Proc. Indian natn. Sci. Acad.
Vol. 43, Part B, No. 5, pp. 159-174 (1977)

Entomology

FIELD DATA ON INTRASPECIFIC VARIABILITY IN MOUND CONSTRUCTION AND NESTING HABITS IN TERMITES AND ITS ECOLOGICAL RELATIONSHIPS

by M. L. ROONWAL, FNA, *Desert Regional Station, Zoological Survey of India, Jodhpur*

(*Received* 18 *August*, 1977)

New as well as known cases of the occurrence of intraspecific variation in mound-structure in termites are discussed in 19 species from various regions, e.g., Oriental, Australian, Ethiopian and Neotropical. (2) In extreme cases, variation may range from 'no mound-formation' to as many as five different types of mounds. (3) Variations are especially common in the Australian and Oriental Regions, and are confined to two families, the Rhinotermitidae (Coptotermitinae) and the Termitidae (Amitermitinae, Termitinae, Macrotermitinae and Nasutitermitinae). (4) In several cases some correlations with ecological habit have been shown to occur but the precise modes of action are not yet fully known.

INTRODUCTION

That mound-and nest-structures in termites (Insecta: Isoptera) are largely species-specific has been known for long, and termites are sometimes identified in the field with the aid of these structures. In recent years, however, data have accumulated which show that in some species the structure of mature mounds of nests may vary greatly in different populations of the same species, and a mound may even be absent. (For this purpose we shall consider only the older and well established mature mounds, for the younger, smaller mounds sometimes differ markedly from the older ones, vide Roonwal, 1977). Since these variations sometimes occur in the same geographical area, we are not dealing here with geographical subspecies. Nor are they due to faulty taxonomy since the determinations have been done by competent and experienced taxonomists. We are, therefore, concerned with genuine cases of eco-physiological and eco-behavioral intraspecific variability which is not evident in morphological characters such as those of size and other features, which are commonly used in isopteran taxonomy. Here, I have described cases of intraspecific variation from various regions and discussed, where possible, the ecological aspects of this variability.

INTRASPECIFIC VARIABILITY IN MOUND CONSTRUCTION AND NESTING HABITS

(A) Oriental Species

(Examples are known from the family Termitidae)

Subfamily 1: Macrotermitinae

1. *Odontotermes assmuthi* Holmgren (Fig. 1)

A widespread Indian species (Roonwal, 1970). In the south (Karnataka) it builds tall, earthen mounds which commonly attain a height of 2-4 m (Basalingappa, 1968, 1971). In the north (Dehra Dun), however, no mounds are built and the species makes diffuse, subterranean nests (Mathur & Sen-Sarma, 1962*a*, *b*).

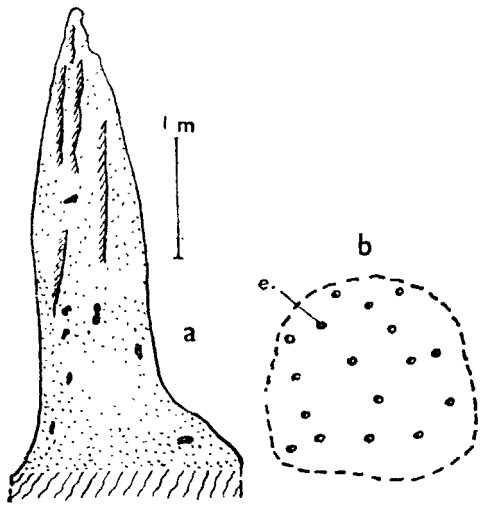

Fig. 1. *Odontotermes assmuthi*. India. Mound and emergence holes. (*a*) A tall mound (c. 4 m high), Karnataka, South India. (*Adapted from Basalingappa*, 1971). (*b*) Emergence holes on ground surface, for swarming alates. North India. *e*, emergence holes.

2. *Odontotermes brunneus* (Hagen) (Fig. 2; and Pl. 1)

Throughout Peninsular India, east to Bengal and northwest to Rajkot in Gujarat (Roonwal, 1970, 1973, 1977, and in press). All over its range it builds, low, dome-shaped, broad-based (diameter up to c. 4 m) earthen mounds. Five types of mounds have been found, and are characterised as follows: *Type I* (Fig. 2a; and Pl. 1a): Sub-conical, c. 1 m high; with smooth outer surface; without papillae, projections or surface holes. Royal chamber lying centrally at ground-level. Rajkot, Gujarat (Roonwal, 1973, 1977). *Type II* (Fig. 2b; and Pl. 1b): Low (c. 1 m high), sprawling and dome-shaped; outer surface rather rugose. With several small (c. 5-7 cm wide) surface holes leading to tunnels; the holes may be temporarily closed. Pune, Maharashtra (Roonwal, present account). (In the same area at Pune are also found the nearly similar mounds of *O. kushwahai* Roonwal and Bose, vide Roonwal and Rathore, in press). *Type III* (Fig. 2c. and Pl. 1c): Low, sprawling, dome-shaped, c. 0.5 m high; surface rather rugose with several large (diameter 14-25 cm) external holes leading to tunnels which join the underground galleries criss-cross. Royal chamber lies eccentrically below ground-level. Found well south in Peninsular India (Coimbatore, Tamil Nadu; and Mysore, Karnataka), which is the southernmost limit of the species (Roonwal, in press). *Type IV* (Fig. 2d, Pl. 1d-f): Dome-shaped, c. 1 m high; surface highly rugose and with

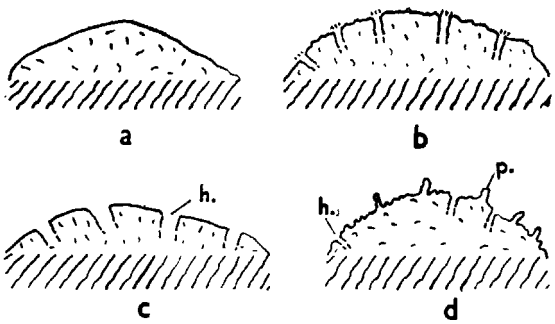

Fig. 2. *Odontotermes brunneus*. India. Various types of mounds. (*a*) Type I : Subconical; surface smooth, without holes. Rajkot, Gujarat. (*b*) Type II : Low (c. 1 m high), sprawling, dome-shaped; surface rather rugose, with several small holes (5-7 cm wide) which may be temporarily closed with earth. Pune, Maharashtra. (*c*) Type III : Low (c. 0.5 m high), sprawling, dome-shaped; like type II, but with large (14-25 cm wide), open holes. Peninsular India : Coimbatore, Mysore. (*d*) Type IV : Low, irregularly dome-shaped; surface very rugose; with small blind papillae. Mota Mava near Rajkot, Gujarat. [A fifth type, at Kirkee near Pune with fine-holed turrets is not shown.] *h*, holes; *p*, papillae.

