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THE NESTS OF *MACROTERMES BELLICOSUS* (SMEATHMAN) FROM MOKWA, NIGERIA

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SUMMARY

Two types of *Macrotermes bellicosus* nests from Mokwa, Nigeria, are described. Both were found under similar conditions of soil, climate and drainage with no clear pattern of distribution to distinguish them. One of these, the spiral plate nest, has a highly developed base-plate which bears spirally arranged hanging vanes.

RESUME

A propos de nids de Macrotermes bellicosus **(Smeathman) de Mokwa, Nigeria**

Deux types de nid de *Macrotermes bellicosus* provenant de Mokwa, Nigeria, sont décrits. Tous deux ont été trouvés dans les mêmes conditions de sol, de climat et d'écoulement d'eau, sans qu'aucun mode de distribution ne les distingue l'un de l'autre. L'un des deux nids, le nid à disque en spirale, est muni d'un socle discoïdal très développé, dont le dessous porte, suspendues, des languettes disposées en spirale.

INTRODUCTION

The structure and function of nests of *Macrotermes bellicosus* (Smeathman) described here were examined as part of a broader study, which included the energetics of this species, in the context of an integrated ecological project on termites in agricultural and natural ecosystems. The project was organised jointly by the Centre for Overseas Pest Research

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(Ministry of Overseas Development, London) and the Institute for Agricultural Research (Ahmadu Bello University, Zaria, Nigeria) and was based at Mokwa (9° 18'N, 5° 04'E) in the Southern Guinea savanna zone of Nigeria. The climate, soils, vegetation and litter production of the area have been described in earlier publications (VALETTE 1973, COLLINS 1977 a).

Since SMEATHMAN's (1781) description of *M. bellicosus* nests, the nests of this species have probably received more attention than those of any other termite. GRASSÉ (1944-1945, 1949) and GRASSÉ and NOIROT (1951, 1958 a, b, 1961) gave precise, illustrated descriptions of nest structures from various parts of West and Central Africa (as *Bellicositermes natalensis*) and RUELLE (1970) considered the nest architecture of this species to be the most elaborate of all the *Macrotermes*. However, the unique constructions found in some nests in the Mokwa region of Nigeria represent a very high level of adaptation that has not previously been described.

The maintenance of microclimatic homeostasis in *M. bellicosus* nests has been studied by RUELLE (1962, 1964) and LÜSCHER (1955, 1956, 1961) (as *M. natalensis*). GRASSÉ and NOIROT (1958 a, b) and NOIROT (1970) disagreed with the latter author on points concerning air circulation within nests and the origin of the high nest temperatures, and the situation has been complicated by the existence of several nest types. GRASSÉ and NOIROT (1961) described regional variation in *M. bellicosus* nests (as *B. natalensis*) and HARRIS (1956) noted that *Macrotermes subhyalinus* Rambur, (as *M. bellicosus*) builds nests with many different styles of architecture under various regimes of soil and climate. HARRIS (1956) considered this variation to be due to modification of behaviour patterns under the influence of local conditions.

The theories of building behaviour in *M. bellicosus* have been complicated still further by the discovery at Mokwa of nests of two distinct types, both on soils of the Kulfo series (VALETTE, 1973), in the same conditions of climate and drainage, with no clear pattern of distribution to distinguish them. Both appear to be built by *M. bellicosus* as re-described by RUELLE (1970).

THE NESTS

1. Macrotermes bellicosus nest with a spiral base-plate

This nest, the " cathedral " type-out, numbered the second type by 40 : 1 and was prevalent between Bida (9°04'N, 6°00'E) and Jebba (9°08'N, 4°51'E). The epigeal mound is conical with vertical flutings, some of which separate from the main cone to produce secondary spires (fig. 1). The mounds reach a height of 6 m (exceptionally 7 m) and a basal diameter of 3-4 m. A survey of 83 mounds gave the following relationship between height and width :

Height = 1.7442 . width — 0.5781

r = 0.935, p = < 0.001. Measurements in metres.

The position of the habitacle, or living area, differs from those shown by GRASSÉ and NOIROT (1961), NOIROT (1970) and HARRIS (1956), in being entirely below ground level. The food stores and fungus combs are distributed as shown in figure 1, with an empty central core immediately below the main shaft of the mound. Fungus combs and food stores are

