Scanning Electron Microscopic Studies of Wing Microsculpturing in Termites (Isoptera). IV. Families Kalotermitidae, Stylotermitidae, Rhinotermitidae and Termiitidae, and General Considerations

M L ROONWAL, S C VERMA* and S S BISEN**
Desert Regional Station, Zoological Survey of India, Paota B Road, Jodhpur

(Received 20 April 1985; after revision 31 December 1985)

This is the fourth and final part of this series and deals with microsculpturing on wing surfaces of four families, 12 genera and 13 species, as follows:—
Family Kalotermitidae: In Bifiditermes beesonii three types of microsculpturing occur, viz., papillae on the margins, and pimples and subcrescentic tubercles all over the wing. Tubercles are the largest (width 7–19 µm). Family Stylotermitidae: In Stylotermes faveolus also three types occur, viz., papillae, pimples and arrowheads. Family Rhinotermitidae: Psammotermes hybostoma wings carry papillae and pimples. In Coptotermes, while C. michaelseni has papillae, pimples and microasters, C. heimi has papillae, pimples and numerous small hairs. Dolichorhinotermes longiflatus wings carry four types, viz., papillae, arrowheads, pimples and tubercles. Family Termitidae: Microcerotermes raja possesses papillae and vase-type microasters with 0–2 central arms. Tuberculitermes bycanistes has papillae and microsetae, while Anguilermes akhorisaiensis carries papillae and microasters, the latter being of two types, viz., vase-type with 1–3 arms (94%) and asteroids (6%). In the Nasutitermitinae, the four genera studied differ considerably from one another. Synotermes molestus has papillae and pimples, and also numerous hairs. In Tumulitermes hastalis there are marginal papillae, a few simple, scattered, minute microasters and numerous granular pimples. Rotunditermes rotundiceps has papillae, pimples and a few simple microasters; also two types of hairs, viz., simple, thin, pointed ordinary hairs with a small, basal articulatory ring, and a thick, blunt type (a new type) with a large articulatory ring. In Mitomitermes giffardi three types occur, viz., papillae, a few simple microasters and numerous spearheads. Some general conclusions on the Isoptera as a whole are drawn.

Key Words: Wing microsculpturing, Termites, Isoptera, Kalotermitidae, Stylotermitidae, Rhinotermitidae, Termiitidae

*Northern Regional Station, Zoological Survey of India, Dehra Dun
**Forest Research Institute, Dehra Dun
Introduction

Light microscope (LM) examination of wing microsculpturing in termites (Isoptera) has been made in a long series of studies by Roonwal (1977–1985) and Roonwal and Co-workers (1967–1985). Eight different types of minute, cuticular elements have been found to densely cover both wing surfaces. Recently, scanning electron microscopic (SEM) studies have been made to determine in detail the nature of these structures (Roonwal 1985a–c and Roonwal & Verma 1985). This is the fourth and final part of the series and deals with four families (Kalotermitidae, Stylotermitidae, Rhinotermitidae and Termitidae), 12 genera and 13 species. Microsculpturing in the order Isoptera as a whole is also discussed and some general conclusions drawn.

Taxonomic details will be found in Snyder's world catalogue (1949). For the more recent taxa, the relevant references are provided.

Results

Family I. KALOTERMITIDAE

Genus (1). Bifiditermes Krishna


1. Bifiditermes beesoni (Gardner) (figure 1; and plate 1)

Material: Imagoes from Lahore (Pakistan).

LM studies (Roonwal & Rathore 1978) have shown the presence of 2 or 3 rows of papillae on the anterior and posterior wing margins, and numerous large tubercles and minute pimplules on the membrane. SEM studies generally confirm this, and further demonstrate the precise nature of these structures, as follows:– Papillae call for little comment; length 2.5–4.0 \( \mu m \). Pimplules scattered all over wing; vary considerably in size (maximum diameter 0.5–2.5 \( \mu m \)) and shape (roundish blobs to longish bodies).

Figure 1 Bifiditermes beesoni. Variation in shape and size of tubercles on surface of forewing. (From scanning electron micrographs). The tubercles generally point distally, but rarely the reverse may occur (figure 1, I).

Tubercles forming the largest and most conspicuous component; shape generally subcrescentic, but may vary considerably; width and height of crescentic margin ca. 7–19 \( \mu m \) and 2–7 \( \mu m \) respectively; crescent generally flat, sometimes high (Index Height/Width 0.25–0.53); wall of crescent generally thicker in middle (maximum thickness 1.5–4.0 \( \mu m \), mostly 2.0–3.5 \( \mu m \)), but sometimes varies irregularly; tubercles occur all over membrane, but are more concentrated in rows on the veins; those near wing margins generally smaller than elsewhere; density 1500–3000/mm\(^2\), higher in anterior half of wing; tubercles point distally, occasionally the reverse (figure 1, I).

