Architecture and morphogenesis in the mound of *Macrotermes michaelseni* (Sjöstedt) (Isoptera: Termitidae, Macrotermitinae) in northern Namibia

J Scott Turner

Department of Environmental & Forest Biology, State University of New York, College of Environmental Science & Forestry, Syracuse, New York 13210, U.S.A.; e-mail: jsturner@mailbox.syr.edu

The mounds of *Macrotermes michaelseni* (Sjöstedt) in northern Namibia have a characteristic architecture, being divided into three structurally distinct components: a central cone-shaped mound, topped by a tall, thin spire which tilts northward at an angle similar to the sun's average zenith angle, and a broad outwash pediment that results from erosion off the mound. Internally, the mound is permeated by a complex network of tunnels that can be divided into three broad types: a capacious central chimney that extends upward through the center of the mound from the colony up to the apex of the spire; a vertically-biased network of surface conduits that lies roughly one to two cm below the surface, and an interweaving network of lateral tunnels that connect the chimney and surface conduits. A model of mound morphogenesis is proposed which accounts for most of these structural features, and which points toward a general model for the relationship between mound architecture and social homeostasis among the macrotermitine termites.

INTRODUCTION

The mounds of the macrotermitine termites of the genus *Macrotermes* Holmgren, 1909, are one of southern Africa's most remarkable landscape features. These structures are common throughout a variety of habitat types, occurring at densities of roughly one to four per hectare (Abe & Darlington 1985; Grassé & Noirot 1961; Pomeroy 1977; Ruelle 1964, 1985). In some regions, these mounds can attain heights of several metres. In Namibia, the genus is represented by four species namely: *Macrotermes natalensis* (Haviland, 1898), *M. subhyalinus* (Rambur, 1842), *M. vitrialatus* (Sjöstedt, 1899) and *M. michaelseni* (Sjöstedt, 1914), with their combined ranges occupying most of the country to the north and east of the 200 mm mean annual rainfall isohyet, which runs roughly from Mata Mata in the southeast to the Ruacana Falls in the northwest (Coaton & Sheasby 1972; Ruelle et al. 1975). This range encompasses most of the arid Savanna Biome in Namibia, as well as some marginal areas of the Nama Karoo Biome.

In the case of *M. michaelseni*, the mound itself is not a habitation for the colony. The colony proper, *i.e.* the locations where the queen, workers and fungus gardens reside, is situated below the mound, occupying a spherical volume roughly 1.5-2 m in diameter (Darlington 1987). Given the prodigious task of constructing the mound, it is worth asking why the termites should build such a structure if not to live within? Currently, most entomologists view the mound as playing some rôle in the regulation of the colony environment, such as its temperature, humidity or the concentration of respiratory gases (Darlington 1987; Lüscher 1956, 1961; Wilson 1971). The mound does this supposedly by promoting ventilation of the colony, and the various mound architectures among the macrotermites seem well suited to particular ventilatory mechanisms (Darlington 1987; Lüscher 1956, 1961; Ruelle 1964). For example, completely enclosed mounds, such as those constructed by *Macrotermes natalensis* or *M. michaelseni*, are permeated with a network of passageways that are seemingly organized to capture energy dissipated from
colony metabolism, and to use it to drive a circulatory flow of air within the mound (Darlington 1985, 1987; Lüscher 1956, 1961; Wilson 1971). Other mounds, such as those commonly built by *M. subhyalinus*, have large diameter openings, sometimes at the tops of vertical chimneys. These presumably capture wind energy to drive air through the colony in a one-way flow (Darlington 1984, 1987; Ruelle 1964; Weir 1973), by a mechanism known as induced flow (Vogel 1978; Vogel & Bretz 1972).

This neat correspondence between mound structure and function implies that termites construct mounds according to a certain plan, and that natural selection has refined this plan so that mounds have the ‘proper’ architecture for the particular ventilatory mechanism they employ. This approach is fraught with difficulty, though, in part because it implies the mound to be the superorganismal analogue of phenotype, with all the attendant difficulties and ambiguities that are inherent in the superorganism concept (Wilson 1971). The challenge for students of social insects is to explain, in a reasonably reductionist way, how mound architecture and function arise, and in the context of the rather limited repertoire of behaviours that workers can bring to the construction of the mound.

As part of a broader exploration of the respiratory function of termite mounds, I have undertaken a detailed examination of the internal structure of the mounds of *Macrotermes michaelseni* (formerly *mossambicus*: vide Ruelle 1975) in northern Namibia. Although the structure of the *M. michaelseni* mound has been described elsewhere (Darlington 1986), descriptions of mound architecture among the macrotermites have, in the interests of descriptive clarity, tended to omit a great deal of the structural complexity of these mounds (Darlington 1984; Inoue et al. 1997; Lüscher 1956, 1961; Ruelle 1964). The mound is a complex structure, however, and I have taken the approach in this paper that this complexity must be part of a full understanding of basic questions of mound morphogenesis and of the link between mound structure and function.

**Figure 1.** Location of the study site. The location of the farm, Namatubis, is indicated by a filled star.

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**MATERIALS AND METHODS**

The study area

The study area was located in northern Namibia, on a private farm roughly 22 km north of the town of Outjo, Outjo District, Kunene region (Figure 1). The farm, Namatubis, consists of several fenced camps, each roughly 300 ha, used for rotational grazing of cattle and domesticated game. The study area was located on one of these camps, 289 ha in extent, centered roughly at the coordinates 16°4.50’E, 19°59.05’S. The habitat is characterized by Coaton & Sheasby (1972) as mopane savanna, dominated by *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Leonard (Fabaceae) intermixed with other trees, including *Acacia tortillis* (Forssk.) Hayne, *Acacia erioloba* E. May., *Acacia mellifera* (Vahl) Benth., *Mundulea sericea* (Willd.) A. Chev. (Fabaceae), *Croton gratissimus* Burch. (Euphorbiaceae), *Petalidium engleranum*, (Schinz). (Acanthaceae), and *Ximenia americana* L. (Olacaceae). The terrain is flat, with sandy red soil overlying a shallow calcareous base which rises occasionally to the surface as chalky
Survey methods and general measurement of mound shape and size

A systematic survey of mounds on this camp was conducted which fixed each mound’s location and recorded simple measures of mound size and shape. The survey was carried out by dividing the camp into 80 north-south corridors, 0.05° of longitude wide (roughly 92 m), and 0.2° of latitude deep (roughly 368 m). Demarcation points for each corridor were located using a hand-held global positioning system (GPS) receiver (Garmin GPS II). The survey was carried by a team of four to six volunteers, who swept locating each mound and fixed each mound’s location and measured its size. Size measurements included the mound’s basal width along its north-south axis, $d_b$, and the mound’s height, $z_M$. Both were measured indirectly, according to the following procedure (Figure 3). One volunteer, the instrument operator, was stationed at some convenient distance to the east or west of the mound (A), whichever afforded the easier access and greater visibility. Another volunteer, the staff holder, held a vertical staff at either the north or south base of the mound (B or C). The staff was equipped with a sound reflecting target which was aimed at the instrument operator. Distance from the instrument operator to the staff (segment AB or AC) was then measured using an ultrasonic range finder. The compass heading from the instrument operator to the staff holder (angles $\alpha$ or $\beta$) was also measured using an electronic sighting compass. The procedure was then repeated for the opposite side of the mound. Once distances

![Figure 2. Detailed map of the camp where the studies were carried out, and the locations of the mounds of *Macrotermes michaelseni* residing therein. The heavy dotted lines indicate fence lines. The fine solid lines indicate the quadrats used in the censusing sweeps. Locations of individual mounds are indicated by open diamonds. Water points are indicated by well towers. The sighting disk symbols indicate base points for the GPS receiver.](image-url)
(segments AC and AB) and directions (α or β) to the north and south bases of the mound was measured, the instrument operator then measured the angle (angle δ) to the mound’s apex, E, using a sighting angle meter. From these measurements, basal diameter (segment BC) and height of the mound (segment A’B) could be calculated trigonometrically. The angle γ was calculated as the difference in compass directions to points C and B:

$$\gamma = |(\alpha - \beta)| \quad [1]$$

The basal diameter, BC, was calculated using the Law of Cosines:

$$BC = \sqrt{(AC^2 + AB^2 - 2 \cdot AC \cdot AB \cdot \cos \gamma)} \quad [2]$$

The height is estimated from the angle δ, the distance DF, and the distance from the ground to the eyes of the observer, AD. The distance DF is estimated from the angle ε, which is calculated from the law of sines:

$$\sin \epsilon = \frac{AC \sin \gamma}{BC} \quad [3]$$

The length of segment DF is equivalent to the distance A’A, and is estimated from the law of sines as the bisector of the basal diameter, segment CB:

$$DF = CB \sin \epsilon / 2 \sin (\delta/2) \quad [4]$$

The length of segment EF is then estimated using the trigonometric identity:

$$EF = DF \tan \delta \quad [5]$$

Height, A’E is then the sum:

$$A’E = AD + EF \quad [6]$$

The mounds of *Macrotermes michaelseni* exhibit a pronounced northward orientation, both in the tilt of the spire and in the skew of the conical base. To quantify this, the azimuth and zenith of the mounds were measured. Azimuth is the heading on the horizon to which the mound points. Zenith is the angle of tilt from the vertical. To estimate azimuth, an observer stood roughly 10 m to the north of the mound and moved to the east or west until the mound profile seemed to the observer to be the most symmetrical. The azimuth was then estimated as the complement of the compass heading from the observer to the apex of the mound. Two methods were used to estimate zenith. In method A (Figure 4), the mound’s basal diameter, $d_b$, was estimated
from the circumference of the base of the mound, $c_b$, measured using a steel tape and the formula:

$$d_b = c_b / \pi.$$  \[7\]

