Proc. Indian natn. Sci. Acad. **B49** No. 5 pp 359-391 (1983)

Evolution and Systematic Significance of Wing Micro-sculpturing in Termites. XIII. Order Isoptera

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(Received 20 May 1982; after revision 5 April 1983)

(1) This is the final part of the current series of papers (Roonwal, and Roonwal et al. 1967–1982) on micro-sculpturing on termite wings. With the abundant material now available from all the major families and subfamilies (79 genera and 238 species were studied), it is profitable to examine the situation in the order Isoptera as a whole. (2) Both the upper and the lower surfaces of wing membranes are densely covered with cuticular microsculptures (sizes 0.5–24 μm; density up to ca. 12570/mm^2), and the total number of the elements on a single wing surface may sometimes be as high as over half a million. (3) At least 7 different types of these elements have been found. Of these, the papillae occur in all the members of Isoptera; the other structures may be present or absent. These structures are: (*i*) *Papillae*: longish, papillate, either finger-shaped or pointed and thorny; directed distally, size ca. 0.5–12 μm, density up to ca. 12570/mm^2; occur universally. (*ii*) *Arrowheads*: Shaped like > or}, sometimes with a third (central) arm; directed distally; sizes ca. 3–23 μm; density low, ca. 1800/mm^2; occur in the Stylotermitidae and a few Rhinotermitidae. (*iii*) *Tubercles*: Large, subcresentic or angular; granular; directed distally; sizes up to 24 μm; density low to moderate, ca. 2600–6300/mm^2; occur in several Kalotermitidae and some Rhinotermitidae. (*iv*) *Pimpules*: Minute (sizes 1–6 μm); density low to high, ca. 900–8885/mm^2; found all over wing; occur in primitive families, rarely in higher ones. (*v*) *Micrasters*: Shapes vary from one-armed (rod-like) to asteroid (8-armed); ten types recognisable; sizes 2–23 μm; densities up to 10870/mm^2; occur in some Hodotermitidae and most of the higher families. (*vi*) *Microsetae*: Thin, setae-like; length ca. 8–16 μm; density moderate, ca. 5000–6000/mm^2; rare, occurring in a few Termitinae and Macrotermitinae. (*vii*) *Rods*: Short to long (2–16 μm); thin, stringy; sub-straight to serpentine; density ca. 2900–8700/mm^2; occur in some Termitinae and some Macroterminae. (4) Detailed distribution in various families is discussed. Microsculpturing is an important *essential* character of the Isoptera, and a new definition of the order is provided. (5) Its evolutionary, phylogenetic and systematic significance is discussed; a key is provided. (6) Micro-sculpturing has important ecological consequences; the theoretical implications are discussed. It adds enormous dead weight to the wings and makes the wing surfaces highly rugose, thus greatly impeding flight and preventing dispersal to distant places. (7) It would be worthwhile to re-examine termite fossils, especially wings, for the presence of micro-sculpturing, particularly papillae.

Key Words: Termites, Isoptera, Wing micro-sculpturing, Evolution, Systematic and ecological significance, Zoraptera

Introduction

This is the final part of the series which deals with all the major families and subfamilies, including 79 genera and and 238 species (Roonwal, and Roonwal et al. 1967–1982, and in press). It deals with the evolution, phylogenetic, systematic, ecological and biological significance of the wing micro-sculpturing in the order Isoptera as a whole. At least 7 types of micro-structures are recognisable, and the number of individual elements on the two wing-surfaces may reach a total of over a million, with densities up to over 12500/mm^2.

Earlier accounts, and also some recent studies, are marked by vagueness, lack of detail, contradictory terminologies and absence of adequate illustrations (Light 1929, p. 426, Emerson 1965, 1969, 1971, Emerson & Krishna 1975, Krishna 1961 and Chhotani 1975).

The first detailed study, on some Macrotermitinae (*Odontotermes*, *Hypotermes* and *Microtermes*), was undertaken by Roonwal and Chhotani (1967). They described the thin, stringy and wavy cuticular rods and illustrated them, giving their sizes, densities, distribution, etc. This was followed by similar studies in the present series by Roonwal et al. (1967–82).

Material and Methods

During the course of these studies all the major families, subfamilies, 79 genera and 238 species of the Isoptera, obtained from all parts of the world, have been examined. Glycerine mounts of wings gave much better definition of micro-structures than stained or unstained Canada balsam mounts. Micro-sculpturing, consisting of various types of minute cuticular structures in enormous number, occurs on both the upper and the lower surfaces of wings. Densities, per mm^2, were calculated from to-scale camera lucida drawings. Photomicrographs were taken extensively and were very useful. They could not, however, be used for density determinations owing to the extreme thinness and the transparency of the wing membranes; the micro-structures of the opposite side often showed through, making their elimination difficult.

Types of Micro-sculpturing and their Characteristics

Recent work (Roonwal, and Roonwal et al. 1967–1982) has established the occurrence of at least 7 types of cuticular micro-sculptures of different shapes and sizes on both the wing-surfaces; they are present in enormous number (sometimes over half-million on a single wing-surface, with densities up to over 12500/mm^2). Shape varies from simple, finger-like or thorny papillae and tiny, rounded pimpules to thin or thick one-armed rods and complex, many-armed, star-shaped micrasters. Size varies from minute (0.5 μm) to relatively large (up to about 24 μm). These structures have been termed as: papillae, arrowheads, tubercles, pimpules, micrasters, microsetae and rods and fall into two groups—directed and undirected. The apices of papillae, arrowheads and tubercles are always directed towards the distal end of the wing, while the others show no fixed orientation.

Micro-sculpturing on wing-scales: On the scale or the basal part of the wings, which remains attached to the thorax after the wings have been shed soon after the nuptial flight, micro-sculpturing gets considerably modified from the 'typical' condition found on the membrane. Here

the structures become smaller and clumpy, often lose their typical shapes, and cannot, therefore, be used effectively for taxonomic purposes (for details, see Roonwal & Rathore 1982).

To avoid repetition, the characteristics of these structures, as typically occurring on the wing membrane, are described below very briefly (for more details, see the various papers in this series; also see chart 1 and tables 1 & 2).

Papillae (figures 1, 2 and plate 1)

Longish, papilliform to thorny, pale yellow to deep brown, hyaline structures, with apex directed distally. Are of two main types: (*i*) Finger-like or tongue-shaped, with a rounded tip; sometimes nipple-shaped (*Syntermes*, *Rotunditermes*) or broad and subcresentic (*Psammotermes*). Usually occurring in the primitive families. (*ii*) Sharply pointed and thorny or spiky. Usually occurring in the higher families. Occasionally, both types may occur on the same wing. May differ in species of the same genus (e.g., finger-shaped in *Heterotermes gertrudae*, pointed and spiky in *H. indicola*). Sizes vary from very small (1 μm $\times$ 0.5 μm) to large (3–12 μm $\times$ 2–6 μm). Are usually well developed; in some species extremely weak and reduced to minute, hardly discernible serrations. Mostly concen-

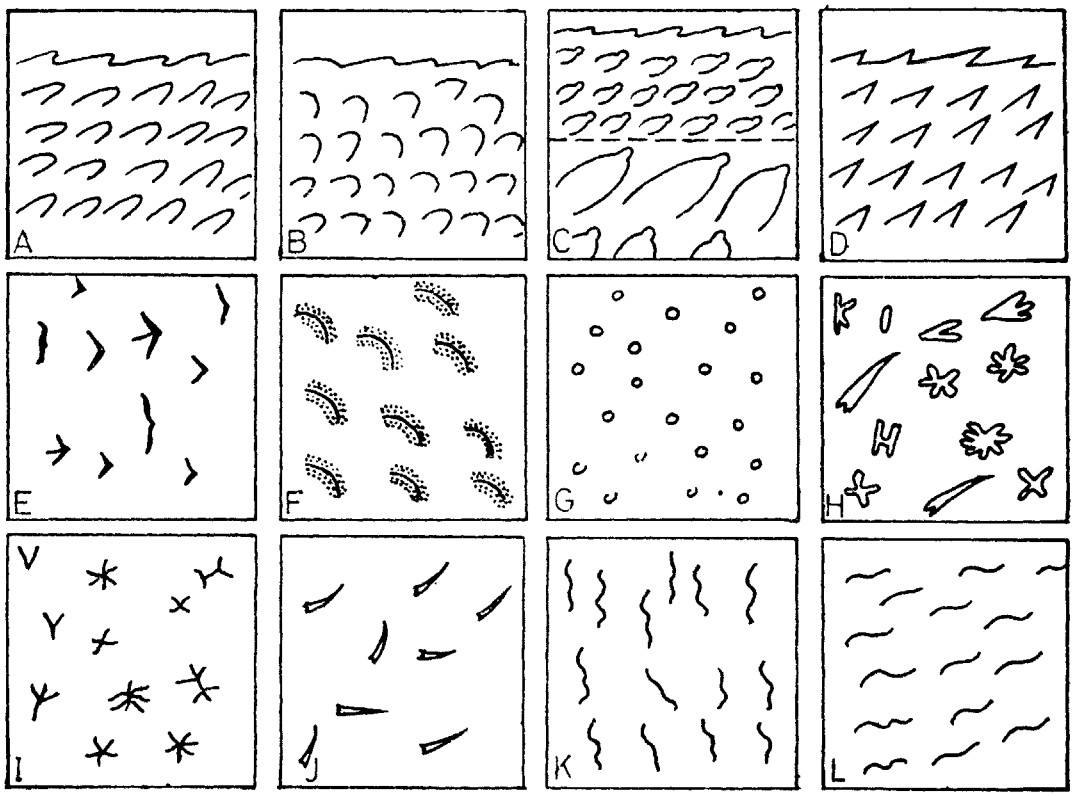

Figure 1 Types of micro-sculpturing on surfaces of termite wings. (**A-D**, papillae, present universally in all Isoptera; **E-L**, other types, may be present or absent.) **A**, Finger-shaped papillae, **B**, Shallower and subcresentic papillae, **C**, Nipple-shaped papillae (in lower half, a few enlarged), **D**, Pointed and thorny papillae, **E**, Arrowheads, **F**, Tubercles, **G**, Pimpules, **H**, Micrasters of thick type, **I**, Micrasters of thin type, **J**, Microsetae, **K**, Rods, subvertical, **L**, Rods, subhorizontal

Table 1 *Wing micro-sculpturing in termites (Isoptera)*

Genera studied	Papillae	Arrow-heads	Tubercles	Pimpules	Micrasters Non-asteroid	Micrasters As-teroid	Micro-setae	Rods	Remarks
1	2	3	4	5	6	7	8	9	10
				Family I. Mastotermitidae (Roonwal, Verma & Thakur 1979a)					
Mastotermes	+	—	—	+	—	—	—	—	—
				Family II. Termopsidae (Roonwal, Verma & Thakur 1979a; Roonwal 1981)					
Zootermopsis, *Archotermopsis*	+	—	—	—	—	—	—	—	—
				Family III. Kalotermitidae (Roonwal & Sen-Sarma 1960; Roonwal & Rathore 1978; Roonwal 1977, 1981)					
(A) Genera studied in detail: 5 genera (see Remarks):	+	—	±	+	—	—	—	—	Genera studied: *Neotermes*, *Bifiditermes*, *Bicornitermes*, *Cryptotermes* and *Ceratokalotermes*. (In *Neotermes* and *Bifiditermes* tubarcles present in some species, absent in others).
(B) Genera studied casually:									
Postelectrotermes	?	?	+	?	—	—	—	—	Roonwal & Sen-Sarma 1960 (their *Neotermes* in part); Roonwal (1977)
Rugitermes	?	?	?	+(?)	—	—	—	—	Krishna's (1961) pimple-like nodules (= my pimpules?).
Glyptotermes	?	?	+(?)	+	—	—	—	—	Krishna's (1961) pimple-like nodules (= my pimpules?); Chhotani's (1975) prominent granules (= my tubercles ?).
Calcaritermes vetus (fossil)	?	?	?	+(?)	—	—	—	—	Emerson's (1969) "conspicuous nodules" (= my pimpules ?).
Incisitermes krishnai (fossil)	?	?	+	?	—	—	—	—	Emerson's (1969) "large tubercles" (= my tubercles).
Epicalotermes	?	—	—	±?	—	—	—	—	Krishana's (1961) hyaline papillae (= my pimpules?)

