// RECORDS

of the

INDIAN MUSEUM

(A Journal of Indian Zoology)

Vol. 58, Parts 3 & 4 September-December, 1960 Pages 131-222

CONTENTS

BIOLOGY AND ECOLOGY OF ORIENTAL TERMITES. NO. 5. MOUND-STRUCTURE, NEST AND MOISTURE-CONTENT OF FUNGUS COMBS IN *ODONTOTERMES OBESUS*, WITH A DISCUSSION ON THE ASSOCIATION OF FUNGI WITH TERMITES

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(With 1 Table, 2 Text-figures, and 4 Plates)

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* Earlier numbers of this series are as follows :—

No. 1. *J. Bombay nat. Hist. Soc.*, Bombay, 1954, **52** (2 & 3), pp. 459-452, 1 pl.
No. 2. *Ibid.*, 1954, **52** (2 & 3), pp. 463-467, 1 pl.
No. 3. *Ibid.*, 1955, **53** (2), pp. 234-239, 2 pls.
No. 4. *Ibid.*, 1959, **56** (3), pp. 511-523. 3 pls.

I—INTRODUCTION

Although *Odontotermes obesus* (Rambur) (Isoptera : Termitidae : Macrotermitinae) is the principal mound-building termite of India, there is some lack of clarity about the structure of its mound. This difficulty arises from a confusion, or rather a lack of adequate information, about its taxonomy. In India only a few species build mounds, and all of them seem to be confined to the genus *Odontotermes*—the mound-building species being *bangalorensis* Holmgren, *obesus* Rambur (and its supposed varieties), *redemanni* Wasmann and *wallonensis* Wasmann. Annandale (1923, 1924) has classified these mounds into two types, *viz.*, (i) the *unilocular* type in which there is single large central cavity containing a large fungus comb ; and (ii) the *multilocular* type in which there are several cavities each containing a fungus comb. According to Annandale (1924), the *unilocular* type occurs in *Odontotermes obesus* var. *oculatus* Silvestri, while the multilocular type occurs in the typical form of *O. obesus* (Rambur) and in *O. redemanni* (Wasmann).

There appear to be the following known forms of *Odontotermes obesus* (Rambur) which is a species confined to India :—

(i) *O. obesus* (Rambur) (typical form).—Practically all over India, except in very cold areas.

(ii) *O. obesus*, var. *gurdaspurensis* Holmgren & Holmgren.—Gurdaspur (Punjab).

(iii) *O. obesus*, var. *oculatus* Silvestri.—Barkuda Island (Chilka Lake, Orissa). In this variety the female (queen) is stated by Silvestri (1923) to have larger eyes than in the typical form, but the soldiers and workers are indistinguishable from that form.

If we accept Annandale's descriptions (1923, 1924) of the mounds of *O. obesus* (identifications of the termites were done for him by the late Professor F. Silvestri, the well-known Italian entomologist and an authority on termites), this single species, has at least three widely divergent types of mounds as follows :—

(i) A large, "unilocular" type, with buttresses. Occurring in *O. obesus* var. *oculatus* Silvestri, on the Barkuda Island (Chilka Lake, Orissa), (*vide* Annandale, 1923, p. 246, Fig. 1 ; and 1924, p. 31, Fig. 4).

(ii) A large, sprawling, "multilocular" type, without buttresses. Occurring in *O. obesus* (Rambur) *forma typica*, also on the Barkuda Is. (Chilka Lake), (*vide* Annandale, 1923, p. 247, Fig. 2). Also found in *O. redemanni* Wasm. in West Bengal, southern India and Ceylon (*vide* Escherich, 1911 ; Annandale, 1924, p. 30, Fig. 30 ; Mukerji & Mitra, 1949 ; and others).

(iii) A comparatively small (about 90 cm. high and 90 cm. in basal diameter), formless mass of earth, nearly solid and with only a few narrow passages. Formed by *O. obesus* occurring in the Andaman Islands (*vide* Annandale, 1924, p. 27). Although the specimens from these mounds were identified by Silvestri simply as "*Odontotermes obesus*", Annandale (1924, p. 27, foot-note) remarked : "Possibly males and females of the Andaman form would show some racial peculiarity"

The mounds of *O. obesus gurdaspurensis* Holmg. & Holmg., from the Punjab have not been described.

It seems to me highly unlikely that the various forms of the same species (which can hardly be distinguished from one another) and some times occur in the same locality, as in the Barkuda Island, build such radically different types of mounds. I cannot help suspecting that these forms might be distinct species, but a clarification of this point must await a future careful taxonomic study, correlated with field work, of the Indian species of the genus *Odontotermes*.

Meanwhile, I have studied in some detail the mound-structure, the nest, the fungus combs, etc., of the "form" of *Odontotermes obesus* as occurring in Dehra Dun and its vicinity in western Uttar Pradesh, and these observations are discussed below. For the reasons stated above, the locale of the "material" has been described below in detail so as to enable comparisons to be made in the future.

Observations on the mound, nest, fungus combs and the related fungi of *O. obesus* have been made by Lefroy (1909), Annandale (1923, 1924), Bose (1923), Beeson (1941), and Bakshi (1951), Roonwal & Gupta (1952), Gupta (1953*a*, *b*), Vishnoi (1955*a*) and Roonwal (1958).

In the present account, a description of the mound-structure, particularly of the underground nest, is provided, together with some observations on the structure, distribution and moisture-content of the fungus combs. Fungus combs in termites have been regarded by some authors to serve as "humidity controls" for maintaining a high humidity inside the nest. In view of this opinion, the moisture-content of the combs has been determined. Finally, a brief account is given of the nature of the association of fungi with termites in general, and the function of the associated fungi and the fungus combs.