Measurements were then made of the distances from the base of the mound to its apex at the north and south sides, $l_N$ and $l_S$, respectively. The three sides, $d_b$, $l_N$, and $l_S$, form a triangle that corresponds to the profile of the mound when viewed from the east or west. The angles $\alpha$, $\beta$ and $\gamma$ can be estimated from the law of cosines:

$$\cos \alpha = \frac{l_N^2 + l_S^2 - d_b^2}{2 l_N l_S} \quad [8a]$$

$$\cos \beta = \frac{l_N^2 + d_b^2 - l_S^2}{2 l_N d_b} \quad [8b]$$

$$\cos \gamma = \frac{l_S^2 + d_b^2 - l_N^2}{2 l_S d_b} \quad [8c]$$

The zenith is indicated by the angle $\phi$ formed by the bisector of angle $\alpha$ and $d_b$, which forms a new triangle with angles $\beta$, $\alpha/2$ and $\phi$. The zenith, $\theta$ is readily calculated as:

$$\theta = 90 - \phi = 90 - (180 - \beta - \alpha/2) \quad [9]$$

Method B for estimating the zenith used a pivoting sighting protractor, consisting of a 2 m long staff of wood with a wooden strip mounted on it so that the strip could pivot about a known point (Figure 5). An observer was stationed roughly 20 m from the east or west face of the mound, whichever offered the clearest view. Another pair of volunteers was stationed about midway between the observer and mound. One of these volunteers held the staff vertically, maintaining its position with the aid of a spirit level. The other volunteer adjusted the pivot until the observer agreed that it paralleled the spire. The zenith was then estimated using measurements from the protractor. Two lengths, designated $l_v$ and $l_A$, were marked lengths on the staff and pivot, respectively, and with the pivot point as their common origin. The distance between the end points of $l_v$ and $l_A$ was then measured using a steel tape measure ($l_T$). The zenith $\theta$ is then estimated from the law of cosines:

$$\cos \theta = \frac{l_A^2 + l_V^2 - l_T^2}{2 l_A l_V} \quad [10]$$

**Mound sectioning methods**

A mound’s internal structure was assessed by sectioning it in a series of flat sections, similar in principle to the sectioning of a tissue block by a microtome. Three types of sectioning were undertaken. In one, designated horizontal section, the mound was sectioned from top to the base in 10 cm horizontal slices. In the second, designated vertical section, the mound was sectioned in 10 cm vertical slices from one side to the other. The third, designated surface section, peeled away the surface in 1 cm slices at four sites located at the mound’s cardinal points. In all types of section, the exposed section face was photographed with ASA 200 slide and print film. Outlines of the mound section and of
the exposed walls of the tunnels were traced using the digitized images of the section faces, and the images analyzed as described below. To ensure proper alignment and scaling of the photographs in the sequence, fiduciary points were set as indicated below.

**Horizontal section**

One mound, about 170 cm tall, was sectioned horizontally. No fiduciary points were set in this case, but alignment of the section sequence was estimated using landmarks visible in the photographs. Each section proceeded as follows. A rough cut was first made using a trenching tool and trowel. Once the overburden of the mound above the section was removed, the exposed face was flattened and smoothed by a progressively finer series of cuts, first with the flat metal edge of a plastering trowel, and finally with a stiff brush. The exposed face was then photographed and the procedure repeated.

In the lower sections, the exposed face had to be reconstructed from several photographs reassembled into a photomontage. This, along with uncertainties in the positions of the alignment landmarks made it impossible to trace with confidence the passage of particular tunnels from one section to the next. This mound was therefore used only for qualitative description and for measurements of the tunnels and exposed faces.

**Vertical sections**

Three mounds were sectioned vertically. In one of the three, serious errors arose in the alignment of the fiduciary points and the information from this mound was therefore not used. In the remaining two, one (designated M03) was sectioned from east to west, while the other (designated M43) was sectioned from north to south. In both mounds, fiduciary points were established by setting up level and parallel reference lines on either side of the mound. The lines were leveled using a spirit line level. Parallelism of the lines was ensured by measuring the perpendicular distance between them at several points. The reference lines were supported on stakes held in place by guy lines. Errors due to stretching of the reference lines were controlled for by marking reference points on each line with brightly coloured nail varnish, which could be aligned with the stakes. Fiduciary points were marked by a small bow of flagging tape tied loosely to each reference line so that the bow could slide along it and be aligned with the cut vertical face of the mound. Parallax errors were minimized by always placing the camera at a set distance from the mound face, *i.e.* the position of the camera advanced along with the sections through the mound. Each mound face was photographed in a single frame, *i.e.* no reconstructions of the image through photomontage were necessary for these sections. However, several close-up photographs of the face were made for verification of the features in the image of the entire face.

The procedure for vertical sectioning was similar to that used in the horizontal sections, that is a rough cut, followed by progressively finer cuts until a smooth vertical face was ready for photographing. The first, or rough cut was laid out by tracing a line 10 cm behind or below the previously cut face, judged by direct measurement from the previously cut face, or with reference to the fiduciary points on the reference lines. The rough cut was made with the flat blade of a trenching tool, followed by a finer set of cuts with the flat blade of a shovel. Recalcitrant portions of the mound face were removed with a broad-bladed cold chisel and hammer. The mound face was then smoothed with the flat edge of a trowel blade, and finally ‘polished’ using a stiff brush.

**Surface sections**

Surface sections were made by ‘peeling’ the mound surface away in 1 cm layers. These dissections were intended to reveal the structure of the surface conduits that underlie the mound’s surface, and to assess their proximity to the surface, their relationship to areas of surface building, and their extent.

Surface sections were made at the cardinal points on the mound surface, roughly 1.5 metres above ground level. The cardinal points were fixed by sighting with an electronic compass. At each cardinal point, a 40 cm by 40 cm square was laid out on the mound surface using a steel tape and chalk line. Fiduciary points were set at points just outside alternate corners of the square, and marked with a piece of flagging tape held in place by nails driven into the mound. A photograph was then taken of each mound surface. Soil was then scraped off to a depth of 1 cm, using a narrow bladed trowel. The exposed face was then smoothed as much as possible, excess dust removed with a brush, and then photographed. This procedure was repeated twice more down to a depth of 3 cm. By this depth, the sectioning had usually penetrated well into the network of tunnels in the mound.
Analysis of images

A flat bed scanner was used to digitize the images at a resolution of 300 dpi. The digitized image was then imported into a graphics program (CorelDraw v8), and tracings made of the outlines of the mound’s exposed faces or of the exposed surface conduits. The digitized images were also used for construction of photomontages in the horizontal sections, and for making any scaling and alignment adjustments necessary. The tracings were then exported to IntelliCAD, in which the areas and perimeter lengths of the outlines of the tunnels and section faces could be measured. These measurements were: the length of the mound’s outer surface outline, \( l_m \); the section area of the exposed face, \( A_m \); the combined circumferences of the tunnels in the exposed face, \( l_t \); and the combined areas of tunnels in the exposed face, \( A_t \). From these measurements, several subsidiary measurements were calculated. Mound surface area, \( A_M \), was calculated as the summed outlines of the mound multiplied by the section thickness, \( l_s \):

\[
A_M = l_s \sum l_m
\]  

[11]

Mound volume, \( V_M \), is similarly calculated from the mound section areas:

\[
V_M = l_s \sum A_m
\]  

[12]

Tunnel surface area, \( A_T \), was estimated from the tunnel outline lengths:

\[
A_T = l_s \sum l_t
\]  

[13]

and tunnel volume, \( V_T \), was estimated from the summed tunnel areas in the sections:

\[
V_T = l_s \sum A_t
\]  

[14]

Rotation of the spire and subsequent effects

To assess the effect of tilt angle on the distribution of temperature and insolation in the spire, spires of two mounds were detached and rotated by 180°. The procedure for rotating the spire was as follows. A mound was chosen, and the cardinal points marked on the spire’s surface using a sighting compass. The cardinal points were marked using nails driven into the spire and tagged with flagging tape. Once the cardinal points were marked, the spire was wrapped in nylon webbing to keep it from crumbling during the operation. A horizontal cut was then made through the spire with a bow saw, detaching it from the rest of the mound. The detached spire was then rotated 180° around its base, as determined by the formerly marked southern cardinal point coming into alignment with a sighting compass stationed to the mound’s north. The spire was then unwrapped and left to stand for twenty-four hours. By this time, the mound had ‘healed’, with damage to the spire and the cut through it sealed by the workers.