small, blind, papillate projections (5-6 cm high) and small holes (2-3 cm in diameter) leading to blinld tunnes. Royal chamberlying centrally at ground-level. Mota Mava near Rajkot, Gujarat (Roonwal, 1973). *Type V*: Fairly high, up to c. 2 m; surface with several turrets, 30 cm high, which are riddled with small holes and crumble easily. Royal chamber lies above, below or at ground-level. Kirkee near Pune, Maharashtra (Holmgren, 1912).

Thus, in at least two cases two different types of mounds occur within a few kilometres of each other — types I and IV in Gujarat (at Rajkot and Mota Mava) and types II and V in Maharashtra (at Pune and Kirkee). The ecological bases of these differences are not clear. In Gujarat, the smooth-surfaced, non-papillate, holeless mounds at Rajkot were on black cotton soil, while the highly rugose, papillate and holed mounds were on coarse, brown soil. In Maharashtra, both the non-papillate, holed mounds at Pune and the turreted mounds at Kirkee were on black cotton soil.

3. *Odontotermes feae* (Wassman) (Fig. 3)

A widespread species (South and Southeast Asia). It lives in large communities and makes massive subterranean nests, up to 2.5 m in diameter, which go down about a metre underground (Roonwal, 1970). Swarming from the nest occurs from tiny surface holes (Holmgren, 1913). On the Barkuda Island (Chilka Lake, Orissa), Annandale (1923) noted its subterranean habits (Fig. 3a). On the same tiny island it also occasionally builds (Roonwal & Chhotani, 1966) low, sprawling, irregularly dome-shaped earthen mounds (height 0.6 m, basal diameter 2 m, Fig. 3b). Several round holes open at the surface and lead into vaults for the lodgement of fungus-combs; the

royal chamber lies eccentrically just below ground-level. Ahmad (1965) also mentioned mounds in Thailand, but gave no details.

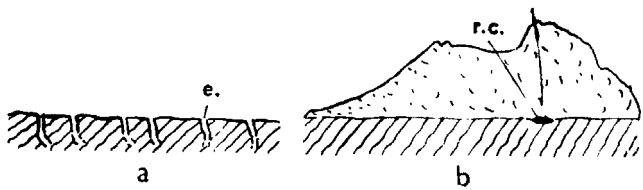

Fig. 3. *Odontotermes feae*. India (Barkuda Island, Chilka Lake, Orissa). (*a*) Nest surface, in vertical section, showing emergence holes. (No mound formed; nest entirely underground). (*b*) A low mound (rare).

e, emergence hole; *r.c.*, royal chamber.

4. *Odontotermes horni* (Wasmann)

A widespread species (South and Southeast Asia; Roonwal, 1970). In India and Sri Lanka it is entirely subterranean, the nest being diffuse (Wasmann, 1902; Escherich, 1911; Mathur & Sen-Sarma, 1962*a*; Roonwal, present account). But in Cambodia it builds about 1 m high earthen mounds (Bathellier, 1927).

5. *Odontotermes obesus* (Rambur) (Figs. 4, 5; and Pl. 2)

The most common mound-building termite of South Asia (India, Pakistan, Bangladesh, Burma); not found in Sri Lanka. It shows a most remarkable range of variations in mature mound-structure, from the tall, buttressed types to no-mound at all. At least five types of mounds have been found as follows, more than one type sometimes occurring in a small, restricted area of a few square kilometres, e.g., the tiny Barkuda Island (Chilka Lake) and the Kanha National Park (Madhya Pradesh).

Type I (Figs. 4a, b; and Pl. 2a, b): Tall, buttressed, 'unilocular' with a ring of some 8-12 buttresses all around; with a single principal underground vault (hence 'unilocular') containing a large fungus-comb and a few small ones; no fungus-comb-carrying vaults lying in the part above ground-level. Mound walls pitted on the inside (Pl. 2b); royal chamber usually underground (Roonwal, 1962, 1977). (This is of the var. *oculatus* Silvestri, the unilocular type of Annandale, 1923, 1924; and type 'A' of Chhotani, 1977). Orissa (Barkuda Island, Chilka Lake), Bihar, Uttar Pradesh, Madhya Pradesh. Best developed in the deciduous 'sal' (*Shorea robusta*) forests in Uttar Pradesh and Madhya Pradesh, where mounds commonly attain a height of 2.5 m, exceptionally of 3.5 m.

Type II (Pl. 2c, d) : Moderately tall, buttressed, but 'multilocular' type as in type I, but smaller (below 2 m in height), with 2-9 buttresses and numerous round, underground vaults (hence 'multilocular'), each carrying a fungus-comb. Peninsular India: Tamil Nadu (Madras, Coimbatore), Karnataka (Mysore, etc.) and Kerala (Nilambur). Apparently confined to the less wet parts of southern India.

Type III (Figs. 4c, d): Low, broad-based, non-buttressed, dome-shaped, subconical or irregularly-shaped, multilocular type composed either of a single unitary

