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Evolution and Systematic Significance of Wing Micro-sculpturing in Termites (Isoptera) X. Subfamily Nasutitermitinae of Family Termitidae

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In the large subfamily Nasutitermitinae, wings of 25 genera and 79 species (given in brackets), as follows, were studied: *Syntermes* (2), *Procornitermes* (3), *Cornitermes* (2), *Rhynchotermes* (2), *Hospitalitermes* (1), *Lacessititermes* (1), *Thailanditermes* (1), *Bulbitermes* (3), *Constrictotermes* (1), *Tenuirostritermes* (1), *Velocitermes* (1), *Diversitermes* (2), *Trinervitermes* (6), *Tumulitermes* (5), *Rotunditermes* (1), *Nasutitermes* (23), *Havilanditermes* (1), *Labiotermes* (2), *Armitermes* (5), *Grallatotermes* (2), *Occasitermes* (1), *Convexitermes* (4), *Subulitermes* (7), *Afrosubulitermes* (1) and *Mimeutermes* (1).

Hairs (length 35–90 μm) are either present or absent. When present, they may be very numerous (density 1000–5100/mm²) or scanty. Micro-sculpturing consists of three types of structures: papillae, pimpules and micrasters. Papillae are universally present, are small to large (3×1.5 μm to 8–10×6–8 μm), distally directed and of localised distribution (in one to several rows on the anterior and posterior wing margins; densities 5000–9100/mm²). Most often they are pointed and thorny, but sometimes, as in *Syntermes* and *Rotunditermes*, they are mostly nipple-shaped (a *new type*). Pimpules are small (1×1 μm to 2×2 μm, rarely larger, 3–7 μm×2–4 μm), non-directional, refractile, glassy, colourless and rounded (rarely somewhat pointed) bodies which are present all over the wing in considerable numbers (densities 3000–7600/mm²). Micrasters are small (2×2 μm to 6–8×6–8 μm; rarely larger and hair-like, 14–23 μm×1.5–3 μm), non-directional bodies, with shapes varying from rod-like (1-armed) to many-armed (up to 8 arms) asteroids. They occur all over (densities 4400–10100/mm²). A *new type* of micraster (long, pointed, 1-armed, hair-like, size 14–23 μm×1.5–3 μm) has been found in *Afrosubulitermes* and *Mimeutermes*.

While Papillae are universal, pimpules may be present or absent. In the primitive genera, only pimpules are present, in the higher ones only micrasters, and in a few others both. Micro-sculpturing has been correlated with the subfamily's phylogeny, and several trends of parallel evolution found. Micro-sculpturing is helpful in separating taxonomic categories, especially at the lower levels (species and subspecies), less so at the generic level.

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Introduction

The Nasutitermitinae is the last major group to be studied by us in this series (Roonwal et al. 1967–1980, and in press, vide the References). This subfamily is the largest among termites, and is widespread and specialised. The majority of genera are characterised by the development, in the soldier caste, of a nose-like growth on the head-dorsum (for the ejection, by squirt-gunning, of a defensive secretion from a head gland), and a corresponding great reduction in the size of the mandibles which become nonfunctional. In the primitive genera the mandibles retain their large size and function.

In the majority of genera, wing micro-sculpturing is fairly uniform and consists of papillae (which are universal in the order Isoptera) and micrasters. In a few genera, marked either by primitiveness *(Syntermes)* or by other features, micrasters of the standard type (described by Roonwal, Verma & Rathore 1974, and regarded here as specialised micrasters) have been replaced either by a peculiar new type of 'micrasters' or by pimpules.

For synonymies and taxonomic status, Snyder's (1949) world catalogue is referred to, while for species and genera described later, the appropriate references and revisions are indicated.

Material and Methods

Imagoes from the following regions were examined, the detailed locations being given under each species—North, South and Central America, the West Indies, Africa, South and Southeast Asia and Australia. A total of 25 genera and 79 species were studied.

The techniques mentioned in the previous parts were used, and densities of micro-sculptures refer to the dorsal wing-surface in its middle part unless otherwise stated. Micro-sculptures are present on both the upper and lower wing surfaces. There are no appreciable differences on the fore- and hindwings. The classification of micrasters into ten types (I–X) and two main groups (nonasteroid and asteroid), as given by Roonwal, Verma and Rathore (1974), has been followed.

Results

Genus (1) **Syntermes** Holmgren

Of this moderate-sized Neotropical genus, two species were available.

1. *Syntermes molestus* (Burmeister) (plate 1). (Snyder 1949, p. 258, Emerson 1945.) South America: Lassance (Minas Gerais, Brazil). Wings semitransparent, pale brown, two anteriormost veins dark brown; without scale 25×7 mm. Entire wing covered with long hairs; length 59–88 μm, density 1000/mm^2. Micro-sculpturing consists of papillae and pimpules.

Papillae: Mostly nipple-shaped (a few are pointed); large (8–10 μm $\times$ 6–8 μm) and in numerous rows in the anterior region (25–30 rows on the front vein, 15–20 on the next vein). In fewer rows and much smaller on the posterior margin. Density (anterior region) 6100/mm^2.

Pimpules: Present densely on proximal half of wing; few or absent elsewhere. Size 2×2 μm; density 6590/mm^2.