Three mounds were treated in this manner. One, CV, served as a control, and was located in a sunny and open situation. A second, T05, had its spire rotated, and was located in a sunny and open situation similar to mound CV’s. A third, T06, also had its spire rotated, but was located in a shady sheltered situation. During the course of a sunny day, surface temperatures and incident radiation were measured using a surface thermocouple and light meter, respectively. The three mounds’ temperatures and insolation at each cardinal point were measured every thirty minutes from about 10:30 AM to 4:30 PM, with measurements taken sequentially from the three mounds, i.e. from CV first, then from T05, then from T06. The mounds were close enough to one another so that all the measurements could be made over a span of 10 minutes. Data were analyzed using a repeated measures analysis of variance, with
RESULTS

External structure of the mound

The *M. michaelseni* mound typically consists of three structurally distinct parts (Figure 6): a cone-shaped base, from which a broad outwash pediment fans, and which is topped by a more cylindrical spire that commonly rises to about twice the height of the base. Within this type, though, there is considerable diversity of shape. Most commonly, the variation comes in how distinct the spire is compared to the conical base. In many mounds, the spire is nearly cylindrical, and contrasts strongly with the sloping walls of the conical base. In other mounds, the base merges more or less imperceptibly into the spire, so that the mound’s overall shape is that of a skewed cone.

The texture of the mound’s surface can usually be differentiated into two distinct types: a relatively smooth and hard surface which has been exposed to smoothing by wind and water erosion, and a highly friable and rough surface that is the site of recent building activity. In roughly 10% of the mounds, however, the surface was more uniform in texture, comprised of very loose soil that flaked when dry. This type of mound was usually darker in colour than the more common reddish sands that comprised most mounds, perhaps as a result of a different soil type being brought up from a different soil horizon at the mound’s location.

The mound is covered to varying degrees by areas of new building (Figure 7). New building is evidenced by an increased surface roughness of the mound, or if it is fresh enough, by a noticeable dampness. There seem to be two types of new building. The spire usually shows signs of being recently worked, most intensely at the spire’s apex. Sites of new building also frequently occur at the sloping sides of the mound’s conical base. These sites of new building are dome-shaped, seeming to billow out from the side of the mound. These sites of new building, designated ‘domes’, are often associated with deep tunnels that extend downward and centripetally to the colony, and with expansive galleries located just below the surface (see below). Less frequently, one finds ‘moundlets’ of new building that occur at some distance from the conical base (Figure 8).

The mounds are frequently associated with trees or other vegetation, even to the extent that trees are found embedded within them. Of a sample of 27 mounds, nine were adjacent to a tree or surrounded by woody vegetation that could afford the mound some significant shading, and a further eleven had

<table>
<thead>
<tr>
<th>Height (m)</th>
<th>Estimated volume (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
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<tr>
<td>Standard deviation</td>
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<tr>
<td>Maximum</td>
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</tr>
<tr>
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<tr>
<td>Median</td>
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</tr>
<tr>
<td>1st Quartile</td>
<td>1.82</td>
</tr>
<tr>
<td>Minimum</td>
<td>0.68</td>
</tr>
</tbody>
</table>

Table 1. Distribution of heights and estimated volumes for 303 censused mounds of *Macrotermes michaelseni* in the Namatubis study site.
trees embedded within them. Despite the close association of mounds with trees, however, the colonies do not appear to use the trees for structural support: seven mounds in the sample stood on their own, with no association at all with woody vegetation. Furthermore, the trees did not appear to serve as significant sources of food. Although bark was frequently stripped from the portions of the trunk embedded within the mound, the embedded trees appeared to be in robust health, suggesting the cambium was left unharmed *vide* Figure 6). Indeed, the trees seem to derive some benefit from the association - in the dry season, trees embedded within mounds frequently supported the only green vegetation on site, with most of the other trees having shed their leaves (S. Turner pers. obs.). The association of trees and mounds probably stems from greater survivorship of natal colonies in the shade provided by these trees or bushes.

*Population density and mound sizes*

The study camp supports a total of 303 mounds over an extent of 289 ha, yielding a population density of 1.045 mounds ha$^{-1}$. The modal distance to mounds' nearest neighbours is roughly 70 m, spanning a range of zero (two mounds immediately adjacent to one another) to 148 m. The average number of mounds in a 0.1'×0.1' quadrat (roughly 3.43 ha) was 3.49, with a variance between quadrats of 3.35. The distribution of mounds per quadrat (Figure 9) was not significantly different from a Poisson distribution ($\chi^2 = 5.23, P = 0.823$), and the similarity of mean and variance of mounds per quadrat indicates a random distribution of mounds, with no evidence of clumping or repulsion of one mound with respect to another. On average, mounds in this sample were 2.16 m high, spanning a range of 0.7 m to 3.75 m (Table 1). Volumes were estimated from the measurements of basal diameter and height, assuming the mound approximated a cone. Estimated mound volumes averaged 3.41 m$^3$, spanning a range from 0.13 to 19.08 m$^3$ (Table 1).

*Mound orientation*

Measurements estimating azimuth and zenith by Method A were carried out on a subsample of 34 mounds on site. Among these mounds, the conical base averaged 7.5 m in circumference, which corresponds to a basal diameter of 2.4 m, assuming

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**Figure 8.** Two examples of accessory moundlets. *a.* A mound with a very narrow conical base and a moundlet emerging in the outwash pediment. *b.* Close-up of a moundlet adjacent to the mound.
A circular base (Table 2). At half-height, the circumference is 42% that of the base. There is a marked asymmetry between the lengths of the north and south faces of the mound, \( l_N \) and \( l_S \). The south face was approximately 11.5% longer than the south face (Table 2), reflecting the mound's northward tilt. A paired \( t \)-test shows the difference to be significant (one-tailed \( p = 0.0417 \)). The mound's average zenith is estimated by this method to be 19.6° N (Table 3). Method B, which estimates zenith more directly, gives an average value of 18.2° N (Table 3). By either method, a Student's \( t \)-test shows the mound's zenith to not significantly different from the average zenith angle of the sun through the year, which is 19.98° at this latitude (For method A, \( p = 0.926 \), and for method B, \( p = 0.161 \)). The mounds' average azimuth is biased about 16° to the west (Table 3): this bias may arise from the inclusion in the sample of one young mound which was oriented to the south-west (Table 3). The median azimuth is 3.7° W. Both zenith and azimuth exhibit considerable variation (Table 3).

**Horizontal sections**

The mound chosen for horizontal section was roughly 170 cm tall, and was sectioned down to about 20 cm above ground level, that is, just to the bottom of the conical base. The horizontal cross section ranges from elliptical in the spire to circular at the base (Figure 10). In the spire (Figure 10, sections +140 to +90), the tunnels are few in number, and branch and merge repeatedly to form a ramifying network of vertically-oriented tunnels. At the conical base (Figure 10, sections +80 to +20), the tunnels of the spire begin to branch laterally. In the centripetal direction, these branches merge into a large elongate open space in the center of the mound, designated the chimney (‘ch’ in Figure 10). Centrifugally, the branches ramify into a series of radial channels (‘rc’ in Figure 10), which eventually project downward and centripetally. Later excavation showed the colony’s fungus gardens to be located about 40 cm below the lowest horizontal section.

### Table 2. Linear measurements of 34 mounds of *Macrotermes michaelseni* at the Namatubis site. Basal circumference is measured at the boundary between the outwash pediment and the conical base of the mound. South and north face lengths are measured from the base of the conical mound to the apex at the respective cardinal points. Half-height circumference is measured at the point halfway between the apex and base of the conical portion of the mound.