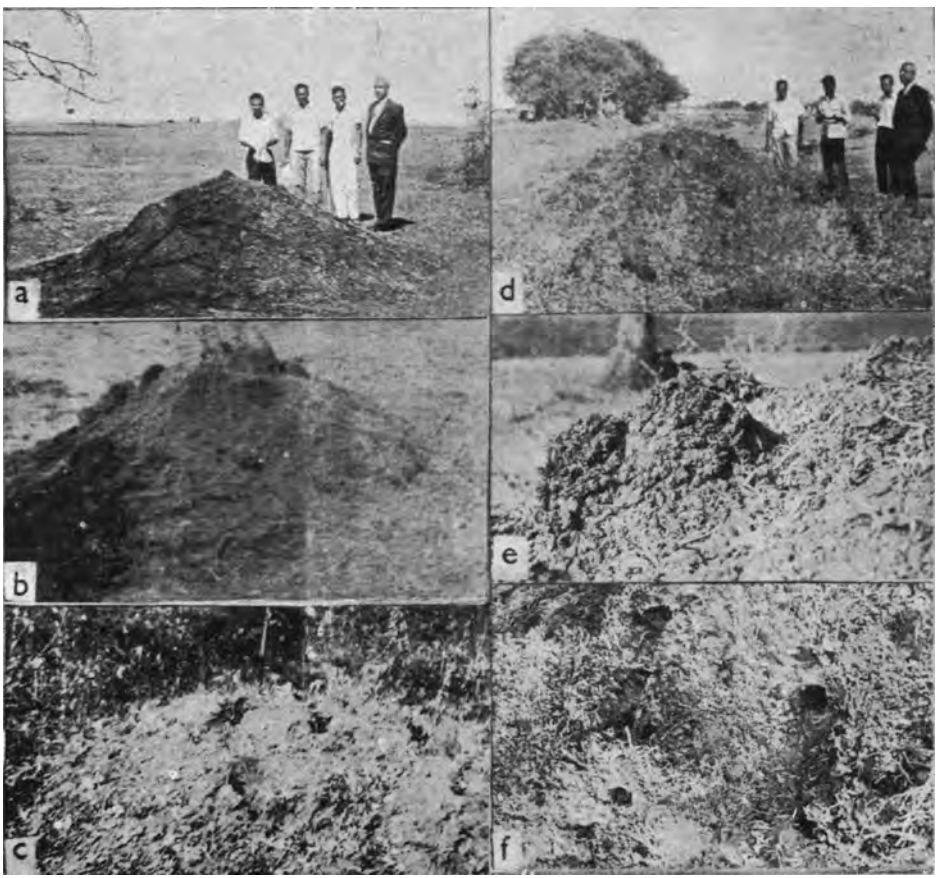

Plate I. *Odontotermes brunneus*. India. Photographs of some mound types. (*a*) Type I : Subconical; surface smooth, without holes. Rajkot, Gujarat. (*b*) Type II : Low, sprawling, dome-shaped; surface rugose, with a few holes which may be temporarily closed. Pune, Maharashtra. (*c*) Type III : Like type II, but with large, open holes. Coimbatore, Tamil Nadu. (*d*) Type IV : Low, irregularly dome-shaped; surface very rugose, and with small blind papillae. Mota Mava, near Rajkot, Gujarat. (*e*) Same, a part enlarged to show rugosity. (*f*) Same, a part enlarged, to show holes. [Figs. a, d, e, f, *from Roonwal*, 1973.]

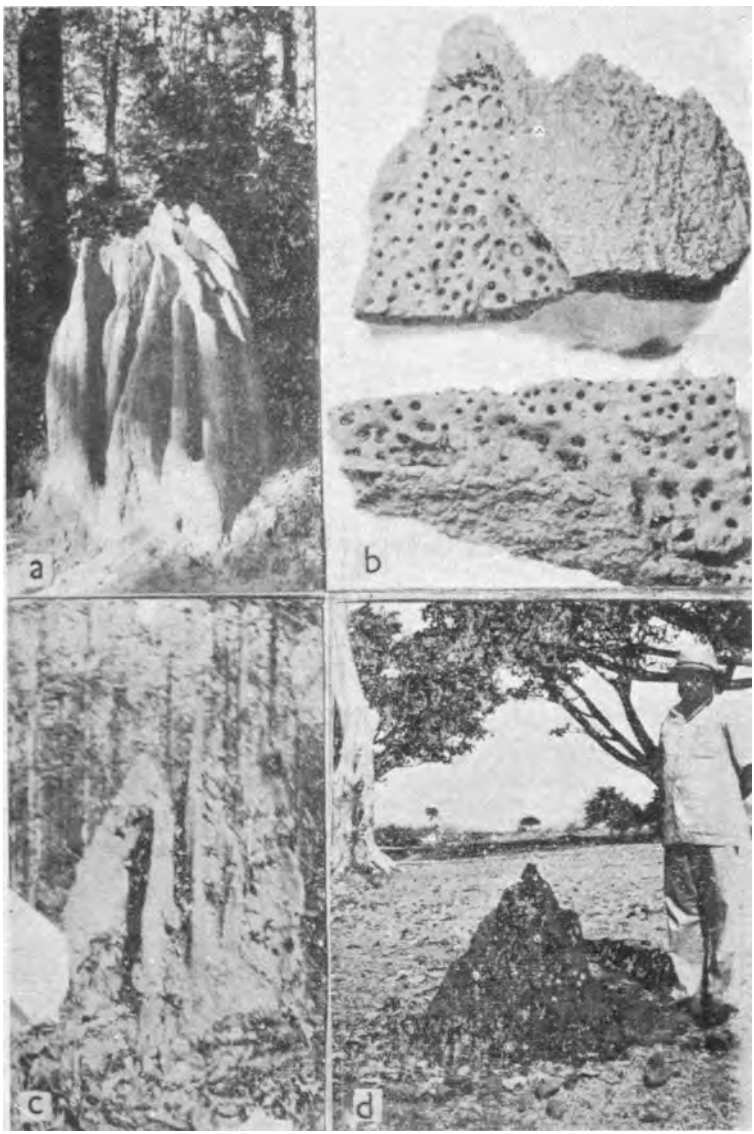

Plate 2. *Odontotermes obesus*. India. Photographs of some mound types. (*a*) Type I : Tall, buttressed, unilocular; height 1.8 m. Dehra Dun (North India). (*b*) Pitted inside wall of same. (*c*) Type II : Moderately tall, buttressed, multilocular; height 1.6 m Nilambur (Kerala). (*d*) Same Type : a smaller mound (height 0.8 m), partly in vertical section, Near Mysore (Karnataka).

structure (Fig. 4d) or of a number of blunt or subconical, hollow 'lumps' arranged either in a line or irregularly scattered (Fig. 4c); rising to a height of about a metre; walls not pitted on the inside; main 'nest' lying underground up to a depth of 1-1.5m); royal chamber above or below ground-level; numerous vaults with fungus-combs scattered all over (multilocular), reaching almost to the top of the mound (This is the mound of 'forma typica' of Annandale, 1923, 1924; mounds in Figs. 22-24 of Roonwal, 1976; and type 'C' mound of Chhotani, 1977). Recorded from the broad-leaved, forested areas of central and southeastern Rajasthan (Ramgarh reservoir near Jaipur, and Kota district), southern India (Karnataka : evergreen forests at Makut, Coorg), and the rather dry Barkuda Island (Chilka Lake, Orissa).