Family II. STYLOTERMITIDAE

[For status of the family, vide Snyder (1949) and Roonwal (1975)]

Genus (2). Stylotermes Holmgren & Holmgren

(Synonyms: Sarvaritermes Chatterjee & Thakur and Operculitermes Yu & Ping.)

2. Stylotermes faveolus (Chatterjee & Thakur) (figures 2 & 3, plate)
Material: Imagoes from Sarvari village (Kulu Valley, Himachal Pradesh, India), emerged ex infested wood of *Alnus nitida*.

Microsculpturing, as studied under SEM, consists of three elements, viz., papillae, pimpules and arrowheads, which may vary greatly in size and shape as follows:- Papillae in a single row; pointed, thorny, size 2.9–3.6 μm × 1.5–3.0 μm; lying at intervals of 2 to 6 μm along anterior wing margin; a similar row of smaller ones on posterior margin. Pimpules minute (1.0–3.5 μm × 1.0–2.5 μm), with various shapes from round to rod-like, bowl-like and flower-like; distribution patchy. Arrowheads V-shaped, scattered in patches (usually on the veins) all over wing, reaching the margins near papillae; density 640–950/mm², higher near margins. Size greatly variable, from minute (1.4 × 1.0 μm) to large (4.2 × 1.8 μm), smaller near margins. Mostly V-shaped with two arms, but some almost straight; inner angle sustained by the two

---

**Figure 2 Stylotermes faveolus.** Some microsculpturing elements on dorsal surface of forewing (figure based on scanning electron micrographs). A, Part of anterior margin of wing, to show papillae and arrowheads; B, Variation in size, shape, etc. of pimpules a, arrowheads; p, papillae

---

**Figure 3 Stylotermes faveolus.** Variation in size, shape, etc. of arrowheads. (From dorsal surface of a forewing, based on scanning electron micrographs.) Arrowheads are usually angular (V-shaped), with the apex pointed distally and the teeth lying on outer margin of the arms. Exceptionally, as in figure O, the apex points in the reverse direction and the teeth lie on the inner margin.
arms varying from acute to obtuse (75°–180°), but is mostly about 15° on either side of a right angle (ca. 75°–110°); most of the Vs flat, but some high-arched; ratio Height/Width 0.2 to 0.9, mostly low, 0.2–0.5; generally, the two arms subequa, but sometimes one of them greatly reduced, or even absent; outer margin toothed, with a large apical and 0–4 prominent marginal teeth on each arm; apex of each arrowhead directed distally, rarely (figure 3, 0), in the same wing completely reversed, with apex pointing proximally and teeth also lying on inner margin instead of outer.

LM studies had been made on two other species (Roonwal 1981, S. fletcheri; and Roonwal, Verma and Thakur 1979a, S. dunensis); microsculpturing in both consists of papillae, pimples and arrowheads. The present SEM studies generally confirm these elements but also show marked differences and throw fresh light on their intimate structure. The papillae are pointed and thorny and occur in a single marginal row instead of being lobular and in several rows. The pimples no longer conform to the previous uniform shapes (minute, rounded bodies), but show great variety, from round and ball-like to rod-like, bowl-like and flower-like. The arrowheads were with smooth arms whereas in S. faveolus the arms are denticulate.

**Family III. RHINOTERMITIDAE**

The Rhinotermitidae is phylogenetically an intermediate family, a position also reflected in its microsculpturing. Five types of elements occur, in various combinations, viz., papillae (universal), arrowheads, pimples, tubercles and micrasters. Three principal groups are recogniseable, thus: (a) A primitive group, without micrasters (Psammotermi- tinae and Rhinotermitinae); (b) an intermediate group, with or without micrasters (Heterotermitinae and Coptotermitinae); and (c) an advanced group, with both simple and complex micrasters (Termotogontinae). In some species of Coptotermes (e.g., C. heimi, etc.) the wing membrane is covered with numerous hairs in addition to the microsculptures (papillae and pimples). One subfamily, Heterotermitinae (Hetero- termes) has been studied earlier (Roonwal 1985a); three others are discussed below.