...Continued

Table 1 (*Continued*)

1	2	3	4	5	6	7	8	9	10
Family IV. Hodotermitidae (Roonwal & Rathore 1978, 1982; and Roonwal Verma & Thakur 1979a)									
Subfam. (*a*) Porotermitinae:									
Porotermes	+	—	—	+	—	—	—	—	—
Subfam. (*b*) Hodotermitinae:									
Anacanthotermes	+	—	—	+	—	—	—	—	—
Subfam. (*c*) Stolotermitinae:									
Stolotermes	+	—	—	—	+	±	—	—	Nonasteroid micrasters in two species, and both nonasteriod and asteroid ones in a third.
Family V. Stylotermitidae (Roonwal, Verma & Thakur 1979a; Roonwal 1981; Emerson 1971)									
Stylotermes	+	+	—	+	—	—	—	—	Also see *Parastylotermes* below.
Parastylotermes (fossil)	?	—	—	+(?)	—	—	—	—	Emerson's (1971) "small microscopic dots or punctuations without radiating extension" (= my pimpules?). Emerson & Krishna (1975, p. 16) record "punctations and micrasters" in both *Stylotermes* and *Parastylotermes*; but no true micrasters actually occur.
Family VI. Rhinotermitidae (Roonwal & Rathore 1977, 1982; Roonwal, Verma & Thakur 1979b; Roonwal 1981)									
Subfam. (*a*) Psammotermitinae:									
Psammotermes	+	—	—	+	—	—	—	—	Emerson & Krishna (1975, p. 16) mention "punctations or micrasters"; but no true micrasters actually occur.
Subfam. (b) Rhinotermitinae:									
Prorhinotermes	+	+	—	—	—	—	—	—	—
Schedorhinotermes	+	—	—	±	—	—	—	—	—
Rhinotermes	+	—	—	+	—	—	—	—	—
Dolichorhinotermes	+	—	+	+	—	—	—	—	—
Subfam. (c) Heterotermitinae:									
Reticulitermes	+	—	—	+	—	—	—	—	—
Heterotermes	+	—	—	—	+	+	—	—	—
Subfam. (d) Coptotermitinae:									

...*Continued*

Table 1 (*Continued*)

1	2	3	4	5	6	7	8	9	10
Coptotermes:									
(*i*) Micrasters absent:	+	—	—	+	—	—	—	—	—
(*ii*) Micrasters present:	+	—	—	±	+	±	—	—	Micrasters mostly non-asteroid only; sometimes bot types present.
Subfam. (e) Termitogetoninae:									
Termitogeton	+	—	—	—	+	+	—	—	—
	Family VII. Serritermitidae								
Serritermes	No detailed information available. Emerson & Krishna (1975) imply absence of micro-sculpturing ("lack punctations", p. 16). But papillae, and probably pimpules expected to occur.								
	Family VIII. Indotermitidae								
Indotermes	No information available.								
	Family IX. Termitidae								
	(Roonwal & Chhotani 1967; Roonwal, Verma & Rathore 1974, 1977 and in press; Roonwal & Verma 1980a, b; Roonwal 1981; Roonwal, Chhotani & Verma 1981)								
Subfam. (a) Amitermitinae									
(A) With only simple, nonasteroid micrasters:									
6 genera (see Remarks)	+	± (rare)	—	—	+	—	—	—	Arrowheads rare, present only in some *Anoplotermes*. Genera studied: *Eurytermes*, *Alyscotermes*, *Anoplotermes*, *Speculitermes*, *Doonitermes* and *Euhamitermes*.
	Family IX. Termitidae (continued)								
(B) With both nonasteroid and asteroid micrasters:									
3 genera (see Remarks)	+	—	—	—	+	+	—	—	Genera studied: *Drepanotermes*, *Eremotermes* and *Microcerotermes*.
Subfam. (b) Termitinae:									
(A) Micrasters present (generally both simple and complex); no microsetae and rods; arrowheads present or absent.									

...*Continued*

(Table 1 *Continued*)

1	2	3	4	5	6	7	8	9	10
15 genera (see Remarks)	+	±	—	—	+	+ (Present in most)	—	—	Micrasters thick or thin. Genera studied: *Allognathotermes*, *Crenetermes*, *Cubitermes*, *Lepidotermes*, *Noditermes*, *Orthotermes*, *Angulitermes*, *Orthognathotermes*, *Crepititermes*, *Termes*, *Cavitermes*, *Promirotermes*, *Protocapritermes*, *Dicuspiditermes* and *Pericapritermes*.
(B) Micrasters absent, microsetae or rods present.									
Megagnathotermes	+	—	—	—	—	—	—	+	Rods resemble those in some Macrotermitinae, but are horizontal-oblique (not vertical-oblique).
Tuberculitermes	+	—	—	—	—	—	+	—	—
Subfam. (c) Nasutitermitinae:									
(A) Micrasters absent; pimpules generally present (rarely absent). Primitive genera:									
4 genera (see Remarks)	+	—	—	± (sometimes absent in *Syntermes*)	—	—	—	—	Genera studied: *Syntermes*, *Procornitermes*, *Cornitermes*, *Rhynchotermes*.
(B) Micrasters present (rarely absent); pimpules generally absent (rarely present)									
21 genera (see Remarks)	+	—	—	+ (rarely present)	+ (rarely absent)	+ (rarely absent)	—	—	Genera studied: *Hospitalitermes* (pimpules present), *Lacessititermes*, *Thailanditermes*, *Bulbitermes*, *Constrictotermes*, *Tenuirostritermes*, *Velocitermes*, *Diversitermes*, *Trinervitermes*, *Tumulitermes* (pimpules present in some), *Rotunditermes*, *Nasutitermes*, *Havilanditermes*, *Labiotermes* (micrasters absent in

...*Continued*

Table 1 (*Concluded*)

1	2	3	4	5	6	7	8	9	10
									some), *Arimitermes* (micrasters, absent in some), *Grallatotermes*, *Occasitermes*, *Convexitermes*, *Subulitermes*, *Afrosubulitermes* and *Mimeutermes*.
Subfam. (d) Macrotermitinae:									
(A) With pimpules:									
Macrotermes	+	—	—	+	—	—	—	—	—
(B) With simple micrasters:									
Allodontermes } *Ancistrotermes* }	+	—	—	—	+	—	—	—	In *Allodontermes* the simple micrasters were earlier called "rods" (Roonwal, Verma & Rathore 1980) but are one-armed, non-asteroid micrasters (see also Roonwal 1981).
(C) With microsetae:									
Pseudacanthotermes	+	—	—	—	—	—	—	—	—
(D) With rods:									
Odontotermes, *Hypotermes*, *Microtermes* }	+	—	—	—	—	—	—	+	—

+, present; —, absent; ±, present or absent.

Table 2 *Summary of wing micro-sculpturing in the Isoptera*

Family	Papillae					Micrasters			
	Finger-shaped or tongue-shaped	Pointed and thorny	Arrow-heads	Tubercles	Pimpules	Non-asteroid (1-6 arms)	Asteroid (1-8 arms)	Micro-setae	Rods
1	2	3	4	5	6	7	8	9	10
Mastotermitidae	+	—	—	—	+	—	—	—	—
Termopsidae	+	+	—	—	—	—	—	—	—
Kalotermitidae	+	—	—	±	+	—	—	—	—
Hodotermitidae	+	—	—	—	±	±	±	—	—
Stylotermitidae	+	—	+	—	+	—	—	—	—
Rhinotermitidae	±	± (rare)	± (rare)	± (rare)	±	±	±	—	—
Serritermitidae	No information. But papillae, and probably pimpules, expected to occur.								
Indotermitidae	No information. But papillae, and probably micrasters, expected to occur.								
Termitidae	± (rare)	± (common)	± (rare)	—	+ (rare)	± (common)	± (common)	± (rare)	±

+, present; — absent; ± present or absent.

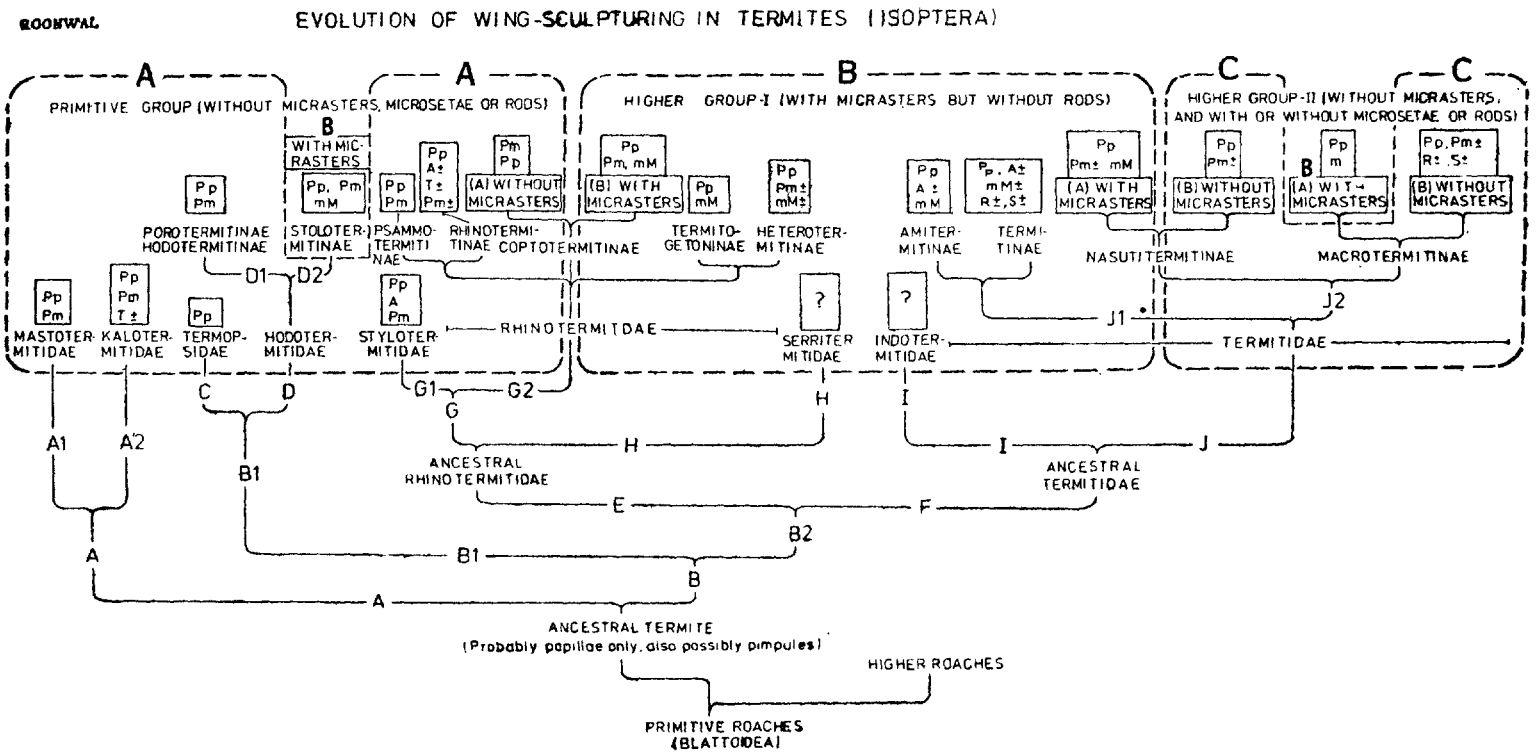

Chart 1 Evolution of wing micro-sculpturing in the Isoptera in three broad groups (A, B, C), the probable routes of descent (A, A^1, A^2, etc.), and the micro-structures present in various families, sub-families, etc.