2. *Syntermes territus* Emerson (figure 1A–D; and plate 2). (Snyder 1949, p. 260, Emerson 1945.) South America: Kartabo (Guyana). Wings and hairs as in *S. molestus*. Wings without scale 22×6 mm;

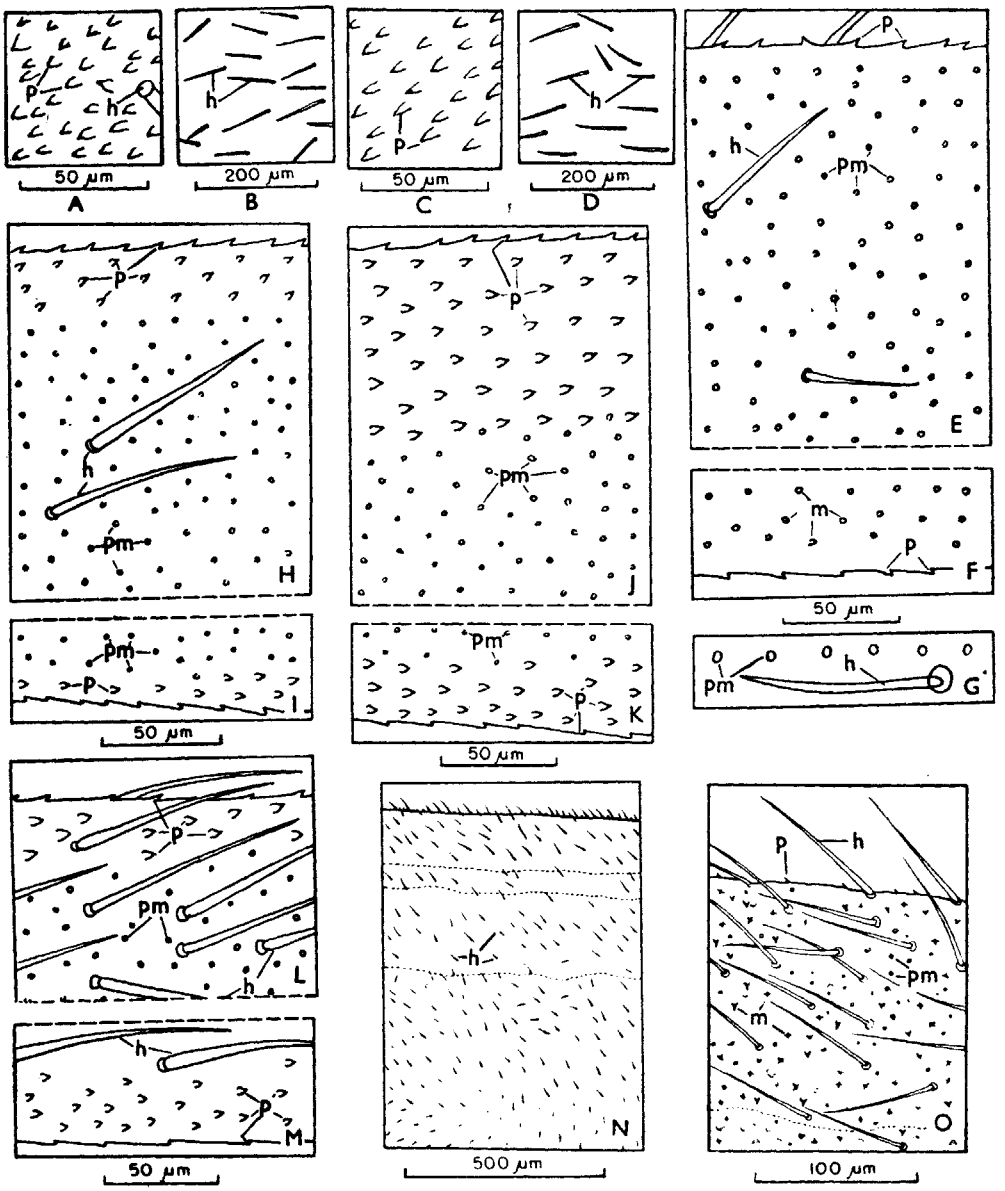

Figure 1 Portions of wing surfaces of some Nasutitermitinae, to show micro-sculpturing. **(A–D)** *Syntermes territus*; *A*, forewing just below anterior margin, to show papillae; *B*, next below, to show hairs; *C*, *D*, same, for hindwing; **(E–G)** *Procornitermes araujoi*; **(H–I)** *Cornitermes cumulans*; **(J–K)** *Rhynchotermes nasutissimus*; **(L–M)** *Rhynchotermes perarmatus*; **(N–O)** *Hospitalitermes monoceros*; (*N*, at low magnification, only hairs visible; at higher magnification in *O*, pimpules and micrasters also visible); *E*, *H*, *J*, *L*, *N*, *O*, anterior margins; *F*, *I*, *K*, posterior margins; *G*, pimpules and a hair in middle of wing, enlarged

h., hairs; **m.**, micrasters; **p.**, papillae; **pm.**, pimpules

hairs 74–103 μm long; density 1000/mm². Micro-sculpturing consists of papillae only. Papillae as in *S. molestus*, mostly nipple-shaped; in 15–20 rows on anterior vein, fewer on the next; size 8–10 μm × 6–8 μm; density 6900–9100/mm². Fewer and much smaller on posterior margin. Pimpules apparently absent.

Genus (2) **Procornitermes** Emerson

Of this small Neotropical genus, 3 species were available.

3. *Procornitermes araujoi* Emerson (figure 1E–G). (Emerson 1952, *Bull. Am. Mus. nat. Hist.* **99** p. 490.) South America: Leme, Taquari (Sao Paolo, Brazil). Wings transparent, pale yellow; without scale 20 × 6 mm. Hairs present all over, including margins; length 40–60 μm, density 1000/mm². Micro-sculpturing consists of papillae and pimpules.

Papillae: Pointed and thorny; in a single row on the anterior margin (size 4–6 μm × 4 μm). Similar but smaller ones in a row on the posterior margin.

Pimpules: Rounded, refractile, small (2 × 2 μm); all over wing, including veins; density 6100/mm².

The other two species are generally like *P. araujoi* and are dealt with briefly.