<table>
<thead>
<tr>
<th></th>
<th>Basal circumference (m)</th>
<th>Half height circumference (m)</th>
<th>South face length (m)</th>
<th>North face length (m)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>11.80</td>
<td>6.85</td>
<td>5.60</td>
<td>4.90</td>
</tr>
</tbody>
</table>

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**Figure 9.** Distribution of mound density in the Namatubis study camp. Solid bars represent the observed numbers of quadrats of the indicated density. Open bars indicate the expected distributions of mound densities.
The sectioned portion of this mound occupied about 0.9 m$^3$, of which 18% on average was occupied by tunnel (Table 4). This figure can only be approximate, given the incomplete coverage of the photographs. The ratio of the mound’s surface area ($A_M$) to its volume ($V_M$) is roughly 4.3 m$^{-1}$, while the ratio of tunnel surface area ($A_T$) to tunnel volume ($V_T$) was roughly 10 times higher, 44.1 m$^{-1}$. This expanded tunnel area presumably indicates the highly folded structure of the mound’s internal air spaces.

The sizes of the tunnels and mound show a two-phase distribution with height, corresponding roughly to the spire and conical base (Figure 11). In the spire, about 25% of the volume of the mound is occupied by tunnel, while in the base, only about 16% of the mound volume is so occupied. This is reflected in the distribution of areas and linear dimensions in the various horizontal sections. In both the spire and conical base, the section areas of the mound, $A_m$, and tunnels, $A_t$, converge slightly with respect to height: in other words, tunnels come to occupy a larger proportional volume of the mound in the higher sections of the mound (Figure 11a). Interestingly, the circumferences of mound sections, $l_m$, and tunnel sections, $l_t$, converge steeply in the spire, but not in the conical base (Figure 11b). This may indicate the more complicated shapes of the tunnels in the portion of the mound experiencing the most recent and intense building.

### Table 3. Distributions of zenith and azimuth angles of mounds of *Macrotermes michaelseni* mounds at the Namatubis site.

<table>
<thead>
<tr>
<th></th>
<th>Zenith angle (degrees), (Method A)</th>
<th>Zenith angle (degrees), (Method B)</th>
<th>Azimuth angle (degrees)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>19.6 N</td>
<td>18.2 N</td>
<td>16.8 W</td>
</tr>
<tr>
<td>N</td>
<td>32</td>
<td>37</td>
<td>32</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>14.7</td>
<td>7.3</td>
<td>36.2</td>
</tr>
<tr>
<td>Minimum</td>
<td>5.9 S</td>
<td>4.6 S</td>
<td>153.7 W</td>
</tr>
<tr>
<td>1st quartile</td>
<td>10.0 N</td>
<td>13.6 N</td>
<td>33.7 W</td>
</tr>
<tr>
<td>Median</td>
<td>14.1 N</td>
<td>18.8 N</td>
<td>3.7 W</td>
</tr>
<tr>
<td>3rd quartile</td>
<td>23.7 N</td>
<td>23.0 N</td>
<td>6.3 E</td>
</tr>
<tr>
<td>Maximum</td>
<td>64.2 N</td>
<td>33.1 N</td>
<td>16.3 E</td>
</tr>
<tr>
<td>Expected</td>
<td>19.98 N (latitude)</td>
<td>19.98 N (latitude)</td>
<td>0.0</td>
</tr>
<tr>
<td>Z</td>
<td>0.450</td>
<td>0.926</td>
<td>0.996</td>
</tr>
</tbody>
</table>

The two vertically-sectioned mounds differed slightly in size, with M43 being about 4% taller than M03, although M43 was about 50% more voluminous (Table 5). As in the horizontal sections, the volume of mound occupied by the tunnels was small, roughly 28% for M03 and 16% for M43. The ratio of surface area to volume, $A_s/V_M$, was similarly small for the mound (2.59 m$^2$ for M03, 2.30 m$^2$ for M43), and remarkably large for the tunnels, $A_t/V_T$ (36.6 m$^2$ for M03, 42.5 m$^2$ for M43).

As in the horizontal sections, the vertical sections revealed a complicated reticulated network of tunnels within the mound, although the vertical sections reveal them with more structural detail. Outlines of the tunnels, exposed colony and mound are given in Figures 12-14 for M03 and Figures 15-17 for M43.

Perhaps the most striking feature of both mounds is the large vertical chimney (‘ch’ in Figures 12-17), which corresponds to the elongate tunnel that appeared in the lower levels of the horizontally-
Figure 10. Tracings of a horizontally sectioned mound of *Macrotermes michaelseni*. The solid outlines indicate mound surface and tunnel outlines that were visible in the photomontage. Dotted outlines indicate hypothetical mound surface that could not be seen in the photomontage. The scale bar represents 30 cm. Labels refer to height of the sectioned face above ground level. Label ‘rc’ refers to a radial tunnel, ‘sc’ refers to a surface conduit, and ‘ch’ refers to the chimney.
sectioned mound (‘ch’ in Figure 10). In the vertical sections, the chimney opens just above the colony, and extends upward into the apex of the mound (Figure 18). Extensive lateral tunnels connect the air space of the chimney to air spaces throughout the mound. In some instances, clear continuous pathways can be seen between the chimney and the surface tunnels (Figure 12, 130 cm; Figure 13, 150 cm, 160 cm; Figure 16, 220 cm). Near the top of the colony, the fungus gardens seem to be serviced by numerous tunnels that appear to wrap around the margins of the colony, merging eventually to form the chimney (Figure 12, 120 cm to 130 cm; Figure 13, 140 cm, 180 cm, 190 cm; Figure 14, 210 cm to 250 cm; Figure 17, 230 cm to 250 cm).

Another common feature of these two mounds is an open chamber that forms at the top of the chimney (Figure 12, 120 cm to 130 cm; Figure 16, 170 cm to 190 cm). This chamber also connects extensively with the surface conduits that run under the outer surface of the mound (Figure 12, 130 cm; Figure 13, 140 cm to 150 cm; Figure 16, 130 cm to 140 cm, 180 cm to 210 cm). The cap of the mound and its associated chamber varies in degree of openness and shape from mound to mound (Figure 19). In many mounds, the cap is rounded, and is covered by a thin friable layer of soil (Figure 19a). In others,
the cap is strongly peaked, and the wall separating the upper chamber from the air is thicker, although seemingly still very porous (Figure 19b). Among other mounds, the chamber space is more disorganized and difficult to trace, with numerous finely divided subchambers and tunnels (Figure 19c).

Conduit forms on the lower part of the mound’s west face (Figure 16, 180 cm), breaking up into numerous small tunnels at 190 cm, and coalescing again at 200 cm through 220 cm.

Both sectioned mounds had extensive networks of large calibre surface tunnels, designated surface conduits, which underlie the entire surface of the mound. For example, an extensive surface conduit underlies the upper two thirds of the north face of M03 (Figure 12, 120 cm), and it can be followed in subsequent sections as it extends downward and to the west (Figure 12, 130 cm; Figure 13, 140 cm to 150 cm). Other surface tunnels appear on this mound’s south face, and again, one can trace the intertwining tunnels through several sections of the mound (Figure 13: 150 cm to 180 cm). Similar features are seen in M43. In this mound, an extensive surface conduit forms on the lower part of the mound’s west face (Figure 16, 180 cm), breaking up into numerous small tunnels at 190 cm, and coalescing again at 200 cm through 220 cm.

The surface conduits are separated from the outside air by a thin friable wall, similar to the thin wall separating the upper chamber from the air at the cap of the mound (Figure 20). Often, the interior surface of the conduits are pitted with small holes, roughly 2 mm in diameter. These usually underlie areas of surface building, and these probably serve as egress holes for worker termites to the surface.

A particularly interesting feature of mound construction are surface ‘boils’, which are narrowly delimited areas of apparently intense building activity. The sections through mound M43 sectioned through two surface ‘boils’ (Figures 22-23), one more extensively built than the other. The intense building activity that accompanies these ‘boils’ is evidenced by the numerous small chambers underlying the ‘boil’ (Figure 22). There is obviously transport of soil to the mound surface during the construction of a ‘boil’, because the texture and colour of the soil sometimes differs from the mound base it is built upon (Figure 21). A more developed ‘boil’ will show extensive working galleries, and the highly convoluted internal surfaces that are characteristic of intense building activity (Figure 22). A particularly interesting feature of these surface ‘boils’ are the centripetal radial channels, which appear to penetrate directly to the colony. Follow the tracings for the tunnels underling the ‘boil’ from 150 cm to 180 cm (Figure 16) - the working gallery pictured in Figure 22 is part of this series. The development of the centripetal tunnel is clearly seen in these sections. The directness of the connection is also seen clearly in Figure 23: the tunnel underlying the ‘boil’ runs straight to the colony.