Type IV (Fig. 4e) : Low, dome-shaped or irregularly-shaped, unilocular type with a large principal vault carrying a fungus-comb near ground-level and a few smaller comb-carrying vaults underground; no vaults above ground; royal chamber above

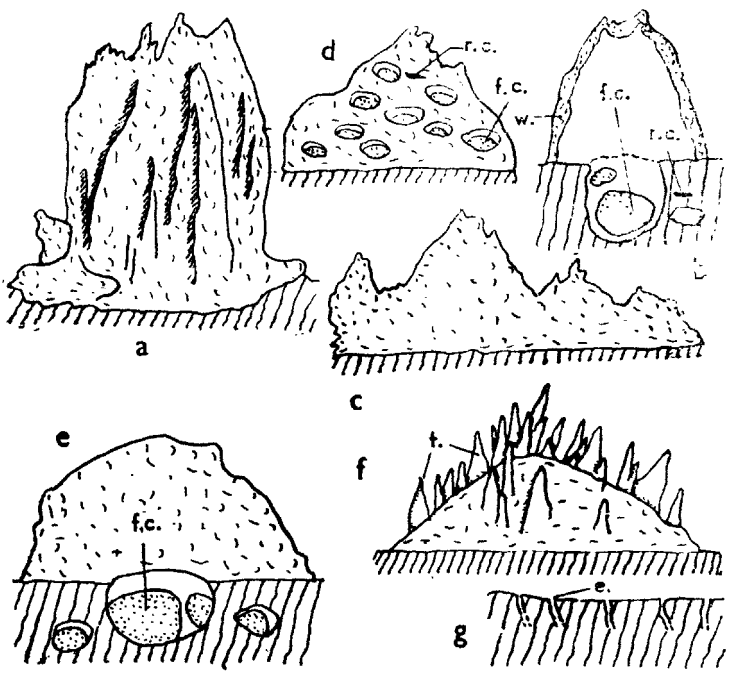

Fig. 4. *Odontotermes obesus*. India. Various types of mounds. (*a*) Type I. Tall (c. 2-3 m high), buttressed; large, 'unilocular' fungus-comb chamber. Barkuda Island, Chilka Lake, Orissa. (*b*) Same type, but younger and smaller, in vertical section. Hardwar, Uttar Pradesh. (*c*) Type III. Broad, low, irregularly-shaped, non-buttressed; 'multilocular' fungus-comb chambers. Barkuda Island. (*d*) Same type (but with single, dome), in vertical section. Forest near Kota, SE Rajasthan. (*e*) Type IV. Broad, non-buttressed but 'unilocular' type. Indian Desert (Western Rajasthan); on banks of water reservoirs. (*f*) Type V : Low, dome-shaped, with turrets; multilocular. Kanah National Park, Madhya Pradesh. (*g*) No-mound; emergence holes in ground surface; nest entirely underground. Indian Desert. (*a* and *c*, *adapted from Annandale; f, from Chhotani.*) *e.*, emergence holes; *f.c*, fungus-combs; *r.c*, royal chamber; *t*, turrets; *w*, wall of mound.

ground-level. Western Rajasthan desert (Mathania, near Jodhpur, on the banks of a water reservoir; Roonwal, 1975, 1976).

Type V (Fig. 4f): Low, broad-based, dome-shaped, multilocular, with numerous small, rugose, hollow, conical turrets Height with turrets about a metre; with several vaults containing fungus-combs in underground portion; royal chamber situated near ground-level. (This is type B of Chhotani, 1977.) Deciduous forests in the Kanha National Park, Madhya Pradesh. [In addition, Chhotani (1977) describes large (height 60-110 m), dome-shaped mounds with large surface holes, from the Kanha National Park, but he regards them as old, deserted mounds of Type V with the turrets gone.]

Finally, in some very arid areas, e.g., the Great Indian Desert, *O. obesus* breeds entirely underground (Fig. 4g) and does not form any mound, except very exceptionally in the vicinity of water, as in type IV above. Thus, in the three ecological zones of Rajasthan (wet, semi-arid and arid, Fig. 5), mounds are practically absent in the last zone.

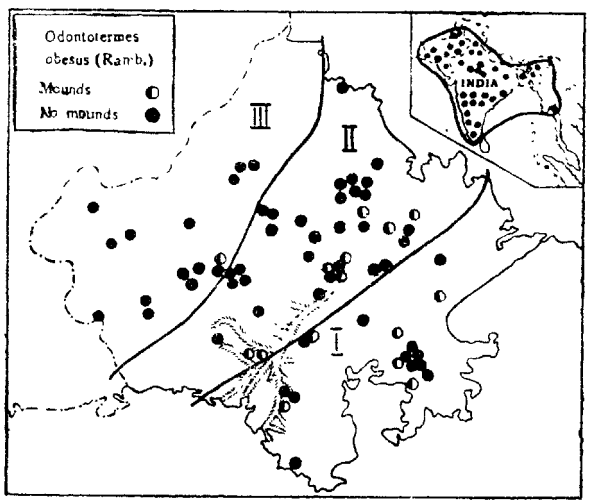

Fig. 5. *Odontotermes obesus.* Map showing known distribution in Rajasthan (India), with mounds and without mounds, in three ecological zones : I, Wet, annual rainfall over 60 cm; II, semi-arid, rain 30-60 cm; III, Arid (desertic), rain below 30 cm. (*Inset* : Distribution of *O. obesus* in South Asia)

We thus have a wide range of variations. The following tentative correlations exist: The no-mound type is characteristic of very dry, desertic habitats (the Great Indian Desert); but where subsoil water is freely available, as on the banks of reservoirs, mounds of type IV are found. The moderately tall, buttressed but multilocular mounds (type II) seem to be confined to the less wet parts, both deciduous forests and semi-scrub, of southern India, and have not ben recorded in the north. The low, broad-based, non-buttressed, multilocular mounds (type III) seem to have a wide ecological range, from the evergreen forests of Coorg to the dry deciduous forests of Rajasthan and Barkuda. The low, dome-shaped, turreted mounds (type V) have

been found only in the deciduous forests of Madhya Pradesh. On the tiny Barkuda Island, two mound-types (I and III) occur, while in the limited area of the Kanha National Park, at least three types (I, III and V) have been found.