4. *Procornitermes lespesii* (Mueller). (Snyder 1949, p. 261.) South America: Ilha Granador (Est. d. Rio, Brazil). Wings small, without scale 13 × 4 mm. Hairs dense all over, length 58–74 μm. Papillae large, pointed, thorny; 7–8 rows on the anterior margin (size 10–12 μm × 4–8 μm; density 7100/mm²), 4–6 rows of smaller ones on the posterior. Pimpules present in proximal region; size 2 × 2 μm, density 7600/mm².

5. *Procornitermes striatus* (Hagen). (Snyder 1949, p. 261.) South America: La Sierra (Uruguay). Wings without scale 16 × 5 mm. Hairs and micro-sculpturing as in *P. lespesii*. Papillae 8–10 μm × 4–6 μm, density 6600/mm². Pimpules as in *P. lespesii*.

Genus (3) **Cornitermes** Wasmann

Of this moderate-sized Neotropical genus, two species were available.

6. *Cornitermes cumulans* (Kollar) (figure 1H, I). (Snyder 1949, p. 262.) South America: Sao Paolo (Brazil). Wings translucent, brown; veins darker. Hairs present all over; length 60–80 μm, density 500/mm². Micro-sculpturing consists of papillae and pimpules.

Papillae: Pointed. 4–6 rows on the anterior margin (size 8–10 μm × 4–6 μm, density 5070/mm²), 2–3 rows on the posterior.

Pimpules: Small, refractile, rounded, size 2 × 2 μm; present all over, especially in the proximal region; density 5000/mm².

7. *Cornitermes pugnax* Emerson (plate 2). (Snyder 1949, p. 262.) South America: Kamekusa (Guyana). Wings and hairs as in *C. cumulans*. Wings without scale 16 × 4.5 mm. Hairs all over; 90–110 μm long, density 500/mm². Micro-sculpturing generally as in *C. cumulans*. Papillae, 8–10 rows on the anterior margin (size 8–10 μm × 4–6 μm, density 6600/mm²), 3–4 rows on the posterior. Pimpules present in proximal region; density 9100/mm².

Genus (4) **Rhynchotermes** Holmgren

Of this small Neotropical genus, two species were available:

8. *Rhynchotermes nasutissimus* (Silvestri) (figure 1 J, K). (Snyder 1949, p. 264.) South America: Guarany (Sao Paolo, Brazil). Wings pale brown, anterior vein darker; size without scale 18 × 4.5 mm.

Hairs absent (cf. *R. perarmatus)*. Micro-sculpturing consists of papillae and pimpules.

Papillae: Short and pointed; 6–7 rows on the anterior margin (size 8–10 μm $\times$ 4–6 μm, density 6100/mm^2), 3–4 rows of smaller ones on the posterior.

Pimpules: Small, rounded, present almost all over; size 2 $\times$ 2 μm, density 7100/mm^2.

9. *Rhynchotermes perarmatus* (Snyder) (figure 1 L, M). (Snyder 1949, p. 264.) Central America: Barro Colorado Island (Canal Zone, Panama). Wings (15 $\times$ 5 mm) as in *R. nasutissimus*, but densely covered all over with hairs (length 56–84 μm, density 1500/mm^2). Micro-sculpturing as in *R. nasutissimus*. Papillae smaller (4–6 μm $\times$ 4 μm) and in fewer rows (2–3). Pimpules present in proximal region.

Genus (5) **Hospitalitermes** Holmgren

Of this small Oriental and Papuan genus, a single species was available.

10. *Hospitalitermes monoceros* (Koenig) (figure 1 N, O; and plate 3). (Snyder 1949, p. 321, Prashad & Sen-Sarma 1960, p. 26, authorship.) South Asia: Colombo (Sri Lanka). Wings transparent, colourless, anterior veins brown; size without scale 13 $\times$ 4 mm. Hairs all over, including margins; length 70–90 μm, density 530/mm^2. Micro-sculpturing consisting of papillae, pimpules and micrasters.

Papillae: A row of small (5–6 μm $\times$ 2–3 μm), thin, pointed, thorny papillae, on the anterior margin; a similar row of smaller ones on the posterior.

Pimpules: Nondirected pimpules (3–7 μm $\times$ 2–4 μm) all over; some of the larger ones are slightly granular (like tubercles) but are, unlike the latter, not distally directed and are therefore classed as pimpules.

Micrasters: (plate 3, figure 4); In the proximal part of wing some nonasteroid micrasters (2–4 arms) present between the veins; apparently absent in the distal part. Arranged in subcircular curves and circles, often with a central micraster. Size 4–6 μm $\times$ 4–6 μm; density 6000–8800/mm^2.

Genus (6) **Lacessititermes** Holmgren

Of this moderate-sized Oriental genus, a single species was available.

11. *Lacessititermes laborator* (Haviland) (figure 2A–C). (Snyder 1949, p. 316.) Southeast Asia: Tandjong Paoh (eastern Sumatra, Indonesia). Wings yellow, anterior veins darker; size without scale 18 $\times$ 4 mm. Hairs densely present all over; length 60–80 μm, density 2000/mm^2. Micro-sculpturing consists of papillae and micrasters.

Papillae: Short, pointed thorny (4–6 μm $\times$ 4 μm); 2–3 rows on the anterior margin (density 6000/mm^2), a single row on the posterior.

Micrasters: Present all over; thin; both nonasteroid (3–5 arms) and asteroid (6–7 arms). Size 6–8 μm $\times$ 6–8 μm; density 9100/mm^2.

Genus (7) **Thailanditermes** Sen-Sarma

(Sen-Sarma 1966, p. 209; Krishna 1970, p. 149, regards it as a synonym of *Lacessititermes* Holmgren.) Of this small genus, a single species was available.

