# The termites of the Savanna Ecosystem Project study area, Nylsvley

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## PREFACE

The Savanna Ecosystem Project of the National Programme for Environmental Sciences is one of several national scientific programmes administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1970 by ICSU (International Council of Scientific Unions) to act as a focus of non-governmental international scientific effort in the environmental field.

The Savanna Ecosystem Project being carried out at Nylsvley is a joint undertaking of more than fifty scientists from the Department of Agriculture, the Transvaal Provincial Administration, the CSIR, the Transvaal Museum and eight universities. As far as possible, participating laboratories finance their own research within the project. The shared facilities at the study area and the research of participating universities and museums are financed from a central fund administered by the National Committee for Environmental Sciences and contributed largely by the Department of Environment Affairs.

The research programme of the Savanna Ecosystem Project has been divided into three phases - Phase I (mid 1974 to mid 1976) - a pilot study of the Nylsvley study area, in particular the description and quantification of structural features of the ecosystem, Phase II (mid 1976 to 1979) - studies in the key components and processes including the development of mathematical models, and Phase III (1979 to 1984) - extension to other sites and the study of management strategies for the optimal use of Burkea savanna ecosystems.

The present report forms part of the description and quantification of the structural features of the ecosystem, namely a study of the distribution, abundance, food preferences and impact of termites (Isoptera) in the ecosystem.

## ACKNOWLEDGEMENTS

I am very grateful to Dr J E Ruelle of the Department of Agriculture, Pretoria, and to Dr S Bacchus of the British Museum (Natural History), London, for their identifications of the termites collected at Nylsvley. I also thank the staff of the Moss Herbarium, University of the Witwatersrand, especially Mrs J Munday, for allowing me to use their special photomicrographic equipment to take the pictures of the termite heads.

ABSTRACT

This report describes the termite fauna of the Savanna Ecosystem Project study area at the Nylsvley Nature Reserve, with an illustrated key for identification of species. Twenty-one species of fifteen genera and two families are recorded, and notes on their biology are given. Most of the species occur in the flatter areas of *Burkea* savanna; three are restricted to open land near the turfvlei. The broad-leaved woodland of Maroelakop lacks two species but has two others restricted to it; *Acacia* patches (including sites of former human settlement) have a much reduced variety of species. The faunal composition is broadly similar to that of west African savannas, but a little impoverished. Main deficiencies are in a variety of Macrotermitinae and *Trinervitermes*; Termitinae are broadly comparable.

SAMEVATTING

Hierdie verslag beskryf die termietfauna van die studie-area van die Savanne-ekosisteemprojek in die Nylsvley Natuurreservaat, met 'n geïllustreerde sleutel vir die identifikasie van spesies. Een-en-twintig spesies van vyftien genera en twee families word aangegee asook aantekeninge oor hul biologie. Meeste van die spesies kom in die gelyke dele van die *Burkea* savanne voor; drie is beperk tot oop veld naby die turfvlei. Die breëblaar bosveld van Maroelakop kort twee spesies maar twee ander is daartoe beperk; *Acacia* gedeeltes (insluitende terreine van vorige mensbewoning) het 'n baie kleiner verskeidenheid van spesies. Die faunale samestelling stem in breë trekke ooreen met die van wes-Afrikase savannes, maar is nie so spesieryk nie, veral in 'n verskeidenheid van Macrotermitinae en *Trinervitermes*; Termitinae is globaal vergelykbaar.

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## INTRODUCTION

Termites are among the more abundant invertebrates in African savannas, and the savanna of the Nylsvley Nature Reserve is no exception. This report lists the termites collected within the South African Savanna Ecosystem Project study area, in the south-eastern part of the reserve, between August 1976 and May 1979. As collecting proceeded it was found that some of the termite species were restricted to individual habitats within the study area, and the work was expanded to include a comparative study of the four principal vegetation types described below. Some species undoubtedly remain to be discovered, for example, *Hodotermes mossambicus* (Hagen) (HODOTERMITIDAE) and *Epicalotermes munroi* (Coaton) (HALOTERMITIDAE), both of which are common in the general area (W G H Coaton, personal communication 1980), but the list covers the majority of termites that occur within the study area.

Some of the points covered in this report have been amplified by Ferrar (1982). An up-to-date, broad view of the termite fauna of southern Africa in general has been given by Ruelle (1978).

## METHODS AND COLLECTING SITES

Termites were collected by examination of all likely termite niches and food sources, by watching for signs of natural activity, by taking soil cores, and by using artificial baits. Specimens were preserved in 80% ethanol, and after initial sorting, representative material was submitted for identification to the National Collection of Isoptera, Pretoria, and to the British Museum (Natural History), London.

The sites of intensive study are shown in Figure 1; they cover the following four main vegetation types:

Type A (sites 1, 2, 3, 4): typical flat *Burkea* savanna (Figure 2), plant association 1.1 of Coetzee et al (1976). A number of other areas with similar vegetation, in all parts of the study area, were examined less intensively, and no differences in the termite fauna were found.

Type B (site 5): steeply sloping, broadleafed savanna of Maroelakop (Figure 3), association 1.2.1 of Coetzee et al (1976).

Type C (sites 6, 7): *Acacia* thorn savanna (at least some of which are areas of abandoned native settlements), association 4 of Coetzee et al (1976). Sites 6 and 7 differed somewhat in vegetation, in that site 6 was more open (Figure 4) while site 7 was more closed and had a greater variety of plant species. There were also differences in the soils, but the broad trends in termite distribution were the same at both sites.

Type D (sites 8, 9, 10, 11): open, grassy areas near the turfvlei, with occasional trees, association 1.3.2.2 of Coetzee et al (1976). Site 9 is shown in Figure 5. There were slight differences in the vegetation between sites 8 and 9 and sites 10 and 11, but the termite faunas were broadly similar throughout these sites.

## IDENTIFICATION OF TERMITES

The taxonomy of many groups of African termites is badly in need of revision, and identification is a task usually best left to experts. However, some of the Nylsvley termites are fairly readily distinguished and the following key, table of measurements, and photographs are provided as a guide.

It is generally only possible for the non-specialist to identify termite soldiers, which may be distinguished from the workers by their heads. Workers have heads that are almost white in colour and circular when viewed from above, with the jaws or mandibles hidden under the top of the head; soldiers have yellow, orange or brown head capsules of assorted shapes (see Figures 8 to 40), with long, pointed mandibles projecting well forward from the head, or with the capsule prolonged forwards as a long horn (nasute soldiers, Figure 6; glands inside this horn produce a defensive secretion that can be squirted from the tip). In some species (both nasute and other) there are two sizes of soldier in the same colony, known as major and minor soldiers. The measurements and terms used below are illustrated in Figures 6 and 7.

One group of soil-feeding termites is soldierless, and notes on distinguishing their workers from the workers of other soil-feeders are provided after the key.

A reference collection of the termites listed in this report has been deposited in the Nylsvley insect collection.

## KEY TO SOLDIERS

1. Soldiers without prominent mandibles, instead with head capsule extending forwards into a long, conical projection (nasute soldiers, both major and minor present, Figures 8 to 17) ........................ 2

Soldiers with prominent mandibles and no nasute projection ........... 4

2. Both major and minor soldiers with head capsule in dorsal view indented at the sides, roughly violin-shaped (Figures 8, 11); dorsal surface of abdomen with stripes of blackish brown sclerotization, head capsule brownish orange.
*Fulleritermes coatoni* (p 23)

Both sizes of soldier with head in dorsal view not indented at sides, roughly pear-shaped (Figures 9, 10, 12, 13); dorsal surface of abdomen with stripes of pale orange sclerotization; head capsule orange.
(genus Trinervitermes) ........................................ 3

3. Nasute horn shorter in relation to head capsule, and broader at base (Figures 14, 16); the smaller Trinervitermes species, head length ca 1,8-2,0 mm (major soldier) or 1,3-1,5 mm (minor) and head width ca 0,9-1,1 mm (major) or 0,5 mm (minor).
Trinervitermes dispar (p 23, 24, 25)

Nasute horn longer in relation to head capsule, and narrower at base (Figures 15, 17); the larger Trinervitermes species, head length ca 2,3-2,4 mm (major) or 0,7 mm (minor), and head width ca 1,3-1,5 mm (major) or 0,7 mm (minor).
Trinervitermes rhodesiensis (p 23, 24, 25)

4. Mandibles with very stout, expanded bases, as in Figure 18; head width ca 1,5 mm, length of individual mandible ca 1,3 mm; head capsule dark blackish brown; found only inside scarcely rotted dead wood (usually of standing trees).
Bifiditermes sibayiensis (p 26)

Mandibles and head not as in Figure 18 ............................... 5

5. Head long and slender, with roughly parallel sides (Figures 19 to 22).
Microcerotermes spp) ........................................... 6

Head not as above ..................................................... 9

6. Smaller species: head capsule plus mandibles ca 2,1-2,2 mm long ............................................................... 7

Larger species: head capsule plus mandibles ca 2,5-2,6 mm long ........ 8

7. Mandibles slightly longer (ca 0,8 mm long) and thinner, and more gently curved towards tips (Figure 19).
Microcerotermes species B (p 26)

Mandibles slightly shorter (ca 0,6-0,7 mm long) and stouter, and more abruptly curved towards tips (Figure 20).
Microcerotermes brachygnathus (p 26)

8. Curve of mandibles more acute at tips (Figure 21).
Microcerotermes species C (p 26)

Curve of mandibles less acute at tips (Figure 22).
Microcerotermes species D (p 27)

9. Labrum tongue-shaped, with a convex anterior edge ............... 10

Labrum not tongue-shaped, with anterior edge straight (Figure 24) or concave (Figures 23, 35, 36, 37) .................................. 14

10. Soldier ca 4,5 mm in total length; mandibles curved strongly inwards, each with a single strong tooth on inner margin (Figure 27); abdomen full of grey food material.
Amitermes hastatus (p 28)

Soldier without all these characteristics ........................... 11

11. One prominent tooth on inner margin of each mandible (Figures 28, 30). .................................................... 12

Mandibles untoothed .................................................. 13

12. Soldier large, ca 9 mm total length (Figure 28).
Odontotermes badius (p 29)

Soldier small, ca 4 mm total length (Figure 30).
Allodontermes rhodesiensis (p 29)

13. Soldiers very small, ca 3,5 mm in total length; mandibles short and slender, almost concealed by labrum (Figure 29).
Microtermes albopartitus (p 29)

Soldiers large, major ca 15 mm total length, minor ca 10 mm (Figures 31, 32, 33, 34).
Macrotermes natalensis (p 30)

14. Soldier with obvious dark gut contents (Cubitermes spp) ........ 15

Soldiers with whitish abdomen, with no visible gut contents .......... 17

15. Labrum broad, the lobes flaring outwards and quite pointed (Figure 35); mandibles stouter and more curved; head width ca 1,5 mm; head profile as in Figure 38.
Cubitermes muneris (p 31)

Labrum not as above; mandibles thinner and straighter ................ 16

16. Labrum less deeply incised (Figure 36); head width not less than ca 1,5 mm; forehead distinctly tinged with dark brown flecks, and whole head capsule with lighter brown tinge; head profile as in Figure 39.
*Cubitermes testaceus* (p 31)

Labrum more deeply incised (Figure 37); head width not more than ca 1,3 mm; forehead and head capsule uniform yellow to pale orange; head profile as in Figure 40.
*Cubitermes pretorianus* (p 32)

17. Labrum moderately bilobed; mandibles very long and slender, curving in to touch near tips and then separating again (Figures 23, 25).
*Promirotermes* sp. (p 27)

Labrum almost straight along anterior edge; mandibles not as above (Figures 24, 26).
*Lepidotermes lounsburyi* (p 27)

Confirmatory evidence may be sought by comparing dimensions of soldiers with those given in Table 1. However, I must stress that the measurements given in the Table are those of the material which I collected, and may not cover the full range that may be found. There is quite a degree of size variability amongst termite soldiers; therefore the measurements should only be used as a guide.