II—MATERIAL

For the reasons stated below, the provenance of the material studied is indicated precisely.

The material on which the present account is based is from the Dehra Dun and Saharanpur districts of Uttar Pradesh (India), especially from Dehra Dun and its vicinity. These districts lie at the foot-hill of the western Himalayas in western Uttar Pradesh. As already discussed above, the exact taxonomic differentiation of the various species of the termite genus *Odontotermes* and their correlation with the various types of mounds is still a desideratum. The principal species involved in the building of these mounds in India appear to be four as follows :—

O. bangalorensis Holmgren, *O. obesus* (Rambur) and its supposed varieties, *O. redemanni* (Wasmann) and *O. wallonensis* (Wasmann).

Of these, *O. obesus* builds high mounds going up to about 2·6 metres (about 9 ft.) or a little more in height and are characterised by a series of buttresses all around (Pls. 8 and 9). Such mounds occur practically all over northern India except Kashmir, the Punjab, Rajasthan and West Bengal. I have seen such mounds abundantly in the deciduous and moist deciduous forests of Uttar Pradesh (Districts of Dehra Dun, Gorakhpur, etc.), Himachal Pradesh (*sal* or *Shorea robusta* forests adjoining the western Uttar Pradesh), Bihar (Ranchi), Orissa (Cuttack and Bhuwaneshwar).

The species concerned, as obtained from the material from Uttar Pradesh, is indistinguishable from *Odontotermes obesus* (Rambur) whose type-locality is the Bombay Presidency (India) and as such the material in the present paper is regarded as *O. obesus*. Whether the species forming the tall buttressed mounds in the other areas mentioned above is identical is not known with certainty and the solution of this problem must await further detailed field and taxonomic study.

The other type of mound generally found is one which is dome-shaped, of low height, and without buttresses. Such mounds occur all over India and may belong to *Odontotermes bangalorensis*, *O. redemanni*, *O. wallonensis* and possibly to other as yet unrecognised species and varieties of the genus *Odontotermes*.

III—STRUCTURE OF TERMITARIUM (MOUND AND NEST) OF *ODONTOTERMES OBESUS*

(Text-figs. 1 and 2 ; and Pls. 8-11)

1. *General*

It may be stated at once that the termitaria of *Odontotermes obesus* to be described here are of the "unilocular" and buttressed type of Annandale (1923, 1924) which that author has assigned to *O. obesus* var. *oculatus* Silvestri. I, however, seriously doubt this identification, and would assign them for the present merely to *Odontotermes obesus*, leaving for future consideration whether the Dehra Dun mounds, on which the present description is based, belong to the typical form of *O. obesus* or to some other race. Generally, Beeson (1941) and other entomologists have regarded the Dehra Dun species as *O. obesus*, and for the present I agree with that view. It is highly unlikely that in the same place more than one form or subspecies of a particular species would occur— as would be the case if we accept Annandale's observations on the Barkuda Island.

In the Dehra Dun form studied by me the entire colony of *Odontotermes obesus* is concentrated, except for the foraging galleries, in a single earthen *termitarium**—by which term we may conveniently include both the mound (above the ground) and the nest (underground). Depending upon the size of the mound, its population consists of about 4,500—90,900 individuals and is composed of soldiers (5·5—7·7 per cent), workers (49·0—66·5 per cent), nymphs (28·0—43·3 per cent), and, of course, the royal pair (one king and one queen) (Gupta, 1953*a*). Exceptionally, two kings and two queens are found in the royal cell or chamber (Roonwal & Gupta, 1952).

The termitarium is divisible into two parts : (i) the "mound", or the portion above the ground ; and (ii) the "nest" or the portion below the ground. The size and shape of the two portions are similar, and may be compared to two tumblers lying one over the other, mouth to mouth (Text-fig. 2 ; and Pls. 8 and 9).

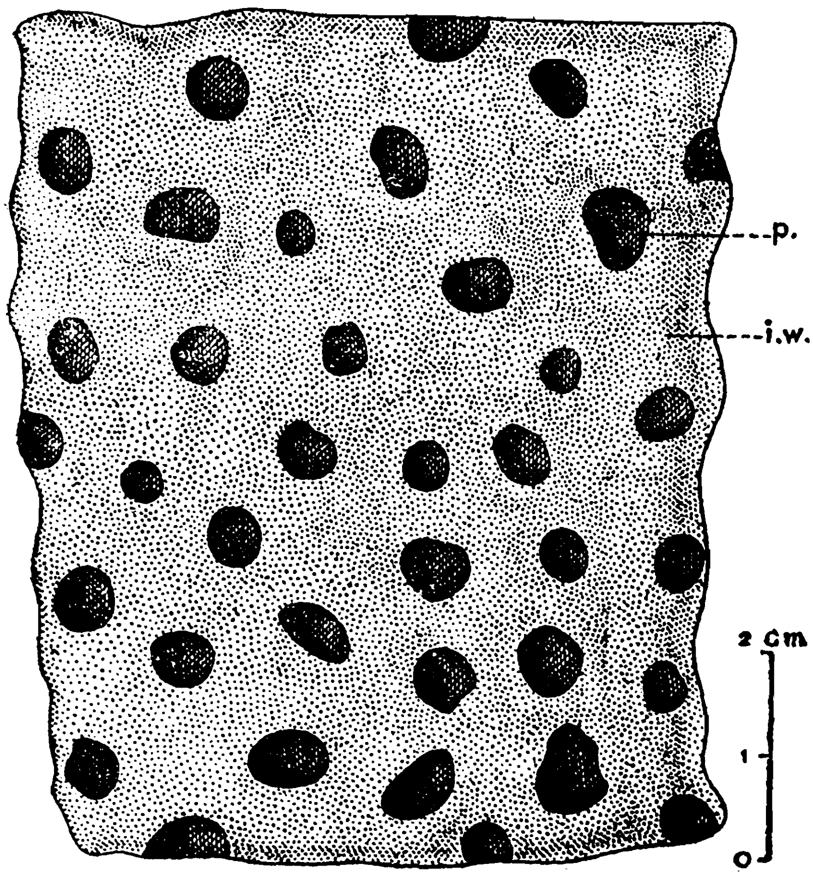
* Snyder (1948, p. 247) has defined the termitarium as follows : "TERMITARIUM a nest, natural or artificial, or a colony of termites."