Surface ‘boils’ appear to be the precursor to the dome-shaped extrusions of soil from the surface, like those pictured in Figure 7. The vertical sections reveal four series through ‘domes’ (‘d’ in Figures 12-17), two on M03, from 60 cm through 90 cm (Figure 12) and again from 190 cm (Figure 13) through 260 cm, and two on M43, from 120 cm through 140 cm (Figure 15) and again from 220 cm (Figure 16) through 320 cm (Figure 17). The last merges into a surface ‘boil’ at 330 cm to 340 cm (Figure 17). The ‘domes’ are clearly areas of intense building activity, particularly toward the surface. Note particularly the gradation from large diameter tunnels in the center of the ‘dome’ to numerous small tunnels toward the surface in the series 230 cm through 270 in M43 (Figure 17).

Figure 18. Photograph through one of the center sections of M03, showing relationship of chimney, fungus gardens and colony. This photograph corresponds to the outline at +160 cm in Figure 13.
Figure 12. Outlines of the vertically sectioned mound M03. Numbers adjacent to the outlines refer to the depth of the section face with respect to the eastern edge of the outwash pediment. Areas filled with dark gray represent the colony, visible in these sections mostly as fungus gardens. Areas filled with light gray represent mound section face. Areas filled with intermediate gray are outlines of tunnels exposed at the face. Labels as in Figure 10. The label ‘d’ refers to a ‘dome’.
Figure 13. Continuation of series of vertical sections from vertically sectioned mound M03. Conventions are as in Figure 12.
Figure 14. Continuation of series of vertical sections from vertically sectioned mound M03. Conventions are as in Figure 12.
Figure 15. Outlines of the vertically sectioned mound M43 of *Macrotermes michaelseni*. Conventions are as in Figure 12.
Figure 16. Continuation of series of vertical sections from vertically sectioned mound M43. Conventions are as in Figure 12.
Figure 17. Continuation of series of vertical sections from vertically sectioned mound M43. Conventions are as in Figure 12.
Despite the similarity of heights (within 3%), the two mounds differ substantially in volume and surface area (Table 5). Nevertheless, the ratios of mound surface area and volume ($A/V_m$) are very similar, between 2.3 and 2.6 m$^{-1}$ (Table 5). This is substantially smaller than the same ratio in the horizontally-sectioned mound (Table 4): the difference is probably due to the horizontally sectioned mound not being sectioned down to ground level, leaving out the substantial volume of outwash pediment that is included in the measurements for both the vertically sectioned mounds.

The size of tunnels in the mounds varies markedly in sections through the mound. In sections through the outwash pediment, tunnels occupied only a small proportion of both mounds (Figure 24), while in sections through the base and center of the mound show a much greater proportion of the section occupied by tunnels, reaching as high as 40% of the section volume, $V_m$. On average, the tunnels occupied 28% of the volume of M03, and about 16% of the volume of M43 (Figure 24). Comparisons of the tunnel surface area with respect to the mound surface area show a similar pattern (Figure 25). On average, the tunnel surface area, $A_T$, is roughly 3.5 to 2.8 times greater than the outside surface area of the mounds, $A_M$ (Table 5, Figure 25). Again, the absence of tunnels in the outwash pediment and their proliferation in the center are evident from the distribution of areas across the sections (Figure 25). In the sections through the outwash pediment, the proportion of the section face occupied by tunnel is visibly small. As the sections proceed through the center parts of the base and spire, the ratio of tunnel area to mound face area increases dramatically. The mound also expands the surface area of ground surface interacting with air by, on average 40% (Figure 26; Table 5). Clearly, the major expansion of ground surface occurs in the central parts of the mound. In the central portion of the mound, the expansion of ground surface is substantially above average, with a maximum ground surface expansion of about 2.3 (Figure 26).

**Surface sections**

The surface conduits form an extensive network that underlies the entire surface of the mound which is illustrated ‘peeling away’ layers of mound surface. Eight series of surface sections were made using the methods described above. A representative sample of three of these series are reproduced in Figures 27-29. A common feature of these sections is the strong vertical orientation of the surface conduits. The conduits are also quite shallowly placed, with nearly all the sections breaking into conduit at depths of only three centimetres, sometimes shallower. Surface conduits frequently are directly under regions of surface building, for example, the south-face series in Figure 27, and the west face series in Figure 28. As often, however, surface conduits are adjacent to regions of surface building, for example in the west-face series in Figure 27, or the east face series south-face.
In one section (south face of Figure 28), in which most of the surface was covered by new building, the surface is penetrated by numerous tiny holes, presumably egress holes and galleries of the newly built surface. The extent of new building on the surface sections averaged about 21%, ranging from 100% to nil (Table 6). On average, the extent of the underlying tunnels doubled for each centimetre of depth, starting at 4% of the sample area at 1 cm depth and increasing to about 20% of the sample area at 3 cm depth. The range of each measure was large, however, ranging from a maximum of about 45% of the underlying area to nil, even in sections as deep as three centimetres (Table 6). The expansion of the tunnels with depth was significant ($F_{2,95} = 7.73$, $p = 0.0008$). However, there was no discernible difference between the samples at the cardinal points, either in the extent of new building on the surface ($F_{3,28} = 1.91$, $p = 0.151$), or in the extent of the tunnels beneath ($F_{3,95} = 0.500$, $p = 0.683$). There was likewise no significant correlation between the extent of the tunnels and the extent of building activity on the overlying surface (Figure 30).

Effect of rotating the spire

Rotating the spire affected the distribution of insolation, temperature and building activity on the mound surface (Figure 31). Overall, mound surfaces facing the north were both warmer ($F_{3,143} = 20.26$, $F' = 2.67$, $p<0.0001$) and more intensely insolated ($F_{3,143} = 86.05$, $F' = 2.67$, $p<0.0001$) than were the other faces (Figure 31). The western faces tended to be both warmer and more insolated than the eastern faces were, primarily because the majority of the measurements were made before solar noon, which biased the distribution of heat within the mound to the west. Also, the western faces of both CV and T05 were relatively free of vegetation that could shade the mound. Rotating the spire 180° also significantly affected both surface temperature ($F_{2,143} = 21.60$, $F' = 3.06$, $p < 0.0001$) and insolation ($F_{2,143} = 39.11$, $F' = 3.06$, $p<0.0001$), with the rotated spires being warmer and more intensely insolated than the unrotated spires (Figure 31). There is also a significant interaction effect for both temperature ($F_{6,143} = 3.08$, $F' = 2.17$, $p = 0.007$) and insolation ($F_{6,143} = 16.96$, $F' = 2.17$, $p < 0.0001$), with the north face warmed and insolated more in the rotated spire than in the unrotated or shaded spire.

Figure 20. The interior surface of a surface conduit, showing egress holes indicated by white arrows. One egress hole opens directly to the outside, as indicated by the light shining through. The black dotted line indicates the outer boundary of the mound. Some of the outer wall of the surface conduit had flaked away during preparation of the mound face.

Figure 21. A newly formed ‘boil’ indicating the different texture of the soil in the mound compared to the ‘boil’. Note also the small working tunnels permeating the ‘boil’.
Subsequent observation of the mounds with rotated spires indicated a greater extent of building activity on the north face of the spire than on other faces. Specifically, on the north face, marker pegs that had been used to indicate the cardinal points on the spire were nearly buried under new building. On the south faces, however, soil around the marker pegs had been eroded away, in one case sufficiently to cause the peg to fall out.

**DISCUSSION**

Much of the classical work on termite mounds has treated these structures as analogous to phenotype, with particular species-specific architectures, or with structural features ‘designed’ to serve a particular function, such as colony homeostasis (Darlington 1984, 1985, 1986; Lüscher 1956; 1961; Weir 1973). Whether purposefully or not, this analogy draws its inspiration from the conception of the insect colony as a ‘superorganism’, with traits and behaviours reminiscent of those observed in conventional organisms, albeit at a higher level of organization (Wilson 1971).

Conventional phenotype can be operationally defined as a structural feature of an organism that is characteristic of the species in which it is found. In turn, this implies that between-species variation in the structure is demonstrably larger than the within-species variation. One striking feature of macrotermitine mounds is their extraordinary structural variation, and how to partition this variation between and among species has long been uncertain. At one time, between-species variation was thought to be the most significant, with certain species thought to construct mounds with distinctive architectures. For example, *Macrotermes subhyalinus* is often described as building relatively low dome-shaped mounds, with large openings that can serve as wind scoops or Venturi vents (Weir 1973). *M. natalensis*, for its part, is usually described as building cone-shaped mounds that are
completely enclosed (Lüscher 1961; Ruelle 1964). *Odontotermes transvaalensis* locates its colony deep underground, and builds vertical open chimneys roughly a metre tall (Ruelle 1985; Turner 1994). Finally, the mound of *M. mossambicus* (now *M. michaelseni*) is described as having a cone-shaped base topped with a thin vertical spire, or steeple (Coaton & Sheasby 1972; Ruelle et al. 1975).