A, arrowheads; *m*, simple (nonasteroid) micrasters; *M*, complex (asteroid) micrasters; *Pm*, pimpules; *Pp* papillae; *R*, thin rods; *S*, microsetae; *T*, tubercles

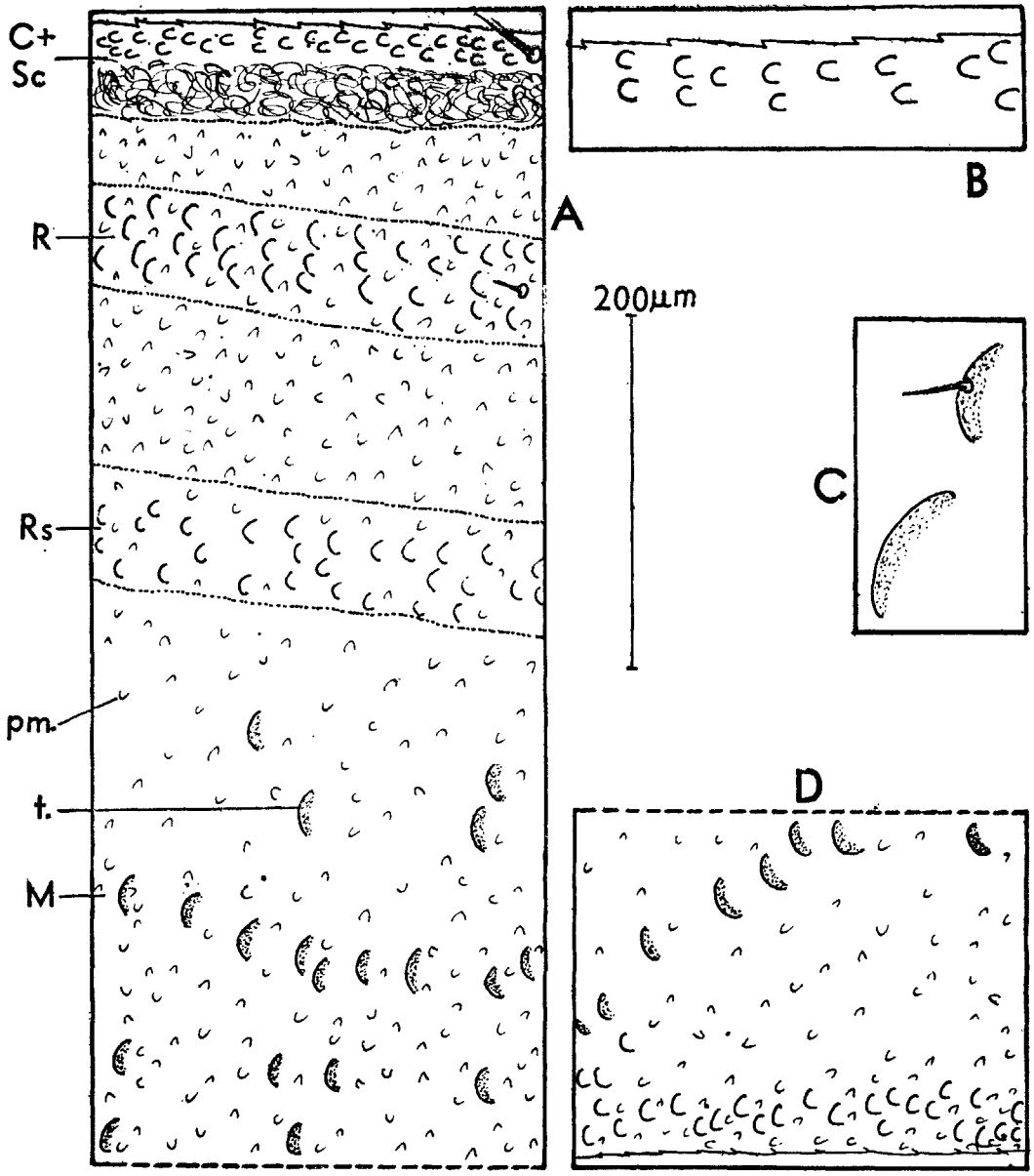

Figure 2 Parts of dorsal surface of left forewing of *Bifiditermes beesoni*, to show micro-sculpturing. **A**, Anterior part, **B**, Same, anterior margin enlarged, to show papillae, **C**, A part enlarged, to show two tubercless (one with a small hair), **D**, Posterior margin, to show papillae, pimpules and tubercles

C + *Sc*, costa + subcosta; *M*, media; *p*, papillae; *pm*, pimpules; *R*, radius; *Rs*, radial sector; *t*, tubercles

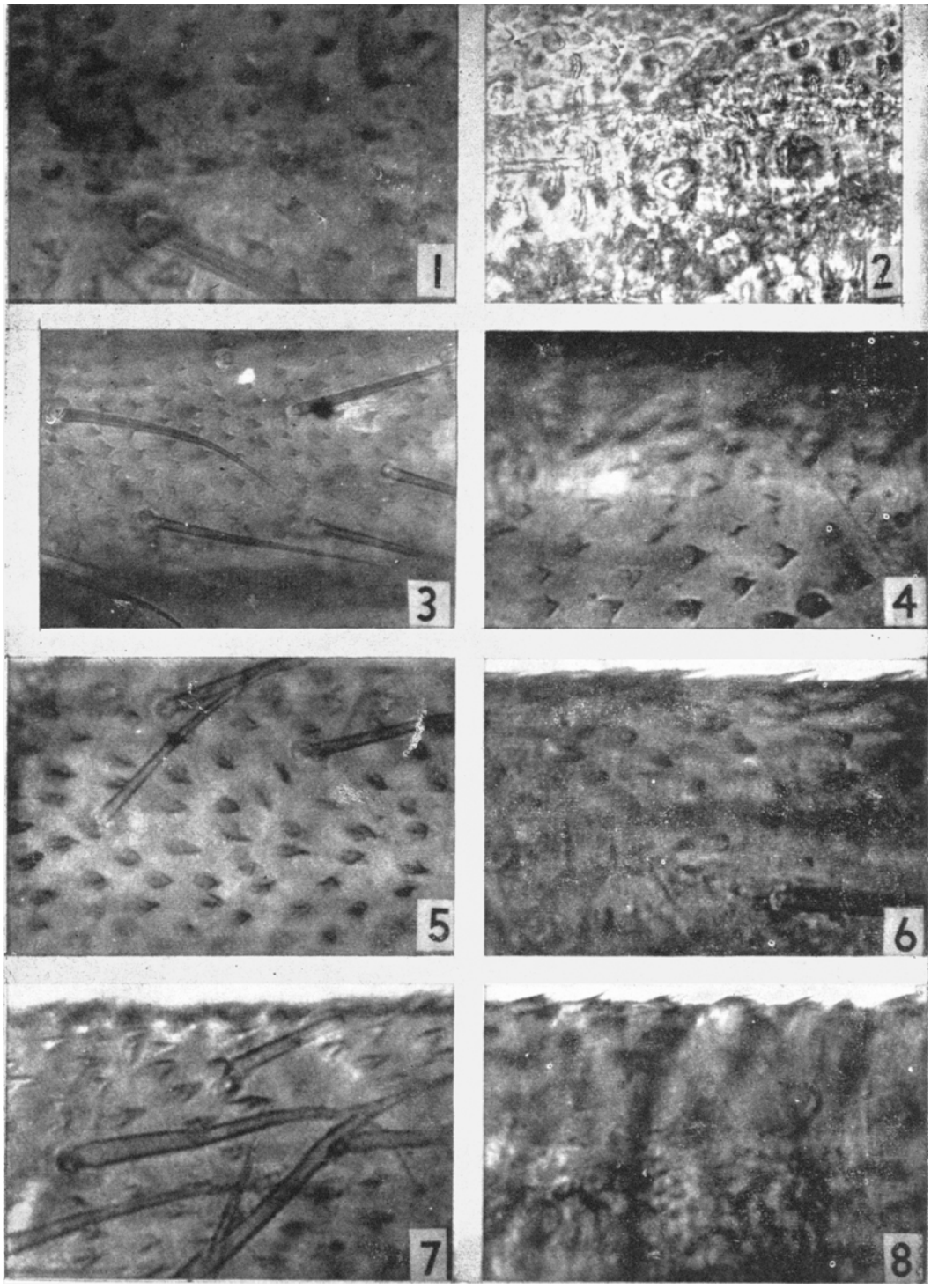

Plate 1 Photomicrographs of anterior margins of wing surfaces of termites, to show papillae. **1**, *Coptotermes testaceus*. Papillae pointed, **2**, *Odontotermes assmuthi*. Papillae tongue-shaped, **3**, Nipple-shaped papillae in *Syntermes territus*, **4**, Same, in *S. molestus*, enlarged, **5**, *Tumulitermes westraliensis*, **6**, *Labiotermes labralis boreus*, **7**, *Trinervitermes bioformis*, **8**, *Armitermes parvidens*. Pointed papillae in the last four species

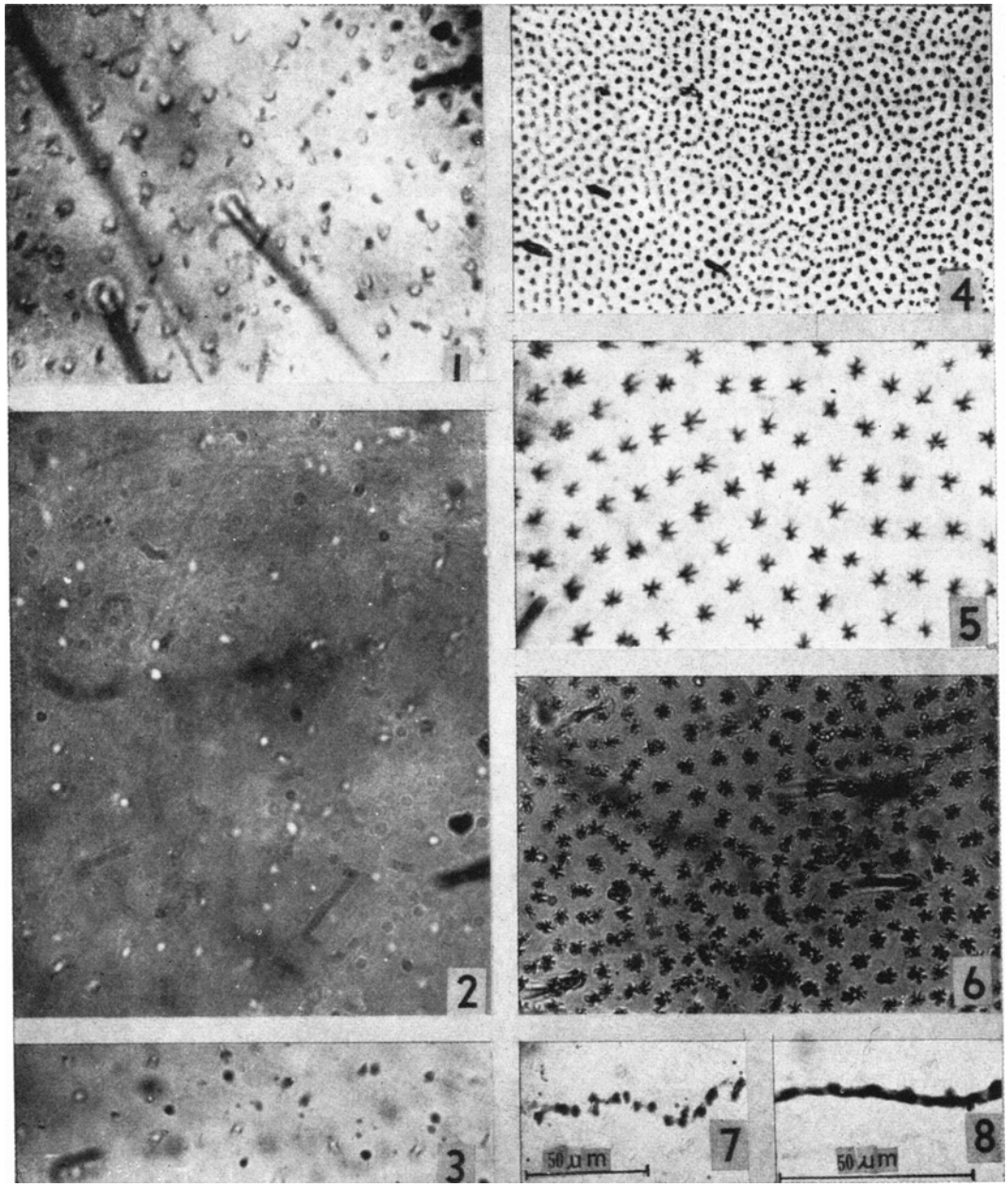

Plate 2 Photomicrographs of wing surfaces of termites, to show micro-sculpturing. (**1–3**, pimpules; **4–8**, micrasters). **1**, *Coptotermes amanii*, near humeral suture, **2**, *Stylotermes dunensis*, **3**, *Tumulitermes hastalis*, **4**, *Nasutitermes dixoni*, **5**, Same, enlarged (thick micrasters), **6**, *Angulitermes jodhpurensis* (thick micrasters), **7**, Same, part of wing in transverse section, unstained. Micrasters seen on either side of wing membrane as dark, raised humps, **8**, Same, stained with eosin and more magnified