2. *The mound-structure*

The mound is made of hard earth cemented together by the termite workers with the help of their saliva. Its colour generally depends upon the colour of the available earth. Thus, in Dehra Dun it is dirty or greyish brown, while in Ranchi (Bihar) it is reddish.

The mound (Pls. 8-10) is a subcylindrical structure, but wider at the base than at the top. When well developed, it may be as much as about 3 metres (*ca.* 10 feet) high and about 1·5 metres (*ca.* 5 feet) in diameter at the base (ground-level). The walls are thick and externally fluted to form a series of about 10-12 hollow buttresses running vertically the entire length of the mound.

When sectioned vertically it is seen to contain usually a wide central shaft (this is sometimes confined to the nest only, *vide* below) which, however, does *not* open to the outside, and a series of irregular chambers and cavities of varying sizes and shapes. The inside wall of these cavities is pitted with numerous small cup-like pits about 5-7 mm. in diameter (Text-fig. 1)*. There are normally no external openings on the mound-



TEXT-FIG. 1.—*Odontotermes obesus* (Rambur). Inner view of a portion of the wall of a mound, to show the pits.
i.w., inside of wall of mound *p.*, pits.

surface (except those caused accidentally through external agencies such as cracking of the wall by excessive drying, or damage by human or other enemies), and it is likely that the termites forage largely through

* According to Annandale (1923, Pl. Fig. 3 ; and 1924, pp. 32-33) these pits are "sentry boxes" in each of which a soldier is stationed at the time of the construction of the wall.

underground galleries, though once they reach the food-object above the ground, such as the bark of a tree, they may make earthen covers or plasters for their movements to and fro. No fungus combs are, as a rule, present in the portion of the mound above the ground.

3. *The nest and the royal cell*

(Text-fig. 2 ; and Pls. 9 and 10)

(a) *General*

The underground nest is usually about as deep below the ground surface as the mound above, and, like the latter, is subcylindrical. Unlike the mound, however, it has no discrete walls, but is merely composed of a central hollow, together with a number large fungus combs, and around them are arranged, irregularly, a number of smaller excavations and tunnels—the former for the lodgement either of one or more fungus combs of varying sizes or of egg-masses, and the latter for the movement of the more active members of the colony.

(b) *The royal cell*

The royal cell usually lies in the nest either at or below (from 0—100 cm.) the ground surface and is generally excentric. Normally it contains a dealated king and a dealated queen, but occasionally (in one out of about 100 cases examined) the royal pair in a cell is duplicated (Roonwal & Gupta, 1952).

A well developed royal cell, containing a large physogastric queen (*i.e.*, a queen in which the abdomen is greatly distended to make room for the large number of eggs produced), is a solid, flat, earthy structure, usually of dark grey colour, and shaped like two irregularly-shaped saucers closed over each other face to face. The outer surface has numerous irregular excrescences, but the inside is smooth and is spindle-shaped in cross-section. (For an illustration *vide* Roonwal & Gupta, 1952, Pl. 1.) A well developed normal royal cell (with one king and one queen) measures about 6—8 cm. in length, 5—6 cm. in width and 2—2·5 cm. in height. The abnormal royal cell described by Roonwal & Gupta (1952), which had two kings and two queens, measured 10 cm. in length, 7·5 cm. in width and 2·6 cm. in height. Tiny round holes about 3—5 mm. in diameter lead from the outside of the royal cell to the royal chamber. These holes are just large enough for the soldiers and workers to pass through and attend upon the royal pair, but are too small for the royal pair itself to creep through—the king has a length (excluding the antennae) of about 10-13 mm. and a maximum width (in the abdominal region) of about 3-4 mm., while an old, well-grown physogastric queen has a length (excluding the antennae) of about 50-75 mm. and a maximum width (in the abdominal region) of about 10-12 mm. The size (length) of the queen is generally directly related to the size of the mound—the larger the mound, the longer the queen (Gupta, 1953*b*). This is evidently an age relationship, as both the mound and the queen grow in size with age.

The inside of the royal chamber was always found scrupulously clean and never was even a speck of food, dirt or refuse met with. A large number of soldiers and workers are found in attendance upon the royal pair.

When the royal chamber is opened, the king usually runs about quite actively, but the queen, because of the weight of its heavy egg-laden abdomen, is hardly able to move. The abdomen of the queen shows regular peristaltic movements from before backwards, and with these movements it extrudes, one by one, a tiny, cylindrical, whitish translucent egg from the hind end of the abdomen at the rate of about one egg per second. (At this rate it would extrude about 3,600 eggs per hour or about 86,400 eggs per day (24 hours). No sooner is an egg extruded, than one of the workers-in-waiting picks it up in its mouth and carries it away presumably to one of the egg-depositories (*vide infra*).