**Subfamily (a) Psammotermitinae**

**Genus (3). Psammotermes Desneux**

3. *Psammotermes hybostoma* Desneux (figure 4 & plate 3)

**Material**: Imagoes from Kasr-el-Gibaly State Farm (near Fayum, Egypt, Africa).

From LM studies (Roonwal, Verma & Thakur 1979) microsculpturing has been shown to consist of papillae at the anterior and posterior margins and pimples all over the membrane. SEM studies confirm this as regards papillae which are finger-shaped

![Figure 4 Psammotermes hybostoma. Shapes, etc. of some microsculpturing elements on surface of forewing. (From scanning electron micrographs.) A, Papillae at the posterior margin; B, Pimples. Vase-shaped, with 0 to 2 central arms, and 5-armed subasteroids (the last figure)
and occur at the anterior and posterior margins (figure 4A; length 3.5–4.0 μm, basal width 1.5–2.5 μm). But the pimplae are different. They are numerous, minute (2.1–5.0 μm × 1.0–2.5 μm), not round but vase-shaped with or without one or two central arms, and occasionally subasteroid. They somewhat resemble microasters but are much smaller.

Proportions of various forms:
- Vase-type without arms 20%
- Vase-type with 1 arm 60%
- Vase-type with 2 arms 10%
- Subasteroids 10%

Subfamily (b) Coptotermitinae
Genus (4) Coptotermes Wasmann

LM studies (Roonwal, Verma & Thakur 1979b) have shown that species fall into two groups: (A) Microasters absent; wing microsculpturing consisting of papillae and pimplae. (B) Microasters present in addition to papillae; pimplae present or absent.

4. Coptotermes michaelensi (Silvestri)
   (figure 5 & plate 4)

Material: Imagines from Merredin (Western Australia).

Falls in group B. From LM studies, microsculpturing has been shown to consist of papillae, pimplae and spearheads (then regarded as a type of microasters). SEM studies confirm this; and further show that the spearheads should be distinguished from true microasters; size small, 1.0–1.6 × 1.0–3.8 μm).

5. Coptotermes heimi (Wasmann)
   (figure 6 & plate 5)

Belongs to group A. From LM studies, microsculpturing has been shown to consist of papillae at the margins and pimplae and hairs on the membrane. SEM studies provide more details of these structures, as follows:

Papillae in 4 or 5 rows of closely packed, distally directed, tongue-shaped, humpy structures of variable sizes (1.5–3.5 × 1.0–2.0 μm)
at anterior margin; occurring on front vein but apparently absent at extreme outer edge. Similar papillae occurring at posterior margin. Rest of wing membrane covered with a few rounded, minute pimplules (diameter 0.5–2.0 μm) and numerous (density ca. 1000/mm²) small hairs (length 10–25 μm, mostly 18–20 μm), each hair with a basal articulatory platelet. Also longer hairs (35–60 μm) occurring at margins and distinguishable from the shorter ones mentioned above.

Subfamily (c) Rhinotermitinae

Genus (5). Dolichorhinotermites Snyder & Emerson

6. Dolichorhinotermites longilabius (Emerson) (figures 7 & 8 plate 6)

Material: Imagoes from Kartabo (Guyana, Central America).

LM studies have shown microsculpturing to consist of papillae on the anterior and posterior margins, pimplules in the anterior one-third of wing and numerous tubercles in one or more rows on the veins. SEM studies confirm some of these findings and also reveal substantial differences, as follows:- Microsculpturing consisting of four types, viz., papillae, arrowheads, pimplules and tubercles. Papillae pointed, thorny, in a single row on anterior margin (size 2.0–2.5 μm × 0.6–1.0 μm), and a similar row of smaller ones on posterior margin. Below papillae, in interspace between first or marginal vein and second vein, lie 4 or 5 rows of arrowheads (size 0.8–3.0 μm × 0.6–1.0 μm), earlier regarded as papillae. On wing membrane lie numerous rows of large (5–10 × 4–7 μm), crescentic tubercles, usually a row on each vein; are specially numerous in anterior one-third of wing. Pimplules minute (1.2–3.0 × 0.5–1.3 μm), widely scattered, round, oblong or V-shaped.

Family IV. TERMITIDAE

The subfamily Macrotermmitinae has been studied earlier (Roonwal 1985a, Microtermes; and Roonwal & Verma, in press, Odontotermes and Macrotermes); the other three subfamilies are discussed below.

Subfamily (a) Amitermitinae

Genus (6). Microcerotermites Silvestri

7. Microcerotermites raja Roonwal & Bose (figures 9 A–M; and plate 7)


Material: Imagoes from Jodhpur (Rajasthan, India).