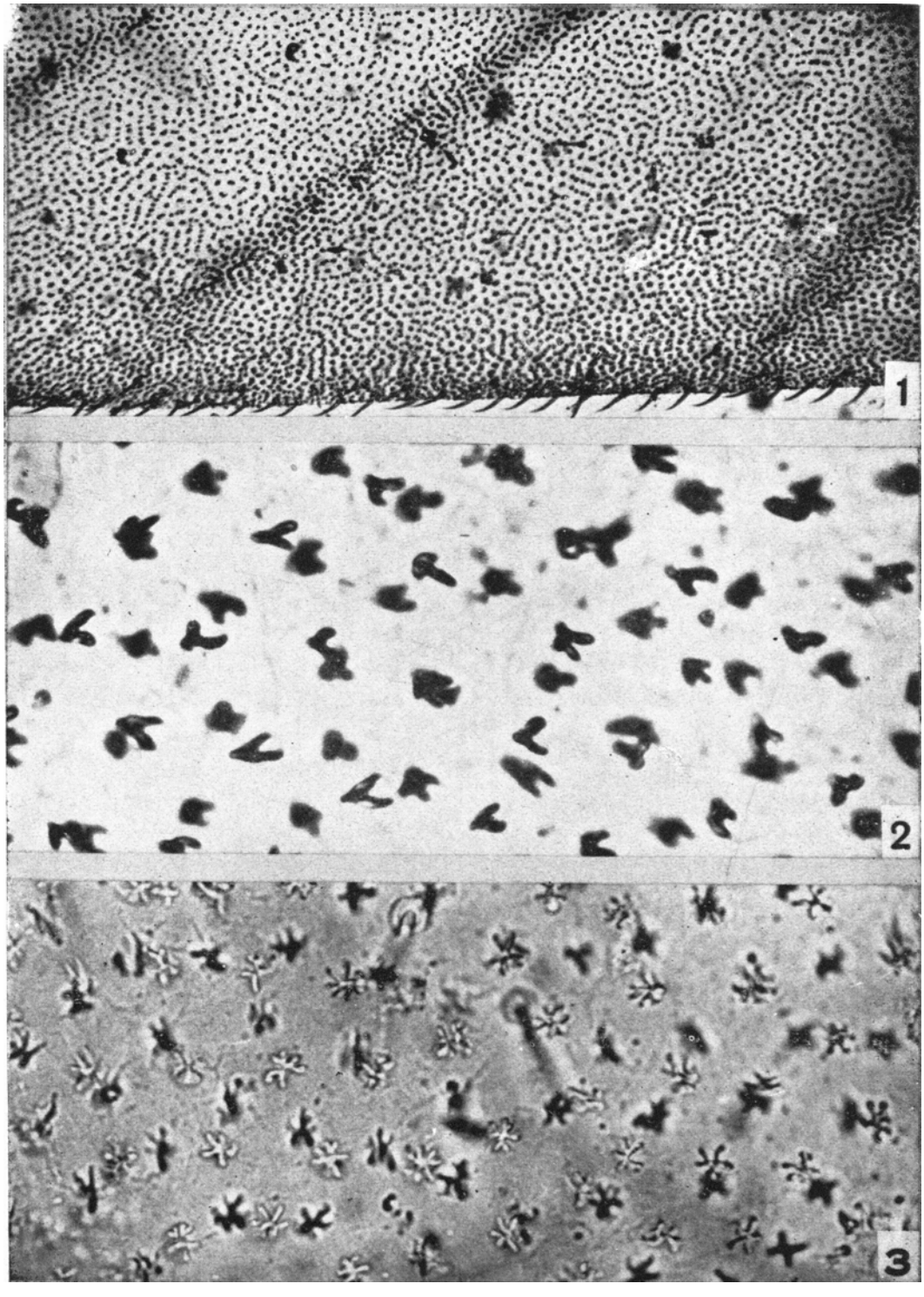

Plate 3 Photo-micrographs of wing surfaces of termites, to show micro-sculpturing (micrasters). **1**, *Speculitermes silvestrii*, **2**, Same, more magnified; thick micrasters, **3**, *Eremotermes paradoxalis*; thin micrasters

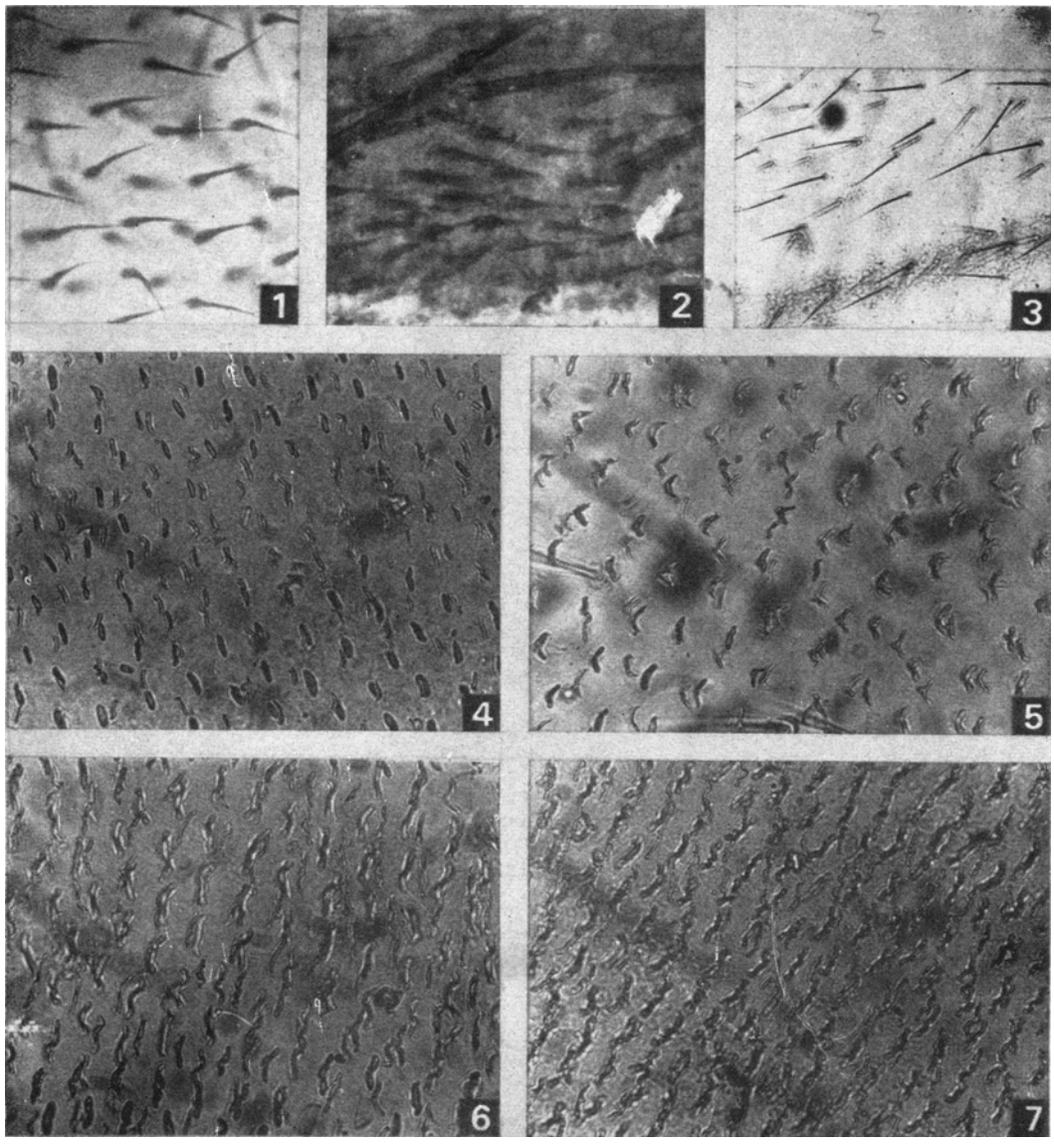

Plate 4 Photomicrographs of wing surfaces of termites, to show micro-sculpturing, **1**, *Afrosubulitermes congoensis*. One-armed, pointed 'micrasters', **2**, Same type, in *Mimeutermes giffardi*, **3**, *Armitermes holmgreni*. Besides papillae, wing covered densely with hairs (seen in figure) and pimpules (not seen), **4**, *Allodontermes schultzei orientalis*. Rods (resemble one-armed 'micrasters', **5**, *Microtermes obesi*. Short rods, often V-shaped, **6**, *Odontotermes obesi*. Long rods, weakly wavy, **7**, *O. formosanus*. Long rods, sinuous

trated, as one to many (ca. 25) closely packed rows near anterior and posterior wing margins, sometimes elsewhere also. Densities (per mm^2) in the concerned wing regions low (ca. 2000, *Porotermes*) to high (10870, *Allodontermes*; 12570, *Coptotermes michaelseni*). Papillae at the anterior margin generally larger and more numerous than those at the posterior, but sometimes the reverse occurs (*Nasutitermes brunneus*).

Papillae were discovered by Roonwal and Rathore (1978, Kalotermitidae) and have subsequently been found to be of universal occurrence on termite wings (Roonwal; and Roonwal et al., vide the References). For distribution, etc., see below.

Arrowheads (figure 1E)

Small, sharply angular, > or }-shaped, hyaline, colourless to pale brown structures; apex directed distally; usually with two arms, sometimes with a third arm in the middle; occasionally merging into subcresentic shapes (*Parrhinotermes simplex*). Sizes vary from small (3–5 μm $\times$ 4–6 μm) to large (4–9 μm $\times$ 7–23μm); the two kinds may be present in the same wing. Generally present in one or more rows on some or all the veins, but may occur elsewhere also except in the region of papillae, and are usually less concentrated than the latter; densities in the concerned wing region low (ca. 1800/mm^2 or lower).

Absent in the primitive families. First appear in the Stylotermitidae, being present in all species of *Stylotermes* (Roonwal et al. 1979a). Thereafter appearing occasionally in the Rhinotermitidae (*Prorhinotermes*, Roonwal et al. 1979 b) and Termitidae (some Amitermitinae and Termitinae, Roonwal & Verma 1980a, b) (also see chart 1 and tables 1 & 2).

Tubercles (figures 1F and 2)

Relatively large, margin either cresentic or subcresentic; brownish, humpy, granular structures with a broad base and a low hump*; apex directed distally. Sizes vary from small to large (1 $\times$ 12 μm to 7 $\times$ 24 μm). Chiefly occurring in sublinear rows on the veins, including the crossveins when present; sometimes on the membrane as well. Moderately dense (density in the concerned wing regions ca. 2600–6300/mm^2). May be present or absent in the same genus (*Neotermes*, *Bifiditermes*).

First described by Roonwal and Sen-Sarma (1960) in the Kalotermitidae; subsequently by Roonwal and Rathore (1978, more Kalotermitidae) and by Roonwal et al. (1979 b, some Rhinotermitidae: *Dolichorhinotermes*).

Pimpules (figures 1G, 2; and plate 1, figures 1–3)

Minute, colourless, hyaline, rounded to slightly pointed structures. (Generally only either round or pointed ones occur in a species, but sometimes both may be present as in *Tumulitermes hastalis*, Nasutitermitinae.) Sizes vary as 1–4 μm $\times$ 1–6 μm. Distributed all over wing membrane or may be localised (confined to proximal half of wing, some *Coptotermes*). Density, per mm^2, low (900, *Cryptotermes dudleyi*) to high (7200, *Macrotermes gilvus borneensis*; 8885, *Coptotermes acinaciformis*).

First described by Roonwal and Rathore (1978) in the Kalotermitidae, and subsequently in several other families (Roonwal 1981, Roonwal et al. 1979–1981). Generally present in the primitive families (except the Termopsidae); only rarely present in the Termitidae. (also see chart 1 and tables 1 & 2).

Micrasters (figures 1H–J, 3–5; and plates 2–4)

Small to large (1–10 μm × 2–12 μm, mostly (3–7 μm × 4–8 μm), colourless to brownish, hyaline structures, which may be either thick or thin and stringy. Varying in shapes from one-armed (rod-like or pointed and hair-like) to many-armed and asteroid. Two broad shape-categories recognisable: (*i*) Simple and nonasteroid (1–6 arms), with shapes like I, V, Y, +, X, K, T, E, H, etc. (*ii*) Complex or asteroid (5–8 arms) with shapes like *. Altogether, 10 types, I-X, recognisable, as follows (figure 3):

Category (A). Non-asteroid.

Type I. Rod-shaped (1-armed), with subtypes A (simple) and B (spearhead shape).

Type II. 2-armed (V- shape).

Type III. 3-armed (Y- and T- shapes), with subtypes A and B.

Type IV. 4-armed (X-, K-, H-, and other shapes), with subtypes A-F.

Type V. 5-armed, with subtypes A–D.