To reliably partition this variation among species requires both a sound understanding of the taxonomic relations among the termites, as well as a good understanding of the variation within those species. Unfortunately, the taxonomy of termites, particularly of the macrotermitines, has long been confused, and many of the classical works on termite mound architecture (e.g. Grassé & Noirot 1961) were done prior to recent revisions of macrotermitine taxonomy (e.g. Ruelle 1970, 1975). As the confused taxonomy of termites has become clearer, and as more descriptions of termite mound architecture have accumulated, it has become obvious that the within-species variation of architecture among the macrotermitines is substantial, perhaps greater than the purported between-species variations that drew the attention of earlier investigators. For example, Ruelle (1964) describes *M. natalensis* mounds in Uganda as characteristically open at the top, while the same species in the Côte d’Ivoire builds mounds that are commonly closed. Grassé & Noirot (1961) describe a vast variation of architecture among mounds of *Bellicositermes natalensis* (= *Macrotermes natalensis*) ranging from low conical mounds to mounds decorated with numerous accessory moundlets to enormous ‘dome’ mounds that span diameters as large as 30 m. Similarly, mounds of *M. subhyalinus* in Kenya exhibit two common morphs (Darlington 1984), with one (the ‘Bissel type’ mound) being low and hemispherical in shape, and penetrated by numerous vent holes, and another (the ‘Marigat type’) being topped by a very tall and thin chimney. Similar degrees of within-species variation have also been described for mounds of the more distantly

**Figure 24.** Distribution of section area for mound ($A_m$) and tunnels ($A_t$) and the ratio of tunnel section area to mound section area through the series of vertical sections. *a.* and *b.* Mound M03. *c.* and *d.* Mound M43. The horizontal lines in *b.* and *d.* indicate the average value over the series of sections.
related Brazilian nasute termite *Cornitermes bequaerti* (Cancello 1991). Less distinct within-species variation in mound architecture has also been described, correlated with climatic gradients. For example, Pomeroy (1977) observed that ‘turrets’ on the mounds of *M. bellicosus* are common in hotter parts of its range, while mounds in cooler parts frequently lack these structures. Harris (1956) has noted that *M. natalensis* mounds tend to have lower profiles at higher elevations than they do at lower elevations. Coaton & Sheasby (1972) have noted similar variations in the mounds of *M. natalensis*, with mounds in the more open and windy areas of the Nama Karoo being low in profile, while mounds in more heavily vegetated arid savanna tend to be taller. Overall, the picture that seems to be emerging is the mound as a dynamic structure which has a relatively minor genetic component, overlain with substantial, perhaps dominant, epigenetic factors that correlate to broad patterns of climate, soil type, vegetation and so forth.

Any attempt to explain this variation of mound architecture must be reconciled with the fairly limited behavioural repertoire that termites bring to mound construction (Emerson 1956; Stuart 1972; von Frisch & von Frisch 1974). Macrotermite mounds also have function, however, and to some degree, this function is dependent upon the mound’s structure. Thus, any explanation for the morphogenesis of termite mounds must also account for how the structure is attuned to its function. In the discussion to follow, I would like to propose such a model. Most of my attention will be devoted to morphogenetic models which explain the major architectural features of the *M. michaelseni* mounds here described. The integration of structure and function is based upon the results of physiological experiments yet to be published, so I shall only touch upon its main features here. Finally, I shall offer a speculative model for the between-species variation of mound architectures amongst the macrotermite termites.

Mound construction results from termites engaging in a simple activity: translocating grains of sand or soil from one spot to another. A worker termite that is disturbed will pick up a grain of soil, either from a spoil pile or from a tunnel wall, carry it for a time,
and then deposit it onto a surface, daubing it into place with adhesive secretions (Stuart 1972; von Frisch and von Frisch 1974). When taken collectively in a colony of 1-2 million inhabitants, this results in termites being prodigious movers of soil, particularly in arid tropical ecosystems (Dangerfield et al. 1998; Lobry de Bruyn & Conacher 1990). For example, the Ugandan termite *Macrotermes bellicosus* transports soil upward into the mound at rates varying from 0.4 to 0.9 m$^3$ ha$^{-1}$ y$^{-1}$.

This upward movement of soil is offset by similar levels of downward movement through erosion, but the building activities are sufficient to support a ‘standing crop’ of soil in termite mounds of 4-8 m$^3$ ha$^{-1}$ (Pomeroy 1976).

Termite mounds are, therefore, dynamic structures, and their architecture is a result of how these movements of soil are directed (Harris 1956). In general, the shape of such a dynamic structure follows from two principal movements of soil. On the one hand, any activity in which work undertaken to deposit soil particles at places they otherwise would not be will result in building, which we might describe using the general term of *blastic*. Blastic processes in mounds are nearly always biological in nature, because the translocation of soil against gravity or weathering processes requires active work being done on the soil by the workers. On the other hand are processes which remove soil particles, perhaps to return them to positions closer to equilibrium, which we will term *clastis*. Clastic processes include abiotic processes, such as erosion, but may also be biological. For example, termites often open holes in the surfaces of termite mounds, either as a normal part of extension of the mound surface (Figure 20), or to open egress holes for the emergence of alates: both involve clastis. Also, the simple act of translocating soil from one part of the mound to another necessarily involves a clastic process, when a grain of soil is dislodged from the mound, coupled to a blastic process, when it is redeposited.
Figure 27. A representative series of surface sections. Columns refer to series at the cardinal points indicated. Rows are the depths of the section in centimeters. Light gray indicates the plot marked on the mound for sectioning, roughly 40 cm by 40 cm. White areas at 0 cm depth refer to areas of new building. Dark gray in the other sections represent outlines of tunnels.

Figure 28. A representative series of surface sections. Conventions are as in Figure 27.

Figure 29. A representative series of surface sections. Conventions are as in Figure 27.

Understanding the architecture of termite mounds thus requires an understanding of how these blastic and clastic processes interact. As a simple example, consider two of the common outward features of the *M. michaelseni* mound: the broad outwash pediment and northward-tilting spire (Figure 6). The origins of the outwash pediment and spire are easily explained by a straightforward interaction between a blastic process that translocates soil directly upward, and a clastic process, like erosion, that transports soil downward again (Figure 32). In the absence of clastis, the upwardly-directed vector of blastis should result in the construction of a cylindrical column (Figure 32a). If a clastic process, like erosion, is now added, there emerges a mound with the central column tapered at an angle steeper than the soil’s angle of repose, and a broad outwash pediment, with the slope of the pediment being similar to or shallower than the soil’s angle of repose (Figure 32b). The northward tilt of the spire results from adding a third vector of blastis (Figure 32c). Imagine that the rate at which a termite builds is dependent upon the termite’s body temperature. Summed across all the workers, the rate at which blastic work is done should vary throughout the mound in parallel with the distribution of temperature within the mound. If the mound is warmed by the sun more on its north side than on its south side (Figure 31), the spire’s north side will grow at a faster rate than will its south, east or west sides. This additional vector of blastis will be oriented in the direction...
Thus, the mound will grow in the direction that equalizes the distributions of temperature around the spire, which will occur when the spire points toward the sun’s average zenith.

The correspondence of the mounds’ tilt with the sun’s average zenith angle at Namatubis is tantalizing, albeit not conclusive, evidence in favor of this model. For example, one would predict from this a systematic variation in the mounds’ northward tilts with latitude, and I am not aware of any evidence that supports or refutes this prediction. However, the patterns of building on the mounds whose spires were rotated does suggest that the rotated spire was slowly growing northward. Furthermore, variations of temperature are known to affect mound architecture of *Macrotermes bellicosus* in ways consistent with this model (Korb & Linsenmair 1998).

Another striking architectural feature of the *M. michaelseni* mound is the size differentiation of the tunnels, with more interior tunnels being larger and more capacious than tunnels closer to the surface. This is evidenced in a number of ways. In the two sets of vertical sections, for example (Figures 12-17), the tunnels in the sections through the outwash pediments and the peripheral portions of the cone appear smaller and fewer in number than the tunnels in the more interior sections of the mound, culminating in the opening of the chimney in the center of the mound (‘ch’ in Figures 12-17). These apparent patterns are substantiated by the various measures of tunnel volume and surface area through the sections (Figures 27-29). Areas in the mound which exhibit intense building activity, such as at the top of the spire (Figures 19b-c), or at the site of a new ‘boil’ (Figure 22), also show a differentiation between small tunnels at the surface grading into larger open spaces toward the interior. Finally, in the surface sections, volume occupied by tunnels roughly doubles for every centimetre of depth (Figures 27-30).