LM studies (Roonwal, Verma & Rathore 1974, Roonwal & Verma 1985, and Roonwal & Rathore 1982) have shown microsculpturing to consist of a few rows of pointed papillae on the anterior and posterior margins and micrasters all over the membrane. SEM studies confirm the presence of papillae and micrasters, and further show their true structure, as follows:-

Papillae pointed and spiky; in 1 or 2 rows of larger ones (2.0–2.5 × 1.0–2.0 μm) on anterior margin and a row of very small ones on posterior. Micrasters (2.0–3.0 × 1.2–1.5 μm) occurring all over membrane (figures 9 A–M; and plate 7); are of the vase-type (Roonwal 1985a) with a gauzy, basal shroud and usually 1 or 2 solid-looking, pistol-like arms projecting from vase, or none at all; no asteroid types (cf. Angulitermes, infra)

Proportions of various types:

Vase-type without arm 16%
Vase-type with 1 arm 71%
Vase-type with 2 arms 13%

Microcerotermites has been well examined (19 species) under LM (Roonwal, Verma & Rathore 1974, Roonwal & Verma 1980a, Roonwal & Rathore 1982) Sharp-pointed papillae occur in rows on the margins. The micrasters cover a wide range, types I to X. SEM studies in M. raja show that only the vase-type, with 0–2 arms, occur and
Figure 7 *Dolichorhinotermes longilabius*. Parts of surface of forewing, to show microsculpturing. (From scanning electron micrographs.) A, Anterior margin, showing papillae, arrowheads and pimplques; B, Middle of membrane, showing tubercles and pimplques

a, arrowheads; f, first vein; p, papillae; pm, pimplques; s, second vein; t, tubercles.

Figure 8 *Dolichorhinotermes longilabius*. Shapes, etc. of microsculpturing elements on surface of forewing. (From scanning electron micrographs.) A, Papillae on anterior margin; B, Arrowheads in anterior one-third of wing, below the papillae; C, Pimplques on membrane; D, Tubercles, usually in single rows on the veins.
there are no asteroids. The vase-type also occurs in some Rhinotermitidae (Roonwal 1985a, Heterotermes) and some Termitidae (Roonwal 1985a, Microtermes; and 1985c, Amitermes and Eremotermes). The Amitermitinae is a relatively primitive subfamily and the uniformity of microsculpturing in its genera emphasise their closeness, in contrast to the Termitinae which shows considerable diversity.

Subfamily (b) Termitinae

Genus 7. Tuberculitermes Holmgren

8. Tuberculitermes bycanistes (Sjöstedt)  
(figure 10; and plate 8)

For synonymy, etc., vide Snyder 1949, p. 174.

Material: Imagoes from Gell River Post, 70 miles from Bahr-el-Gebel (the Sudan, Africa). LM studies (Roonwal & Verma 1980b) have shown two types of microstructures, viz., rows of pointed papillae on the margins
Figure 10 *Tuberculitermes bycanistes.* Microstructures on surface of forewing. (From scanning electron micrographs.) A, a hair. Note the large size and the basal platelet (ring of articular membrane, which is wanting in microsetae); B–O, Variation in microsetae

pl., platelet; s., shaft of hair
and irregularly distributed microsetae all over the membrane. SEM studies generally confirm these findings and throw new light on the structure of the microsetae. Microsculpturing is as follows:-

Papillae sharply pointed and thorny; occurring in 3–4 rows on anterior margin and in 1–2 rows on posterior; anterior papillae larger (3.0–4.5×2.5–3.5 μm) than posterior (2.5–3.0 μm). Microsetae occurring all over membrane; vary considerably in size and shape; length 1–7 μm, basal width 0.6–1.0 μm, those in middle of wing generally longer; shape generally straight with a broad base and tapering to a sharp point, sometimes both ends taper more or less; base broad and irregular, the end sometimes incurved; no basal platelet or articular ring which is characteristic of true hairs (vide figure 10A, and plate 8, figure 1). From LM studies, the microsetae were regarded as having a “basal articulation” (Roonwal 1983b, p. 376), but SEM studies show the absence of such an articular ring. Microsetae are, therefore, not merely minute hairs but are structures sui generis.

Genus 8. Angulitermes Sjöstedt

9. Angulitermes akhorisainensis Chatterjee & Thakur

(figure 9 N–V; and plate 9)


Material: Imagoes from Tehri Garhwal (Uttar Pradesh, India).

LM studies (Roonwal, Verma & Rathore 1974, Roonwal & Verma 1980b, and Roonwal & Rathore 1982) have shown microsculpturing to consist of pointed papillae at the margins and micrasters (both asteroid and nonasteroid) all over the membrane. SEM studies confirm them and further reveal the intimate structure of these bodies, as follows:-

Papillae (plate 9) forming a single row of pointed, thorny structures on anterior margin (size 1.5–3.0×1.0–2.5 μm) and a row of similar but somewhat smaller ones on posterior margin. Micrasters (figures 9N–V and plate 9) mostly (94%) vase-shaped with a basal, petal-like shroud of thin, gauzy material and 1–3 central, pistil-like rods or arms sprouting out of vase; a few (6%) asteroid with 5–8 arms. Sizes 1.8–2.0×1.6–2.4 μm; generally longer than wide, occasionally the reverse.