Silvestri (1923, p. 224) stated that in Annandale's Barkuda Island examples, in imagoes from the buttressed mounds (his var. *oculatus* Silvestri), eyes are larger than in the typical form, but no differences in alates or soldiers have been found anywhere else on more abundant material, and it is difficult to sustain Silvestri's separation. The older taxonomists were aware of the problem of mound variability (see Wasmann, 1902, pp. 159-160).

Subfamily 2 : Nasutitermitinae

6. *Trinervitermes biformis* (Wasmann) (Fig. 6) [Syn. *T. heimi* (Wasmann)]

Widespread in South Asia (Pakistan, India, Sri Lanka). In the north it is entirely subterranean and does not build mounds (Roonwal, 1975, 1976, Rajasthan), but in the south (Tamil Nadu and Karnataka) it builds low, dome-shaped earthen mounds about 8-25 cm in height and 20-60 cm in basal diameter; beneath the mound lies the bowl-shaped underground nest (Sen-Sarma and Mathur, 1961; and Roonwal, in press).

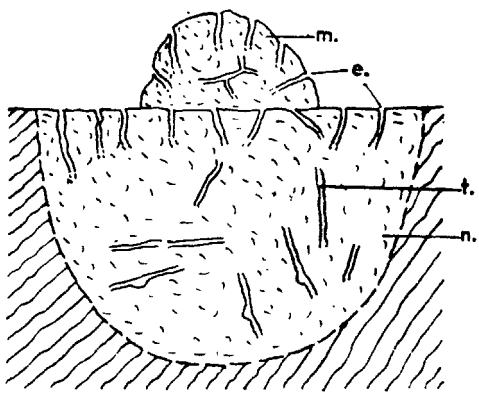

Fig. 6 *Trinervitermes biformis*. India. Mound and nest, in vertical section South India. Diagrammatic.

e, emergence hole; *m*, mound; *n*, nest; *t*, tunnels.

(B) Australian Species

(Several examples are known from the Australian Region)

Family (a) Rhinotermitidae

Subfamily : Coptotermitinae

1. *Coptotermes acinaciformis acinaciformis* (Froggatt)

Widespread in Australia, with a wide range of ecological tolerances, being found in areas with low annual rainfall (20 cm) to as high as 150 cm (Gay & Calaby, 1970). Also shows considerable variation in mound and nest-building habits. In the north and southwest it builds mounds, but eleswhere it breeds either entirely

underground or in stumps, holes of wood piles or in trunks of dead and living trees. In all these cases it maintains a connection with ground soil. But occasionally it nests in situations where a soil connection is impossible, as in the timbers of ferry boats.

Ecologically (Gay & Calaby, 1970), it occurs in three different situations: (i) In tropical Queensland, the Northern Territory and on the Cape York Peninsula, it is consistently a mound-builder, probably because the eucalyptuses of the northern Australian woodlands do not have the physical dimensions to contain its large colonies. (ii) In subtropical and temperate Australia it nests entirely within tree trunks and no mounds are built. (iii) In southwestern Australia, though it is largely a tree-nester, it also occasionally builds dome-shaped mounds in the sclerophyll woodland and mallee (thickets of dwarf eucalyptus). Regional differences also occur. In tropical Australia, mounds are large (2m or more in height), and the honeycombed carton lumps, where breeding occurs, lie deep underground. In the northern territory there is a definite nursery area at ground-level, but in northern Queensland there is none. Mounds in southwestern Australia are small, hardly a metre high, with very thick walls, and the nursery lies below ground level (Calaby & Gay, 1956; Gay & Calaby, 1970).

An allied subspecies, *C. a. raffrai* Wasmann, is found only in southwestern Australia; it attacks in-service timber as well as living trees, but is not known to build mounds.

2. *Cotpotermes frenchi* Hill

Occurs from Northern Queensland to Western Australia in eucalyptus communities. In forests and savannah woodlands it nests within tree trunks and does not build mounds. But from western New South Wales across to western Australia, in semi-arid dwarf eucalyptus communities (mellee) and sclerophyll woodland, it builds symmetrical, dome-shaped, 30-60 m high mounds (Gay & Calaby, 1970).

3. *Coptotermes lacteus* (Froggatt) (Fig. 7a)

Common in eastern Australia from Victoria to southern Queensland in dense or open forest or in pastureland; up to c. 1,060m. It generally builds mounds which

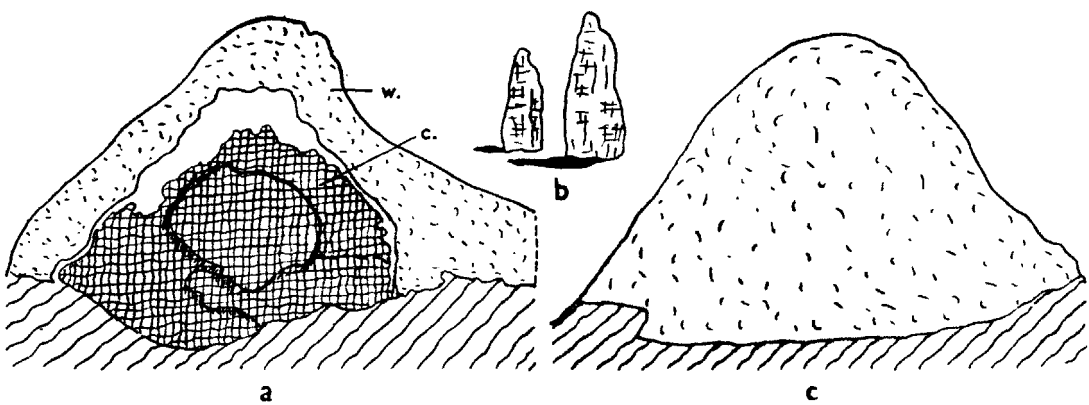

Fig. 7. Mounds of Australian termites. (*Adapted from Gay & Calaby*, 1972.) (*a*) *Coptotermes lacteus*, in vertical section. (*b*) *Amitermes vitiosus*. (*c*) *Nasutitermes exitiosus*.

c, carton nest; *w*, wall of mound.

attain a height of about 2.5 m and a basal diameter of 2.1 m; the outer wall is 15-30 cm thick and encloses a mass of dense carton material, the nest (Fig. 7a). In the rain forests of northern New South Wales and southern Queensland it nests in rotting logs and does not build mounds. (Gay & Greaves, 1940; Calaby & Gay, 1956; Gay & Calaby, 1970.)