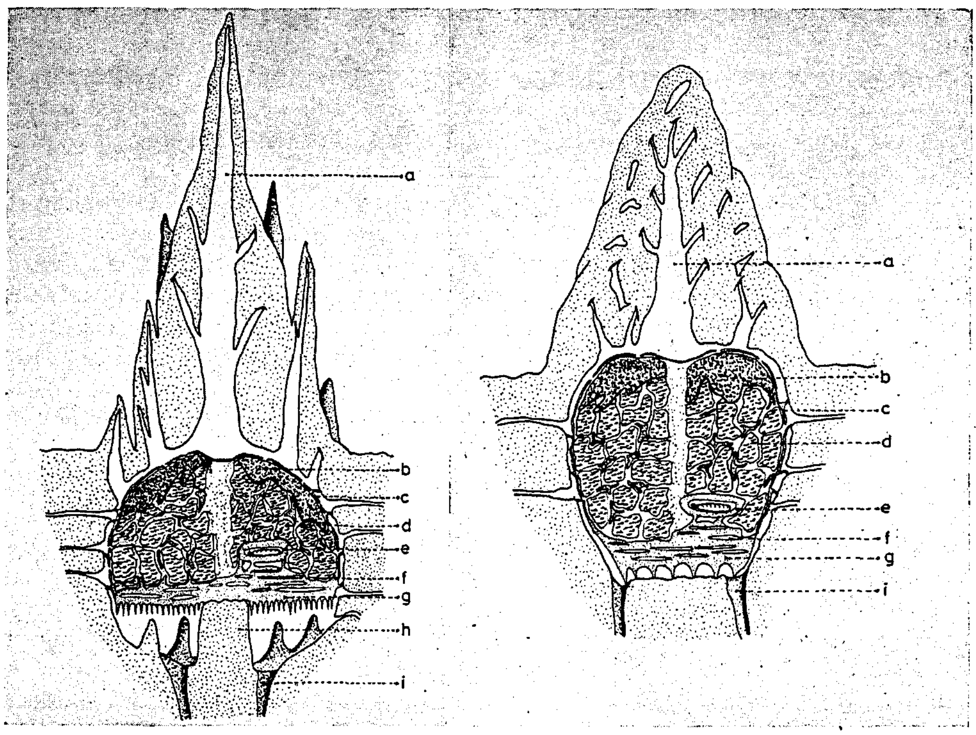

Fig. 1 Fig. 2

Fig. 1. — The spiral plate type nest of *Macrotermes bellicosus*.
a : main shaft, b : food stores, c : idiotheque, d : fungus combs, e : royal cell, f : larval galleries, g : base-plate with spiral, h : pillar, i : deep galleries.

Fig. 1. — Le nid du type à disque en spirale de *Macrotermes bellicosus*.
a : la cavité centrale, b : amas de nourriture, c : l'idiothèque, d : meules à champignons, e : la cellule royale, f : galeries aux larves, g : le socle en spirale, h : le pilier, i : galeries profondes.

Fig. 2. — The non-spiral (conventional) nest of *Macrotermes bellicosus*.
a : main shaft, b : food stores, c : idiotheque, d : fungus combs, e : royal cell, f : larval galleries, g : base-plate with supporting cones, i : deep galleries.

Fig. 2. — Nid conventionnel, à socle sans spirales, de *Macrotermes bellicosus*.
a : la cavité centrale, b : amas de nourriture, c : l'idiothèque, d : meules à champignons, e : la cellule royale, f : galeries aux larves, g : le socle avec les piliers coniques, h : galeries profondes.

surrounded by the idiothèque (GRASSÉ and NOIROT, 1958 a, b), a thin mud sheet usually fairly complete in young colonies but increasingly perforated in older ones. The queen cell is raised slightly above the levels of the wide larval galleries which ramify through the surface layers of the base-plate. The base-plate itself, which supports the termites and their fungus combs, is unique among the constructions of social insects. In plan view the plate is circular, up to 3.5 m across and supported centrally by a solid pillar approximately a quarter of the width of the plate. Very small cones protruding from the underside of the plate, fit into cavities on the pillar surface, but plate and pillar are not physically bonded, the plate merely resting on the pillar surface. The underside of the base-plate bears a remarkable series of clay vanes hanging downwards to a depth of up to 10 cm in large mounds and encircling the plate in a series of spirals (fig. 4). Three or four complete turns of the spiral are common before a break occurs and a new spiral begins. The vane is stalactitic in cross-section less, up to 2.5 cm thick at its attachment, 1 mm thick and very fragile at the irregularly wavy fine edge. The vanes are generally coated with a white layer of mineral salts (fig. 3), increasing in thickness with age of mound. The cellar in this