Type VI. 6-armed, with subtypes A and B.

Category (B). Asteroid.

Type VII. 5-armed.

Type VIII. 6-armed, with subtypes A and B.

Type IX. 7-armed, with subtypes A and B.

Type X. 8-armed.

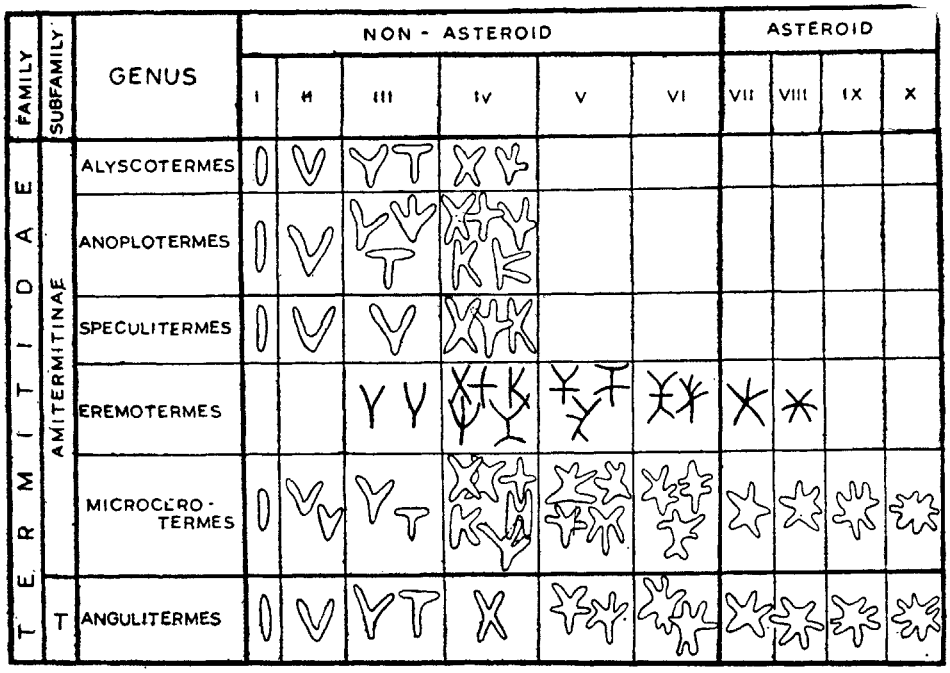

Figure 3 Distribution of various categories and types of micrasters on wings of some Amitermitinae (family Termitidae)

*A second type of tubercle, with an angular margin and with a few large granules besides the numerous small ones has been found in the Kalotermitid genus *Glyptotermes* (Roonwal & Verma, in press).

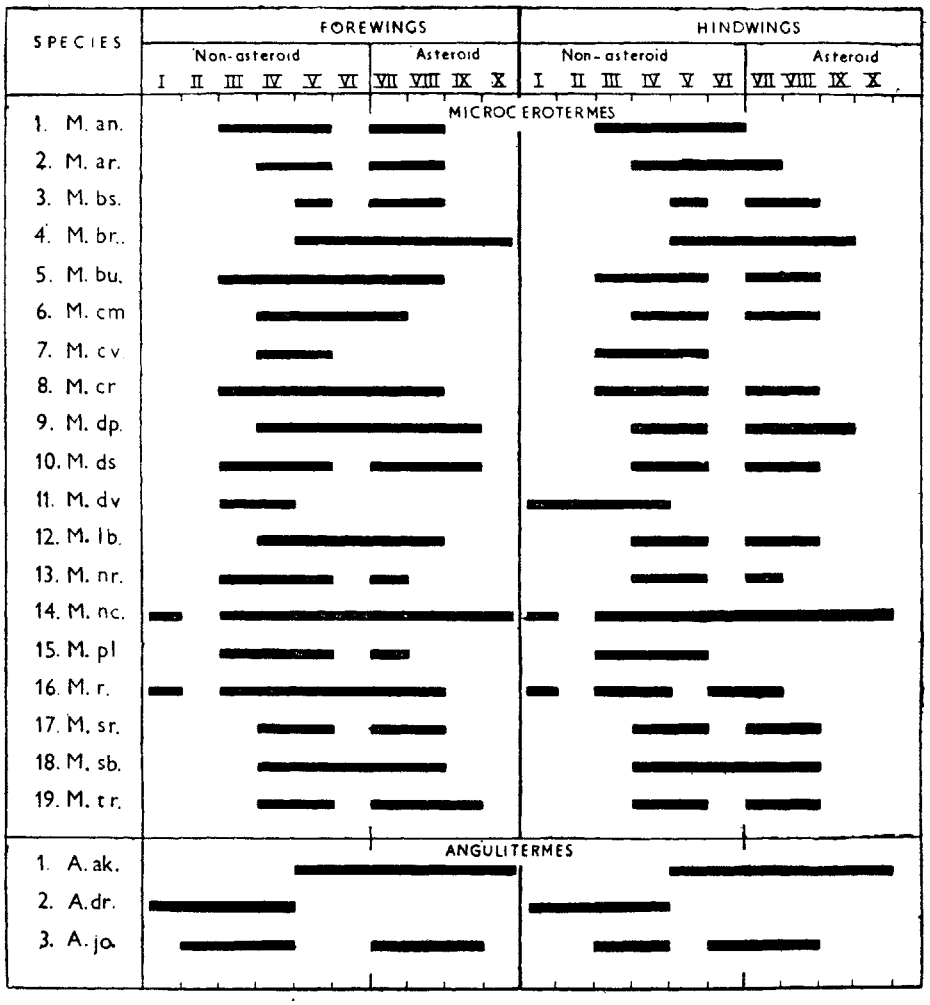

Figure 4 Distribution of various types of micrasters on wings of the genera *Microcerotermes* and *Anguliterme*s (Ex. Roonwal, Verma & Rathore)

Microcerotermes: 1, *anandalei*, 2, *arboreus*, 3, *beesoni*, 4, *biroi*, 5, *burmanicus*, 6, *cameroni*, 7, *cavus*, 8, *crassus*, 9, *depokensis*, 10, *distinctus*, 11, *diversus*, 12, *los-banosensis*, 13, *nervosus*, 14, *nicobarensis*, 15, *palestinensis*, 16, *raja*, 17, *serratus*, 18, *subtilis*, 19, *turneri*. Anguliterme*s*: 1, *akhorisainensis*, 2, *dehraensis*, 3, *jodhpurensis*

In different species, the range of types varying from a few to the entire gamut of ten, thus: Amitermitinae: *Speculitermes silvestrii*, types III and IV; *S. sinhalensis*, I-III; *Microcerotermes beesoni*, V-VIII; *M. nicobarensis*, I-X. Macortermitinae: *Allodontermes*, I only; *Ancistrotermes*, I-III. Considerable variation may occur within the same genus, e.g., *Microcerotermes* (figure 4).

One-armed micrasters of two types: (*i*) Simple, rod type: Short and straight, with both ends rounded (some Hodotermitidae, some Coptotermitinae, most Amitermitinae and Termitinae, and some Nasutitermitinae and Macrotermitinae (figures 1H, 3). (*ii*) Spearhead type: Short to long (up to 23 μm), straight to slightly curved, tapering apically with the apical end pointed and the basal end broad. Short (3–6 μm) and straight, with the basal end incurved (*Coptotermes michaelseni* and *C. testaceous*); or long (14–23 μm) and slightly curved and hair-like, with the basal end incurved or tripod-shaped (some Nasutitermitinae: *Afrosubulitermes* and *Mimeutermes*, figure 1H; and plate 4, figures 1, 2). The two types (rod type and spearhead type) may occur simultaneously in the same species (*Mimeutermes giffardi*).

Micrasters generally occur all over wing except in the region of the papillae; often, but not always, absent on the veins. Broadly arranged in curved lines, e.g., circles and spirals with one or more micrasters at the centre (figure 5). Densities, per mm², moderate to high (3330, *Speculitermes rongrensis*; 10870, several Amitermitinae; 11595, some Termitinae). Are absent in the primitive families and common in the higher ones, finally almost disappearing in the Macrotermitinae (vide infra). Though known earlier cursorily, micrasters were first studied in detail by Roonwal et al. (1974, some Termitidae), and subsequently in several other groups (Roonwal 1977, 1981; Roonwal et al. 1979-1982 and in press).

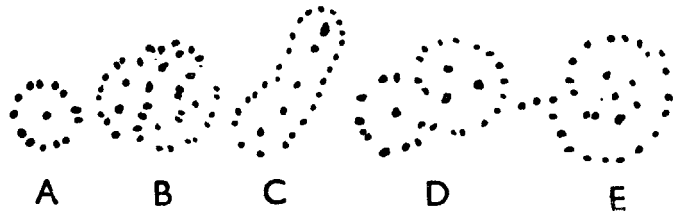

Figure 5 Some types of arrangements of micrasters (*Speculitermes silvestrii*). Circles, spirals, etc. (Ex. Roonwal & Rathore)

Microsetae (figure 1J)

Thin, tiny, setae-like, pointed, hyaline structures, with a basal articulation. Differ from hairs in being extremely small (length 8–16 μm; hairs much longer, usually 50–100 μm or more). Present all over membrane except near anterior and posterior margins where papillae are present. Are rare, found so far in only two genera (Termitinae: *Tuberculitermes*, Roonwal & Verma 1980b; and Macrotermitinae: *Pseudacanthotermes*, Roonwal et al. 1980).

Rods (figures 1 K, L; and plate 4, figures 4–7)

Short to long (2–16 μm), thin, stringy, hyaline, colourless, weakly curved to sinuous and serpentine structures. (Differ from the rod-like, one-armed micrasters described above, the latter being much stouter and generally straight or with only a single, weak curve.) Cover the entire wing membrane (densities low to high, 2910–8700/mm²) except in the region of the papillae. Distribution restricted to a few genera of the higher termites, as given below. Are of two types (both not present together in the same species): (*i*) Subhorizontal: Nearly horizontal but

with a slight oblique tilt. Occur in *Meagnathotermes* (Termitinae, Roonwal & Verma 1980b). (*ii*) Subvertical: Nearly vertical but with a slight oblique tilt. Occur in *Odontotermes*, *Hypotermes* and *Microtermes* (Roonwal & Chhotani 1967, Roonwal et al. 1980).

Hairs (plates 1; 3, figure 1; and 4, figure 3)

Not strictly a part of micro-sculpturing, hairs (setae or macrotrichia of authors) form an important component of termite wings. Are basally articulated, hyaline, colourless to brown and short to long (about 35–210 μm). Always present on margins in greater or lesser abundance. On membrane, present or almost absent; sometimes present in abundance (densities up to ca. 5000/mm^2), e.g., *Coptotermes*, *Syntermes*, etc. are generally few in the primitive families and again in the higher ones, and fairly abundant in the intermediate ones (for their origin, etc., vide infra).

Micro-sculpturing in Various Families (Tables 1 and 2)

There is some diversity of opinion about Isopteran classification. The following family and subfamily classification, as adopted here (based on Roonwal 1975, 1979, keys), is considered as adequate to reflect the evolutionary trends of micro-sculpturing as well as other features:

Fam. 1. Mastotermitidae.

Fam. 2. Termopsidae.

Fam. 3. Kalotermitidae.

Fam. 4. Hodotermitidae (subfamilies Porotermitinae, Hodotermitinae and Stolotermitinae).

Fam. 5. Stylotermitidae.

Fam. 6. Rhinotermitidae (subfamilies Psammotermitinae, Rhinotermitinae, Heterotermitinae, Coptotermitinae and Termitogetoninae).

Fam. 7. Serritermitidae.

Fam. 8. Indotermitidae.

Fam. 9. Termitidae (subfamilies Amitermitinae, Termitinae, Nasutitermitinae and Macrotermitinae).

The condition in the various families may now be discussed (for the genera studied, see table 1).

Family 1. Mastotermitidae

A primitive family, the most primitive in some respects. Contains a single living genus and species, *Mastotermes darwiniensis* Froggatt, from Australia.

Micro-sculpturing: In his revision of the family, including fossil forms, Emerson (1965) made no mention of wing micro-sculpturing. Later, Emerson and Krishna (1975) stated that *Mastotermes* wings "lack punctations" (p. 16). *M. darwiniensis* was studied in detail by Roonwal et al. (1979 a). Finger-shaped papillae on the veins in considerable density (6860–9430/mm^2) and minute, rounded, refractile pimpules all over membrane are present.

Hairs: A few small hairs present on wing margins; membrane hairless.