## IDENTIFICATION OF SOLDIERLESS TERMITES

At least three species of soldierless termites occur at Nylsvley. A monograph on African soldierless termites has been published by Sands (1972), but the identification of individual genera is a specialist's task. However, it is possible for the non-specialists to distinguish soldierless workers as a group from other soil-feeding workers by the appearance of the gut loops in the abdomen when viewed ventrally. This subject has been discussed more fully by Johnson (1979).

Soil-feeding workers as a whole can be distinguished by their relatively swollen abdomens (compared to wood-feeders), which contain bulging segments of intestine full of grey matter. On dissection this material is found to contain many mineral particles. The termites of this type at Nylsvley are *Amitermes*, *Cubitermes* (3 spp), *Lepidotermes* and *Promirotermes*, all of which have soldiers, and three soldierless species (*Aganotermes oryctes*, *Astalotermes brevior* and an undescribed genus). Soldiers of *Amitermes* and usually *Promirotermes* are readily found amongst their workers, so there is little chance of these being taken for soldierless species. However, *Cubitermes* soldiers in particular may be very difficult to find at some times of the year. The appearance of the gut segments in ventral view of the abdomen of workers of a soldierless termite and of a *Cubitermes* are shown in Figures 41 and 42.

TABLE 1. Dimensions of termite soldiers

| Species | Total length (mm) (tip of mandibles or nasute horn to end of abdomen) | Head length (mm) (tip of mandibles or nasute horn to back of head capsule) | Head width (mm) | Length of mandible (mm) |
|---|---|---|---|---|
| Bifiditermes sibayiensis | 5,7- 6,8 | 3,5-3,6 | 1,4-1,5 | 1,3 |
| Allodontermes rhodesiensis | 4,1- 4,6 | 2,1-2,3 | 0,9-1,0 | 0,5-0,6 |
| Macrotermes natalensis MAJOR | 14,8-15,2 | 7,3-7,5 | 4,0 | 2,2-2,3 |
| MINOR | 10,3-10,4 | 4,8-5,0 | 2,4-2,5 | 1,5-1,7 |
| Microtermes sp nr albopartitus | 3,1- 3,7 | 1,4-1,5 | 0,8 | 0,4-0,5 |
| Odontotermes badius | 8,9- 9,5 | 4,4-4,5 | 2,4-2,8 | 1,2-1,3 |
| Fulleritermes coatoni MAJOR | 2,5- 3,5 | 1,4 | 0,75 | |
| MINOR | 2,1- 2,8 | 1,2 | 0,5 | |
| [a]Trinervitermes dispar MAJOR | 3,0- 4,5 | 1,8-2,0 | 0,9-1,1 | |
| MINOR | 2,6- 3,4 | 1,3-1,5 | 0,5 | |
| [a]Trinervitermes rhodesiensis MAJ | 5,6- 6,1 | 2,3-2,4 | 1,3-1,5 | |
| MINOR | 3,7- 4,1 | 1,8-1,9 | 0,7 | |
| Amitermes hastatus | 4,4- 4,6 | 1,9-2,0 | 1,0-1,1 | 0,6 |
| Cubitermes muneris | 6,3- 7,1 | 3,1-3,2 | 1,5 | 1,4 |
| Cubitermes pretorianus | 6,3- 6,5 | 2,9-3,0 | 1,2-1,3 | 1,1-1,2 |
| Cubitermes testaceus | 5,0- 5,5 (mandibles crossed) | 2,3-2,6 (mandibles crossed) | 1,5-1,6 | 1,5-1,6 |
| Lepidotermes lounsburyi | 3,1- 3,3 (mandibles crossed) | 1,7-2,0 (mandibles crossed) | 1,0-1,1 | 1,1 |
| Microcerotermes species B | 4,8- 4,9 | 2,1-2,2 | 0,8 | 0,8 |
| Microcerotermes brachygnathus | 5,0- 5,3 | 2,1 | 0,7-0,8 | 0,6-0,7 |
| Microcerotermes species C | 5,3- 5,6 | 2,5-2,6 | 0,9 | 0,9-1,0 |
| Microcerotermes species D | 5,3- 5,6 | 2,5-2,6 | 0,9 | 1,0-1,1 |
| Promirotermes sp | 4,0 | 2,7-3,0 | 0,9-1,1 | 1,4-1,5 |

[a]The two species of Trinervitermes may also be distinguished by the sizes of their major workers. In T dispar the largest workers are ca 4,6 mm in total length and ca 1,1 mm in head capsule width; in T rhodesiensis the largest workers are ca 6,0 mm long and ca 1,5 mm in head width.

Those of the other species and genera are broadly similar to the Cubitermes (see illustrations of Johnson 1979), and none has the distinctive tube-like section arrowed on the right of the illustration of the soldierless termite (Figure 41). This section is apparently characteristic of all soldierless termites.

Measurement of size may be an additional help, as the soldierless termites do not have very large workers. Total length of workers in this study did not exceed 4,0 mm (Aganotermes), 4,1 mm (Astalotermes) and 3,3 mm (unidentified sp), while maximum width of abdomen was 1,2 mm (Aganotermes), 1,4 mm (Astalotermes) and 0,7 mm (unidentified sp) (which may not quite be the maximum size possible).

## SYSTEMATIC LIST

Class INSECTA: Order Isoptera (termites)

Family Kalotermitidae (lower termites)

*Bifiditermes sibayiensis* (Coaton) (Figure 18). Found wherever there are trees in the study area, in galleries in dead branches of living trees and in standing (or recently fallen) dead trees. Feeds only on hard, scarcely rotted wood which it opens up for subsequent fungal attack. Nests within its galleries in the tree and has no contact with the ground. Live colonies are only moderately common, but a high proportion of dead branches and trees show signs of past attack by this species. Nests were found in *Acacia*, *Lannea*, *Combretum* and *Burkea* trees, and a wide range of tree species had signs of old attack.

Family Termitidae (higher termites)

Subfamily Apicotermitinae

*Aganotermes oryctes* (Sands). Probably the commonest termite at Nylsvley, found throughout the study area. Soil-feeding, found in foraging galleries in the soil, under fallen objects, in soil packed in hollow, rotten wood, and in the nests of other termites. During the wetter months of summer it is hard to find a square metre of soil in which these termites are not working just beneath the soil surface. Uses abdominal dehiscence (Sands 1972) for defence.

*Astalotermes brevior* (Holmgren). One small specimen taken from soil on Maroelakop, and a few specimens apparently of this species taken at other sites. Owing to the difficulty of distinguishing species of soldierless termites the distribution and abundance of this species at Nylsvley have not yet been fully determined.

Genus undescribed. One series of a small, slender soldierless termite, apparently of an undescribed genus, was taken on Maroelakop. A few specimens probably of the same termite were also taken on other parts of the reserve, but as with *Astalotermes* the difficulties of identification have so far prevented further study. However, apparently not very common.

Five other species of soldierless termite have been recorded from the northern Transvaal by Sands (1972), and some of these may possibly also occur at Nylsvley but have been overlooked because of difficulties in identification.

Subfamily Macrotermitinae

Allodontermes rhodesiensis (Sjöstedt) (Figure 30). Found in open areas near the turfvlei (sites 8 and 9), in a dead tree stump, in foraging galleries in loose soil, in the outer shell of a live Macrotermes mound, and attacking toilet roll baits. Wood and litter feeding, this species plasters the outside of food sources with loose earth, rather like Macrotermes. Biological and distributional notes on the genus in southern Africa have been given by Ruelle (1979).

Macrotermes natalensis (Haviland) (Figures 31 to 34). Found throughout the broad-leaved savanna, principally in the more open, grassy areas where it is most abundant towards the turfvlei; possibly occurs in the Acacia areas and on Maroelakop as well, but all obvious mounds there are unoccupied. In the broadleafed savanna there are also patches in which all the mounds are unoccupied, and the cause of this is not obvious.

Macrotermes builds conical mounds (Figure 43) on average 75 cm high, with 140 cm basal diameter (ground level) and 375 cm basal circumference. Large mounds may be up to 130 cm high, 175 cm basal diameter and 525 cm basal circumference. Unoccupied mounds become much tunnelled (Figure 44), and are a refuge for assorted reptiles, birds and mammals.

Macrotermes forages extensively in dead wood, dead grass, dung and other vegetable litter, and to a lesser extent on live vegetation; also feeds on toilet roll baits, discarded cardboard boxes, etc. Forage is often plastered with loosely cemented sand on the outside before being eaten (Figure 45). Biological and distributional notes on the genus in southern Africa have been given by Ruelle, Coaton and Sheasby (1975).

Microtermes sp, probably albopartitus Sjöstedt (Figure 29). Plentiful in all areas, and especially abundant in the Acacia patches. Forages in dead wood, old cow and antelope dung (and toilet roll baits); also found in shallow soil galleries and in nests of other termites. Nests of Microtermes with reproductives and fungus combs have been found built into the edges of Cubitermes mounds.

Odontotermes badius (Haviland) (Figure 28). Found in all habitats; apparently quite common, but only seen when foraging in food sources such as wood, old antelope dung, leaf litter, dead grass, and toilet roll baits. The food source is often plastered outside with earth, and one tree trunk was found completely sheathed in a crust of cemented soil to quite a height (Figure 46). The nest is subterranean, and none were excavated at Nylsvley.

Subfamily Nasutitermitinae

Fulleritermes coatoni (Sands) (Figures 8, 11). Moderately common in the Burkea, and quite abundant on Maroelakop and at sites 9 and 10 near the turfvlei. Found in the mounds of other termites, including Amitermes and Cubitermes, and in dead mounds of Macrotermes. Also found in toilet roll baits, though it was not clear whether it was actually eating the paper. Distributional and ecological notes on this species have been given by Coaton and Sheasby (1973).

The food sources of this species were not determined. Coaton and Sheasby (1973) recorded it as foraging in cattle dung, rotted wood and deposits of grass in derelict Trinervitermes mounds, while Sands (1965a) stated that the genus is wood-feeding. At Nylsvley, when found in Cubitermes mounds, it was often in ones built against a piece of wood. However, it was once found in an Amitermes mound that was 11 m from the nearest tree or obvious surface wood (though tree roots probably ran nearer).

Tunnels and nests of this species have a lining of black faecal material. When the nest is breached the soldiers rush out to defend it while the workers remain motionless and closely pressed against the black walls, against which surface their blackish bodes are remarkably well camouflaged. This strategy is adopted also by Trinervitermes (see below).

Trinervitermes dispar (Sjöstedt) (Figures 9, 12, 14, 16). Found principally in the flatter Burkea areas, where it is fairly common; also on Maroelakop (site 5) and near the turfvlei (site 8). It was found in toilet roll baits though, as with Fulleritermes, it was not clear to what extent it was actually eating the paper. Also found in shallow soil galleries, and nesting within live Cubitermes mounds. It does not store food in its nest, and its sources of forage were not determined. Its tunnels and nest cells have a lining of speckled brown and black faecal material, against which the orange and grey bodies of the workers are well camouflaged when they are motionless (see note for Fulleritermes above). Distributional notes on this species have been given by Sands (1965a).