Proportions of various types:

- Vase-shaped with 1 arm 33%
- Vase-shaped with 2 arms 37%
- Vase-shaped with 3 arms 24%
- Asteroids with 5–8 arms 6%

Subfamily (c) Nasutitermitinae

LM studies (Roonwal, Chhotani & Verma 1981, Roonwal & Rathore 1982, and Roonwal 1983b) have shown three types of microsculpturings, viz., papillae, pimples and micrasters (of two types). SEM studies broadly confirm these findings and add a fourth type, the spearheads, and also a new type of hair.

Genus (9) Syntermes Holmgren

10. Syntermes molestus (Burmeister)

(figure 11; and plate 10)

Material: Imagoes from Lassance (Minas Gerais, Brazil, S. America).

LM studies have shown microsculpturing to consist of papillae and pimples; in addition, hairs are present all over. SEM studies generally confirm these findings, and further reveal the great variety of form and size of the various elements which are as follows:-

Papillae in numerous rows: shallower, smaller (2.5–6.0×1.5–3.0 μm) and denser in upper rows of anterior margin; more conical (some nipple-shaped), larger (3–6×3–6 μm) and more scattered in lower rows, with the base irregular, not smooth. Pimples scattered irregularly over membrane, especially in proximal part; size varies greatly (ca. 0.6×1.2 to 1.6×3.0 μm); shape varying from round or oblong blobs to those with a narrow
projection. Hairs (length 25–50 μm) present densely near margins and in irregular groups on membrane.

Genus (10) **Tumulitermes** Holmgren

11. **Tumulitermes hastalis** (Froggatt)
(plate 11)

*Material:* Imagoes from Brooks Creek (Northern Territory, Australia).

LM studies (Roonwal, Chhotani & Verma 1981) have shown microsculpturing to consist of papillae on the margins, pimplules all over and a few micrasters. SEM studies generally confirm this and provide more details of their structure, as follows:-

Papillae pointed, small (2.0–2.5 × 1.0–2.0 μm), in a row on anterior and posterior margins; a few very small (1.5–2.0 × 1.0–1.5 μm) V-shaped, Y-shaped and rod-like micrasters on anterior one-third of membrane; and numerous odd-shaped, mostly roundish, pimplules elsewhere, varying greatly in size (2.5–3.5 × 2.5–2.5 μm to extremely small ones, less than a micron) producing a granular appearance.

Genus (11) **Rotunditermes** Holmgren

12. **Rotunditermes rotundiceps** Holmgren

*Material:* Imagoes from Chaquimayo (Carabaya, Peru, S. America).

LM studies (Roonwal, Chhotani & Verma 1981) have shown microsculpturing to consist of rows of papillae on the margins and simple micrasters elsewhere; ordinary hairs are also present. SEM studies confirm these elements and provide more information on their true structure and also reveal a new type of hair, as follows:-

Papillae occurring in 3 or 4 rows on anterior margin and in 1 or 2 rows on the posterior; are small (1.5–2.0 × 1.0–2.0 μm) and of two types: pointed and spiky at the edge, arrowhead-like below it. Micrasters few, simple (V-shaped with or without a central arm), small (0.8–3.0 × 0.6–2.2 μm) and rather atypical. Hairs of two types: (i) Ordinary type; thin, sharply pointed, with a small basal articulatory ring; marginal ones thicker and longer (40–60 μm) than those on membrane (15–20 μm); distribution on membrane patchy. (ii) A new type; have a short shaft (12–15 μm long) with a blunt, rounded tip
Plate 1 Bifiditermes beesoni. SEM of dorsal surface of forewing, to show microsculpturings. 1. Anterior margin of wing in middle region, to show papillae (near the edge) and pimples and small tubercles below (×1000); 2. Same, posterior margin; tubercles (×2000); 3. Middle of wing membrane, to show tubercles and pimples (×500); 4. Same, more magnified (×1000).
Plate 2  *Stylotermes faveolus*. Scanning electron micrographs of dorsal surface of left forewing, to show microsculpturings.  1, Anterior margin of wing, near basal (proximal) end, to show hairs (× 500); 2, Anterior margin near middle region, to show thorny papillae (at the edge) and groups of small arrowheads (× 2000); 3, Same, near distal part, to show larger arrowheads (× 2000); 4, Same, more magnified (× 5000); 5, Middle of membrane, to show pimplles (× 1000); 6, Same, more magnified (× 2000)
Plate 3 *Psamnotermes hybostoma*. Scanning electron micrographs of surface of forewing, to show microsculpturing. 1, Middle of wing membrane, to show pimples (×1000); 2, Same, more magnified (×2000); 3, Same, another part of membrane (×2000); 4, Near posterior margin, to show one or two rows of finger-shaped papillae near margin and pimples elsewhere. (×2000).