Family 2. Termopsidae

A small, primitive family with only 3 genera; nearctic and oriental. (Some authors regard it as a subfamily, Termopsinae, of family Hodotermitidae.)

Micro-sculpturing: Emerson and Krishna (1975) stated that wings of *Archotermopsis* "lack punctations" (p. 16). Two genera studied in detail (*Zootermopsis*, by Roonwal et al. 1979a;

and *Archotermopsis*, by Roonwal 1981). In both only papillae (fairly large and pointed, sometimes with rounded or subcresentic margins) present on veins, apparently absent on membrane.

Hairs: A few short hairs scattered on wing margins; membrane hairless.

Family 3. Kalotermitidae

A moderately large, cosmopolitan and primitive family; members live and breed in wood.

Micro-sculpturing: Light (1921) and Tsai and Chen (1963) casually mentioned its occurrence in some species of *Cryptotermes*. Roonwal and Sen-Sarma (1960) recorded and illustrated large tubercle-like structures on the wing membrane in several genera. Krishna (1961), Emerson and Krishna (1975) and Chhotani (1975) mentioned the occurrence of nodules, papillae, punctations and granules in several genera, but these terms were neither defined nor were the structures illustrated. In some fossils Emerson (1969) noted "conspicuous nodules" in *Calcaritermes vitus* Emerson (p. 41) and "large tubercles" in *Incisitermes krishnai* Emerson (p. 49).

Detailed studies are by Roonwal (1977, 1981), Roonwal and Rathore (1978) and Roonwal and Verma (in press) in several genera (*Neotermes*, *Kalotermes*, *Ceratokalotermes*, *Bifiditermes*, *Bicornitermes*, *Cryptotermes* and *Glyptotermes*). Sculpturing consisting of papillae and pimpules, and quite often also of large tubercles; the last mentioned occasionally absent (sometimes in different species of the same genus, e.g., *Neotermes*, *Bifiditermes*). Papillae finger-like, fairly dense (4650–8880/mm^2); confined to the front vein. Pimpules minute, present all over membrane. Tubercles large, subcresentic or angular; granular; generally on the veins.

Hairs: A few small hairs present on wing margins, membrane hairless or with a few scattered hairs.

Family 4. Hodotermitidae

A medium-sized, widespread, somewhat primitive family with 3 subfamilies (some authors include a fourth, Termopsinae, which is here treated as a separate family).

Micro-sculpturing: Studied by Roonwal and Rathore (1978, *Anacanthotermes*) and Roonwal, Verma and Thakur (1979a, several genera). In the two primitive sub-families, Porotermitinae (*Porotermes*) and Hodotermitinae (*Anacanthotermes*), only papillae (in several rows on anterior veins) and pimpules (all over membrane) present; micrasters absent. In the third subfamily, Stolotermitinae (*Stolotermes*), micrasters (both simple or nonasteroid and complex or asteroid) present fairly densely (3000–4500/mm^2) all over membrane; in addition, papillae present, but pimpules absent.

Hairs: Wings almost hairless or with a few hairs on margins.

Family 5. Stylotermitidae

A small primitive family with a single living, oriental genus, *Stylotermes* (syn. *Sarvaritermes*) and a single fossil palaearctic and nearctic genus, *Parastylotermes*. Is characterised by the rare condition of 3-segmented tarsi. (Some authors regard it as a subfamily, Stylotermitinae, of family Rhinotermitidae; for its phylogeny and taxonomic status, see Roonwal 1975.)

Micro-sculpturing : Earlier records are imprecise and contradictory. Emerson (1971) credited the wing membranes of both genera with "small microscopic dots or punctations without radiating extensions" (pp. 289–291). Latter, Emerson and Krishna (1975) spoke of

"rounded punctations or micrasters" (p. 16) in both *Stylotermes* and *Parastylotermes* but, as shown below, no true micrasters occur.

Stylotermes studied in detail by Roonwal, Verma and Thakur (1979a) and Roonwal (1981). Three types of micro-sculptures present: a few rows of weakly pointed papillae on anterior margin; rows of arrowheads on anterior and other veins; and minute pimpules on lower and proximal parts of membrane. No micrasters present.

Hairs: Wings practically hairless.

Family 6. Rhinotermitidae

A moderate-sized, widespread family; intermediate in evolutionary position. With 5 subfamilies, excluding the Stylotermitinae which is here treated as a separate family.

Micro-sculpturing: Earlier authors (Emerson 1971; Emerson & Krishna 1975) vaguely referred to "dense punctations" and "micrasters", but made no distinction between different types. Detailed studies are by Roonwal and Rathore (1977, *Heterotermes*), Roonwal et al. (1979 b, all subfamilies) and Roonwal (1981, Heterotermitinae).

Sculpturing in the Rhinotermitidae consisting of 5 types of structures (papillae, arrowheads, tubercles, pimpules and micrasters). All not present together in the same species, but papillae present in all. The following combinations occur:- (*i*) Only papillae : Some Rhinotermitinae (most *Schedorhinotermes*); (*ii*) Only papillae and pimpules: Psammotermitinae, some Rhinotermitinae (a few *Schedorhinotermes*, *Rhinotermes*) and some Coptotermitinae; (*iii*) Only papillae and arrowheads: *Prorhinotermes*; (*iv*) Papillae, pimpules and tubercles: Some Rhinotermitinae (*Dolichorhinotermes*). (*v*) Only papillae and micrasters: Some Heterotermitinae, some Coptotermitinae, and Termitogetoninae. (*vi*) Papillae, pimpules and micrasters: Some Coptotermitinae.

Papillae usually finger-like (occasionally shallow and subcresentic), sometimes pointed and spiky. Different shapes may occur in the same genus (finger-like in *Heterotermes gertrudae*, spiky in *H. indicola*). Arrowheads and tubercles occurring rarely. Pimpules frequently present, occurring all over membrane or in restricted areas; may be present or absent in the same genus (*Schedorhinotermes*). Micrasters, both simple and complex, occurring in higher groups (some Heterotermitinae, some Coptotermitinae, and Termitogetoninae); may be present or absent in the same genus (*Coptotermes*). The ascending order of evolution of micrasters (moving downward in the following scheme) in the Rhinotermitidae is as follows:

A. Primitive, with no micrasters (Psammotermitinae and Rhinotermitinae).

B. Intermediate, with or without micrasters (Heterotermitinae and Coptotermitinae). (a) Species without micrasters. (b) Species with micrasters : (*i*) Species with simple micrasters. (*ii*) Species with both simple and complex micrasters.

C. Advanced, with both simple and complex micrasters (Termitogetoninae).

Hairs: In several Rhinotermitidae (especially Coptotermitinae: *Coptotermes*) longish hairs, 60-135 μm long, present in fair abundance all over wing (densities up to ca. 2300/mm^2); in others, hairs few or almost absent.

Family 7. Serritermitidae

A small, neotropical family (Brazil), with a single genus and species, *Serritermes serrifer* (Bates, in Hagen). (Regarded by some authors as a subfamily, Serritermitinae, of family Termitidae. For family status, see Emerson 1965, p. 17; characters elaborated by Emerson & Krishna 1975).

Micro-sculpturing: No detailed information available. Emerson and Krishna (1975) gave some preliminary and incomplete information as follows:– (*i*) Hairs absent "on the costal margins, inner margins, membranes, and strong veins beyond the humeral suture. . . ." (p.12), a condition which they regard as "derivative" (i.e., secondary). (*ii*) Wing membranes "lack punctations" (p. 16). The precise meaning is not clear, but "punctations" are apparently different from micrasters, since later in the same paragraph these authors speak of "rounded punctations or micrasters" in several genera of other families, e.g., *Termitogeton*, *Heterotermes*, etc.

Family 8. Indotermitidae

A small, oriental family, with a single genus and three species. Was created by Roonwal and Sen-Sarma (1960) to accomodate a new genus, *Indotermes*, characterised, among other things, by the presence of the rare condition (found, in addition, only in the Stylotermitidae) of 3-segmented tarsi. (Some authors place this genus in the Amitermitinae of family Termitidae but without justification; for its phylogeny and taxonomic status, see Roonwal 1975.)

Nothing is known about its micro-sculpturing. Judging from its phylogenetic position, the presence of micrasters or allied structures (in addition to the universal papillae) may be expected to occur.

Family 9. Termitidae

A large, widespread family with four subfamilies: Amitermitinae, Termitinae, Nasutitermitinae and Macrotermitinae. (Sands 1972 has relegated several genera of the Amitermitinae to a fifth subfamily, Apicotermitinae, abolishing the Amitermitinae, but I consider the simpler arrangement given above as being more natural.)

Micro-sculpturing: Termitidae studied in detail by Roonwal et al. (1967-1982, and in press, vide the subfamilies below). Family characterised by several features, suggesting its advanced evolutionary status, broadly in the ascending order: Amitermitinae, Termitinae, Nasutitermitinae and Macrotermitinae. The following structures occur, though not all together: Papillae (universal), arrowheads (rare), pimpules (rare), micrasters (common), microsetae (rare) and rods (in some); tubercles absent. Papillae almost always pointed and thorny.
Arrowheads occurring rarely (only in some Amitermitinae and Termitinae), Pimpules also rare (occurring in a few Nasutitermitinae and Macrotermitinae). Micrasters present in all Amitermitinae and most Termitinae (rarely absent: *Megagnathotermes*, *Tuberculitermes*) and Nasutitermitinae (absent in the primitive genera *Syntermes*, *Procornitermes*, *Cornitermes* and *Rhynchotermes*, and a few others); have virtually disappeared in the Macrotermitinae (simple ones present only in *Allodontermes* and *Ancistrotermes*), being replaced by either microsetae or rods. Microsetae occurring rarely, found in some Termitinae (*Tuberculitermes*) and some Macrotermitinae (*Pseudacanthotermes*). Thin, stringy

cuticular rods occurring in several Macrotermitinae (*Odontotermes*, *Hypotermes*, *Microtermes*) and some Termitinae (*Megagnathotermes*).

Hairs: Are either absent or few and scattered.

The position of sculpturing in the various subfamilies is discussed below briefly.

Subfamily (*a*) *Amitermitinae*

(Roonwal et al. 1974; Roonwal & Rathore 1977, 1982; Roonwal & Verma 1980a.)

Micro-sculpturing: Is simple, consisting of papillae and micrasters ; rarely, arrowheads also present (some *Anoplotermes*). Papillae pointed and thorny, not finger-like; are tiny to moderate-sized. Micrasters either thick or thin and stringy; occurring all over membrane. Genera fall into two groups (table 1): (*i*) Primitive genera having simple, nonasteroid micrasters. (*ii*) Advanced genera (*Drepanotermes*, *Eremotermes*, *Microcerotermes*) having complex or asteroid types also in addition to the nonasteroids.

Hairs: Generally present in a few rows on margins; membrane either hairless or carrying only a few hairs.

Subfamily (*b*) *Termitinae*

(Roonwal et al. 1974, Roonwal & Verma 1980b, Roonwal & Rathore 1982)

Micro-sculpturing: Consisting of five types of structures, viz. papillae, arrowheads, micrasters, microsetae and thin rods, in various combinations. Papillae universal; are pointed and spiny, not finger - like. Arrowheads occurring occasionally (*Cubitermes*, *Orthognathotermes*, *Crepititermes*, *Termes*, *Dicuspiditermes*). Micrasters common; usually of both nonasteroid and asteroid types and either thick or thin; rarely absent, being replaced by microsetae (*Tuberculitermes*) or thin rods (*Megagnathotermes*). Genera fall into two groups (see table 1): (*i*) Micrasters present (generally both simple and complex); no microsetae or rods; arrowheads present or absent. (*ii*) Micrasters; absent; either microsetae or rods present. Micrasters attaining maximum development in the Termitinae.

Hairs: As in the Amitermitinae.

Subfamily (*c*) *Nasutitermitinae*

(Roonwal et al. 1981, Roonwal & Rathore 1982)

Micro-sculpturing: Consisting of three types of structures: Papillae, pimpules and micrasters. Papillae universally present; generally pointed and thorny, but sometimes mostly nipple-shaped (*Syntermes*, *Rotunditermes*); confined to anterior and posterior marginal areas. Pimpules minute and present all over membrane; occurring in a few genera (*Snytermes*, *Procornitermes*, *Cornitermes*, *Rhynchotermes*, where micrasters absent), but sometimes present along with micrasters (*Hospitalitermes*, *Tumulitermes*, *Armitermes*). Micrasters usually present (simple nonasteroid in some and both nonasteroid and asteroid in others; thick or thin); absent in a few genera (*Syntermes*, *Procornitermes*, *Cornitermes*, *Rhynchotermes*, and some *Labiotermes* and *Armitermes*); usually moderate-sized (6–8 μm $\times$ 6–8 μm), sometimes (*Afrosubulitermes* and *Mimeutermes*) much longer (14–23 μm), pointed and hair-like. Genera fall into two groups (table 1): (*i*) Micrasters absent; pimpules generally present (primitive genera). (*ii*) Micrasters present (rarely either absent or present in the same genus); pimpules generally absent.