This distribution of tunnel sizes can be explained by a type of conservation mechanism, in which the translocation of a grain of soil from one place to another involves the simultaneous appearance of a ‘heap’ - a grain of soil glued to something, either a tunnel wall, or a previously deposited grain of soil - and a ‘hole’, a space previously occupied by that grain of soil (Figure 33). In the absence of any biasing of the movements of the termites, soil translocation will be random, as will the spatial distribution of heaps and holes. If the movement of termites carrying soil is biased in a particular direction, however, the distribution of heaps and holes no longer will be random, and will reflect the bias in the locomotory activities of the termites. One consequence of such a bias will be distribution of hole sizes similar to that seen in the mound. Suppose, for example, the termites tend to translocate soil centrifugally, from the center of the mound to the surface.

### Table 6. Proportion of surface section areas occupied by new building or tunnels. Numbers are reported as mean (standard deviation) [ minimum - maximum].

<table>
<thead>
<tr>
<th>Depth of section (cm)</th>
<th>Proportion of area occupied by new building</th>
<th>Proportion of area occupied by tunnel</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface</td>
<td>0.21 (0.23) [1.000 - 0.000]</td>
<td>0.04 (0.07) [0.275 - 0.000]</td>
</tr>
<tr>
<td>-1 cm</td>
<td>0.10 (0.10) [0.309 - 0.000]</td>
<td>0.20 (0.13) [0.444 - 0.000]</td>
</tr>
</tbody>
</table>
As soil is deposited at the surface, i.e. as new heaps are added there, the mound surface grows outward. However, the material to supply these new heaps must result in the appearance of holes, and because termites only carry soil for a limited distance, the new hole either appears at the site of a nearby heap, leveling it, or from a previously created hole, enlarging it (Figure 33). Thus, mound building involves a sort of ‘bucket-brigade’, with outward extension of the mound surface being supported by increasing amounts of excavation from the interior parts of the mound. This results in a direct correlation between the age of a tunnel and its size. When a tunnel is newly formed, it has not served as a source of soil for new heaps for very long, and its size - reflective of the number of ‘holes’ opened there - will therefore be small. Whereas older tunnels will have served as a source for longer period, and it will therefore be large. Consequently, the capacious chimney probably results simply from this region of the mound having served for the longest time as a source of material for extending the mound surface outwards.

Probably the most common biasing mechanisms in mound construction involve gradients of concentrations in respiratory gases (including water vapor) and temperature (Emerson 1956; Stuart 1972). There is much anecdotal evidence that these alter building behaviour of termites and other social insects (Nicholas & Sillans 1989; Stuart 1972). For example, macrotermite termites will begin to excavate openings in their nests when nest CO$_2$ concentrations increase from 1% to 2% (Nicholas & Sillans 1989). Termites kept in glass cases will tend to concentrate their building near the case’s vent holes (Stuart 1972). Behaviours of ants and termites can be altered by exposure to small alterations of concentrations of oxygen, carbon dioxide, humidity or gentle movements of air (Stuart 1972).

It follows that the structure of a mound could be shaped in part by gradients within the mound of the concentrations of respiratory gases (i.e. $pO_2$, $pCO_2$, $pH_2O$) or temperature (Korb & Linsenmair 1998). Consider, for example, the sequence of behaviours that follow the opening of a breach in the mound wall of $M. michaelseni$ (S. Turner pers. obs.). When the mound wall is first breached, worker termites are
rare or absent. After about five minutes, workers begin to appear near the breach and to deposit grains of sand on nearby tunnel walls. Initially, the deposition is haphazard, but as the initial repair work proceeds, there is continued recruitment of workers to the task of repair, and increased numbers of deposited grains of sand. Eventually, worker termites seeking to deposit grains of sand are likely to encounter previously deposited grains, and this biases deposition of new grains toward those previously deposited, a process known as ‘stigmergy’. The result is the erection of the pillars, walls and roofed galleries that grow to eventually seal off the tunnels leading to the breach. Once sealed, the workers recruited to the repair work drift away to other tasks.

The curious thing about this behaviour, particularly in response to a large breach in the mound wall, is that it occurs mostly at some distance inward from the breach. As a consequence, the repair does not replace the damaged wall: rather it seals the tunnels leading into the breach. This is consistent with the workers’ activities being concentrated at a particular threshold of $pO_2$, $pCO_2$, or $pH_2O$, or with translocation being directed down gradients in the concentrations of these gases. When the mound wall is breached, colony air with high $pCO_2$ and

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**Figure 32.** Hypothetical scheme for the development of the outwash pediment and spire, and the northward tilt of the spire. *a.* Growth with vertical blastis only. *b.* Tapered spire and fanned outwash pediment resulting from vertical blastis and downward clastis. *c.* Growth of a tilted spire resulting from vertical blastis, temperature-directed blastis and downward clastis. Details are discussed in text.
$pH_2O$ and low $pO_2$ is brought into contact with outside air with low $pCO_2$ and $pH_2O$, and high $pO_2$. Gradients in these concentrations will inevitably follow, but the mixing of these two air masses, and hence the location and steepness of the gradients, will be influenced by the interaction of the two energy sources that drive the mixing. From the colony interior, metabolic energy in the form of heat and humidity will drive colony air out toward the breach, while wind energy will drive outside air in. If the effect of the winds is great, as they could be expected to be in the case of a large breach, the gradients will be pushed inward, concentrating building activity there. However, a different pattern of repair results when the opening in the mound wall is small (S. Turner pers. obs.). Part of my physiological work with these mounds has required me to drill small holes (25 mm diameter) into the surface conduits. In those circumstances, repair work is always concentrated on the mound’s outer surface. For small holes such as these, the admission of wind energy might be smaller, the metabolic energy driving colony air outward may prevail, and gradients in $pO_2$, $pCO_2$, and $pH_2O$ may actually extend outwards from the hole, concentrating building activity there.

If building activity is generally biased by fields of $pO_2$, $pCO_2$ and $pH_2O$, it may help explain the mound-building habit in general: mound-building results from termites translocating soils along fields of concentration in respiratory gases, temperature and perhaps momentum in air (proportional to velocity).

These fields will radiate outward from the colony, and soil translocation will also be outward. Furthermore, termites can only extend the mound surface outward by opening up small egress holes in the mound, such as those depicted in Figure 20. If these act similarly to the small holes I have drilled in mounds, this may concentrate building on the mound’s outer surface, causing it to grow outward.

In this conception, architecture emerges from the ways a mound interacts with all the factors that influence its concentration fields for the respiratory gases. These could include colony metabolism, temperature distribution or kinetic energy in wind. The crucial thing is that mound structure is both result and cause of the concentration fields, in other words, mound architecture is part of a closed-loop system in which feedback interactions are likely to play an important rôle.

How might such feedback loops operate? The quantitative measurements of tunnel and mound dimensions suggest that the mound consists of two structurally distinct components: the spire, and the conical base (e.g. Figures 11, 24-26). This might imply two such closed loops commonly operate to generate the building of the mound. I suggest that both loops operate as positive feedback loops, with mound growth being driven by a kind of autocatalytic process whereby an action taken to correct a problem (i.e. structural alteration of the mound to correct an anomalous concentration of respiratory gases) serves only to aggravate the stimulus that initiated the action.

Let us first turn to the upward growth of the spire (Figure 34). Colony metabolism changes not only the composition of the colony air but also its density, by warming and humidifying it. Consequently, colony metabolism imparts buoyant forces to the colony air that will tend to loft it upwards. In the initial stages of mound growth, these forces will be small, because the colony metabolism will be small, and the mound should grow uniformly outward with no particular bias. As the mound grows, however, it will begin to excavate large internal spaces, according to the ‘bucket brigade’ model outlined in Figure 33, and its metabolic rate will increase, which magnifies the buoyant forces on colony air. Thus, colony air will likely be more forcefully lofted upwards through the newly-opened large tunnels in the center of the mound. Consequently, gradients of the respiratory gases and water vapor will steepen in the upper parts of the chimney, and blastis should be most
intense there, causing the mound to grow upwards. As the mound grows upwards, however, it also grows into the gradient of wind speeds that comprise the surface boundary layer. Because these higher winds will bring more wind energy to the mixing of colony air, these should also steepen the concentration gradients at the uppermost parts of the spire, stimulating blastis there, with the stimulus intensifying as the spire grows upwards into ever more energetic winds. Eventually, this aggravating effect of increasing wind speeds will taper off as the mound grows high enough to get into the free stream (where momentum no longer varies with height), or where the mound height equilibrates between rates of upwardly directed blastis, and erosion-mediated clastis (Figure 34).

