and it is no longer possible to identify different floors (Fig. 3 bottom). One can descend in the nest doing sharp turns along this helix (Fig. 2 bottom) or by following the outer wall of the nest in the same direction (left-handed in the case of Fig. 2 (bottom), see https://www.youtube.com/watch?v=bcWY_VqmOak for a fly through).

IV.   GETTING RAMPS AND HELICES IN A 3D MODEL OF SELF-ORGANIZED NEST CONSTRUCTION

The construction of ramps and helices could result from the spatial and the temporal lag that exists in the growth of
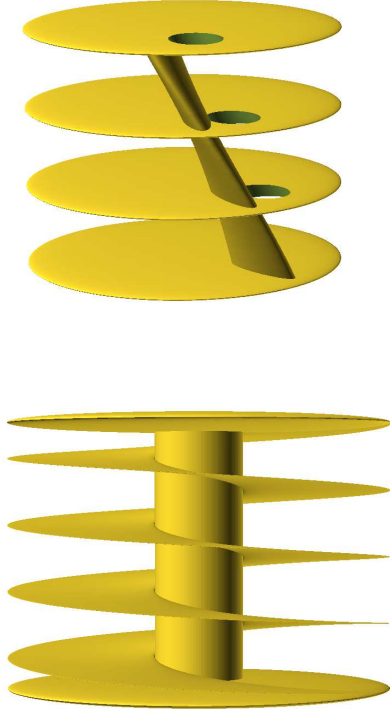
Figure 3. Schematic differences between ramps and helices. (top) Ramp: the layers remain well identifiable. (bottom) Helix: all twists of the helix form one single layer.
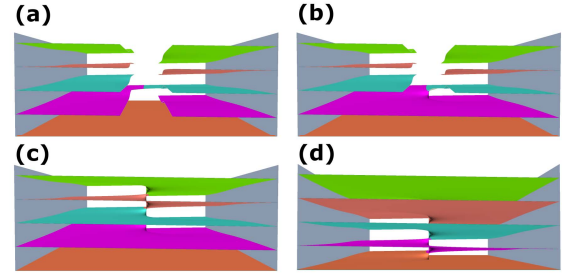

Figure 4. Scenario how a helicoidal ramp may emerge during self-organized nest construction. (a) Layers start growing from different origins. A different colour is used for each layer. One layer (in this case of level 2) is mistakenly connected to a layer of higher or lower level (in this case a layer of level 3). (b) At some other spatial position the same layer is correctly connected to a layer of the same level. (c) As some of the possible connections are already occupied, the topological defect propagates and the helical structure grows. (d) Eventually the helix terminates by forming a triple connection.

their different parts and also from the constant remodelling activity. One possible mechanism leading to the formation of straight ramps could be the following one: termites start building a pillar and when the pillar has reached the critical height they expand it to form the floor of a new layer. However, on one side of the pillar the floor does not grow because of intense traffic of termites, resulting in the appearance of a hatch. The process is then repeated at the upper layers. Geometric or chemical templates (e.g. a pheromone associated to the material used to build the first flight of ramp), coupled with termite traffic (which is channelled by the already formed portion of ramp) trigger the building of a new pillar in the proximity of the already formed ramp originating from lower layers, so that the process is repeated.

The formation of helices seems compatible with a different morphogenetic process, illustrated in Fig. 4. Termites start building layers simultaneously from different origins. As the height of layers is not homogeneous everywhere, at some spatial position the floor of one layer is mistakenly connected to the floor of the layer above or below (Fig. 4a). However, at some other spatial position the floors are correctly paired with floors of the same level (Fig. 4b). As some pairing possibilities are already taken, the wrong pairing of floors propagates determining the vertical propagation of the helix (Fig. 4c) that can only be arrested by

the formation of a triple junction (one layer - in this case the bottom layer of Fig. 4d - simultaneously connects to the layer of the same level and to the layer above or below).