There is some evidence that occasionally, due to causes still unknown, the old royal cell is deserted and, adjoining them, a new royal cell is formed where the royal pair is transferred presumably by the workers. This suggestion received support from the discovery (Gupta, 1953*b*) of deserted royal cells in *Odontotermes obesus*, and the finding by Vishnoi (1955*a*) of very large holes (about 15 mm. wide) in the royal cell through which, according to that author's presumption, the queen is transported to a new royal cell by other members of the colony.

The question whether the royal cell and the queen lie in a particular direction of the compass has been somewhat controversial. Deoras (1944) stated that in the mound-forming termite (species not mentioned, but probably *Odontotermes redemanni* Wasm.) in peninsular India (?. Poona), "the 'queen' invariably lies nearly parallel to the magnetie N. and S. in her cell which is N.-E. or in a very few cases S.-W. of the central point of the 'live' mound". Vishnoi (1955*a*) also stated that in "*Odontotermes obesus* var. *oculatus*", in Dhampur, western Uttar Pradesh, the queen lies in the N.-S. direction in the royal chamber. These claims, however, do not receive support from the detailed work of Gupta (1953*b*) on *O. obesus* in Dehra Dun, who showed that neither the royal cell nor the queen lie in any particular favoured position.

(c) *The egg-depositories and nurseries*

As mentioned above, there are in the nest small rounded excavations of varying sizes (diameter about 4-12 cm. or more). These vaults are flat below and have a dome-shaped roof, and the walls and the ceiling are smooth. Here one finds either fungus combs (one, or sometimes two or three, in each vault) or masses of eggs heaped together in groups of thousands. In a single nest, up to half a dozen such egg-depositories are found. Egg masses are also found inside the cells of some of the fungus combs.

Also in the fungus combs, and sometimes in the vaults serving as egg-depositories, are found numerous tiny nymphs along with a number of workers and a few soldiers. According to the observations of Gupta

(1953*a*), the proportion of nymphs is higher, and of soldiers lower, in the fungus combs than elsewhere in the nest, thus :

	Percentage of various castes		
	Workers	Soldiers	Nymphs
1. N FUNGUS COMBS :	17·8	2·8	79·4
2. ELSEWHERE IN MOUND :			
(i) In non-mound building months	49·0	7·7	43·3
(ii) In mound-building months .	66·5	5·5	28·0

IV—FUNGUS COMBS OF *ODONTOTERMES OBESUS*

(Text-fig. 2 ; and Pls. 8-10)

1. *General observations*

As mentioned above, a well developed nest of *Odontotermes obesus* usually contains a large number (about 20-30) fungus combs of varying sizes. The peripheral combs are generally smaller than those situated more centrally. Except perhaps initially in the young colony, there is no large central comb as occurs in *O. obesus* var. *oculatus* Silvestri (*vide* below, Annandale, 1923) or as in *O. redemanni* (Wasmann). The combs lie in shelf-like excavations or vaults made by the termite. All the fungal combs lie, as a rule, wholly below the ground surface, except in rare cases when a small portion (about 3 or 4 centimetres high) of the comb-bearing area may lie above the ground surface.

It is noteworthy that the fungus combs are usually found in the "nest" only, *i.e.*, below the ground surface, and not in the "mound" above ground. (This is in contrast to what occurs, according to Annandale (1923, 1924) in *O. obesus*, *forma typica*, and in the allied species, *Odontotermes redemanni* (Wasmann) (Escherich, 1911, and Mukerji and Mitra, 1949) where the combs occur in the mound portion also.

The fungus combs are made by the workers from rounded pellets of excreta. Combs in early stage of formation are shown in Pl. 10, Fig. 3. The individual combs are irregularly rounded spongy masses, coloured greyish-brown with orange or reddish tinge, and vary in size greatly from pieces about 2 cm. or less in diameter to those about 20 cm. or more (Pls. 9 and 10). Each piece usually lies separately in a small earthen rounded excavation in the nest (Pls. 9 and 10).

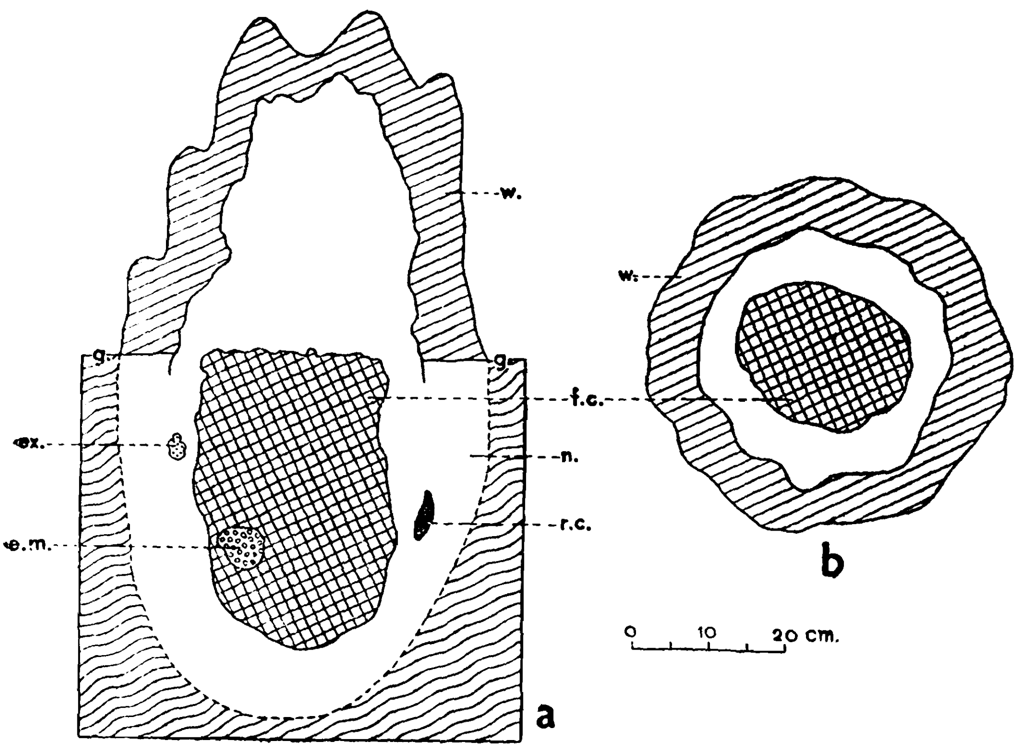
The fungus combs harbour a population of termites consisting of workers, soldiers, nymphs and eggs, the nymphs being more numerous than the others (*vide* above).