Trinervitermes rhodesiensis (Sjöstedt) (Figures 10, 13, 15, 17). Apparently restricted to open grassland near the turfvlei (sites 10 and 11) where it constructs flattish domed mounds (Figure 47) of somewhat oval cross section, up to 37 cm high, 70-115 cm diameter (of oval shape at ground level), and 290 cm ground level circumference. The mound is typical of Trinervitermes, with a hard outer shell of cemented sand, and a softer inner structure of rather open cells and galleries, the walls of which are crumbly sand coated with speckled brown and black faecal material (against which the orange and grey bodies of motionless workers are well camouflaged; see note for Fulleritermes above). Distributional notes on this species have been given by Sands (1965a).

The mounds contain sizeable amounts of stored forage (Figure 48), mostly grass but with some seeds and wood and leaf fragments. The pieces range from 2,0-9,3 mm long by 0,2-1,2 mm broad. Two small nests that were sampled contained about 3 g and 16 g dry mass of forage respectively. If larger nests contain extra forage in proportion to their increased nest volume (which seems likely from examination) then they could contain in the vicinity of 500 g dry forage per nest.

Subfamily Termitinae

Amitermes hastatus (Haviland) (Figure 27). Found near the turfvlei (sites 9 and 10) where it constructs flattish grey mounds (Figure 49) with a surface that is nodular on young mounds and honeycombed on older ones. The construction is fairly soft and sandy, with cells separated by rather massive walls. Also found in the outer shell of a live Macrotermes mound. Distributional notes on this species have been given by Sands (1959).

The food of this termite was not determined. The guts of both workers and soldiers contained a substantial quantity of soil, but they were never located when feeding. Skaife (1955) states that they eat well-rotted vegetable matter, including wood and plant stems but not leaf mould or humus. At Nylsvley the nests are in open areas with very little surface wood, though tree roots would be present below the surface. Deligne (1966) indicated a correlation between the structure of termite mandibles and their diet; those with transverse grinding ridges on the mandibles of the workers ingest whole vegetable matter (in which group he listed the genus Amitermes), while humivorous species lack the ridges and have a concavity in the mandible with a cusp at one end. A hastatus lacks grinding ridges and seems closer to the second type. Perhaps it feeds on soil containing a high proportion of well-rotted grass or other vegetable matter.

Cubitermes pretorianus Silvestri (Figures 37, 40). Common throughout the study area, except for the Acacia patches from which it is absent. A soil-feeder, this species is found in shallow soil galleries and in blackish brown mounds with a nodular or honeycombed surface (Figure 50). Each mound is roughly spherical, slightly broader than tall, and mostly buried in the soil with only the top of the mound above the soil surface; in size they average 20 cm diameter, 65 cm circumference, and 17 cm height of which 1 to 6 cm is above ground. The density of mounds measured in two rectangles at site 1 was 385 and 500 mounds ha$^{-1}$. Cubitermes mounds occur near the turfvlei as well as throughout the Burkea, but in the vlei area Cubitermes is also found as a resident in mounds of Amitermes and Trinervitermes rhodesiensis. On Maroelakop C pretorianus seems to nest mainly in the mounds of the other Cubitermes spp.

The mound comprises many cells about 15x15x10 mm across, each with one or more small access holes 1,5 mm in diameter; the cell walls are of thick, hard, blackish brown, cemented faecal material. When the mound is breached workers immobilize attackers such as ants by biting them and hanging on, the weight of soil in the termite's gut greatly impeding the movement of the attacker. Meanwhile other workers retreat to the nearest intact cell and quickly seal the tiny access hole with a few quick-drying defaecations. Sometimes grains of sand are placed in the hole to speed the closure. Soldiers generally do not come to the defence but withdraw towards the queen and eggs. There is no special queen cell or nursery area in the nest; the queen is quite mobile and can move quickly from cell to cell to escape pursuers.

Thirteen of these mounds were dug up intact for sampling; in every nest at least one other species of termite and usually one or two species of ant were also present. The termites sharing the nest included Aganotermes, Microcerotermes (brachygnathus and species B), Microtermes, Trinervitermes dispar, Fulleritermes and Lepidotermes; the ants were Crematogaster sp and Monomorium sp. The counts of termites in the mounds are given in Table 2. Relatively early in the sampling it became obvious that the termites had a seasonal cycle of egg production. To illustrate this, the results for the three calendar years of sampling have been placed in monthly order within one annual cycle, starting in mid-November when the winged termites have just flown.

Two other quite distinct species of Cubitermes also occur at Nylsvley. They appear morphologically to be the same as the following two species recorded in East Africa by Williams (1966), but their habits are quite different from the East African species. When the genus is revised in southern Africa they may turn out to be separate species.

Cubitermes muneris (Sjöstedt) (Figures 35, 38). A soil-feeding species, restricted almost entirely to Maroelakop where it is quite common, though one soldier and a few workers were found in a shallow earth cell near site 1. Found in mounds similar in construction to those described for C pretorianus except that they are almost invariably built under the overhang of a boulder or tree stump, and are irregularly shaped to fit into the available space. These nests usually contain both this species and Cubitermes testaceus, and it is difficult to say which of the two species initiates the mound; C pretorianus may be present as well, but less commonly.

Cubitermes testaceus Williams (Figures 36, 39). A soil-feeding species found only on Maroelakop in nests with the preceding species where it is fairly common.

Lepidotermes lounsburyi (Silvestri) (Figures 24, 26). This species is found in shallow soil galleries, soil cells and in Cubitermes mounds in the Burkea. It is a rather uncommon soil-feeding species.

Microcerotermes brachygnathus (Silvestri) (Figure 20). Common throughout the study area, especially in the Burkea and on Maroelakop. Forages in fallen timber, in dry dung, in the woody stubble at the junction of stem and root of grass plants, and in toilet roll baits. Nests are made of tightly packed, concentric layers of yellow-brown "carton", sometimes alone in the soil but often incorporated within a Cubitermes mound or, near the turfvlei, with Trinervitermes rhodesiensis or Macrotermes.

Two or perhaps three other Microcerotermes spp also occur at Nylsvley but in the absence of a modern revision of the genus in southern Africa no reliable specific names can be given.

Microcerotermes species B (near apricitatis Fuller and durbanensis Fuller) (Figure 19). As for M brachygnathus except that specimens were also taken from branches of standing trees. The species is present but scarce on Maroelakop. Significant ecological differences between the two species were not detected.

TABLE 2. Termite populations of sampled *Cubitermes* mounds

| Date sampled | Genus | Workers | Soldiers | White soldiers | Royal pairs | Eggs | Apterous larvae | Alate nymphs | Alate adults | Ants[c] |
|---|---|---|---|---|---|---|---|---|---|---|
| 11 Nov 76 | *Cubitermes* | 8 520 | 97 | 14 | 1 | | | | | |
| | *Aganotermes* | 16 | | | | 9 750 | 5 870 | | | *Mono* |
| | *Microtermes* | 280 | 34 | 6 | 1 | | | | | |
| 11 Dec 78 | *Cubitermes* | 10 400 | 83 | 3 | 1 | | | | | |
| | *Aganotermes* | 120 | | | 1 | 11 200 | 7 180 | | | *Crem* |
| 12 Dec 77 | *Cubitermes* | 2 460 | 15 | 2 | | | | | | |
| | *Microcerotermes*[a] | 320 | 1 | | | 1 550 | 1 540 | | | |
| 8 Jan 79 | *Cubitermes* | 5 450 | 32 | 11 | | | | | | |
| | *Aganotermes* | 280 | | | 1 | | | | | |
| | *Trinervitermes* | 1 440 | 86 major | 20 maj | 1 | 6 250 | 3 580 | 2 | 5 | *Crem* |
| | | | 185 minor | 26 min | | | | | | *Mono* |
| 9 Feb 77 | *Cubitermes* | 8 830 | 41 | 13 | 1 | | | | | |
| | *Aganotermes* | 70 | | | | 5 650 | 4 720 | 217 | | *Mono* |
| | *Microcerotermes*[a] | 2 780 | 13 | 1 | | | | | | |
| 5 Mar 79 | *Cubitermes* | 11 220 | 56 | 15 | 1 | | | | | |
| | *Aganotermes* | 650 | | | 1 | | | | | |
| | *Trinervitermes* | | 1 maj | | | 7 100 | 7 200 | 220 | | *Mono* |
| | | | 10 min | | | | | | | |
| | *Microcerotermes*[b] | 3 570 | 24 | 51 | | | | | | |
| 3 Apr 78 | *Cubitermes* | 8 620 | 44 | 9 | 1 | | | | | |
| | *Aganotermes* | 570 | | | | 2 020 | 8 530 | 24 | 4 | *Crem* |
| | *Microcerotermes* | 3 780 | 55 | 22 | | | | | | *Mono* |
| 12 May 77 | *Cubitermes* | 10 330 | 63 | | 1 | | | | | |
| | *Lepidotermes* | | 34 | | 1 | | | | | |
| | *Aganotermes* | 370 | | | | | | | | |
| | *Trinervitermes* | 430 | 94 maj | | | 500 | 1 250 | 740 | | *Crem* |
| | | | 121 min | | | | | | | *Mono* |
| | *Microcerotermes*[a] | | 106 | 4 | 1 | | | | | |
| | *Microtermes* | 16 500 | 21 | | | | | | | |
| 24 Jun 77 | *Cubitermes* | 14 650 | 214 | | 1 | | | | | |
| | *Aganotermes* | 480 | | | | 4 500 | 10 | 450 | | *Mono* |
| 19 Aug 77 | *Cubitermes* | 4 900 | 42 | | 1 | | | | | |
| | *Aganotermes* | 800 | | | 1 | 4 700 | 555 | 150 | | *Crem* |
| | *Microtermes* | 1 300 | 105 | | 1 | | | | | *Mono* |
| 18 Sep 78 | *Cubitermes* | 4 330 | 28 | 1 | 1 | 2 670 | 1 100 | 170 | | *Crem* |
| | *Aganotermes* | 180 | | | | | | | | *Mono* |
| 11 Oct 77 | *Aganotermes* | 730 | | | | | | | | *Crem* |
| | *Microcerotermes*[b] | 1 070 | 11 | 10 | | 430 | 370 | | 14 | *Mono* |
| 18 Oct 77 | *Cubitermes* | 5 940 | 34 | 12 | 1 | | | | | |
| | *Aganotermes* | 750 | | | | | | | | |
| | *Fulleritermes* | 440 | 3 maj | | 1 | 17 240 | 6 700 | | 2 100 | *Crem* |
| | | | 60 min | | | | | | | *Mono* |
| | *Microcerotermes*[b] | 8 350 | 3 | 52 | | | | | | |
| | *Microtermes* | | 68 | 106 | | | | | | |

[a] *M Brachygnathus*

[b] *Microcerotermes* species B

[c] Ants: *Crem* = *Crematogaster*; *Mono* = *Monomorium*

Microcerotermes species C (near sanctaeluciae Fuller and thermarum Fuller) (Figure 21). One sample was taken from the dead branch of a standing Burkea tree in flat savanna, and several were taken from standing and fallen dead wood on Maroelakop. This species is a little larger than the preceding two species, and a number of other samples of similarly large-sized workers were taken from the branches of standing trees; however, in the absence of soldiers no positive identification could be made.

Microcerotermes species D (Figure 22). One sample, taken from a dead branch of a standing Diplorhynchus tree on Maroelakop, seemed to be slightly different from species C and may be a separate species. Its habits are likely to be similar to those of species C.