In order to test if helices can actually be produced by a more realistic insect building behaviour, we use an agent based model of nest building behaviour developed for ants [20]. In this model, the 3D discrete space is defined by a 200 × 200 × 200 cubic lattice with a unit side length $\Delta l = 0.5$ mm. The building material is made of particles whose elementary size corresponds to that of a single cell. Each insect occupies a single cell, can only perceive its 26 neighbouring cells (hereafter denoted as V26) and perform a random walk on the surface of the growing structure.

During one time step, insects can only move to adjacent locations (i.e., to the six orthogonal locations around the insects' current position), and then they can either (i) choose to pick up a particle from the ground if they are not already carrying one with a probability P(pick), (ii) deposit a particle with a probability P(drop), or (iii) simply keep walking. The stochastic decision process is local and Markovian: there is no effect of the amount of time an insect has spent either moving unloaded on P(pick) or carrying a particle on P(drop).

As suggested by the experiments on ants, insects add a pheromone to the building material that may enhance further depositions of pellets at the locations where pheromone intensity is high enough. In the model, this chemical marking of building material is included and once it has been deposited, a particle is labelled by the time of its deposition.

An insect can pick up any particle on the bottom layer of V26 and deposit a pellet on its current position, both as a function of previously deposited pellets in V26. However, P(drop) increases with the total amount of pheromone in the surrounding building material. The model also includes a body-template effect that leads to the lateral depositions of pellets on the sides of pillars that are tall enough. The functions to model P(pick) and P(drop) as well as the values of all parameters were chosen as in [20] with the exception of two parameters as described below.
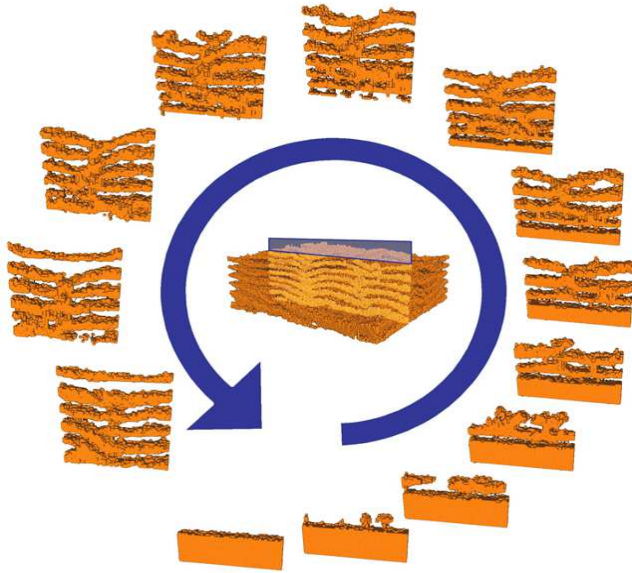
Figure 5. Simulation of the nest construction dynamics with the individual based model of Khuong et al (2016). Insects start to build pillars thanks to the positive feed-back induced by a building pheromone. When pillars become high enough, pieces of material are added on their sides; this rapidly increases the surface over which the material can be dropped, leading to the formation of globular capitals over the pillars. Roofs are built through the progressive merging of the growing capitals and new pillars are built over the successive floors. The cross section shows the construction of an helicoidal ramp between successive layers, resulting from the merging of different layers.

While the ant nests that the agent based simulation was intended to model are very different from *Apicotermes* nests, we observed that changing only 2 parameters (the spontaneous deposition rate and the lifetime of the cement pheromone) allowed the model to produce layered structures similar to those built by *Apicotermes*, comprising large layers and helicoidal ramps. The appearance of one such helicoidal ramp is illustrated in Figs. 5 and 6. The two changed parameters were not chosen by chance: spontaneous deposition rate determines the initiation of new pillars (it was set to 0.0001 s^{-1} instead of the 0.025 s^{-1} in [20]), while the pheromone evaporation rate determines the spacing between pillars (set to 0.000016 s^{-1} instead of the range 0.0008-0.00125 s^{-1} in [20]). Both changes lead to larger spacing between pillars as preliminary measurements indicate to be the case in *Apicotermes* nests.