The combs also serve as the substratum for the growth of fungal mycelia which throw off numerous tiny translucent white " spheres " (Pl. 11, Fig. 2) which, according to some authors, are eaten by the workers —this question has been discussed in some detail in the next section.

It is noticed that if fungus combs, along with the broken remnants of the nest and colony, are kept in a large closed box, within less than 12 hours the fungal mycelia in the combs throw up long, finger-like, dark-greyish processes of a fungus, which has been identified as *Xylaria nigriceps*, and the entire colony is quickly killed. This "choking" does not happen in the living, flourishing colony in the live nest where the growth of *Xylaria* is, in some unknown manner, prevented.

2. *Development of fungal combs in a young colony*

It would appear that during the development of the mound and the colony, at first a large central fungus comb is formed, and the other smaller ones are formed later as the colony develops. This method is suggested by the study of a small mound of *O. obesus* in a forest near Hardwar (western Uttar Pradesh). The young mound (Text-fig. 2),



TEXT-FIG. 2.—*Odontotermes obesus* (Rambur). A young termitarium, about 45 cm. high, near Hardwar (Uttar Pradesh, India).

(*a*). The termitarium (mound and nest in vertical section). (*b*). Ditto, in cross section, at the ground level.

e.m., egg-mass ; *ex.*, mass of dried excreta ; *f.c.*, fungal comb ; *g.*, ground-level ; *n.*, nest portion of the termitarium : *r.c.*, royal cell ; *w.*, wall of the mound.

which was of the usual unilocular and buttressed type, was about 45 cm. high and had a basal diameter also of about 45 cm. The walls were about 7-8 cm. thick and were smooth outside but heavily pitted on the inside with small circular pits each of which was about 5-6 mm. in diameter. The "nest" was underground and extended about 45 cm. below the mound. There was a single, central, huge, rounded fungus comb, about 22 cm. in diameter and about 38 cm. deep ; it lay almost wholly underground, except for 2-4 cm. of its portion which jutted above the ground surface. The dry weight of the fungal comb (dried at 105°C) was 1,129 gms. The royal cell, containing a king and a queen, lay on one side of the fungal comb and about 20 cm. below the ground surface.

Excentrically, on the side opposite the one where the royal cell was situated and about 20 cm. below the ground surface, there was in the fungus comb a large mass (about 5 cm. ×5 cm.) composed of thousands of tiny eggs—this was the *egg-nursery* of the termite. Innumerable tiny nymphs were also swarming in the " nursery "

In two places in the nest, by the side of the fungal comb, there were small flat masses (each mass measuring about 2·5 cm. ×2·5 cm.) of comparatively dried up excreta (*cf.* fungus combs, which are always moist) assembled in a heap. These were undoubtedly the beginnings of the " fungus combs " which had not yet been innoculated with fungus. Their colour was pale yellowish-brown and the characteristic greyish colour of fungus combs containing active fungus was wanting.

3. *Moisture content of fungus combs*

(Table 1)

The moisture content of the various fungus combs, taken out of a large termitarium in New Forest, near Dehra Dun, in late December was determined (Table 1). Eight samples, composed of a total of 11 different pieces of varying sizes were weighed. Immediately each piece was dug out of the nest it was put in a small air-tight metal box to prevent loss of moisture, and the wet weight was determined in a chemical balance within a few minutes of the collection. The combs were then dried in an air oven at 105°C. until the weight was constant. The wet weight of the individual combs varied from 6·80—343·79 gms., the dry weight from 3·22—164·52 gms. and the moisture-content from 50·4-52·6 per cent (mean 51·63 per cent). This fairly high moisture content would suggest that the combs may serve as a permanent source of moisture for the humidity-conditioning of the nest.

4. *Discussion*

Lefroy (1909, p. 118, Pl. VIII), briefly referred to and illustrated the " fungus chambers " (which are what we today call fungus combs) of *Odontotermes obesus* (his " *Termes obesus* ") probably obtained in Pusa (Bihar). According to him there were large "main" and small " subsidiary chambers ", but their number in each mound was not mentioned. In the illustrations given by him, the "chambers" are subround ; the large one is about 24 cm., and the smallest one about 15 cm., in diameter. The fungus combs of *O. obesus* (Rambur) *forma typica* and *O. obesus* var. *oculatus* Silvestri, both from the Barkuda Island in the Chilka Lake, Orissa, were described and illustrated by Annandale (1923). According to him (p. 240), the combs of *O. obesus* are compact from the first and even when very small have a distinct " cellular " structure. He further wrote : " In the mounds of *O. obesus* typicus there is no single large fungus garden, but there are many (sometimes as many as twenty or thirty) small gardens. The largest chambers are rarely more than 9-10 cm. in diameter and the gardens in them a few centimetres less, but both vary considerably in size." The internal cells of the fungus comb are regular, transverse (not vertical) and comparatively uniform, the