Family (b) Termitidae

Subfamily 1: Amitermitinae

4. *Drepanotermes rubriceps* (Froggatt)

Widespread in Australia. In inland New South Wales, southwestern Queensland, and the coastal areas of the northern territory it is entirely subterranean; and the ground surface above the nest forms bare concrete slabs over an area of several square metres. Sometimes, portions of these slabs are raised either as several small humps or into large dome-shaped, 2 m high mounds (Gay & Calaby, 1970).

5. *Amitermes laurensis* Mjöberg

Widespread in Northern Queens land. It is basically a mound-builder, the mounds showing a remarkable degree of variation (Gay & Calaby, 1970). In Townsville, on rocky slopes, many of the mounds are pyramidal in shape and go up only to 0.5m in height, but on the plains they are round-conical and rise up to nearly 2 m. On well drained soils mounds are circular at the base, but in ill-drained, clayey depressions or swampy habitats they are laterally compresed so as to give them a north-south orientation, such 'meridional' mounds being as high as 3.6 m. Occasionally, the species does not build mounds and the nest is entirely subterranean. The ecological relationships are obscure.

6. *Amitermes vitiosus* Hill (Fig. 7b)

Common in northern Queensland and the northern territory. It generally constructs columnar, subconical mounds which have a basal diameter of up to 0.6m and a height of a little over a metre. In the same locality they are very numerous on poor grazing land, such as well-drained sandy or gravelly elevations, but on hard, poorly drained, grey soil flats they are not only scarce but also laterally compressed, with a north-south 'meridional' orientation (cf. *A. laurensis*).

7. *Microcerotermes serratus* (Froggatt)

Widespread in Australia. In some areas it builds small, pointed or dome-shaped mounds which contain a well formed royal chamber. Elsewhere, it builds 'nests' on tree trunks not far above the ground which are about a metre long and 10 cm thick; these 'nests' do not contain functioning reproductives, the latter being present underground in a true nest in contact with buried timber (Gay & Calaby, 1970).

Subfamily 2: Nasutitermitinae

8. *Nasutitermes exitiosus* (Hill) (Fig. 7c)

Occupies the southern half of Australia and is known for its populous colonies containing one to two million individuals. It builds dome-shaped mounds. In low rainfall belts mounds are very low, and the nest is mostly, or entirely, underground. In

forests mounds are much larger, up to a metre high and 1.2 m in basal diameter (Fig. 7c). They have an outer earthen wall, an inner woody wall, and a central nursery of fragile woody material (Holdaway, 1933; Fyfe & Gay, 1938; Holdaway & Gay, 1948; Gay & Calaby, 1970.)

9. *Tumulitermes pastinator* (Hill)

Occupies the northern half of Australia and is a mound-builder. Generally, mounds are low and dome-shaped with a height of about 0.6 m and a basal diameter of a metre or less (occasionally 1.2 m and 2 m respectively). At other places they have a truncated apex and deeply sculptured sides (Gay & Calaby, 1970). The ecological relationships are not known.

10. *Tumulitermes westraliensis* (Hill)

Confined to western Australia. It builds variable mounds. Some are wide and flat (about 25-30 cm high and 40-45 cm in basal diameter); others are tall, conical and rather narrow (height 100 cm, basal diameter 76 cm). The ecological relationships are not known.

(C) Ethiopian Species

(Only two examples, both Termitidae, are known)

Subfamily 1 : Termitinae

1. *Cubitermes fungifaber* (Sjostedt) (Fig. 8)

Widespread in equatoral Africa. It builds complex mushroom-shaped mounds composed of one or more vertical columns, each 15 cm or more thick and several times higher than wide; the columns are topped by several umbrellas or none. In full grown mounds there are 1 to 6 vertical columns each bearing up to five caps or none. Internally, there are numerous intercommunicating cells. Once built, the different portions of the mound are not modified, though new additions may be made without any order and without any connection with the old plan; the nest is thus of the 'mosaic' type. There is thus considerable intraspecific variability, from a single-columned, uncapped mound to those with many columns and many caps (Fig. 8). No ecological relationships have been established (Noirot & Noirot-Timothée, 1962; & Noirot, 1970.)

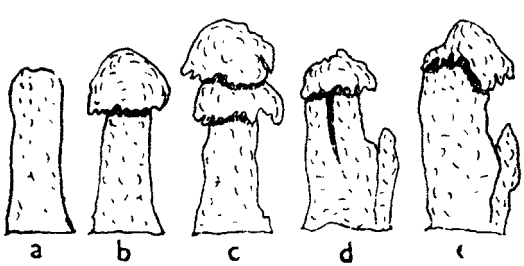

Fig. 8. *Cubitermes fungifaber*. Equatorial Africa. Variations (a-e) in mound types. *Adapted from Noirot*, 1970)

Subfamily 2 : Macrotermitinae

2. *Macrotermes subhyalinus* (Rambur)*

In East Africa (the Kajiado district and the Rift Valley), Dorlington (personal communication) found two extreme types of mounds and an intermediate type which he could correlate with soil types as follows: *Type I*: Kajiado clay type. Has a highly differentiated internal structure, with a distinct underground 'hive chamber' containing large fungus-combs; numerous air passages going up to the roof ; mound of coarse, hard earth with a network of passages without, external openings; royal cell lying deep underground, surrounded by massive elaborate defensive structures. Found on hard, clay soil. *Type II*: Ologesailie diatomite type. 'Hive chambers' small and mostly above ground; fungus-combs small; air passages open to the surface and extend well down; royal cell without distinctive structures or surrounding defences. Found on soft, friable soils. *Type III*: Intermediate type. 'Hive' partly above ground; closed air passages extend down into the hive structure and not opening from the roof; fungus-comb galleries with thick walls instead of thin lamellae and pillars. Found on light, sandy soils at Kajiado.

(D) Neotropical Species

A single example (Termitidae, Nasutitermitinae) of mound variability is known. Holmgren (1906) had described variations in carton nests of the Nasutitermitinae, but these were age variations and not correlated with ecology. [Also see Addendum].