The mound’s conical base may also grow outward by a similar autocatalytic process, although one differing in some detail from that proposed for the spire (Figure 35). The similarity of ‘boils’ (Figures 21, 22), ‘moundlets’ (Figure 8) and ‘domes’ (Figure 7) suggests a developmental sequence whereby the ‘boil’ is precursor to the ‘moundlet’, which is precursor to the ‘dome’. The process probably begins with the appearance of a diagonal tunnel that emerges from the colony (‘rc’ in Figures 12-17, Figures 22-23), which Darlington (1984) has identified as egress holes constructed for emergence of the alates. However, their location and size indicate that they may also be formed by the emergence of mushrooms of the symbiotic fungus cultivated by the termites. Irrespective of how the holes are formed, though, immediately following their opening, the termites work to seal the hole. Because of the small calibre of these holes, the gradients in respiratory gas concentrations might extend outward from the mound’s outer surface, thus concentrating the repair work there, forming the ‘boil’ (Figure 21). As the ‘boil’ grows, however, its outside surface area also expands, which enhances the capacity of the growing ‘boil’ for gas exchange and for interaction with momentum in winds (Figure 35). The direct connection of the ‘boil’ to the colony through the radial channel also provides a direct conduit for mixing energy from colony metabolism. The ‘boil’ may therefore grow autocatalytically, with the attempt to seal the hole intensifying the stimulus that initiated the building in the first place, which worsens the more the termites work to fix it (Figure 35).

Thus, several of the architectural features of the M. michaelesi mound can be explained through such autocatalytic feedback loops. This suggests a general model of mound morphogenesis which can be summarized roughly as follows (Figure 36). In the young mound, which is small and in the shape of a simple heap, partial pressure gradients are uniform, reflecting the diffuse and relatively disorganized arrangement of tunnels in the mound (Figure 36a). As the mound grows, and as ‘bucket-brigade’ soil transport continues, large spaces begin to open in the mound center, and which are the precursor for the chimney. These serve to channel the increasingly buoyant colony air up to the top of the mound, steepening the concentration gradients of the respiratory gases there, and consequently focusing blastis there (Figure 36b). The result is the upward elongation of the mound to form the spire (Figure 36c). Once the colony has attained sufficient size, either to produce alates or a crop of
mushrooms, the resulting diagonal tunnels will provide a direct channel for the movement of colony air to the surface, with gradients of carbon dioxide, oxygen and water vapor being steepened there as they are in the upper parts of the chimney (Figure 36c). These steepened gradients will elicit blastis there, which will develop eventually into the autocatalytic growth of the ‘dome’. As the autocatalytic growth proceeds, working galleries will develop beneath the developing ‘dome’ (as in Figure 22), which will eventually grow and ramify to form the surface conduits. Add to this the subtle biasing effects of solar heating and erosion (Figure 32), and a reasonably simple model for morphogenesis in the *M. michaelseni* mound emerges.

One of the tantalizing aspects of this model of mound morphogenesis is that it may help explain how social homeostasis emerges from the construction of the mound. Social homeostasis, in which the collective activities of a colony’s inhabitants results in the regulation of the colony environment, has been a long-standing problem in the biology of social insects, in part because it draws its inspiration from the problematic concept of the insect colony as a superorganism (Wilson 1971). Yet, how do the inhabitants of the colony know when their nest has attained the ‘correct’ structure, and how are corrections to deviant structures carried out?

A solution to these quandaries can be found by considering homeostasis not as a regulatory phenomenon, but as a process that brings it about. Homeostasis results when the fluxes of matter and energy into and out of the colony are matched. For example, when the rate of oxygen consumption by the colony is matched to the rate of oxygen flux across the boundary separating the colony from its environment, a homeostasis of oxygen concentration in the colony is the result. If soil translocation and the mound structure that results affects the concentration gradients for oxygen in the mound, this may, in turn result in the matching of oxygen flux to oxygen consumption. Social homeostasis, then, is not the product of a regulatory process, as it is in the regulation of, say, body temperature. Rather, it is a simple by-product of soil transport by termites, insofar as the soil transport both affects, and is affected by the gradients in oxygen concentration within the mound.

This simple model also might point the way to understanding morphogenesis of mound structure among other macrotermitines. The model of mound morphogenesis I have outlined is based upon five principal assertions:

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**Figure 35.** Hypothetical scheme for the autocatalytic growth of a ‘dome’. Details in text. *a.* The repair of a small egress hole results in the continued outward growth of the mound, culminating in the development of a ‘dome’. *b.* Series of positive feedback steps which result in autocatalytic outward growth.
1. Soil translocation occurs along gradients in concentrations of oxygen, carbon dioxide, water vapor and momentum.

2. The intensity of soil translocation, i.e. the rate of translocation work, or more succinctly, the translocation power, is proportional to the steepness of these gradients.

3. Any factor which ‘verticalizes’ these gradients, i.e. steepens them in the vertical dimension, will tend termite colonies toward the construction of mounds. Such factors can include metabolic rate of the colony, porosity of the soil compared to tunnels excavated by termites, and concentration of metabolic power into compact colonies.

4. Gradients in the respiratory gases can also be influenced by external environmental factors, such as winds, insolation or rainfall. The interaction of soil translocation and colony metabolism with these external factors can involve worker termites into autocatalytic loops of building, which cause the mound to grow uncontrollably.

5. The tendency of mounds to open through chimneys or large vents is dependent upon how intensely verticalized the gradients in the mound are. The steeper these gradients are in the vertical dimension, the more likely it will be that the mound will open through a chimney.

This model is admittedly speculative, but it does offer an explanation for some of the major variation in mound architectures to be found amongst the macrotermitines. Consider, for example, the dramatic variations described by Grassé & Noirot (1961) for *Bellicositermes (= Macrotermes) natalensis*, the mound as a broad, low hillock, or as a strongly vertically oriented mound. The hillock type of mound is correlated with a broadly dispersed colony, with fungus gardens, and the metabolic power that emanates from them, scattered over a broad extent. The vertical mound, in contrast, has its fungus gardens concentrated in a ‘cap’, roughly 1.5 to 2 m in diameter, that sits atop the colony. In the hillock mound, even if the metabolic production of the colony was prodigious, the metabolic heat and humidification of the air can be blunted by conduction into the surrounding soil, reducing the buoyant forces that could produce strong vertical gradients in respiratory gases. Blastis in the colony will be broadly distributed, but locally weak, and more likely to be leveled by erosion, with the result being a low hillock mound. Concentrating the colony, on the other hand, will also concentrate the release of metabolic energy that heats and humidifies the colony air, which will magnify the resulting buoyant forces, and hence the vertical steepness of the gradients in the mound. The local concentration of blastis will result in a columnar mound.

Properties of the soil also are likely to influence how strongly verticalized the gradients in respiratory gases are. A very porous soil, for example, will enable horizontal movements of gases by diffusion, reducing the vertical dimensions of gas movement, and the vertical translocation of soil commensurately. A very compact soil, on the other hand, will bottle up respiratory gases, and their movements will be strongly biased by the pathways termites themselves open through the soil. This may help explain the tendency of mounds to produce, in some circumstance, many ‘moundlets’ or ‘boils’, while mounds in other circumstances do not. On the one hand, in a mound that is built from very compact soil, any egress hole, whether it be for the exit of alates, or for mushrooms, or for workers, as seen in Figure 20, will result in the formation of a ‘boil’, and potentially into a ‘dome’. If the mound is very porous, on the other hand, the opening of any egress hole may have less effect on the concentration gradients in the tunnels, and hence on the stimulation of ‘boils’ and ‘domes’.

Figure 36. A model of morphogenesis in the mound of *Macrotermes michaelseni*. Details in text.
Similarly, the vertical position of the colony might operate through this mechanism to alter whether the mound opens through a chimney or not. In general, mounds that are located deep underground are more likely to have open chimneys than those that are not. Two widespread species with open chimneys, *Macrotermes subhyalinus* and *Odontotermes transvaalensis*, both locate their colonies more deeply than closed-mound types such as *M. michaelseni* or *M. natalensis*. Again, how vertically oriented the gradients can be will depend upon the extent of horizontal movements of the gases. In a deeply buried colony, the possibilities for horizontal movements may be limited more than they would be in a colony that extends upward into the mound as does the *M. michaelseni* colony. A severe enough restriction on the horizontal movements of gases may eventually force the gradients to ‘spill out’ over the tops of the mound, with the result being a continual translocation of soil out and over the top, producing a chimney.

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REFERENCES


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