12. *Thailanditermes thailandicus* Sen-Sarma (figure 2 D–F). (Sen-Sarma 1966, *Indian J. Ent.* **28** p. 203.) Southeast Asia: Chanthaburi (Thailand). Wings brown, anterior veins darker; size without scale 13.5 $\times$ 4.5 mm. Hairs densely present all over; length 52–66 μm, density

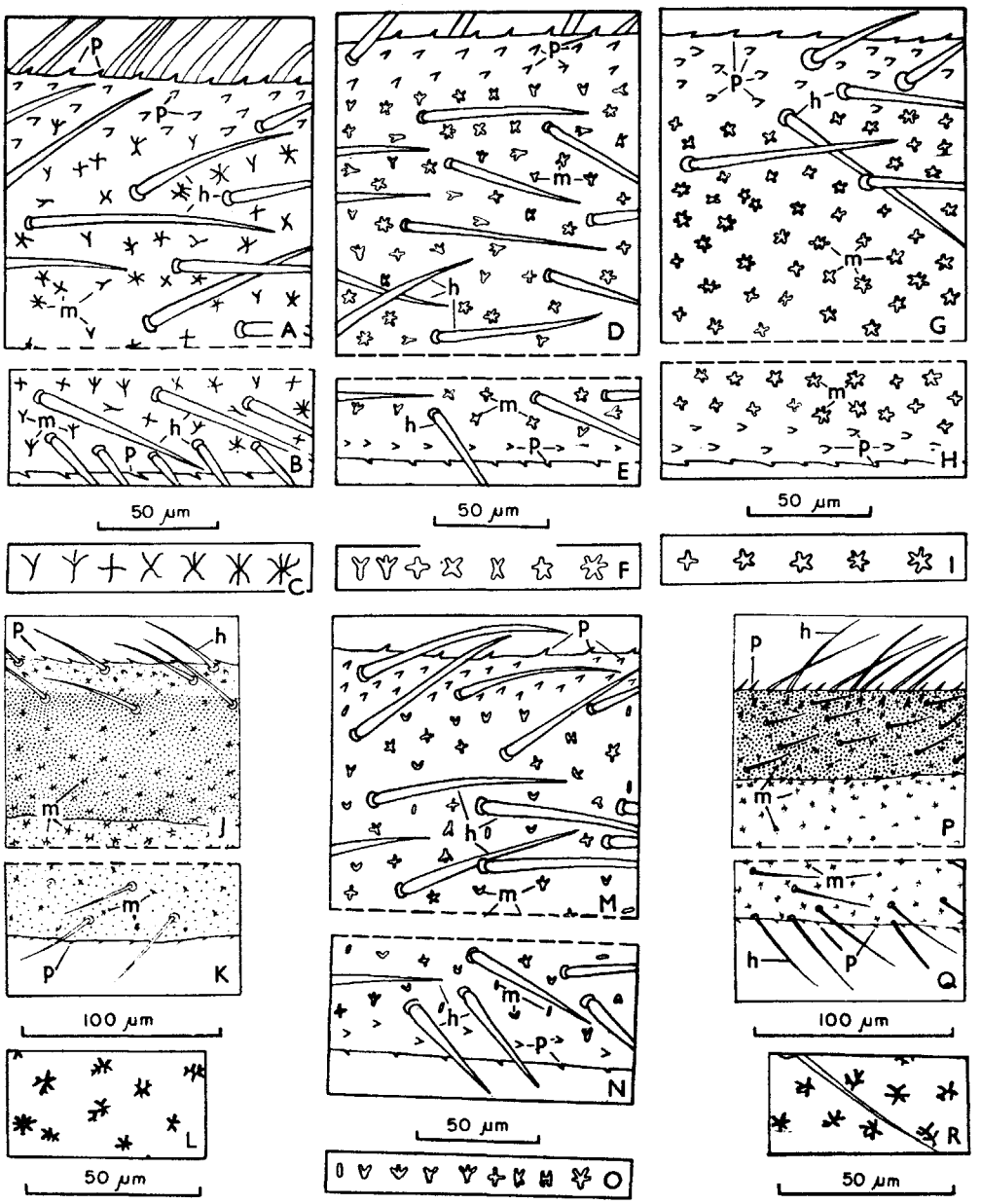

Figure 2 Portions of wing surfaces of some Nasutitermitinae, to show micro-sculpturing. Veins, where darker, are stippled. **(A–C)** *Lacessititermes laborator;* **(D–F)** *Thailanditermes thailandicus;* **(G–I)** *Bulbitermes constrictiformis;* **(J–L)** *Constrictotermes cavifrons;* **(M–O)** *Tenuirostritermes tenuirostris;* **(P–R)** *Velocitermes barrocoloradensis; A, D, G, J, M, P,* anterior margins; *B, E, H, K, N, Q,* posterior margins; *C, F, I, L, O, R,* micrasters in middle of wing, enlarged (Lettering as in figure 1)

1000/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Short, pointed, spiny; 2–3 rows on the anterior margin (size 4–6 μm × 4 μm, density 5100/mm²), 1–2 rows of smaller ones on the posterior.

Micrasters: All over; thick. Both non-asteroids (3–4 arms) and asteroids (5–6 arms) present. Size 6–8 μm × 4–6 μm; density 8600/mm².

Genus (8) **Bulbitermes** Emerson

Of this moderate-sized Oriental genus, 3 species were available.

13. *Bulbitermes constrictiformis* (Holmgren) (figure 2 G–I, and plate 3). (Snyder 1949, p. 308.) Southeast Asia: Gap (Fraser's Hill, Malaysia). Wings brown, veins darker; without scale 15 × 4.5 mm. Hairs all over, denser on distal half; length 60–80 μm, density 500–1000/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Short, pointed, thorny; 3–4 rows on the anterior margin and 2–3 rows on the posterior. Size 8 × 4 μm, density 7000/mm².