Armitermes neotenicus Holmgren

Occurs in Bolivia, Peru and Guiana. It is a species of virgin forest, avoids dry areas, and shows considerable variations in the selection of sites for nest building (Araujo, 1970). It makes "arboreal nests, earthen nests on tree trunks, and round nests in thin artificial and natural forests . . . " (p. 553). Further details are lacking.

Discussion — Correlation with Ecology

As shown above, intraspecific variation in mound and nest-construction is known in at least 19 species from different regions (Oriental 6, Australian 10, Ethiopian 2, and Neotropical 1) and from two families (the Rhinotermitidae and the Termitidae). Taxonomically, these variations seem to be confined to the Coptotermitinae among the Rhinotermitidae, but is more widespread among the Termitidae. Variations have so far been found largely in the Oriental (especially Indian) and the Australian regions. This bias is, at least in part, due to the comparative paucity of studies in the other regions. The range of variations is sometimes narrow, and at others very large. In extreme cases it may extend from nesting completely underground or inside trees (the "no-mound' situation) to the building of large, conspicuous mounds (*Coptotermes a. acinaciformis* and *Drepanotermes rubriceps*) in Australia, and *Odontotermes obesus* in India). The mounds too may be highly variable in shape, size, inner construction and abundance (in *Odontotermes brunneus* and *O. obesus* five types are known).

* For synonymies and nomenclatural position, see Ruelle, 1970, *Bull, Br. Mus. (nat. Hist.), Eutom.* **24** (9), 365-444.

In some cases the relationship between mound and nest types and the nature of the ecological habitat is fairly clear, while in others this is not so. These variations are not geographical since in the same area, within a few kilometres, different types of construction are encountered (*O. brunneus*, at Rajkot; *O. obesus*, on the Barkuda Island and in the Kanha National Park; and *Macrotermes subhyalinus* at Kajiado. It also seems that different species may react differently to similar habitats. A few examples of ecological correlations will suffice to illustrate the main points. In the Indian Desert, *Odontotermes obesus* nests entirely underground (except rarely, where subsoil water is available in plenty as on the banks of water reservoirs), but it constructs well built mounds in the wetter areas (Figs. 4, 5) (Roonwal, 1975, 1976, and in press). In the same species different types of mounds are made in various ecological habitats (vide supra). In the Australian species *Amitermes laurensis*, mounds are small and pyramidal in rocky areas, and tall and laterally compressed in the plains. In tropical forests *Coptotermes a. acinaciformis* and *Nasutitermes exitiosus* build mounds, but *C. frenchi* and *C. lacteus* nest in trees; in low rainfall areas, *C. a. acinaciformis* nests in trees but *C. lacteus* builds mounds. While in a number of species the variations have been correlated with certain types of ecological habitats, the precise mode of action is not known, except perhaps in the case of *Odontotermes obesus* where subsoil moisture seems to govern mound formation.

References

Ahmad, M. (1965). Termites (Isoptera) from Thailand. *Bull. Amer. Mus. nat. Hist.*, **131**, 1-113.

Annandale, N. (1923). The habits of the termites of Barkuda. *Rec. Indian Mus.*, **25**, 233-252.

———(1924). Termite mounds. *J. Bombay nat. Hist. Soc.*, **30**, 25-35.

Araujo, R. L. (1970). Termites of the Neotropical Region. In: *Biology of Termites* (ed. K. Krishna and F. M. Weesner), Vol. 2, pp. 527-576. Academic Press, New York.

Basalingappa, S. (1968). The replacement of the primary reproductives in termites. *J. anim. Morph. Physiol.*, **15**, 183-187.

———(1971). Association of *Speculitermes cyclops*, *Dicuspiditermes* (*Capritermes*) *incola* and an undetermined species of *Microtermes* with *Odontotermes assmuthi*. *Indian Zoologist*, **2**, 67-72.

Bathellier, J. (1927). Contribution a l'etude systematique et biologique des termites de l'Indochine. *Faune Colon. Franc.* **1**, 4+125-365.

Beeson, C.F.C. (1941). *The Ecology and Control of the Forest Insects of India and the Neighbouring Countries*. Vasant Press, Dehra Dun. 1007 pp. (Reprint 1961, 8 +10+767 pp.). Manager of Publ., Govt. of India, Delhi.

Calaby, J. H. & Gay, F. J. (1956). The distribution and biology of the genus *Coptotermes* (Isoptera) in Western Australia. *Austral. J. Zool.*, **4**, 19-39.

Chhotani, O. B. (1977). Termites of Kanha National Park (Madhya Pradesh), India. *Rec. Zool. Surv. India*, **72**, 367-388, 5 pls.

Dorlington, J. B. E. L. An investigation of the mounds of *Macrotermes subhyalinus* (Rambur). Personal Communication.

Escherich, K. (1911). *Termitenleben auf Ceylon*. G. Fischer, Jena. 263 pp.

Fyfe, R. V. & Gay, F. J. (1938). The humidity of the atmosphere and the moisture conditions within mounds of *Eutermes exitiosus* Hill. *Pamphlet Counc. Sci. industr. Res. Australia*, No. **82**, 1-22.

Gay, F. J. & Calaby, J. H. (1970). Termites of the Australian Region. In : *Biology of Termites* (ed. K. Krishna and F. M. Weesner), Vol. 2, pp. 393-448. Academic Press, New York.

Gay, F.J. & Greaves, T. (1940). The population of a mound colony of *Coptotermes lacteus* (Froggatt) *J. Counc. sci. industr. Res. Australia*, **13**, 145-149.

Holdaway, F. G. (1933). The composition of different regions of mounds of *Eutermes exitiosus* Hill. *J. Counc. sci. industr. Res. Australia*. **6**, 160-165.

Holdaway, F. G. & Gay, F. J. (1948). Temperature studies of the habitat of *Eutermes exitiosus* with special reference to the temperature within the mound.—*Australian J. Sci. Res.*, B **1**, 464-493.

Holmgren, N. (1906). Studien uber sudamerikanische Termiten. *Zool. Jahrb. (Syst.)*, **23**, 521-676.

———(1912). Termites from British India (Bombay) collected by Dr. J. Assmuth S. J. *J. Bombay nat. Hist. Soc.*, **21**, 774-793.