Promirotermes spp (Figures 23, 25). Moderately common in the Burkea and quite common on Maroelakop, in shallow soil galleries, in earth cells beneath fallen objects (including toilet roll baits), and in earth plastering inside hollow rotten wood. Seems to select soils of high organic content.

DISTRIBUTION WITHIN VEGETATION TYPES

The distribution of species within the four main vegetation types is summarized in Table 3. The termites of the flat Burkea savanna probably represent the basic spectrum of species in the South African savanna fauna. Most of the species also occur in steep rocky areas such as Maroelakop; Lepidotermes may or may not occur, as it is an elusive species, while Macrotermes has at least existed there one time, since two old, crumbled mounds found on the hillside can only have been constructed by this genus. The rocky habitat also attracts two species of Cubitermes which are not, or scarcely, found elsewhere in the study area. Drainage is unlikely to be the deciding factor in their distribution, as the more elevated parts of the flat savanna are very well drained. However, it may be that the presence of boulders is necessary for nest construction in these Cubitermes species.

The fauna of the strip adjacent to the turfvlei contains most of the basic species, plus Allodontermes, Amitermes and Trinervitermes rhodesiensis. Factors which may be relevant in attracting these extra species are the openness of the area (and thus a greater variety and abundance of grasses for harvesters) and the higher water table, due to the proximity of the flood plain, which may promote rotting of food materials.

The most striking difference is in the Acacia, which has a much depleted fauna. At least some of the Acacia patches are the sites of old native settlements (confirmed by soil cores taken at site 6 which yielded a number of rough pottery fragments), but their presence is part of a natural mosaic of vegetation in the area. Wood, Johnson and Ohiagu (1977) have described how human interference reduces or eliminates many species of termite, while increasing one or two others such as

TABLE 3. Distribution of termites within vegetation types at Nylsvley.

(NB The number of crosses indicates that the species is more (++) or less (+) abundant in a particular area compared to the other areas, but comparisons should not be made between species; eg *Microtermes* in *Burkea* (+) is more numerous than *T dispar* in *Burkea* (++).)

| | *Burkea* | Maroelakop | *Acacia* | Turfvlei |
|---|---|---|---|---|
| *Bifiditermes sibayiensis* | + | + | + | |
| *Aganotermes oryctes* | ++ | ++ | ++ | ++ |
| *Astalotermes brevior* | ? | + | ? | ? |
| Soldierless genus indet | ? | + | ? | ? |
| *Allodontermes rhodesiensis* | | | | + |
| *Macrotermes natalensis* | + | ? | ? | ++ |
| *Microtermes* sp prob. *albopartitus* | + | + | ++ | + |
| *Odontotermes badius* | + | + | + | + |
| *Fulleritermes coatoni* | + | ++ | | ++ |
| *Trinervitermes dispar* | ++ | + | | + |
| *Trinervitermes rhodesiensis* | | | | + |
| *Amitermes hastatus* | | | | + |
| *Cubitermes muneris* | + | ++ | | |
| *Cubitermes pretorianus* | ++ | + | | + |
| *Cubitermes testaceus* | | ++ | | |
| *Lepidotermes lounsburyi* | + | | | |
| *Microcerotermes brachygnathus* | ++ | ++ | + | + |
| *Microcerotermes* species B | ++ | + | + | + |
| *Microcerotermes* species C | + | + | | |
| *Microcerotermes* species D | | + | | |
| *Promirotermes* sp | + | ++ | | |

*Microtermes*. This appears to have happened in these *Acacia* patches, where all the nasutes and soil-feeding Termitinae (and apparently also *Macrotermes*) have disappeared but *Microtermes* has increased substantially (as shown by soil coring and by foraging in toilet roll baits). However, Wood, Johnson and Ohiagu (1977) referred to human interference such as mechanical cultivation, and as far as is known the *Acacia* sites 6 and 7 have never been subject to such treatment. To the human eye they look quite natural (Figure 4), and any mechanical effect, such as trampling by herded cattle, ceased years ago (at least 50 and probably more; B J Huntley, personal communication 1978). The soil is apparently still more compacted in these areas than in the *Burkea*, and the soil nutrient status is different in some respects; the leaf litter input from microphyllous *Acacia* trees is also quite different. The patches are able to support one soil-feeding species *Aganotermes*, which thrives there, and the reasons for the lack of colonization by other species are not clear.

## RELATIONSHIP WITH OTHER AFRICAN SAVANNA FAUNA

Among the many studies on African termites there are relatively few in which the total termite fauna of a savanna ecosystem has been surveyed. Those that do exist make an interesting comparison with Nylsvley. Comparative physical data for the sites are given in Table 4, and the termites of each in Table 5. This should only be regarded as a broad comparison since collecting techniques will have differed to varying extents (for example, one or two of the studies appear to have concentrated on termites in contact with the soil and to have ignored tree-dwelling Kalotermitidae). Furthermore, termite taxonomy, especially of difficult genera, has varied over the 15-year period covered by these reports.

It is clear that, despite its great distance from the other areas, Nylsvley has a broadly comparable termite fauna. It is therefore likely that this approximate balance of genera is characteristic of all African savannas. The Nylsvley fauna is somewhat impoverished compared to the others, and three factors may be relevant, namely the greater distance from the Equator, the higher altitude and the relatively low rainfall. The area in the Table most comparable in vegetation to Nylsvley is the southern Guinea savanna of Nigeria, and at that site half as many species again occur in a small fraction of the area. Nylsvley seems to be lacking mainly in diversity of Macrotermitinae and Trinervitermes; Termitinae are roughly comparable.

TABLE 4. Physical data for savannas surveyed for termites

| | Sahel, Senegal (Lepage 1972) | N. Guinea savanna, Nigeria | S. Guinea savanna, Nigeria | Lamto-Pakobo Ivory Coast (Josens 1972) | Lower Ivory Coast (Bodot 1967) | Nylsvley (present study) |
|---|---|---|---|---|---|---|
| Latitude[b] | 16°13'N | ca 11°N | 9°18'N | 6°13'N | ca 5°30'N | 24°39'S |
| Altitude[c] (m) | <100 ? | 700 | 200 | 75-125 | <100 ? | 1080-1140 |
| Mean rainfall[d] (mm yr$^{-1}$) | ? between 380-650 | 1170 | 1175 | 1290 | 2000 | 630 |
| Area surveyed[e] (ha) | 100 | 10 | 6 | part of 2700 | 50 000 | 745 |

Notes

[a]Data published by Wood et al (1977), but Collins (1977) gives figures for extra unidentified species that are included here

[b]For N. Guinea savanna, taken as that of Zaria

[c]For Sahel and Lower Ivory Coast, estimated from atlas contours

[d]For Sahel, presumed to be between averages of stations 632 (Linguere) and 652 (St Louis) of Walter and Lieth (1960)

[e]For Lamto-Pakobo, 2700 ha was surveyed but only part of this was savanna, and only the savanna termites are included in Table 5; for Lower Ivory coast from Bodot (1964)

TABLE 5. Total termite fauna of some African savanna ecosystems

| | Sahel | N. Guinea savanna | S. Guinea savanna | Lamto Pakobo | Lower Ivory Coast | Nylsvley |
|---|---|---|---|---|---|---|
| Kalotermitidae | | | | | | |
| *Bifiditermes* | | | | | | 1 |
| *Cryptotermes* | | | | 1 | | |
| *Neotermes* | | | | 1 | | |
| Rhinotermitidae | | | | | | |
| *Coptotermes* | 2 | | 1 | 1 | | |
| *Psammotermes* | 1 | | | | | |
| Termitidae | | | | | | |
| Apicotermitinae | | | | | | |
| Soldierless termites | | >1 | 3 | 4 | 3 | 3 |
| Macrotermitinae | | | | | | |
| *Allodontermes* | | 1 | 1 | | 1 | 1 |
| *Ancistrotermes* | | >1 | 1 | 2 | 2 | |
| *Macrotermes* | 1 | 2 | 2 | 2 | 2 | 1 |
| *Microtermes* | 1 | >1 | 5 | 1 | 1 | 1 |
| *Odontotermes* | 1 | >1 | 2 | 3 | 1 | 1 |
| *Pseudacanthotermes* | | 2 | | 1 | | |
| Nasutitermitinae | | | | | | |
| *Eutermellus* | | | 1 | 2 | | |
| *Fulleritermes* | | | 1 | 1 | | 1 |
| *Mimeutermes* | | | | 1 | 1 | |
| *Nasutitermes* | | | | 1 | | |
| *Trinervitermes* | 5 | 5 | 5 | 5 | 2 | 2 |
| Termitinae | | | | | | |
| *Allognathotermes* | | 1 | | | 1 | |
| *Amitermes* | 3 | 1 | 2 | 1 | 1 | 1 |
| *Angulitermes* | 1 | | | | | |
| *Basidentitermes* | | | 1 | 1 | 1 | |
| *Cubitermes* | | 1 | 1 | | 2 | 3 |
| *Eremotermes* | | | 1 | | | |
| *Euchilotermes* | | | | | 1 | |
| *Hoplognathotermes* | | | | | 1 | |
| *Lepidotermes* | | | | | | 1 |
| *Microcerotermes* | 2 | >1 | 1 | 3 | | 4 |
| *Noditermes* | | | 1 | | | |
| *Ophiotermes* | | | | | 1 | |
| *Pericarpritermes* | | 1 | 1 | 1 | 1 | |
| *Procubitermes* | | 1 | | 1 | | |
| *Promirotermes* | 1 | >1 | 1 | 2 | | 1 |
| *Tuberculitermes* | 1 | 1 | | 1 | | |
| Total | 19 | >29 | 30 | 36 | 22 | 21 |