Micrasters: Thick type; present all over and arranged in curves. Both non-asteroids (4 arms) and asteroids (5–6 arms) present. Size 4–6 μm × 4–6 μm, density 7600–8100/mm.

14. *Bulbitermes sarawakensis* (Haviland). (Snyder 1949, p. 309.) Southeast Asia: Baram (Borneo, Indonesia). Wings yellowish brown, without scale 17 × 4 mm. Scattered hairs (length 60–72 μm) all over; more numerous (1000/mm²) in distal half. Micro-sculpturing generally as in *B. constrictiformis*, with papillae and thick micrasters.

15. *Bulbitermes singaporiensis* (Haviland). (Snyder 1949, p. 309.) Southeast Asia: Singapore. Wings (without scale 11 × 4 mm) and hairs as in *B. sarawakensis*. Micro-sculpturing generally as in *B. constrictiformis*, with papillae and thick micrasters.

Genus (9) **Constrictotermes** Holmgren

Of this small Neotropical genus, a single species was available.

16. *Constrictotermes cavifrons* (Holmgren) (figure 2 J–L; and plate 3). (Synder 1949, p. 318.) South America: Oko River (Guyana). Wings transparent, colourless, veins dark brown; without scale 15 × 4 mm. Hairs (length 48–60 μm) in 1–2 rows on margins, practically absent on membrane. Micro-sculpturing consists of papillae and micrasters.

Papillae: Longish and pointed; 1–3 rows on the anterior margin (size 6–8 μm × 2–4 μm, density 5600/mm²), fewer (1–2 rows) and smaller on the posterior.

Micrasters: Numerous, brown, thick ones all over. Mostly large asteroids (6–8 arms) present; also a few non-asteroids (5–7 arms). Size 6–8 μm × 5–8 μm; density 6100/mm².

Genus (10) **Tenuirostritermes** Holmgren

Of this small Nearctic and Neotropical genus, a single species was available.

17. *Tenuirostritermes tenuirostris* (Desneux) (figure 2 M–O; and plate 1). (Snyder 1949, p. 313.) North America: Basin Chisos Mts. (Texas, USA). Wings yellow, anterior veins darker; size without scale 21 × 6 mm. Hairs all over wing, including margins; length 60–80 μm, density 1000/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Small, pointed; 2–3 rows on the anterior margin (size 2–3 μm × 1–2 μm,

density 5600/mm²), 1–2 rows of smaller ones on the posterior.

Micrasters: Thick; nonasteroids (1–5 arms) all over; 6–8 μm × 6–8 μm, density 6600/mm².

Genus (11) **Velocitermes** Holmgren

Of this small Neotropical genus, a single species was available.

18. *Velocitermes barrocoloradensis* (Snyder) (figure 2 P–R; and plate 3). (Snyder 1949, p. 312.) Central America: Borro Colorado Island (Canal Zone, Panama). Wings small (without scale 9–10 mm × 3 mm), brown, anterior veins darker. Hairs all over, including margins and veins; length 40–70 μm. Micro-sculpturing consists of papillae and micrasters.

Papillae: 1–3 rows of longish, brown, pointed, thorny papillae on the anterior margin (size 6–8 μm × 3–4 μm, density 6000/mm²); a row of similar but smaller ones on the posterior margin.

Micrasters: Numerous, thick, asteroids (5–8 arms) all over; size 5–6 μm × 4–6 μm, density 6400–7200/mm².

Genus (12) **Diversitermes** Holmgren

Of this small Neotropical genus, two species were available.

19. *Diversitermes eidmanni* Emerson (? MS name) (figure 3 A–C). (Listed in Mathur & Thapa 1962, p. 79.) South America: Sao Vicente (Porchal Island, Sao Paolo, Brazil). Wings small, semi-transparent, brown, anterior veins darker; size without scale 11 × 3 mm. Hairs mostly on distal half of wing and on margins; length 36–50 μm, density 500/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Pointed, thorny; 2–3 rows on anterior margin (6–8 μm × 3 μm, density 5000/mm²); similar but smaller ones on posterior margin.

Micrasters: Thin. Present all over; asteroid (5–8 arms); size 6–8 μm × 6–8 μm, density 8100/mm².

20. *Diversitermes needhami* Emerson (? MS name). (Listed in Mathur & Thapa 1962, p. 80.) South America: Guarany (Sao Paolo, Brazil). Wings as in *D. eidmanni;* size without scale 13 × 4 mm. Hairs all over; length 40–60 μm, density 1000/mm². Micro-sculpturing as in *D. eidmanni.* Papillae pointed; 5–6 rows on the anterior margin (size 6–8 μm × 4–6 μm, density 6000/mm²), 2–3 rows on the posterior. Micrasters small (2–3 μm × 2–3 μm), simple, nonasteroid (1–2 arms, I- and V-shaped); present mostly on the anterior one-third of wing, especially in proximal half, few elsewhere.

Genus (13) **Trinervitermes** Holmgren

Of this large Ethiopian and Oriental genus, 6 species were available.

21. *Trinervitermes biformis* (Wasmann) (figure 3 D–F; and plates 1 and 3). [Synonyms: *T. heimi* (Wasmann) and *T. longinotus* (Snyder)]. (Snyder 1949, p. 324, Prashad & Sen-Sarma 1966, p. 7, synonymy.) South Asia (India): Pune and Bhogi Forest, Koregaon (Maharashtra); Coimbatore (Tamil Nadu); and near Nagaur (Rajasthan). Wings large (without scale 14–17 mm × 4–5 mm); transparent, colourless, anterior part and veins brown. Hairs all over; length 40–60 μm (longer on margins, 80–90 μm); density 1000/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Pointed, thorny, 8–15 rows on the anterior margin (size 6–8 μm × 4–6 μm, density 7100/mm²); 1–5 rows of smaller ones on the posterior.