Plate 4 *Coptotermes michaelseni*. Scanning electron micrographs of surface of forewing, to show microsculpturing. 1, Anterior margin, to show papillae (at the edge) and pimples (×2000); 2, Same, more magnified (×5000); 3, Middle of membrane, to show spearheads and a few pimples (×2000); 4, Same, more magnified (×5000)
Plate 5 Coptotermes heimi. Scanning electron micrographs of surface of forewing to show microsculpturing. 1, Anterior margin, to show hairs and papillae. (×1000); 2, Same, middle part, more magnified, to show tongue-shaped papillae and a single hair (×2000); 3, Membrane, to show a few minute pimples and numerous hairs (×200); 4, Same, more magnified. (×1000); 5, Posterior margin, to show papillae (×2000); 6, Same, middle parts more magnified (×5000)
Plate 6 *Dolichorhinotermes longilabius*. Scanning electron micrographs of surface of forewing, to show microsculpturing. 1, Anterior margin, showing papillae (on the edge) and rows of arrowheads below (×2000); 2, Same, arrowheads more magnified (×5000); 3, Anterior one-third of wing, to show pimples (×2000); 4, Posterior margin, to show small papillae (at the edge) and a few pimples (×2000); 5, On membrane, to show rows of tubercles (×500); Same, more magnified. (×1000)
Plate 7 Microcerotermes raja. Scanning electron micrographs of surface of forewing, to show microsculpturing. 1, Anterior wing margin. Note the long hairs, the small, pointed papillae (at the edge) and a few micrasters in lower half (×2000); 2, Posterior margin. Note the long hairs (at the edge) and micrasters elsewhere (×1000); 3, Middle of membrane, showing micrasters (×1000); 4, Same, more magnified (×2000); 5, Same, still more magnified (×5000); 6, Same, another part (×5000)
Plate 8 *Tuberculitermes bycanistes*. Scanning electron micrographs of dorsal surface of forewing, to show microsculpturing. 1. Anterior margin, showing long hairs, papillae (pointed and thorny) at the anterior margin, and several small microsetae elsewhere. (×2000); 2. Posterior margin. Small papillae at the edge and microsetae elsewhere (×2000); 3. Microsetae on membrane (×2000); Same, part more magnified (×5000)
Plate 9 Angulitermes akhorisainensis. Scanning electron micrographs of dorsal surface of hindwing, to show microsculptures. 1, Anterior wing margin. Note the long hairs, the pointed papillae at the anterior edge and micrasters elsewhere (×2000); 2, Posterior margin. Note the pointed papillae at the posterior edge and micrasters elsewhere (×2000); 3, Middle of wing membrane, to show micrasters (×1000); 4, Same, part more magnified (×2000); 5, Same, still more magnified (×5000); 6, Same, another part (×5000)
Plate 10 *Syntermes molestus*. Scanning electron micrographs of surface of forewing, to show microsculpturing. 1, Anterior margin, to show hairs at the margin and a little below it; papillae (below margin) too small to be clearly seen (cf. figure 2) (×200); 2, Just below the anterior margin. Region of papillae, more magnified (×1000); 3, Region below figure 2, to show scattered papillae (×2000); 4, Same, another region nearby (×2000); 5, Membrane, to show pimples (×2000); 6, Same, more magnified (×5000)
Plate 11 Tumultitermes hastalis. Scanning electron micrographs of surface of forewing, to show microsculpturing. 1, Anterior margin, to show papillae at the edge, long marginal hairs and microasters in the lower half (×1000); 2, Membrane, to show papillae (×2000); 3, Membrane, more magnified, showing papillae (×5000); Same, another part, with papillae (×5000)

Plate 12 Rotunditermes rotundiceps. Scanning electron micrographs of surface of forewing, to show microsculpturing. 1, Anterior margin, to show papillae (at the edge) and hairs (×1000); 2, Same (from another wing), more magnified, to show several rows of papillae, the bases of the large marginal hairs and a single, round-tipped special hair in foreground (×2000); 3, Membrane, to show several hairs. A few basal pieces (ring of articulatory membrane and the central alveolus or pit also seen, with the hair shaft removed) (×1000); 4, Membrane, to show a few microasters, the distal parts of the shafts of two special hairs and a single basal piece of the same (×2000)
Plate 13 *Mimeutermes giffardii*. Scanning electron micrographs of surface of forewing, to show microsculpturing. 1. Anterior margin, to show papillae (at the edge), micrasters (a few) and spearheads ($\times$1000); 2. Membrane, to show micrasters and spearheads. ($\times$1000); 3. Middle of membrane, showing spearheads and a few micrasters ($\times$1000); 4. Membrane, to show a few micrasters, the distal parts of the shafts of two special hairs and a single basal piece of the same ($\times$2000); 5. Same, Still more magnified. Two spearheads ($\times$10000); 6. Membrane from another wing. Spearheads ($\times$5000).