V.   DISCUSSION AND CONCLUSIONS

Social insect colonies of different species can build a large variety of nest structures ranging from the disordered and twisted chambers built by *Lasius niger* ants to the regular structures of *Apicotermes* shown in this paper. In this latter case one can find regularly spaced floors connected by straight or helicoidal ramps. All these different structures result from self-organisation [26]. Our simulations indicate that small changes in model parameters (such as the

evaporation time of a cement pheromone) can determine the transition between these different structures. The similarity of mechanisms that potentially lead to the building of different nest plans provides us information about how nest building might have evolved in different species.

One of the most astonishing aspects of self-organisation in living systems is to produce regular, plastic and efficient structures from the interactions of stochastic units. In *Apicotermes* nests, the noisy control of the height of nest layers (in the model implemented by the stochastic deposition rate combined with the body template effect) is probably one of the factors determining the formation of helicoidal ramps. In this system, noise, coupled with the self-organised morphogenetic process is hence essential to produce specific structures, such as the helicoidal ramps, that have a functional value (they guarantee the vertical connectivity across the nest). Further work should increase our detailed understanding of these currently rather exploratory results: get a detailed quantitative description of the spatial arrangement of linear and helicoidal ramps, both in the nests and in the simulation results; explore the initial conditions that lead to the appearance of ramps as opposed to helices, in order to understand why these two different types of connections coexist in the same nests; modify the initial conditions in the model, as for example suggested in Fig 4, to provoke the construction of helicoidal ramps; further investigate the mechanisms underlying linear ramp formation across several layers; explore the adaptive value of either linear or helicoidal ramps with respect to termite traffic in the nest. While from the functional point of view it
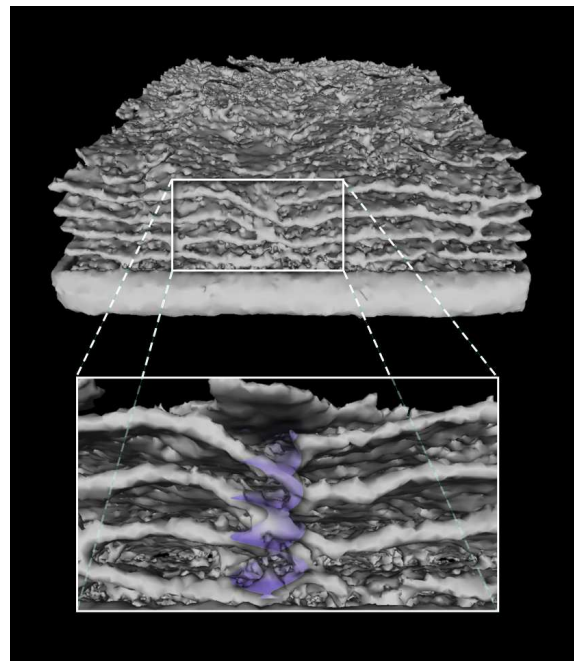

Figure 6.   Helicoidal ramp in a 3D model of nest construction. The emerging nest is organized as a set of regularly spaced layers. Helicoidal ramps are not explicitly encoded into the behavioral rules of the insects. They result from the spatial and the temporal lag in the growth of the different parts of a nest and from remodeling activity.

seems unlikely that ramps and helices fulfill different functions, ramps might be more plastic features of a nest, as they do not impose a complete reorganization of the floors that they interconnect. For such a reason, they could be produced and removed ad hoc when traffic needs across the nests change due to seasonal differences or changes in nest population. We are confident that a further exploration of our simulation model, together with a more detailed analysis of nest features, will allow us to answer this and a number of related questions. For instance, if ramps are added and removed at different times, we should expect the pillars that do not form ramps to be aligned in a similar way to pillars that formed ramps (because they were once part of a ramp).

We can imagine that reaching a detailed understanding of the mechanisms of nest building behaviour in social insects will provide inspiration for the design of human made systems capable of building similarly complex structures with limited resources. However, our example also illustrates that such artificial systems need careful calibration to ensure that the desired architecture emerges; slight changes in parameter values can be amplified to produce dramatic differences in the final outcome in such nonlinear complex systems.

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