Hairs: Generally present on margins,

veins and membrane, sometimes in considerable abundance (densities up to ca. 5000/mm^2); in others much fewer, and in a few cases almost absent.

Subfamily (*d*) *Macrotermitinae*
(Roonwal & Chhotani 1967, Roonwal et al. 1980, Roonwal 1981, Roonwal & Rathore 1982).

Micro-sculpturing: Consists of 5 types of structure, viz. papillae, pimpules, micrasters, microsetae and rods, in various combinations. Papillae with apex rounded or pointed; occurring in several rows on anterior and posterior margins. Apart from papillae, genera fall into four groups (table 1): (*i*) With pimpules only (*Macrotermes*). (*ii*) With simple micrasters only (*Allodontermes*, *Ancistrotermes*). (*iii*) With microsetae only (*Pseudacanthotermes*). (*iv*) With rods only (*Odontotermes*, *Hypotermes*, *Microtermes*).

Hairs: Short to long (50–160 μm). Generally present in a few rows on margins, and sometimes in single rows on veins. Membrane with either a few or no hairs or with fairly numerous hairs (*Macrotermes*, density 300/mm^2).

Evolution and Phylogenetic and Systematic Significance of Micro-sculpturing

Evolution of Micro-sculpturing (Chart 1 and Table 1)

(*a*) *Evolutionary trends*

With the extensive information now available, it is possible to visualise the probable evolution of micro-sculpturing in the order Isoptera. Briefly, the following are the principal conclusions which emerge:–

1. At least seven different types of micro-structures densely cover both the upper and lower wing-surfaces. In some cases as many as over a million elements may be present on a single wing.

2. Papillae occur universally in isopteran wings*. The other types are more restricted in distribution, occurring (in various combinations) in some groups or species, and are either rare or absent in others (chart 1 and table 1).

3. It is possible to broadly associate some of these structures with primitive groups and others with higher ones.

4. Finger-shaped or tongue-shaped papillae (with a rounded tip) largely characterise the primitive groups (Mastotermitidae, etc.) and pointed, thorny ones the advanced groups (Termitidae); the Rhinotermitidae occupies an intermediate position.

5. Arrowheads are absent in the most primitive families and first appear in the Stylotermitidae. Thereafter, they occur occasionally, probably *sui generis*, in the higher groups. Their evolutionary significance is not clear.

6. Tubercles occur widely but not universally in the Kalotermitidae, but are absent in the other primitive families (Mastotermitidae, Termopsidae, Hodotermitidae and Stylotermitidae). They then make a rare and probably *sui generis* appearance in the intermediate family Rhinotermitidae (*Dolichorhinotermes*), and are altogether absent in the higher groups.

7. Pimpules are common in the primitive families (they are curiously absent in the Termopsidae), then occur irregularly and *sui generis* in the remaining groups, including occasionally the highest ones (the higher Termitidae).

8. Micrasters, rods and microsetae are absent in the most primitive families and

*In addition to their universal occurrence on termite wings, papillae also occur on tibial spines and spurs in a few primitive termites (*Mastotermes* and *Archotermopsis*, (Roonwal 1972, 1974, and Roonwal & Bose 1970)

characterise the intermediate and higher ones, Rhinotermitidae and Termitidae. (There is a curious and inexplicable exception, the genus *Macrotermes* of subfamily Macrotermitinae, where these structures are wanting and pimpules occur instead.)

9. Of these structures, micrasters are the most widespread. They first make their appearance in the subfamily Stolotermitinae (of family Hodotermitidae) and continue to occur irregularly in the Rhinotermitidae (being absent in the primitive subfamilies Psammotermitinae, Rhinotermitinae and some Coptotermitinae, and well developed in the remainder). They reach their maximum development in the two lower subfamilies (Amitermitinae and Termitinae) of the family Termitidae, occur irregularly in the third (Nasutitermitinae) and virtually disappear in the highest (Macrotermitinae where they occur occasionally in their simplest form, probably a *vestigeal* condition. The evolutionary sequence thus is: Absence →appearance→abundance→disappearance.

10. Microsetae and rods are found rarely in a few genera of the higher subfamilies, Termitinae and Macrotermitinae.

11. Hairs on wing membranes are virtually absent in the primitive families. In the intermediate family Rhinotermitidae they are sometimes absent but often irregularly present in numbers, occasionally even in great abundance. In the highest family, Termitidae, they are again either absent or present in small numbers.

12. On the bases discussed above, it is possible to broadly divide the Isoptera into three major evolutionary groups, A, B and C, which are characterised as follows, the evolutionary routes (A, A1, A2; B, B1 B2; etc.) indicating probable lines of descent (chart 1).

Group A: Primitive group, without micrasters, microsetae and rods. Includes the following families which carry the micro-structures mentioned against each:

(*i*) Mastotermitidae: Papillae and pimpules.

(*ii*) Kalotermitidae: Papillae and pimpules; tubercles present or absent.

(*iii*) Termopside; Papillae only.

(*iv*) Hodotermitidae (in part):

Subfamilies Porotermitinae and Hodotermitinae: Papillae and pimpules. [Subfamily Stolotermitinae, of route D 2 (with micrasters), belongs to group B.]

(*v*) Stylotermitidae: Papillae, arrowheads and pimpules.

(*vi*) Rhinotermitidae (in part):

(a) Psammotermitinae: Papillae and pimpules. (b) Rhinotermitinae: Papillae, arrowheads, tubercles and pimpules (the last three present or absent). (c) Coptotermitinae (in part, section A: Papillae and pimpules). [Section B falls in the higher group, B.] (d) Heterotermitinae (in part, *Reticulitermes*: Papillae and pimpules.)

Group B (Higher Group I): Generally with micrasters (rarely absent); and without rods and microstae (these occasionally present). Includes the following families which carry the micro-structures mentioned against each:

(*i*) Hodotermitidae (in part: Subfamily Stolotermitidae.

(*ii*) Rhinotermitidae (in part):

(a) Coptotermitinae (in part, Section B): Papillae, pimpules (present or absent) and micrasters. (b) Heterotermitinae (in part, *Heterotermes*): Papillae and micrasters. (c) Termitogetoninae: Papillae and micrasters.

(*iii*) Termitidae (in part):

(a) Amitermitinae: Papillae, arrow-

heads (rare) and micrasters. (b) Termitinae (in part): Papillae, arrowheads (present or absent) and micrasters. (Rarely, micrasters absent and either microsetae or rods present.) (c) Nasutitermitinae (in part, Section A): Papillae, pimpules (rare) and micrasters (rarely absent). [Section B falls in the Higher Group C.] (d) Macrotermitinae (in part, Section A): Papillae and simple micrasters. (e) The tiny, single-genus families, Serritermitidae and Indotermitidae, also probably belong to Group B, but precise information is lacking.

Group C (Higher Group II): Without micrasters and with or without microsetae or thin rods. Includes the following families which carry the micro-structures mentioned against each:--
Termitidae (in part):
(a) Nasutitermitinae (in part, Section B): Papillae and pimpules (the latter rarely absent). (b) Macrotermitinae (in part, Section B): Papillae and pimpules (the latter rare); and either with or without microsetae and rods.

(b) *Origin and relationship of micro-sculptures*

It is difficult to trace the precise origin of the varied micro-sculptures in the Isoptera partly because detailed studies in other insectan orders are generally wanting. That they do not arise from hairs is pretty obvious, since hairs, sometimes in fair abundance, are present simultaneously with them. They recall similar structures found in certain Lepidoptera, e.g., the "fixed hairs" of Kellog (1894) and Comstock (1918), the "Stacheln" of Spuler (1895), the "aculei" of Busk (1914) and the "small surface hairs" of Marshall (1915). They are apparently different from the fine hairs or "microtrichia" described by Tillyard (1918) on wing membranes in the more primitive orders of the group Holometabola (Endopterygota), viz. the primitive members of the Panorpoid Complex (Neuroptera, Mecorptera, etc.), vide also Imms, 1957, p. 38; the microtrichia have a basal articulation which the isopteran microstructures lack (except in the case of the microsetae).

Do the seven different kinds of microstructures in the Isoptera have phylogenetic continuity, or did each of them arise *sui generis*? To start with, we may note that papillae, arrowheads and tubercles have mutual similarity, all being directed distally on the wing. Papillae, being universal in occurrence, may be regarded as the precursors, and arrowheads and tubercles (which occur here and there) as their derivatives.

All the remaining types are "non-directed". Pimpules are primitive and probably arose *sui generis*: they cannot be connected with other structures. They arise early in termites, and then tend to fade out in the higher groups, though they crop up here and there (some Macrotermitinae). Micrasters also seem to be structures *sui generis* which have a wide spectrum of variation from the simple 1-armed to the complex 8-armed. They must have arisen polyphyletically several times, after their first appearance (with the full range of variation) in the Hodotermitid stock (Stolotermitinae). Generally, the simpler, few-armed types may be considered as more primitive than the many-armed ones. Microsetae and rods are again structures *sui generis*. They arose much later (in the highest termites) and occur only in a few genera, probably arising polyphyletically.

Thus, we have the following scheme of origin and evolution of the micro-structures, with 5 independent types:--

1. Papillae-group (distally directed).
   (a) Simple papillae (various types, e. g. finger-like and thorny).
   (b) Arrowheads.
   (c) Tubercles.
2. Pimpules.
3. Micrasters.
   (a) Simple (nonasteroid, with one to a few arms).
   (b) Complex (asteroid, with many arms).
4. Microsetae.
5. Rods.
   (a) Subhorizontal (horizontal-oblique).
   (b) Subvertical (vertical-oblique).

Phylogenetic significance

There are a number of phylogenetic schemes, each with its own merits, of the origin of various families and subfamilies of the Isoptera. The main schemes are those by Holmgren (1911–1913), Snyder (1949), Ahmad (1950), Krishna (1970), Emerson (1965–1971) and Roonwal (1975), and are based on various structural characters, e.g., head, mandibles, wing venation, tarsal segmentation, etc. For the present purpose, division into 9 families and various subfamilies in the order (as given above in Section IV, and also by Roonwal 1975) will suffice, and considerations of wing micro-sculpturing broadly support this scheme. Thus, the Termpopsidae, with the simplest micro-sculpturing (papillae only) would appear to be an even more primitive family than the Mastotermitidae, though on other characters the latter is the more primitive one. The Kalotermitidae, with the presence of tubercles, seems to follow a special line. In the Hodotermitidae, the subfamily Stolotermitinae (with its micrasters) is more advanced than the Porotermitinae and the Hodotermitinae. The family Stylotermitidae, with the absence of micrasters, seems to be primitive, but has some special features such as the presence of arrowheads and also the rare 3-segmented nature of the tarsi.

The Rhinotermitidae is a mixed assemblage, with a primitive component without micrasters (subfamilies Psammotermitinae, Rhinotermitinae, some Heterotermitinae and some Coptotermitinae) and an advanced component with micrasters (Termitogetoninae, some Heterotermitinae and some Coptotermitinae).

The highest family, Termitidae, also has two principal components : a more primitive one with micrasters (all Amitermitinae, most Termitinae, most Nasutitermitinae and a few Macrotermitinae) and a more advanced one without micrasters and with or without microsetae or rods (most Macrotermitinae and, curiously, some primitive Nasutitermitine genera, e.g., *Syntermes*, etc.).

Comparison with the Zoraptera

Closely allied to the Isoptera is the small but widespread insectan order Zoraptera with a single genus, *Zorotypus* (family Zorotypidae), containing only about 22 species. Like the Isoptera, members of this order also shed their wings at a basal fracture, leaving only stumps. The female alate form of *Z. hubbardi* Caudell (from Hunter, Virginia, U.S.A.) was available to me for examination.