A, Micrasters; B, Spearheads.
Figure 12 *Rotunditermes rotundiceps.* Variation in shape, etc. of microsculpturing elements on surface of forewing. (From scanning electron micrographs.) A, Papillae at the anterior margin. The group on the left lies at the extreme edge, that on the right below the edge; B, Micrasters; C, Hairs on membrane (numerous); D, Special hairs on membrane (few and scattered). The figure at the extreme right shows only the basal alveolus or pit and the ring of articulatory membrane in surface view (hair shaft removed).

Figure 13 *Mimeutermes giffardi.* Variation in shape, etc. of microsculpturing elements on surface of hindwing. (From scanning electron micrographs.) A, Micrasters; B, Spearheads.
(not sharply pointed) and a large basal articulatory ring; are few in number, lying scattered over membrane; function unknown, but probably sensory.

Genus (12) *Mimeutermes* Silvestri

13. *Mimeutermes giffardi* (Silvestri)

(figure 13; and plate 13)

*Material:* Imagoes from Adipodoume near Abidjan (Ivory Coast, West Africa).

LM studies (Roonwal, Chhotani & Verma 1981) have shown microsculpturing to consist of thorny papillae on the anterior and posterior margins and ‘two types’ of micrasters on the membrane (numerous, long ‘spearhead’ type and a few of the typical ones); also hairs are present in several rows on the margins and a row on each of the veins. SEM studies generally confirm this, and provide new information on the intimate structure of these elements, as follows, and also show that spearheads must be separated from micrasters:

Papillae occurring in one or two rows on the margins. Micrasters proper small (2.0–3.5×0.8–2.5 μm), few and scattered on membrane. Spearheads (earlier bracketed with micrasters) large (5–10×1–4 μm), narrow, pointed, present in large numbers all over membrane; vary greatly in size; hair-like but lack the basal articulatory ring; base ‘naked’, sometimes jagged or with a knob-like projection.

**III. General Conclusions**

With considerable scanning electron microscopic data now available (Roonwal 1985a-c, Roonwal & Verma, 1985 and the present account), some general conclusions on the order Isoptera may now be drawn. While SEM studies have broadly confirmed the light microscope findings, several new results have come to light, especially in the following respects:

(i) The intimate structure of the various elements has been revealed, especially in the micrasters, papillae and pimples.

(ii) A new type of micraster, the vase-type with 0–4 central arms, has been found. (iii) A new type of hair (blunt and with a large, basal articulation) has come to light. (iv) some pimples, though still extremely small, look like simple micrasters.

At least eight different kinds of elements occur, not all simultaneously. The papillae occur universally; of the remainder, not more than two or three types may occur in a species. The principal characteristics of these bodies, as revealed by SEM, are given below briefly.

1. *Papillae.* Are either finger-like (tongue-shaped) or pointed and thorny, sometimes nipple-shaped. Two types may occur on the same wing. Occur universally on the anterior and posterior margins in all species. Directed distally.

2. *Arrowheads.* Angular, arrowhead-like structures found in some intermediate families (Stylotermitidae, Serritermitidae). Either absent, or present only occasionally, in the primitive families on the one hand and the higher ones on the other. Directed distally.

3. *Pimples.* Minute (ca. 1.0×1.0 μm to somewhat larger, 2.5×1.5 μm). Appeared to be rounded in LM images but show, in SEM studies, a greater variety of shape, from round or rod-like to flower-like and leafy (thus resembling simple micrasters, but differing from the latter in their minuteness).

4. *Micrasters.* In LM studies showed a wide range of structures, from simple rod-like to complex asteroid shapes with up to 8 arms. But SEM studies reveal a substantially different structure of the simpler, nonasteroid ones which have leafy, vase-shaped outer bodies of thin, gauzy material, with 0–4 solid-looking, pistil-kile arms or rods sprouting out from the inside base. Generally absent in the lowest and highest termites; abundant in the ‘intermediate groups’, especially
the Amitermiteinae, Termitinae and many Nasutitermitinae.