TABLE 1.—Odontotermes obesus (*Rambur*). *Weight, and moisture-content, etc., of fungus combs collected from a large mound in New Forest, near Dehra Dun, in December.*

Sample No.	Number of pieces	Approximate size (in cm.) after drying	Wet weight (in gms.)	Dry weight (in gms.)	Loss of weight (=water-content) (in gms.)	Percentage of weter-content
1	1	5×5×9	55·20	26·14	29·06	52·6
2	2	4×8×12 ; 3×8×10	125·20	62·13	63·07	50·4
3	3	4×13×15 ; 4×10×14 ; 4×6×6	343·79	164·52	179·27	52·1
4	1	4×7×9	47·24	22·47	24·77	52·4
5	1	4×7×7	25·76	12·62	13·14	51·0
6	1	5×7×8	51·59	25·40	26·19	50·8
7	1	4×7×8	56·37	27·87	28·50	50·6
8	1	3×3×4	6·80	3·22	3·58	52·6
	11	RANGE :	6·80—343·79	3·22—164·52	3·58—179·27	50·4—52.6%
						MEAN : 51·63%

size of each cell being about 6-15 mm. ×3-5 mm. The combs are similar to those of *O. redemanni* (Petch, 1906).

In *O. obesus* var. *oculatus*, on the other hand, the fungus gardens, according to Annandale (1923), are extremely massive and have a capacity of many litres. " The whole basal part of the mound is occupied by a single large garden, incompletely divided by partitions that hang from the roof or rise from the floor of the large garden-chamber like stalagtites and stalagmites in a cave, the garden nearly fills the chamber, of which it is practically a cast. Sometimes there are two or more tiers of comb " (p. 239). According to the same author, there is a considerable difference in the internal structure of the older and younger parts of the comb. The younger parts, which are situated near the periphery of the mass have the external surface covered with irregular grooves and small circular apertures leading into internal cells or cavities but mostly orientated with their major axis at right angles to that of the whole mass. Superficially the older parts look like the younger ones, but in a section it is seen that the internal cells in the older parts are more vertical and more regular in shape and size (average : 12 mm. high and 5 mm. broad).

Annandale (1923) noted, on the Barkuda Island (Orissa), that the fungus combs of *O. obesus* were shifted from one part of the nest to another, depending upon the season. He noted (p. 241) that in mounds opened in February " the upper garden-chambers which are situated well above ground, will be found to be empty ", but in April or May, " all the garden-chambers in the mound are empty. In both months the interior of the empty chambers is perfectly clean, and no trace of the gardens can be discovered " Annandale concluded that in the dry season, and especially when the weather is hot as well as dry, the workers remove the gardens bodily underground. He gave two reasons for this removal, namely, (i) the impossibility of maintaining the correct temperature and moisture for the growth of the fungi above ground in hot and dry weather ; and (ii) the danger to the community if the upper parts of the nest are occupied too near the surface at such times.

Bose (1923) identified the fungus occurring in the mound of *O. obesus* on the Barkuda Island as an agaric, *Collybia albuminosa* (Berk.) Petch, and stated that different forms of another fungus, *Xylaria nigriceps*, were found in mounds abandoned by the termite colony. Bakshi (1951) has re-studied the fungi occurring in mounds of this species in Dehra Dun (U.P.) and his conclusions, as summarised by Roonwal (1958, p. 87) are as follows :—

" Mycelia and spheres are common within fungus combs. Hyphae are abundant, cottony, thin-walled (or slightly thick-walled), hyaline, separate (simple), and 2-5μ broad. Chalamydospores develop rarely, and when present are about 11-13×8-9μ in size. Some of these hyphae unite to form small whitish spheres which are 0·5—0·8 mm. in diameter when mature, and have been identified as *Termitosphaeria duthei* Berkeley belonging to the Moniliales. Such a sphere is composed of a short stalk which swells up into a head, the latter becoming spherical with age. The spheres can be cultured easily in malt-agar. Stoma of *Xylaria nigriceps* were sometimes found on the surface of deserted combs."

V.—DISCUSSION ON THE ASSOCIATION OF FUNGI WITH TERMITES

1. *Historical*

Observations on the "fungus combs" of termites of the Indian region, including Ceylon, have been made by a number of workers, *viz.*, König (1779), Petch (1906-13), Lefroy (1909), Bugnion (1914), Hegh (1922), Annandale (1923-24), Bose (1923), Beeson (1941), Mukerji & Raychaudhuri (1943), Mukerji & Mitra (1949), Bakshi (1951) and Roonwal (1958).

The pioneer observations of König (1779) deserve more than passing attention. He was the first to give an account of the fungus combs of a termite, and his was, in fact, the first scientific account of any aspect of termites ever to be published. He described the mound and fungus combs of an unnamed species, probably *Odontotermes redemanni* (Wasm.), of a southern Indian mound-building termite in Tanjore. He regarded these combs as the "dwellings" of the termite, and wrote as follows (Fletcher's translation, 1921) :—

"Their dwellings [*i.e.*, the fungus combs] have, as stated, the shape of the vault [in which they are placed] except that they are separated everywhere from the inside wall by a small interval ; also on the bottom there is not to be found the slightest trace that they are made firm somehow or other by an adhesive substance or by any other means."

And further :

"They consist of innumerable intercommunicating passages, which are their cells, whereto most entrances enter from below, a few from above and fewest vertically."