The wing membrane (figure 6) is densely covered (density c. 1030/mm^2, on one surface) with small hairs (length c. 15-60 μm) all over on both sides, including the margins; the marginal hairs are appreciably thicker and longer (25-60μm). In a Canada balsam mount I could find no trace of any wing micro-sculpturing. Zorapteran wings recall the hairy wings of some primitive Isoptera (e.g., some species of *Coptotermes*) minus their micro-sculpturing. This suggests that micro-sculpturing is peculiar to the

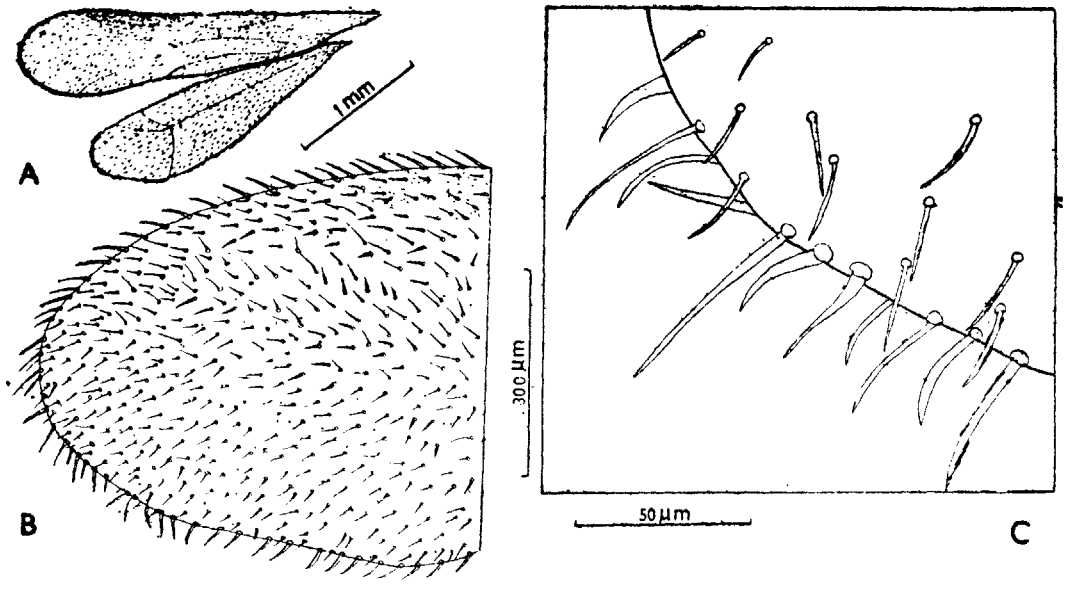

Figure 6 Left wings of *Zorotypus hubbardi* (Zoraptera, U.S.A.). **A**, Both wings, **B**, Distal part of forewing, enlarged, **C**, Same, a small part near margin more magnified, to show sizes of hairs

Isoptera. (For details of wing venation, etc. in the Zoraptera, see Denis 1941, Imms 1965, and Weidner 1970b.)

Systematic significance

(a) *Significance*

Though unmistakable phylogenetic trends are discernible as discussed above, clear separation of families and subfamilies on the basis of wing micro-sculpturing alone is not possible, except in rare cases. Thus, the Stolotermitinae can be separated from the other subfamilies of the Hodotermitidae by the presence of micrasters. Assistance in the lower taxonomic categories, e.g., genera and species, is, however, much more substantial, and a few examples (which can be multiplied) will suffice to illustrate the point.

1. In the Macrotermitinae (Termitidae) *Odontotermes* and *Hypotermes* are closely allied genera (formerly regarded as subgenera of a common genus) and have nearly identical micro-sculpturing by means of long thin, stringy rods, while another allied genus *Microtermes* can be separated by having much shorter rods.

2. Within the genus *Odontotermes*, the species *O. obesus* has thinner and weakly sinuous rods, while *O. assmuthi* has thicker and almost serpentine rods.

3. In the subfamily Amitermitinae (of family Termitidae), *Eremotermes* has thin, stringy micrasters, while an allied genus, *Microcerotermes*, has thick micrasters. These differing conditions of 'thinness' or 'thickness' of micrasters are spread over several subfamilies and genera, and evidently arose *sui generis*.

4. In *Microcertotermes*, some species have only simple, nonasteroid micrasters with low density (*M. cavus*, c. 4455/mm^2) and others have mostly micrasters with high density (*M. nicobarensis*, c. 8775/mm^2).

5. In *Heterotermes gertrudae* (Rhinotermitidae) papillae are finger-shaped with

rounded tips, while in an allied species, *H. indicola*, they are sharply pointed and spiky.

6. In *Nasutitermes longipennis* the papillae are finger-like, while in other species of the genus they are pointed and thorny.

7. The following key, while illustrating the difficulties of neat phylogenetic separation, is of practical use when wings alone are available for identification; micro-sculpturing can be used in combination with differences in hairs and venation.

(*b*) *Key based on micro-sculpturing*

A tentative key for the identification of the major families, subfamilies and genera-groups, based on wing micro-sculpturing is given below. Pipillae are present in all Isoptera; the other types of sculpturing may be present or absent. (The key excludes the tiny, single genus families Serritermitidae and Indotermitidae for which no information is available.)

A (H). Micrasters, microsetae and rods absent (primitive families).

B (C). Only papillae present; no other types.
1. Termopsidae (*Zootermopsis*, *Archotermopsis*).
2. Some Rhinotermitidae (some Rhinotermitinae: most *Schedorhinotermes*).

C (D). Besides papillae, other types present (pimpules, arrowheads, tubercles).

D (E). Only papillae and pimpules present; no other types.
1. Mastotermitidae (*Mastotermes*).
2. Some Hodotermitidae:
   (a) Porotermitinae (*Porotermes*).
   (b) Hodotermitinae (*Anacantho termes*).
3. Some Rhinotermitidae:
   (a) Psammotermitinae (*Psammotermes*).
   (b) Some Rhinotermitinae (some *Schedorhinotermes*; *Rhinotermes*).
   (c) Some Coptotermitinae (some *Coptotermes*).
   (d) Some Heterotermitinae (*Reticulitermes*).
4. Some Termitidae:
   Primitive Nasutitermitinae (some *Syntermes*, *Procornitermes*, *Cornitermes*, *Rhynchotermes*, some *Tumulitermes*).
5. Some Macrotermitinae (*Macrotermes*).

E (F). Besides papillae and pimpules, either arrowheads or tubercles present.

F (G). Arrowheads present.
1. Stylotermitidae (*Stylotermes*).
2. Some Rhinotermitidae (Rhinotermitinae: *Prorhinotermes*).
   [Arrowheads also occur in some Amitermitinae and Termitinae, but without pimpules.]

G (F). Tubercles present.
1. Kalotermitidae (rarely absent).
2. Some Rhinotermitidae (some Rhinotermitinae: *Dolichorhinotermes*).

H (A). Besides papillae, either micrasters, microsetae or thin rods present.

I (J). Only micrasters present (pimpules and arrowheads present or absent).
1. Some Hodotermitidae (Stolotermitinae: *Stolotermes*).
2. Some Rhinotermitidae:
   (a) Some Coptotermitinae (some *Coptotermes*).
   (b) Termitogetoninae (*Termitogeton*).
   (c) Some Heterotermitinae (*Heterotermes*).
3. Some Termitidae:
   (a) Amitermitinae.
   (b) Most Termitinae.
   (c) Most Nasutitermitinae.
   (d) A few Macrotermitinae (*Allodontermes* and *Ancistrotermes*, both with simple, nonasteroid micrasters).

J (I). Only microsetae or thin rods present.
1. Some Termitidae.
(a) A few Termitinae (*Megagnathotermes*, rods ; *Tuberculitermes*, microsetae).
(b) Several Macrotermitinae (*Pseudacanthotermes*, microsetae; and *Odontotermes*, *Hypotermes* and *Microtermes*, rods).

(c) *Wing micro-sculpturing an essential isopteran character*

In view of the invariable presence of wing micro-sculpturing on termite wings, this character should be regarded as one of the important and essential characters of the order Isoptera and is summed up as follows:--

Isoptera : Both wing surfaces invariably and more or less densely micro-sculptured (density up to over 12500/mm^2, the total on a wing surface may go up to over half a million), with a variety (at least 7 types are known) of minute, cuticular structures of which not more than 3 or 4 types are present simultaneously in a species. Of these, papillae are universal, micrasters very common (but not universal) and the remainder (arrowheads, tubercles, pimpules, microsetae and rods) much less common.

In the light of these findings it would be worth while to re-examine termite fossils, particularly wings, espesially those which are preserved in transparent media, e.g., amber, for the presence of micro-sculpturing, especially papillae.

Ecological and Biological Aspects of Micro-sculpturing (Table 3)

The two pairs of termite wings are nearly equal and identical. Basically, each wing is, as in most insects, a very thin, resilient, double-layered, cuticular membrane which is strengthened by veins. The latter structures are thick and tough at the front margin; the hind margin is delicate and not so strengthened. The wing length varies from about one-half to as long as 3 or 4 centimetres. The membrane may carry a great abundance of hairs, which may be as long as 100 μm or

Table 3 *Approximate total number of some micro-sculpturing elements on the wing surface of some Isoptera*

Species	Approximate total area of one surface (dorsal) of wing (excluding the humeral scale)	Microstructure elements concerned	Density of micro-structure (per mm^2)	Total number of micro-structure elements	
				On one surface (dorsal)	On both surfaces (calculated)
1	2	3	4	5	6
Heterotermes gertrudae (Rhinotermitidae: Heterotermitinae)	16 mm^2 (forewing)	Micrasters	6000	96000	192000
Speculitermes sinhalensis (Termitidae: Amitermitinae)	27 mm^2 (hindwing)	,,	3850	103950	207900
Eremotermes paradoxalis	Forewing : 12 mm^2	,,	5670	68040	136080
(Termitidae: Amitermitinae)	Hindwing : 13 mm^2	,,	6000	78000	156000
Angulitermes jodhpurensis (Termitidae: Termitinae)	13 mm^2 (hindwing)	,,	8100	105300	210600
Odontotermes obesus	Forewing : 137 mm^2	Thin rods	4520	619240	1238480
(Termitidae: Macrotermitinae)	Hindwing : 145 mm^2	,,	4410	639450	1278900

more, or the hairs may be almost absent. In addition, both sides of the membrane carry in great abundance at least seven different kinds of micro-sculptures (not all together but in various combinations in different species), ranging in size from the tiny papillae and pimpules (barely one-half to 3 or 4 microns across) to micrasters (several microns across and well raised from the wing surface, plate 2, figures 7, 8). Their density may be of the order of about 2000 to over 12500/ mm^2. The overall impression is that of a heavily embroidered *sari* of an Indian lady. Each wing may thus be loaded with several hundred thousand to over a million of the principal elements, e.g., micrasters, rods, etc. (table 3); to this may be added the lighter and fewer elements, e.g., papillae, pimpules, etc. All these additions must effect the functioning of the wings, as discussed below.

Effect on flight, and its consequences: Precise data are not available, but on theoretical grounds the following features, briefly, seem to be involved in the functioning of termite wings and their ecological and biological consequences.

1. Micro-sculpturing (including hairs) directly results in two consequences: (*i*) It adds enormous dead weight to the otherwise thin and light wings; and (*ii*) it causes extreme rugosity (plate 2, figures 7,8) to the otherwise nearly smooth wings. These features must greatly impede the aerodynamic efficiency of wings. The additional weight would require greater energy for wing flapping, and the increased rugosity would impede air flow over the wing-surface.

2. This reduced flight efficiency may be responsible for the slow, erratic flight which is characteristic of termites during the short nuptial flight, lasting an hour or two, following periodical swarming usually only once or twice a year.

3. The heavily weighted wings may also prevent termites from being easily blown away by strong wind.

4. Micro-sculpturing may give added strength to wings and prevent them from being torn in strong wind.

5. An important biological consequence of these effects is that dispersal, by intrinsic means alone, to distant and perhaps ecologically unsuitable environment and terrain, is avoided, and swarms start fresh colonies within a short distance (perhaps no more than a kilometre or two) of the swarming site. Dispersal is largely achieved through extrinsic agencies, such as strong wind, driftwood and commerce. (Numerous instances of such dispersal, especially by the last two means, are well known.)

6. The primitive families carry fewer and smaller micro-sculpturing elements (either papillae only, or papillae and pimpules, see tables 1 & 2), and should theoretically have faster flights and better powers of dispersal than the higher families which carry more numerous and larger elements which impede flight.

Acknowledgements

I am obliged to the following for assistance:- To Dr N S Rathore, the late Dr S C Makwana and Dr R C Dhiman (all of the Zoological Survey of India, Jodhpur) for assistance in laboratory work and in some drawings. To the Head, Entomology Division, Indian Agricultural Research Institute, New Delhi, for the loan of Zorapteran material.

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