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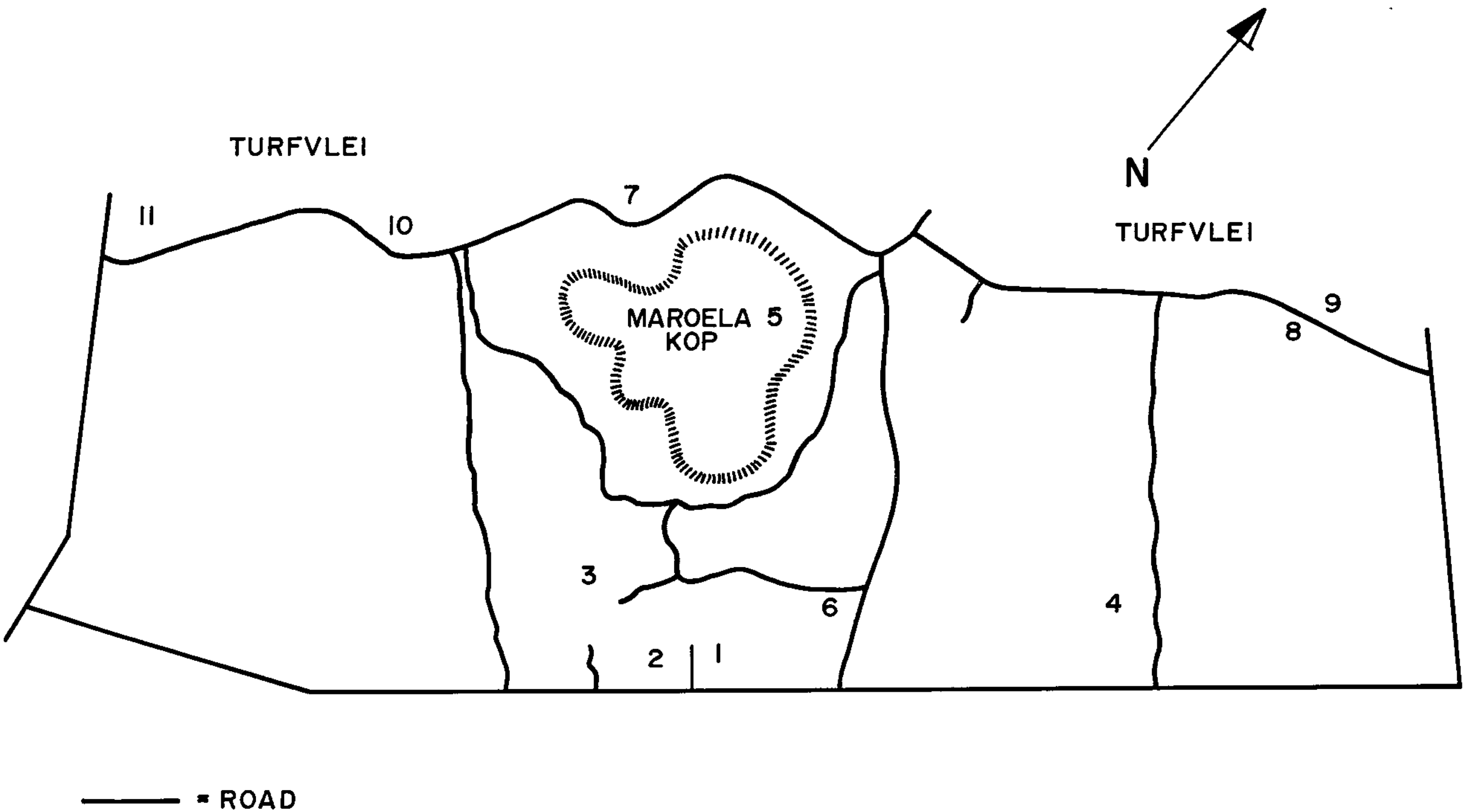


**FIGURE 1**

**( FERRAR-TERMITE REPORT )**

FIGURE 1. Map of study area showing main termite collecting sites.

FIGURE 2. Burkea savanna.

FIGURE 3. Maroelakop.

FIGURE 4. Acacia thorn savanna.

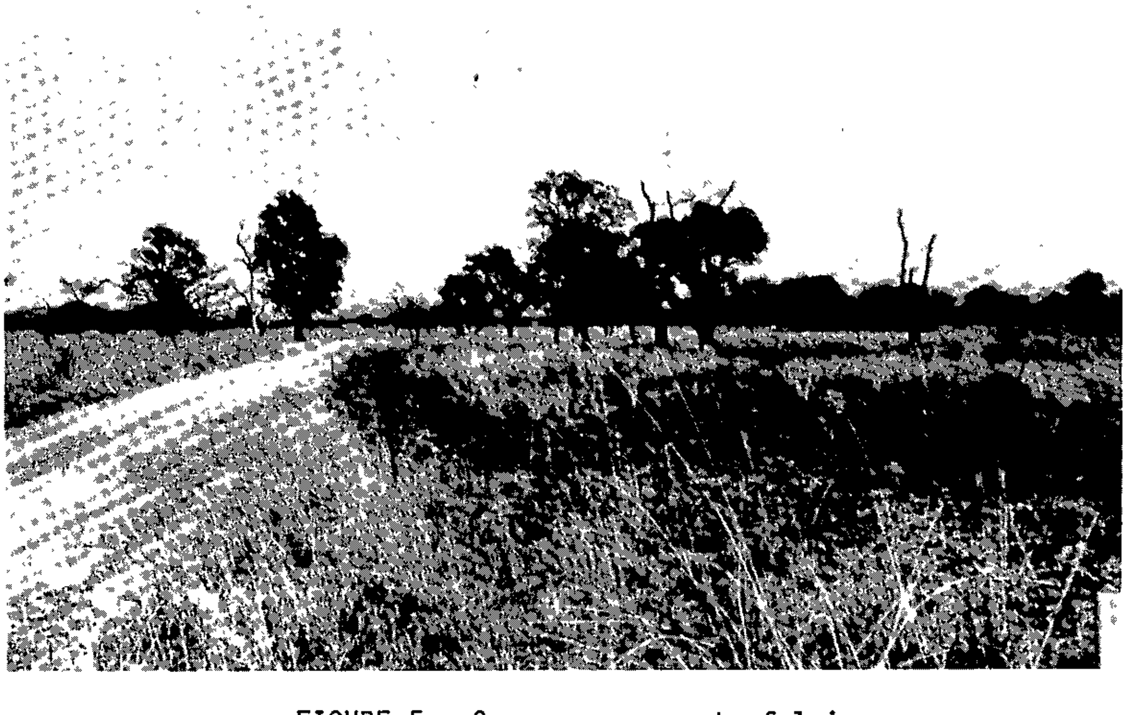

FIGURE 5. Open area near turfvlei.

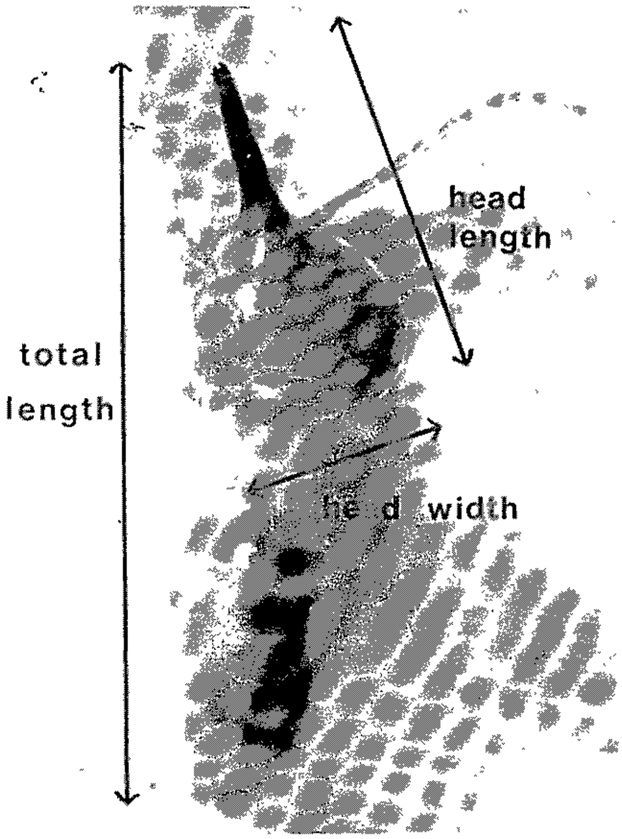


FIGURE 6. Terms and measurements used in key to Nasute soldiers.

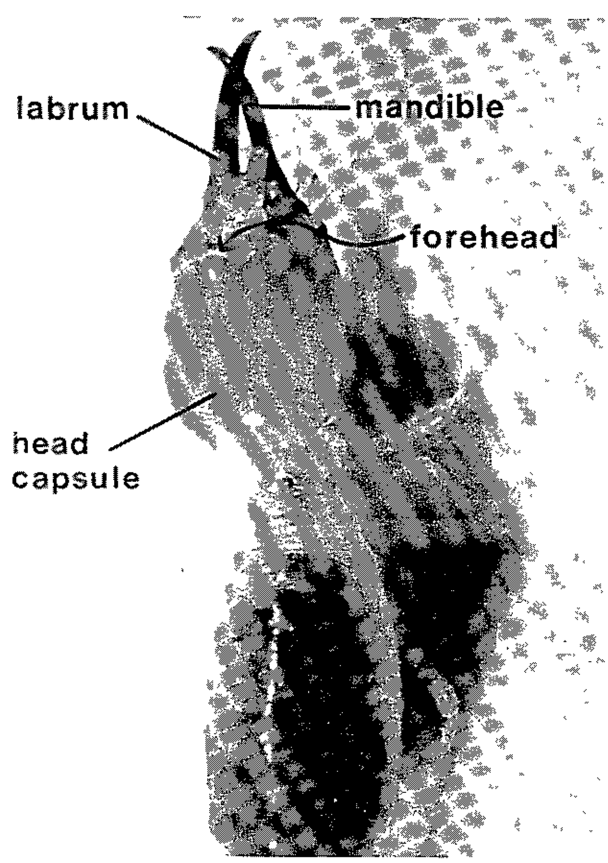


FIGURE 7. Terms and measurements used in key to Mandibulate soldiers.


FIGURE 8. *Fulleritermes coatoni*, major soldier, dorsal.


FIGURE 9. *Trinervitermes dispar*, major soldier, dorsal.


FIGURE 10. *Trinervitermes rhodesiensis*, major soldier, dorsal.


FIGURE 11. *Fulleritermes coatoni*, minor soldier, dorsal.


FIGURE 12. Trinervitermes dispar, minor soldier, dorsal.

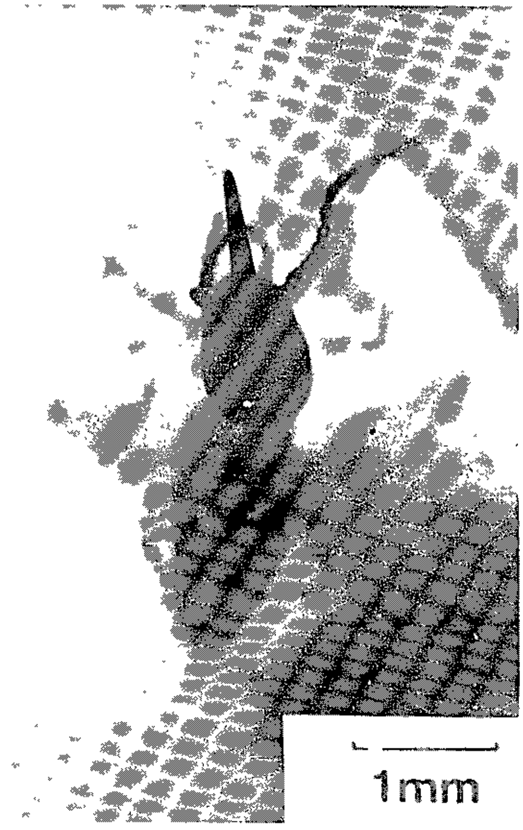


FIGURE 13. Trinervitermes rhodesiensis, minor soldier, dorsal.

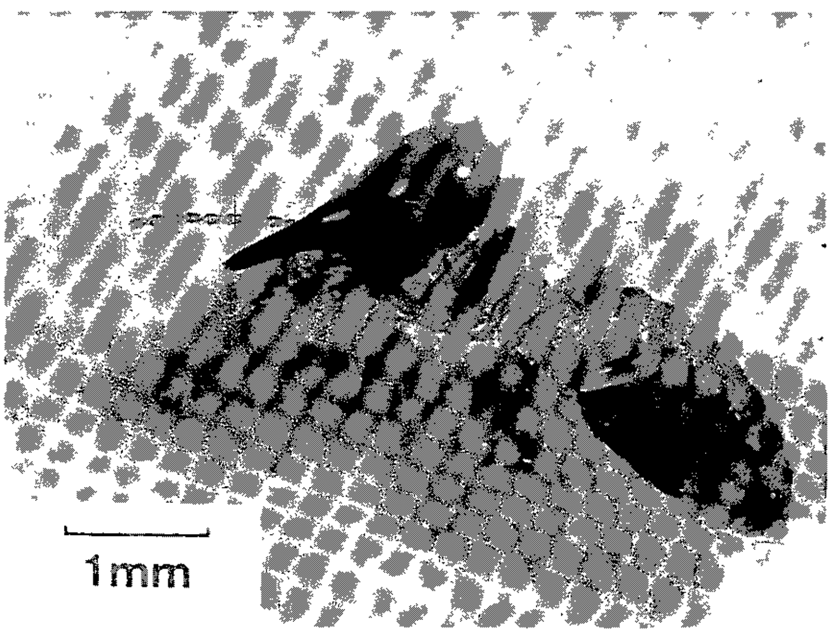


FIGURE 14. Trinervitermes dispar, major soldier, lateral.