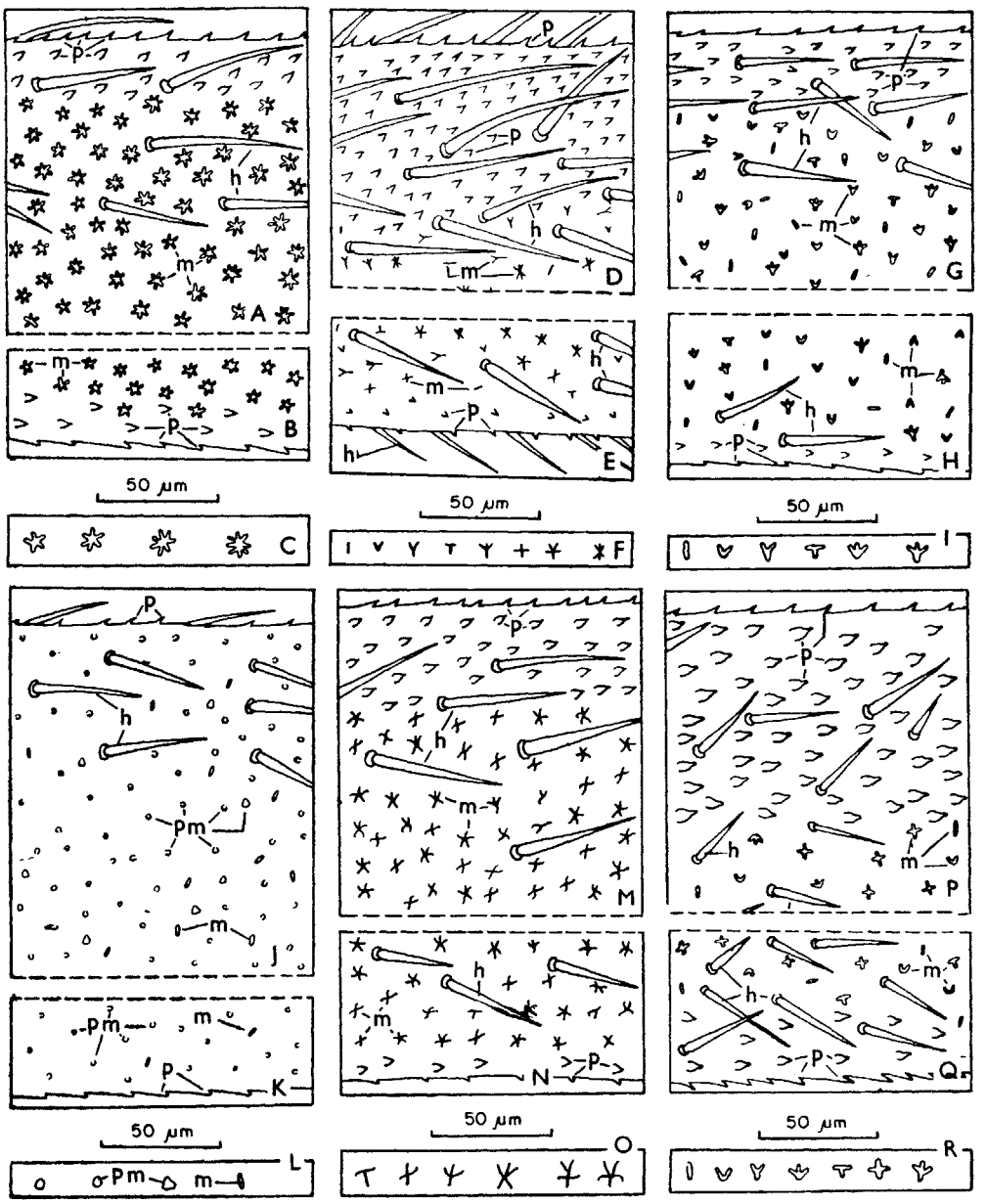

Figure 3 Portions of wing surface of some Nasutitermitinae to show micro-sculpturing. **(A–C)** *Diversitermes eidmanni;* **(D–F)** *Trinervitermes biformis;* **(G–I)** *Tumulitermes apiocephalus;* **(J–L)** *Tumulitermes hastalis;* **(M–O)** *Tumulitermes pastinator;* **(P–R)** *Rotunditermes rotundiceps; A, D, G, J, M, P,* anterior margins; *B, E, H, K, N, Q* posterior margins; *C, F, I, L, O, R, micrasters,* in middle of wing, enlarged (also pimpules in L) (Lettering as in figure 1)

Micrasters: All over. Thin; only non-asteroids (1–6 arms). Size 4–6 μm × 4–6 μm, density 5600–8600/mm².

22. *Trinervitermes ebenerianus* Sjostedt. (Snyder 1949, p. 325.) West Africa: Accra (Ghana). Wings brown, anterior veins darker; size without scale 18.5 × 5 mm. Hairs all over, 50–90 μm long. Micro-sculpturing as in *T. biformis*. Pointed papillae, 9–10 rows on the anterior margin (density 7600/mm²), and 2–3 on the posterior. Micrasters thin, only non-asteroids (3–6 arms); density 7600/mm².

23. *Trinervitermes nigrirostris* Mathur and Sen-Sarma. (Mathur & Sen-Sarma 1959, *Z. angew. Ent.*, Hamburg **45** p. 71.) South Asia (India): Mandapam (Tamil Nadu). Wings yellow, anterior veins darker; size without scale 15–16 mm × 5 mm. Hairs all over; length 48–60 μm, density 1000/mm². Micro-sculpturing as in *T. ebenerianus*.