König also noticed the fungal conidia growing in these combs, and further thought that they might be the food for newly-patched young ones. He wrote :

"... I must mention a small plant which grows tolerably abundantly and invariably inside the walls of the cells [of the fungus combs]. According to Sir C. von Linné it will be a Mucor and is situated on a stalk bearing rounded composite snow-white bodies [=conidia]. It is very small and has quite a short stalk on which, as its fruit-part, the small head is to be found and this latter is composed of very minute globules and is of snow-white colour. Here and there also, as if strewn, on the afore-said walls there occur small, bent, white filaments which terminate sometimes in a small head, and sometimes are club-shaped."

And further :

"May not a wise Providence have ordained these minute plants to grow here, perhaps for the immediate nourishment of the newly hatched animals, whilst otherwise no nourishment is present in the nest nor can any foraging be done. This I only suppose : I have not observed it, because these young animals are all at once very feeble so soon as they come out of the ground into the open air and into daylight."

König also noticed that in these combs were abundantly present the young ones and eggs of the termite, and that some of the combs were full of eggs. He wrote :

"The eggs are usually cylindrical, rounded at both ends, small, smooth, shining, milk-white, somewhat transparent withal, on one side rather more opaque. They were slightly fastened together one upon another, without order, on the walls in the interior of the combs ; some of the large combs were filled out with them, their number was very large at this time of the year. By which of these animals they have been brought there (*i.e.*, into the combs) and how, I have not been able to observe.

2. *Nature of the association of fungi with termites*

As stated above, the association of fungi with termites has been known for a long time, and was first noticed by König (1779) in the southern Indian mound-building termite—species not mentioned, but probably *Odontotermes redemanni* (Wasmann). The main form in which this association occurs is the cultivation of "fungus gardens" by the higher termites (Termitidae) in their nests. These fungus gardens usually take the shape of irregular, spongy masses of varying sizes and shapes constructed by the termites themselves and believed to be composed of their excreta. On these masses or "fungus combs", which are usually lodged in shelves or other places inside the termitaria, the termites cultivate fungi which are, by some unknown means, prevented by the termites from fruiting. Tiny whitish spheres or conidia, which almost appear to be sessile but actually have a tiny stalk, are, however, formed fairly abundantly, and the termites have been observed to sometimes feed up on them. Removal of these combs from the nest, and the consequent discontinuance of their connection with live termites in the colony do away with the "control" which the termites exercise on fungal growth in some unknown manner, and within a few hours, or a day or so, under favourable conditions of high humidity and high temperature, the fungi grow long, cylindrical, fruiting bodies of a species of *Xylaria* which are often 20-30 cm. long. According to some authors, these *Xylaria* are weeds which come up only when the colony dies, and the original fungus of the combs is a different species. (In this connection the accounts of Doflein (1905-06), Petch (1906-13), Escherich (1909-11), Bugnion (1914), Hegh (1922), Annandale (1923-24), Bathellier (1927), Grassé (1937-59), Grassé & Heim (1950), Grassé & Noirot (1948-58), Ghidini (1938) and Geyer (1951) may be consulted.)

In rare cases, as in the African termite, *Sphaerotermes sphaerothrax* (Sjöstedt), the so-called "fungus combs" are present but they are without fungi (Grassé & Noirot, 1949).

Another form of association of fungi with termites is that which occurs in many of the wood-inhabiting species, such as for example members of the genera *Kalotermes*, *Reticulitermes*, *Zootermopsis*, *Gnathotermes*, etc. Here no "fungal gardens" are cultivated, but several species of fungi occur in the nests and galleries of the termites. Thus, Hendee (1946) isloated representatives of 33 different genera of fungi from colonies of termites of the genera *Kalotermes*, *Reticulitermes* and *Zootermopsis* in the United States, but found no evidence of any specific relationship between a given species of termite and any genus of the fungi ; the significance of the fungi remained problematic.

3. *Functions of fungi associated with termites.*

The "fungus gardens" in termite nests have been variously regarded as a possible source of food (König, 1779; Petch, 1906-13; Annandale, 1923) and of vitamins (Grassé, 1949), as maintaining the high humidity in termite nests (Ghidini, 1938; Lüscher, 1951), as producing heat and thus maintaining the high temperatures inside mounds (Geyer, 1951 ; Lüscher, 1951), and as egg-depositories and nurseries (König, 1779 ; Annandale, 1924 ; Mukerji & Raychaudhuri, 1943). In the case of the wood-inhabiting species, the fungi may be useful in breaking down the wood into components which are easily digestible by the termites (Snyder, 1948 ; Grassé, 1959). The more important relevant details may now be discussed.

Direct observations that the fungal conidia are actually eaten by the termites are wanting (except for the rare observation of Lüscher, 1951, *vide* below), and the belief that they serve as food is conjectural. Thus, Annandale (1923, p. 242) wrote about *Odontotermes obesus* as follows :—

> " The royal chamber is apart [from the fungus gardens] and if the adult males and females feed on fungus-products, they must be brought them by the workers. The eggs, however, are carried by the workers to the gardens, in which both they and the young are often found in large numbers, and I have little doubt that the young eat the food-bodies there produced. Possibly the workers and soldiers do so in times of stress, but in damp weather they make long excursions outside the nest to feed on dead wood, dead leaves and other dead organic matter."