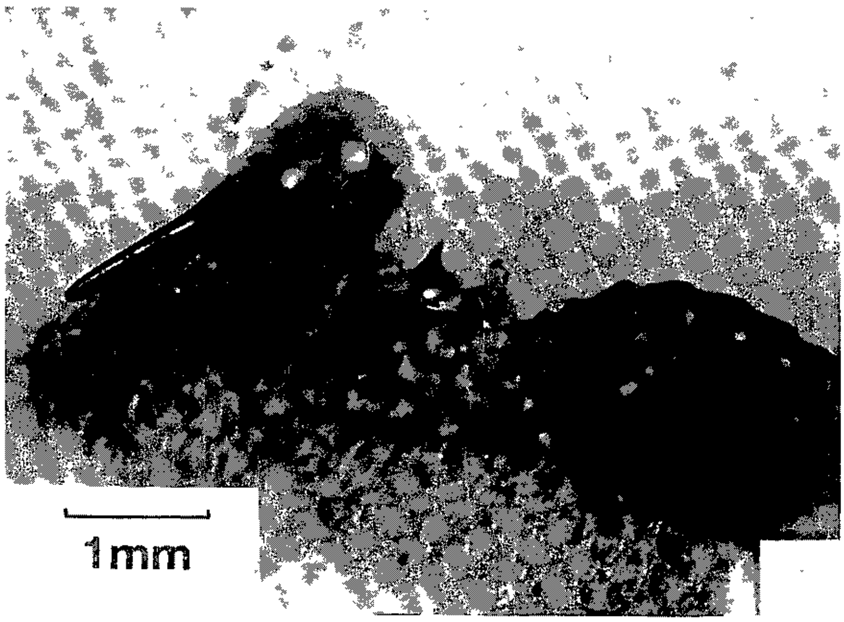


FIGURE 15. *Trinervitermes rhodesiensis*, major soldier, lateral.

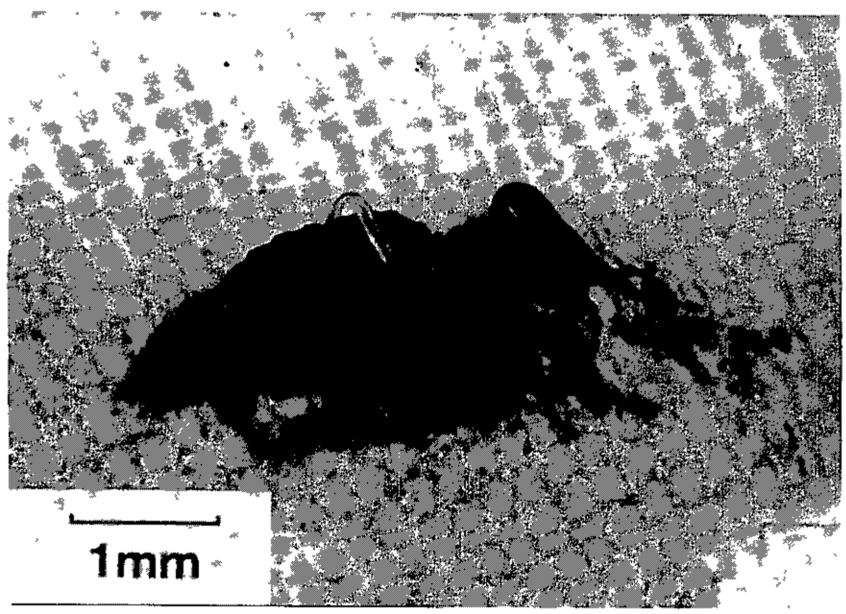


FIGURE 16. *Trinervitermes dispar*, minor soldier, lateral.

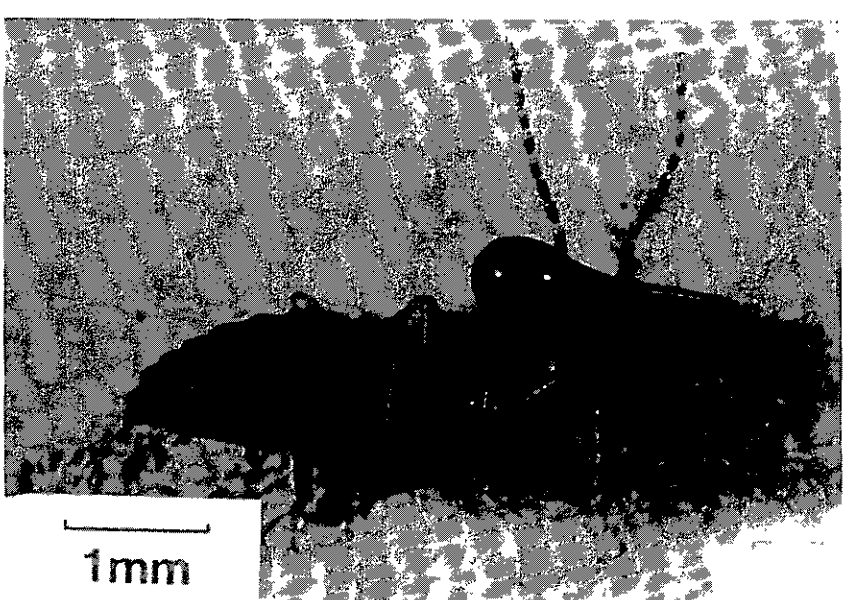


FIGURE 17. *Trinervitermes rhodesiensis*, minor soldier, lateral.


FIGURE 18. Bifiditermes sibayiensis.

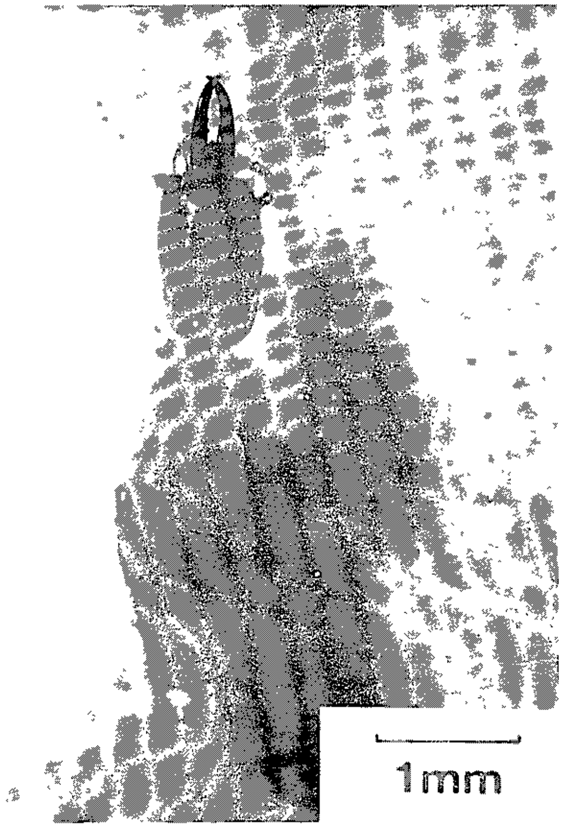


FIGURE 19. Microcerotermes species B.


FIGURE 20. Microcerotermes brachygnathus.


FIGURE 21. Microcerotermes species C.


FIGURE 22. *Microcerotermes* species D.


FIGURE 23. *Promirotermes* sp, dorsal.

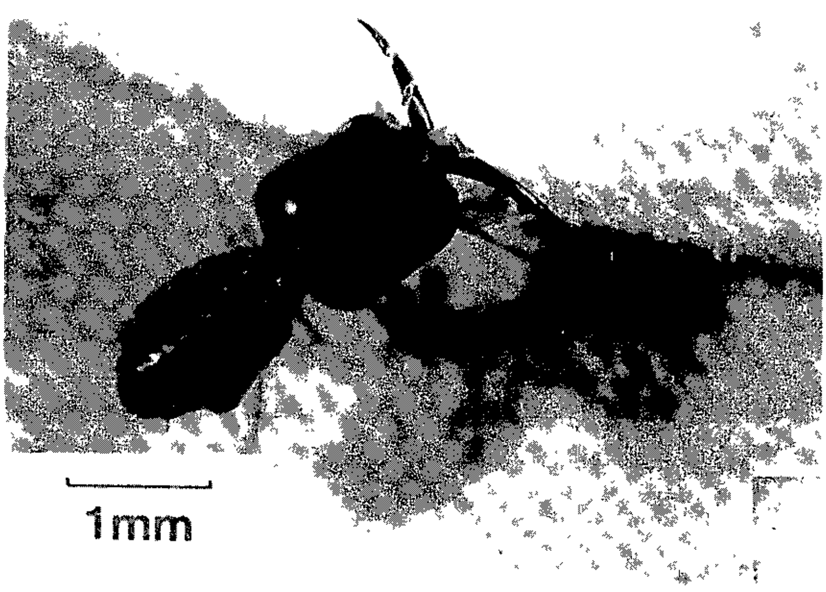


FIGURE 24. *Lepidotermes lounsburyi*, dorsal.

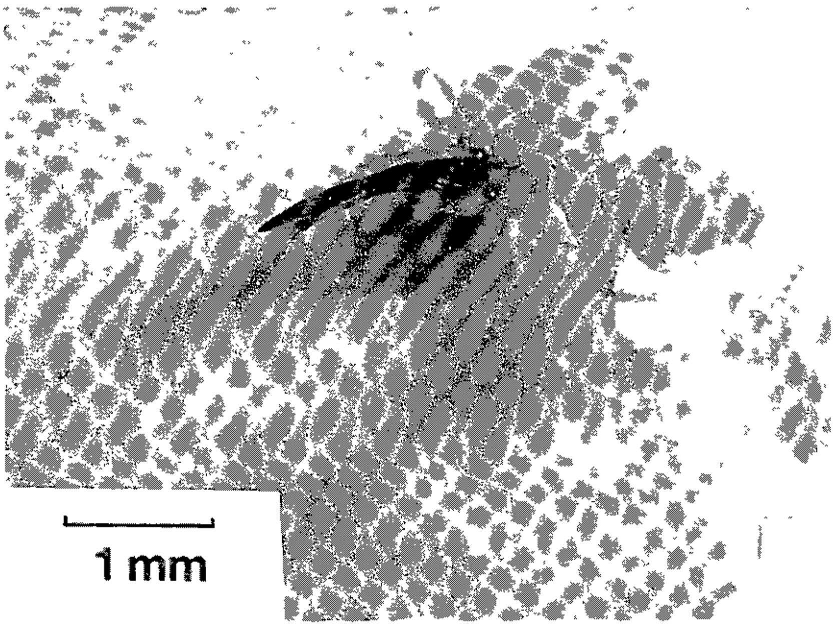


FIGURE 25. Promirotermes sp, lateral.


FIGURE 26. Lepidotermes lounsburyi, lateral.