24. *Trinervitermes roseni* (Holmgren). (Snyder 1949, p. 330.) Central Africa: "Belgian Congo" (=Zaire). Wings brown; size without scale 16 × 5 mm. Hairs all over; length 40–60 μm, density 500–1000/mm². Micro-sculpturing: Papillae and micrasters as in *T. biformis*.

25. *Trinervitermes rubidus* (Hagen). (Snyder 1949, p. 330.) South Asia: Kotte (Sri Lanka). Wings brown; size without scale 13 × 4 mm. Hairs all over; as in *T. roseni*. Micro-sculpturing: Papillae and micrasters generally as in *T. biformis*.

26. *Trinervitermes trinervius* (Rambur). (Snyder 1949, p. 332.) West Africa: Liberia. Wings brown; without scale 16 × 5 mm. Hairs all over; as in *T. roseni*. Micro-sculpturing: Papillae and micrasters as in *T. ebenerianus*.

Genus (14) **Tumulitermes** Holmgren

Of this moderate-sized Australian genus, 5 species were available

27. *Tumulitermes apiocephalus* (Silvestri) (figure 3 G–I). (Snyder 1949, p. 301.) Australia. Wings brown, veins darker; size without scale 9 × 3 mm. Hairs: 2–4 rows on margins, few or absent elsewhere; length 56-58 μm. Micro-sculpturing consists of papillae and micrasters.

Papillae: Pointed and thorny; 3–4 rows on the anterior margin (6–8 μm × 4 μm, density 5000/mm²); 1–2 rows of smaller ones on the posterior.

Micrasters: All over. Thick, simple, nonasteroid (1–4 arms); size 2–6 μm × 2–6 μm, density 9100/mm².

28. *Tumulitermes hastalis* (Froggatt) (figure 3 J–L; and plate 2) (Snyder 1949, p. 302.) Australia: Brooks Creek (Northern Territory), Wings transparent, colourless to yellowish, veins brown; size without scale 9–10 × 3 mm. Hairs as in *T. apiocephalus*. Micro-sculpturing consists of papillae, pimpules and micrasters.

Papillae: Pointed, thorny, small (4 × 2 μm). A row each on the anterior and posterior margins.

Pimpules: All over; rounded to slightly conical; density 4000–4400/mm². Are of two types, with mixed distribution: (a) Small and round (1 μm × 1 μm); are common. (b) Slightly larger (1.5-2 μm × 1.5-2 μm) and pointed, almost subconical are fewer.

Micrasters: A few simple, nonasteroid, rod-like, 1-armed micrasters scattered all over; size 4–7 μm × 0.5 μm, density 60/mm².

29. *Tumulitermes pastinator* (Hill) (figure 3 M–O). (Snyder 1949, p. 303.)

(Australia: Brooks Creek, Northern Territory). Wings brownish, large (without scale 19×5 mm). Hairs all over; length 50–80 μm; density 1000/mm². Micro-sculpturing generally as in *T. apiocephalus*. Papillae, pointed; 4–5 rows on the anterior margin (size 5–6 ×2–3 μm, density 7100/mm²), 1–2 rows on the posterior. Micrasters thin; nonasteroids (3–5 arms); present all over wing; size 6–8 μm×6–8 μm, density 7600–9100/mm².

30. *Tumulitermes tumuli* (Froggatt). (Snyder 1949, p. 309.) Australia: Gosnells (Western Australia). Wings brownish; size without scale 12×3 mm. Hairs (length 40–60 μm) in 3–4 rows on the anterior margin, and 1–2 rows on the posterior; also scattered on distal half of membrane, few or none elsewhere. Micro-sculpturing generally as in *T. apiocephalus*. Papillae pointed; 3–4 rows on the anterior margin, 1–2 on the posterior. Micrasters thin; nonasteroid (1–4 arms); size 4–6 μm×4–6 μm, density 6600/mm².

31. *Tumulitermes westraliensis* (Hill) (plates 1 and 2). (Snyder 1949, p. 304.) Australia: Gosnells and near Armdale (Western Australia). Wings and hairs as in *T. tumuli;* wings without scale 9×3.5 mm. Micro-sculpturing generally as in *T. apiocephalus*. Papillae in 2–3 rows on the anterior margin (size 4–6 μm × 4 μm, density 5100/mm²), 1–2 rows on the posterior. Micrasters thick, small, nonasteroid (2–5 arms, mostly 4); size 4–6 μm ×4–6 μm, density 4800–6100/mm².

Genus (15) **Rotunditermes** Holmgren

Of this small Neotropical genus, a single species was available.

32. *Rotunditermes rotundiceps* (Holmgren) (figure 3 P–R). (Snyder 1949, p. 300.) South America: Chaquimayo (Carabaya, Peru). Wings brownish, anterior veins darker. Hairs all over, including margins; length 40–60 μm, density 1000/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Large (6–8 μm×4–6 μm); some pointed and thorny but mostly nipple-shaped, as in *Syntermes*. 8–12 rows on the anterior margin, and 2–3 rows on the posterior (the latter rather *longer*). Density 7100/mm².

Micrasters: All over. Thick, nonasteroid (1–4 arms); 3 μm×3 μm, density 9100/mm².

Genus (16) **Nasutitermes** Banks

(The author of the genus is Banks 1920, not Dudley 1890, vide discussion in Prashad & Sen-Sarma 1959, p. 2.)