Grassé (1945) observed in African termites that though the conidia on the " fungal combs " are sometimes eaten by the workers and are found in the alimentary canal, they cannot be of any great significance as a source of food. He further suggested that they may serve as a source of vitamins (1949). Lüscher (1951) observed in artificial nests of the termite *Synacanthotermes zanzibarensis* Sjöstedt that, except on two occasions, the termites never attacked or ate the fungal conidia. He wrote (pp. 34-35), thus :

> " We may conclude that the conidia are immune for a long period ; but that they are sometimes suddenly attacked and then eaten completely within a very short time [within about 20 minutes], probably after having reached a certain degree of ripeness. This may explain why the actual process of devouring the conidia has never been observed previously, and also why partly destroyed conidia are never found in the ' fungus garden. They are attacked so rarely that they can scarcely play a large part in the nutrition of the termites, though they may possibly serve as a source of vitamins, as Grassè has supposed[5].
>
> [[5]Grassè, P.-P. " Traite de Zoologie ", **9** (Masson, Paris, 1949).]"

Lüscher (1951) has suggested, from field observations on *Macrotermes bellicosus* Smeathman in Africa, that the fungus gardens generate heat, probably by means of fermentation processes going on in them, and thus serve to raise the nest temperature in the region of these gardens ; here the temperature remains constant at about 30°-30·5°C. as contrasted with an appreciably lower and fluctuating temperature in the more superficial wall-layers (*ca.* 27°-29°C.). They also serve to raise the relative humidity which was about 85 per cent in the wall, and 95 per cent in the ' fungus garden ' area.

König (1779) found some of the large combs of a southern Indian mound-building species, probably *Odontotermes redemanni* (Wasm.), full of egg-masses, and Escherich (1911, p. 41) confirmed this observation in *Odontotermes redemanni* (Wasm.) in Ceylon. Escherisch found masses of a large number of eggs either inside the cells of the fungus combs, on their surfaces or between the two adjoining fungus combs. The number of eggs in a mound was estimated by Escherich as several hundred thousand—a single fungus comb, with a surface area of 250 sq. cm. might contain as many as 300,000 to 350,000 eggs. Mukerji & Raychaudhuri (1943) noted in that same species (in West Bengal, India) that the smaller fungus combs in the mound serve as " nurseries since the larvae or immature forms occur there along with the mature or adult soldiers and workers" (p. 175). In addition, these latter authors noted another kind of fungus comb which contains only eggs, and thus serves as an "egg-depository" They wrote (p. 175) :

> "Quite different from this type of combs or the fungus gardens there is another comb which is exceedingly moist and is dark brown in colour and papery in texture. It is of a different pattern from the rest and is the largest in size. It is located deep down in the centre of the mound. In this comb, eggs alone, but no larvae or other stages, are found. Close to this, but quite separate from it, the royal chamber is situated."

Mukerji & Mitra (1949) further noted in the same species that, because of its close proximity to the royal chamber, eggs laid by the queen are first stored in the large central fungus comb mentioned above and then transferred to the neighbouring combs.

As stated above, in rare cases, as in *Sphaerotermes sphaerothorax* "fungus combs" are present but are without fungi (Grassé & Noirot 1949).

In the case of certain wood-feeding genera (*vide supra*). there is some evidence that the fungi present in the nest and the galleries break down the cellulose and lignin of the wood into easily digestible components. For the North American genus *Amitermes* (*Gnathamitermes*), Snyder, (1948, p. 100) stated as follows :—

> "Since species of *Gnathamitermes* do not contain the usual symbiotic intestinal protozoa, either fungi alter the vegetation so as to make it available to them as food, or the fungi themselves are important in the diet of the termites. These termites will also cover wood with similar earth mats and eat off or scour the surface, but never bore into or destroy wood ; they merely erode the surface."

Grassé (1959) has brought forth evidence that the fungi serve to break down cellulose and lignin. He has further shown that the termites of the subfamily Macrotermitinae present a case of double symbiosis which is unique in the animal kingdom—first, symbiosis wlth a fungus, and secondly, symbiosis with bacteria. Both these methods help the termites to digest wood.

VI—SUMMARY

1. Results of observations, as made in the region of western Uttar Pradesh (Dehra Dun and Saharanpur Districts), are given on the structure of the termitarium (mound and nest) and fungus combs of the termite *Odontotermes obesus* Rambur (Isoptera : Termitidae : Macrotermitinae).

2. The "termitarium", which contains the entire colony, is composed of two parts of subequal diamensions—the earthen "mound" above the ground and the "nest" below the ground. In shape these two parts may be compared to a pair of tumblers touching each other mouth to mouth.

3. The mound is a high, subcylindrical, thick-walled earthen structure, narrowing somewhat at the top, and rising up to about 3 metres (10 ft.) in height, and is further characterised by a ring of about 10-12 vertical buttresses running the entire length of the mound. The inside of the mound has a wide central shaft and a number of galleries and excavations.

4. The nest lies immediately below the mound and is similarly shaped, but in reverse. It does not have any discrete walls, but consists of a series of large to small chambers (or vaults) and galleries—the former for the lodgement of fungus combs and egg-masses, etc. (egg-depositories and nurseries) and the latter for the passage of the active members of the colony.

5. The queen lays eggs at the rate of about one per second. No sooner is an egg extruded than one of the workers-in-attendance picks it up in its mouth and carries it away, presumably to one of the egg-depositories.

6. There is generally a large central fungus comb and numerous smaller ones. They have on their walls numerous tiny, white spheres or conidia of fungi.

7. The fungus combs contain about 50·4 - 52·6 per cent. (mean 51·63 per cent.) water. Dried fungus combs may weigh from about 3 to 1129 gms., depending upon their size.

8. The development of fungus combs in a young colony was observed.

9. The association and function of fungus combs and fungi with termites in general is discussed.

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