———(1913). Termites from British India (near Bombay, in Gujarat and Bangalore) collected by Dr. J. Assmuth S. J. *J. Bombay nat. Hist. Soc.*, **22**. 101-117.

Mathur, R. N. & Sen-Sarma, P. K. (1962a). Notes on the habits and biology of Dehra Dun, termites. III. *J. Timber Dryers' Preserv. Assoc. India*, **8**, 1-18.

———(1962b). Imago caste of *Odontotermes assmuthi* (Holmgren) (Isoptera: Termitidae). *Bull. Ent., Madras*, **3**, 7-12.

Noirot, C. (1970). The nests of termites. In : *Biology of Termites* (ed. K. Krishna and F.M. Weesner), Vol. 2, pp. 73-125. Academic Press, New York.

Noirot, C. & Noirot-Timothee, C. (1962). Construction et reconstruction du nid chez *Cubitermes fungifaber* Sjost. *Sympos. Genet. Biol. Ital.*, Pavia, 11 (Atti 4th Congr. Un. intern. Etud. Insectes sociaux (1961), pp. 181-188.

Roonwal, M.L. (1958). Recent work on termite research in India (1947-57). *Trans. Bose Res. Inst.* Calcutta, **22**, 77-100, 4 pls.

———(1960). Biology and ecology of oriental termites. No. 5. Mound-structure, nests and moisture-content of fungus combs in *Odontotermes obesus*, with a discussion on the association of fungi with termites. *Rec. Indian Mus.*, Delhi, **58**, 131-150.

———(1970). Termites of the Oriental Region. In : *Biology of Termites* (ed. K. Krishna and F. M. Weesner), Vol. **2**, pp. 315-391. Academic Press, New York.

———(1973). Mound-structure, fungus combs and primary reproductives (king and queen) in the termite *Odontotermes brunneus* (Termitidae) in India. *Proc. Indian natn. Sci. Acad.*, B **39**, 63-76.

———(1975). Thar Desert termites. In : *Environmental Analysis of the Thar Desert* (ed. R.K. Gupta. and I. Prakash), pp. 393-422. English Book Depot, Dehra Dun.

———(1976). Field ecology and eco-biogeography of Rajasthan termites : A study in desert environment. *Zool. Jahrb. (Syst.)*, Berlin, **103**, 455-504.

———(1977). Growth ratios in termite mounds (*Odontotermes* : Termitidae). *Comp. Physiol. Ecol.* Jodhpur, **2**, 141-143.

———Bioecological and economical observations on termites of Peninsular India. *Zeit. angew. Ent.*, Berlin and Hamburg (In press).

Roonwal, M.L. & Bose, G. (1964). Termite fauna of Rajasthan, India. *Zoologica*, Stuttgart, **40** (3) (Heft 113) : 58 pp.

Roonwal, M. L. & Chhotani, O. B. (1966). The mound of the termite *Odontotermes feae* in India, *Proc. 2nd All-India Congr. Zool.* (Varanasi, 1962), Calcutta, Pt. 2 (*(Sci. Papers)*, pp. 426-428.

Roonwal, M. L. & Rathore, N. S. The mound-structure and primary reproductives (king and queen) of the termite *Odontotermes kushwahai* (Termitidae) (In press).

Sen-Sarma, P. K. & Mathur, R. N. (1961). *Trinervitermes biformis* (Wasmann), a mound-building termite in South India. *Indian Forester*, Dehra Dun, **87**, 252.

Silvestri, F. (1923). The fauna of an island in the Chilka Lake. Part III, No . 1. The termites of Barkuda Island. *Rec. Indian Mus.*, Calcutta, **25**, 221-232.

Wasmann, E. (1902). Termiten, Termitophilen und Myrmekophilen, gesammelt auf Ceylon von Dr. W. Horn, 1899, mit anderer Ostindischen Material bearbeitet. *Zool. Jahrb. (Syst.)*, Jena, **17**, 99-164.

Addendum

Since the above was written, additional information for the Neotropical Region has come to light. Mathews (1977) has mentioned variations in mound structure in a restricted 20 km² area at the "Base Camp" at Serra do Roncador (latitude 12° 49′ S, longitude 51° 46′ W) in the northeastern part of the State of Mato Grosso in central Brazil. Intraspecific variations, apparently related to vegetation types, have been recorded in three species of the Termitidae, as follows :

Subfamily : Amitermitinae

1. *Microcerotermes exiguus* (Hagen)

It builds a small, subcylindrical mound which reaches a height of about 16 cm and a basal diameter of 11 cm. In the 'Cerrado' forest type about 65% of the mound is below ground-level; the buried part somewhat tapers downward, and the exposed part is rounded and flat-topped. In the 'Cerradao' (a denser form of Cerrado) the mound is smaller; only about 45% of it is buried, and that part strongly tapers downward.

2. *Microcerotermes indistinctus* Mathews

It makes carton nests (a mixture of mineral soil particles and ligneous, probably faecal, material) on tree trunks. Mounds are taller than broad; a large one may attain a height of 40 cm, a width of 35 cm and a thickness of 25 cm, but they are generally smaller. The height attained by them varies with the vegetation type, as follows: in Cerradao type 1.0—3.2 cm (M 2.23); in Valley Forest type 1.8—10.0 cm (M 5.65); and in Dry Forest type 5.5—11.0 cm (M 8.85). This difference, according to Mathews (1977), suggests a relationship with canopy height, the higher mounds being in forests with higher canopies. This may either represent a microclimatic requirement of the mound or may simply reflect the availability of more living space or mound sites.

Subfamily : Nasutitermitinae

3. *Cornitermes snyderi* Emerson

It makes large, dome-shaped mounds in various vegetation types; they attain a height 80 cm and a basal diameter of 100 cm. A mound begins underground as a subcylindrical structure and then rises up slowly above ground level. The original cylinder is sometimes capped by turret-like structures of other termites, especially *Velocitermes heteropterus*. Mounds in Deciduous Seasonal forest with markedly heavier soils are much more shallowly domed than those in very sandy soils of the Cerrado and Campo vegetation types, and the protective layer of the dome is much thinner and harbours far fewer other species.

Mathews, A. G. A. (1977). *Studies on Termites from the Mato Grosso State, Brazil.* 4= 267 pp.—Rio de Janero (Academia Basileira de Ciencias).