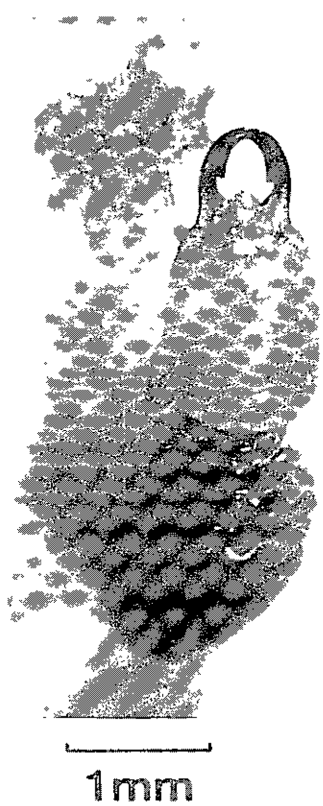


FIGURE 27. Amitermes hastatus.

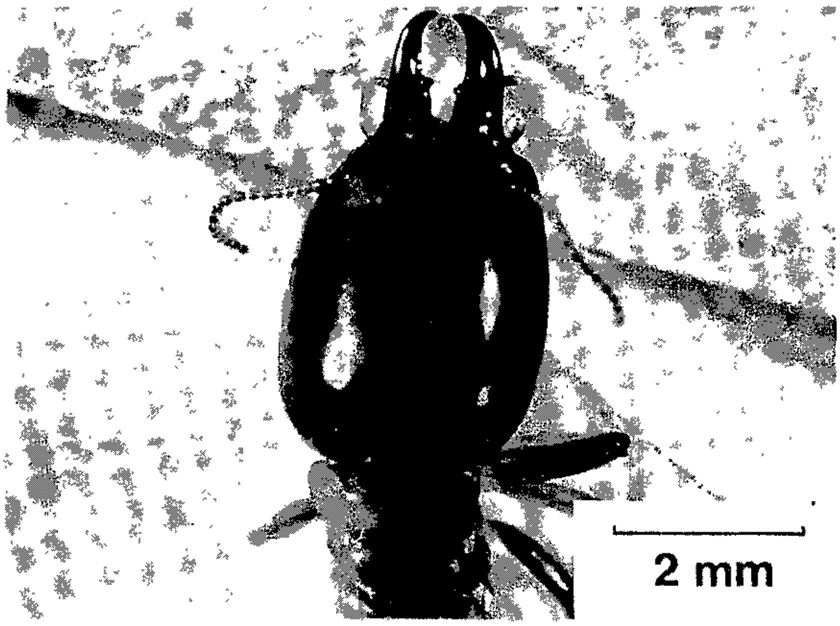


FIGURE 28. Odontotermes badius.


FIGURE 29. Microtermes sp, probably albopartitus.


FIGURE 30. Allodontermes rhodesiensis.

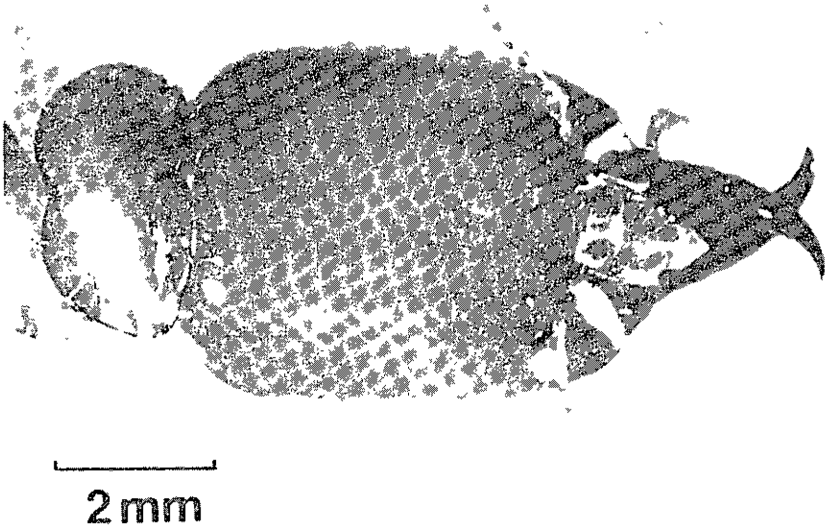


FIGURE 31. Macrotermes natalensis, major soldier, dorsal.

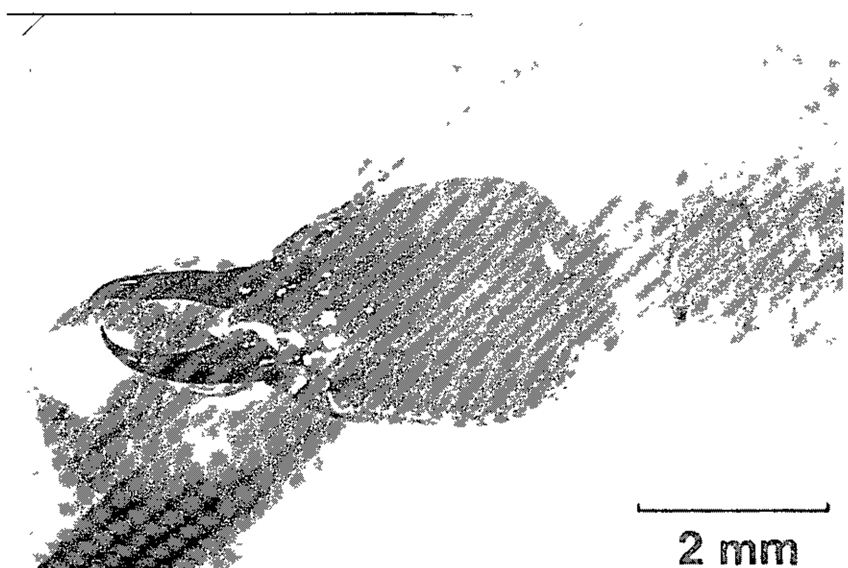


FIGURE 32. Macrotermes natalensis, minor soldier, dorsal.

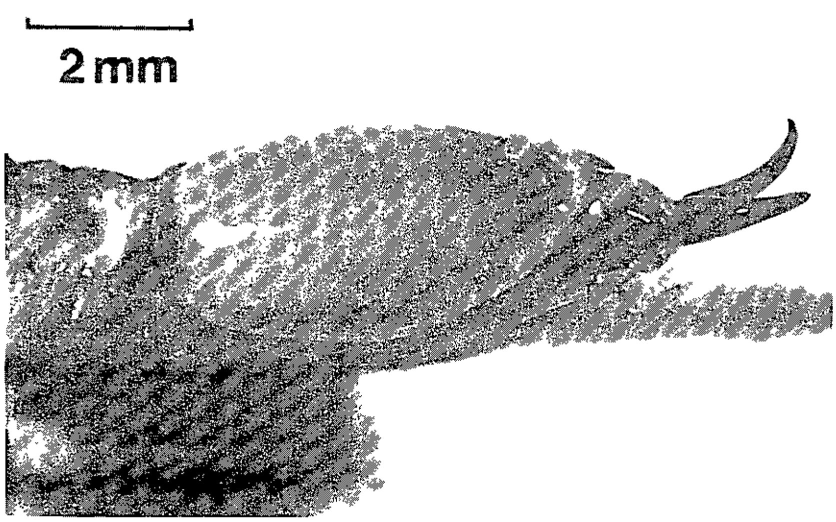


FIGURE 33. Macrotermes natalensis, major soldier, lateral.

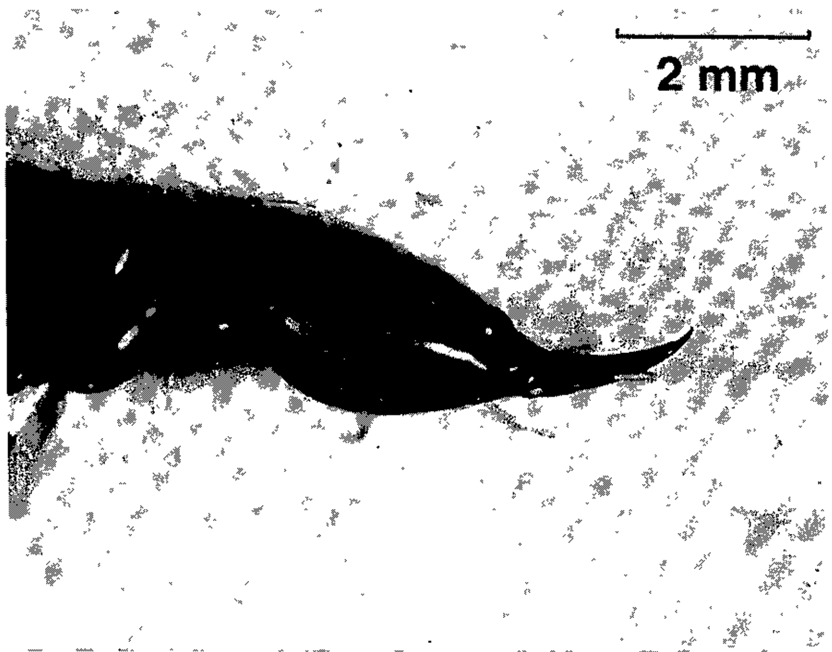


FIGURE 34. Macrotermes natalensis, minor soldier, lateral.


FIGURE 35. Cubitermes muneris, dorsal.

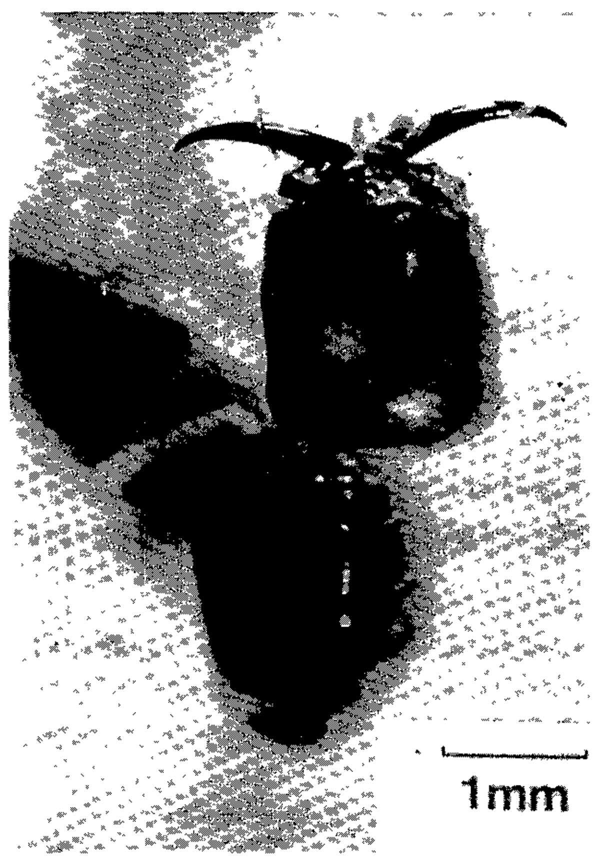


FIGURE 36. Cubitermes testaceus, dorsal.