5. Rods. Substraight rods of varying thickness; either subvertical (Odontotermes, Macrotermiteinae) or subhorizontal (Megagynothotermes, Termitinae). (Falsely appear to be sinuous in LM images).

6. Tubercles. Relatively large bodies (1×12 μm to 7×24 μm) with a broad base, with either subcrescentic or angular hump. Generally occur in linear rows on veins (occasionally also on membrane) in some lower families (some Kalotermitidae and Rhinotermitidae). May be absent or present in the same genus (Bifiditermes). Directed distally.

7. Spearheads. Broad-based, spearhead-like bodies, sharp-pointed at tip and blunt or irregularly jagged at base. Occur irregularly in some primitive genera (e.g., some Coptotermes) and again in higher Nasutitermitinae (Afrosubulitermes and Mineutermes). Distally directed.

8. Microsetae. Sharp-pointed, hair-like, with a narrow base (cf. spearheads); devoid of basal articulatory platelet (which characterises hairs), the narrow base blunt or jagged. Not common; so far found only in two genera (Tuberculitermes, Termitinae; and Pseudacanthotermes, Macrotermiteinae).

Hairs. Not strictly a part of wing microsculpturing, they occasionally occur (some Coptotermes, Syntertes, etc.) in considerable numbers on the wing membrane along with the true microsculptures. These are the ordinary hairs (found in all insect orders) and are characterised by a long or short, distally pointed shaft and a small basal articulatory ring or platelet. SEM studies have shown the rare occurrence (Rotunditermes rotundiceps) of a new type of hair (which may be sensory) characterised by a small (12–15 μm), distally blunt or rounded shaft and a large basal articulatory ring.

Microsculpturing is of considerable phylogenetic, taxonomic and ecological significance (Roonwal, 1983b, 1985b).

Acknowledgements
For the scanning electron microscopic facilities we are indebted to Dr P K Sengupta (Director of Biological Research, Forest Research Institute, Dehra Dun) and to Dr R Guggenheim (Director, Laboratory of Scanning Microscopy, Geological-Palaeontological Institute of the University of Basel, Switzerland). To Dr R C Sharma and Dr N S Rathore (Zoological Survey of India, Jodhpur) we are obliged for assistance with the drawings.

References
— 1983a Universal occurrence of external cuticular microscopic papillae and allied structures as an essential character of termites (Isoptera, Insecta), and redefinition of the Order; *Zool. Anz.*, Jena 211 137–144
1985b Recent researches on wing microsculpturing in termites (Isoptera), and its evolutionary and biological significance; *Proc. Indian natn. Sci. Acad.* **B51** 135–168

1985c Scanning electron microscopic studies of wing microsculpturing in termites (Isoptera). II. Genera *Amitermes* and *Eremotermes* (Termitidae, Amitermitinae); *Proc. Indian natn. Sci. Acad.* **B51** 310–318

— and Chhotani O B 1967 Wing microsculpturing in termite genera *Odontotermes*, *Hypoterme* and *Microtermes* (Termitidae: Macrotermitinae), and its taxonomic value; *Zool. Anz.*, Jena **178** 236–262, 1 table


— and — 1986 Wings and wing microsculpturing in the termite family Indotermidae (Indotermes, Isoptera), and their bearing on phylogeny; *Proc. Indian Acad. Sci. (Anim. Sci.), Bangalore* (In press)


— and — 1980b Evolution and systematic significance of wing microsculpturing in termites (Isoptera). IX. Subfamily Termitinae of family Termitidae; *Proc. Indian natn. Sci. Acad.* **B46** 455–469

— and — 1983 New data on wing microsculpturing in termites (Kalotermitidae, Thinotermitidae and Termitidae); *Annals Ent., Dehra Dun* 1 (1) 27–34

— and — 1985 Scanning electron microscopic studies of wing microsculpturing in termites (Isoptera). III. Genera *Odontotermes* and *Macrotermes* (Termitidae, Macrotermitinae); *Proc. Indian natn. Sci. Acad.* **B51** 405–412


—, — and Thakur M L 1979a Evolution and systematic significance of wing microsculpturing in termites (Isoptera). V. Families Mastotermitidae, Termopsoidae, Hodotermitidae and Stylotermitidae; *Proc. Indian natn. Sci. Acad.* **B45** 115–128

—, — and — 1979b Evolution and systematic significance of wing microsculpturing in termites (Isoptera). VI. Family Rhinotermitidae; *Proc. Indian natn. Sci. Acad.* **B45** 332–353

Synder T E 1949 Catalog of the termites (Isoptera) of the world; *Smithson. misc. Colls., Washington*, 112 1–499