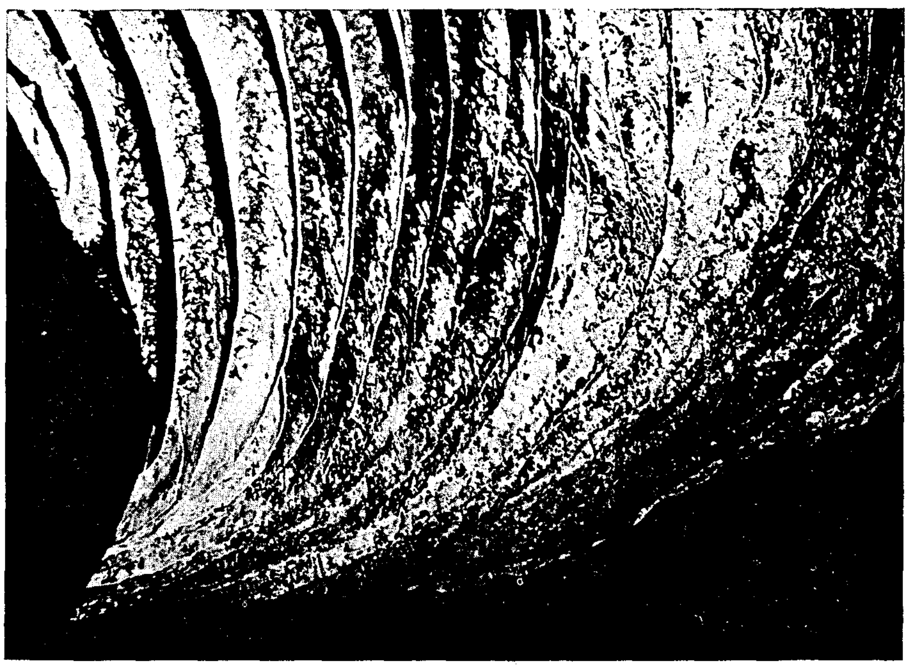

Fig. 3. — View of the spiral plate from below. The mineral deposits on the spirals are clearly visible. The pillar is on the left.

Fig. 3. — Le disque en spirale, vu de dessous. Les dépôts minéraux apparaissent clairement sur les spirales. Le pilier se trouve sur la gauche.

type of nest is very large and at the sides of the pillar wide shafts (up to 20 cm) descend vertically to a depth of 2-3 m (fig. 1). Observations on workers repairing damaged nests suggest that these shafts are used as a source of wet mud. Domed solid earth pillars rising from the floor of the cellar are of unknown function and may have been left behind as the cellar was extended. The entire habitacle is surrounded by an air space traversed by fragile earth bridges leading to the main shafts of the mound and to the slit-like openings of the subterranean foraging galleries, which may extend considerable distances before surfacing. An isolated colony with a 2 m mound was found to have a regular foraging circle of 15 m radius, with occasional further extensions.

Fig. 4. — Close-up of the spiral vanes and part of the pillar. *Macrotermes bellicosus* soldiers and workers show the scale.

Fig. 4. — Détail des languettes en spirale et d'une partie du pilier. Des soldats et des ouvriers de *Macrotermes bellicosus* indiquent l'échelle.

2. Macrotermes bellicosus nest without a spiral base-plate

The structure of this nest is essentially identical to the conventional nests described by Grassé and Noirot (1961) from the Ivory Coast, except that at Mokwa the habitacle is entirely below ground level (fig. 2). The mound may reach 2-3 m high and is rounded, without distinct flutings or spires. The mound shafts are smaller and more reticulated and the spiral vane and supporting pillar are absent. The habitacle is supported on conical projections, up to 15 cm long, which extend from the underside of the base-plate and rest with the points on the cellar floor.

DISCUSSION

Physical and chemical examination of the soils surrounding three mounds of each type revealed no significant local variations in percentage of sand, clay, nitrogen or organic carbon. The nests themselves were composed mainly of clay-rich sub-soil and were similar in both nest types but with a marginally higher sand fraction in components of the conventional nests (type 2 above). In addition, examination of the soldiers and workers of each nest type showed no clear morphological characteristics to distinguish them. The differences in nest type might arise from sibling species or some as yet unrecognised environmental factor.

The precise function of the extraordinarily complex spiral plate is a matter for conjecture. Temperature measurements in five spiral plate nests gave a very stable series of mean temperatures ranging from 30.67-31.22°C and the spiral plate itself may be a specialised response to the microclimatic requirements of the colonies. The layers of mineral salts on the spiral vanes indicate that their high surface area promotes evaporation (and therefore cooling) from the underside of the base-plate. The maintenance of nest temperatures near 30°C is of advantage in facilitating both larval development (MUKERJI, 1970) and the growth of *Termitomyces* on the fungus combs (M.J. SWIFT and R.J. THOMAS, pers. comm.). No temperature studies were done on plateless nests so temperature stability and levels cannot be compared. However, it was noted that the spiral plate colonies developed mounds and populations significantly larger than plate-less colonies (COLLINS, 1977 C), an observation that may be related to the significance of the plate.

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