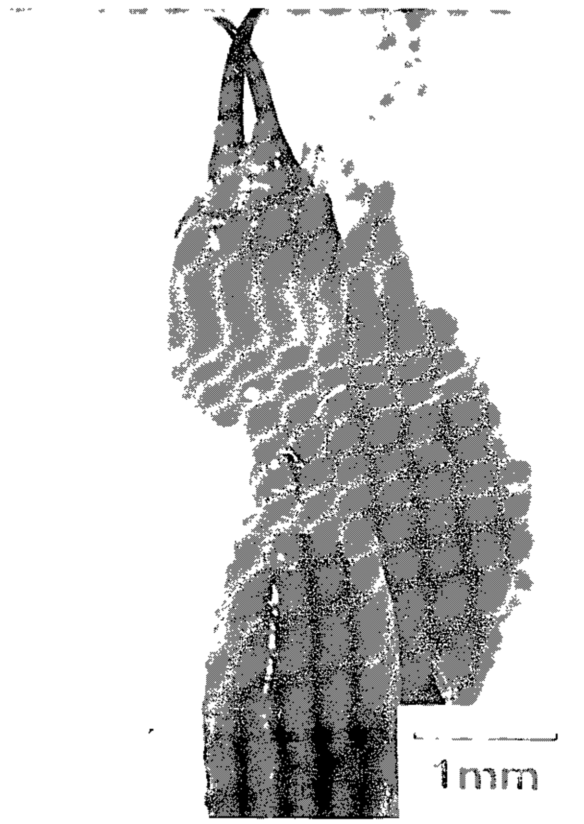


FIGURE 37. Cubitermes pretorianus, dorsal.


FIGURE 38. Cubitermes muneris, lateral.


FIGURE 39. Cubitermes testaceus, lateral


FIGURE 40. Cubitermes pretorianus, lateral.

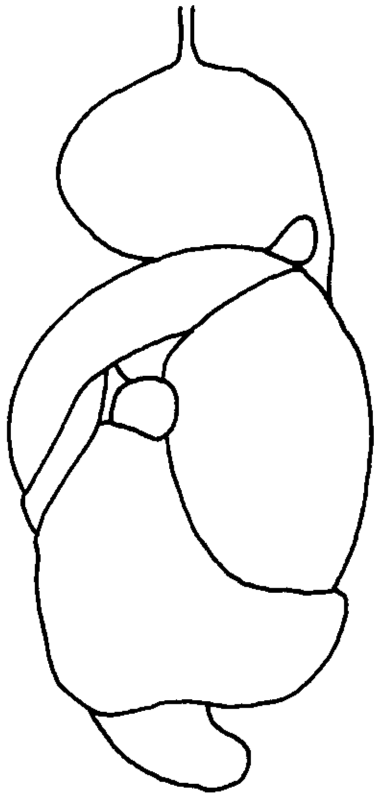

FIGURE 41. Appearance of gut in ventral view of abdomen of the soil-feeding termite Adaiphrotermes choanensis (Fuller).

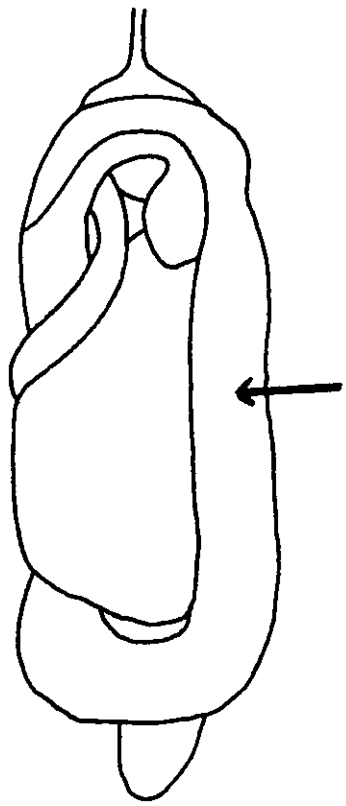

FIGURE 42. Appearance of gut in ventral view of abdomen of the soil-feeding termite Cubitermes oculatus (Silvestri).

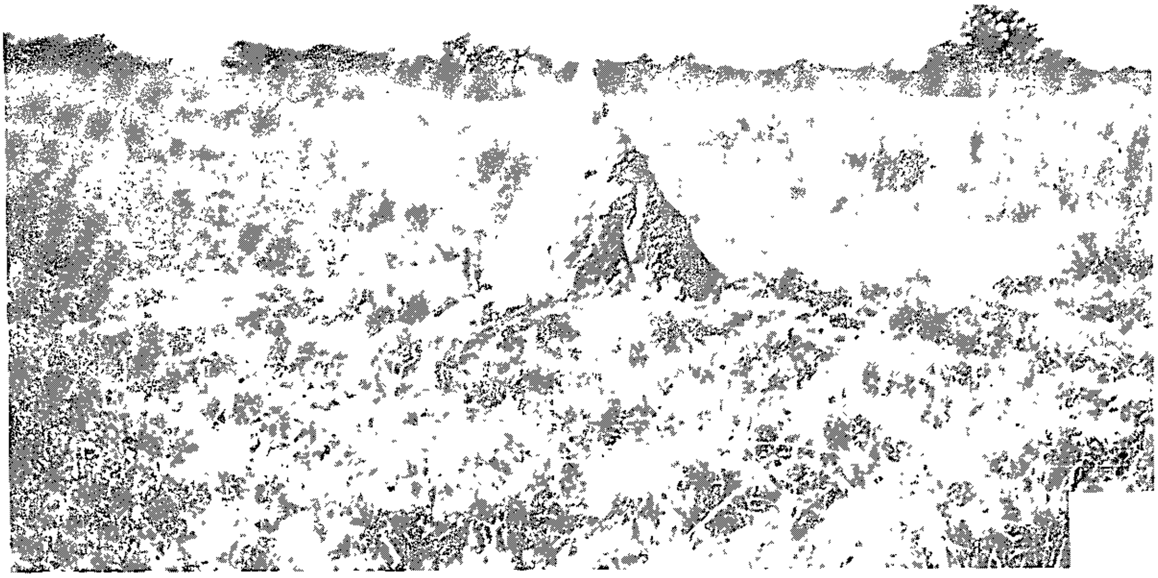

FIGURE 43. Live mound of Macrotermes natalensis.

FIGURE 44. Dead, tunnelled mound of Macrotermes.

FIGURE 45. Plastering by Macrotermes natalensis on grass for foraging.

FIGURE 46. Plastering by Odontotermes badius on tree for foraging on bark.

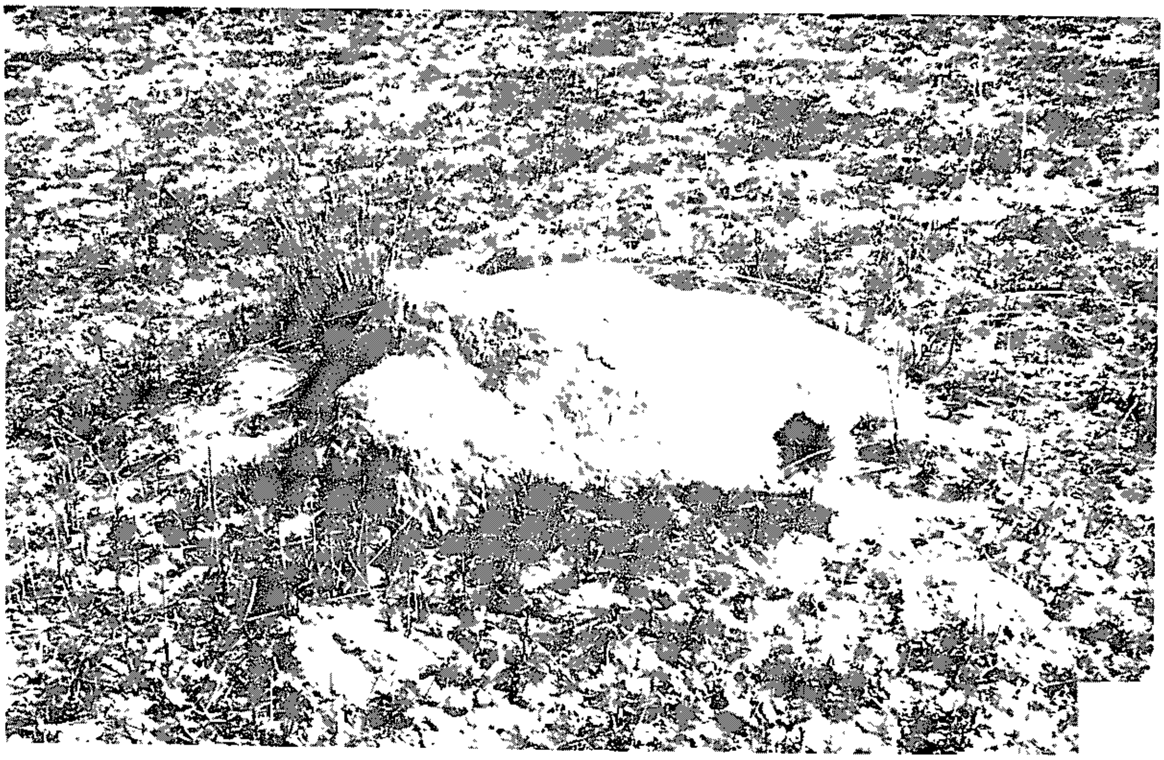

FIGURE 47. Mound of Trinervitermes rhodesiensis.

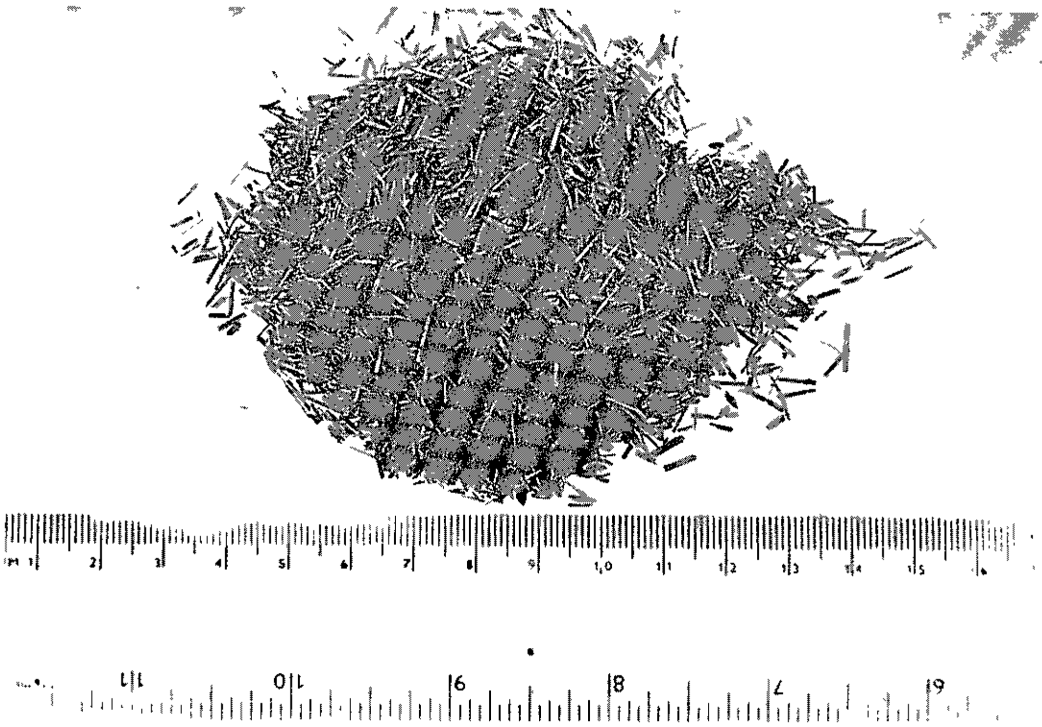

FIGURE 48. Stored forage from small mound of Trinervitermes rhodesiensis.

FIGURE 49. Mound of Amitermes hastatus.

FIGURE 50. Mound of Cubitermes pretorianus.

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