Of this large and widespread genus, 23 species were available. The genus is fairly uniform, and micro-sculpturing in all species studied consists of papillae and micrasters only. Wings are generally transparent and colourless, with the veins yellowish to dark brown. Wing sizes vary with the species from small to large, 8–19 mm ×2–6 mm. Hairs are generally present, being longer on wing margins than elsewhere; lengths vary as 40–90 μm, and density as 500–1500/mm². The proximal part of wing generally carries fewer hairs.

Papillae are longish, pointed and thorny and vary with the species from small to large (3–9 μm×1–4 μm). They occur in several (5–6) rows on the anterior margin and 2–4 on the posterior. Those on the anterior margin are generally longer and stouter than those on the posterior, but the reverse occurs in some species (e.g., *N. brunneus*). Density 6600–8100/mm².

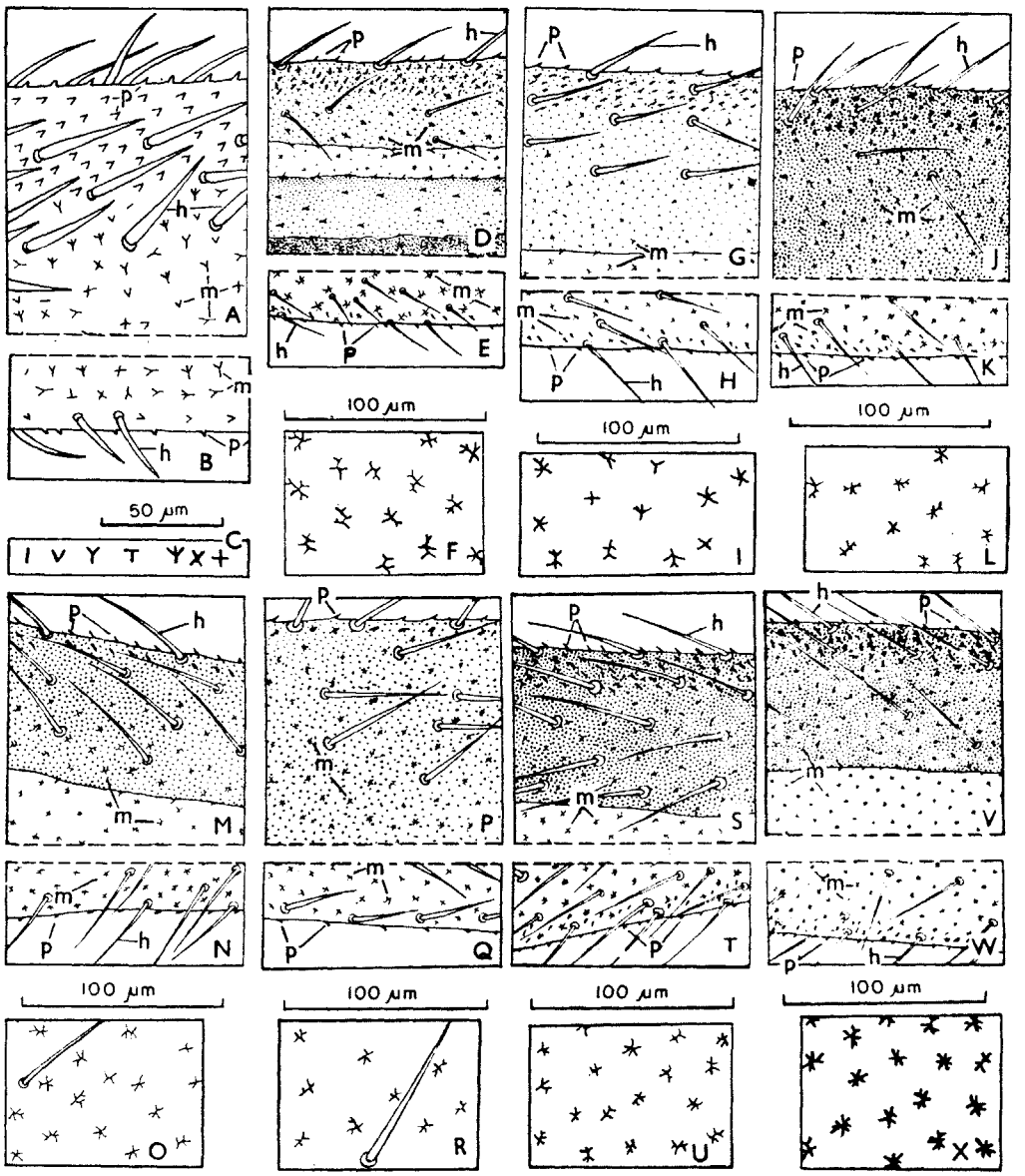

Figure 4 Portions of wing surfaces of *Nasutitermes* spp. Veins, where darker, are stippled; **(A–C)** *N. corniger;* **(D–F)** *N. beckeri;* **(G–I)** *N. exitiosus;* **(J–L)** *N. fumigatus;* **(M–O)** *N. garoensis;* **(P–R)** *N. longipennis;* **(S–U)** *N. luzonicus;* **(V–X)** *N. dixoni. A, D, G, J, M, P, S, V,* anterior margins; *B, E, H, K, N, Q, T, W,* posterior margins; *C, F, I, L, O, R, U, X,* micrasters in middle of wing, enlarged. (Lettering as in figure 1)

Micrasters are present all over the wing, densities varying as about 6600–10100/mm². Both nonasteroid (1–8 arms) and asteroid (5–8 arms) shapes occur. Further, some have thin, and others thick, micrasters. To save space, the species are grouped into 'thin' and 'thick' types, with one species described in detail in each type, the rest being dealt with only briefly.

(A) *Nasutitermes with thin micrasters*

33. *Nasutitermes corniger* (Motschulsky) (figure 4 A–C). (Snyder 1949, p. 272.) Central America: Guatemala. Wings transparent, colourless, anterior veins dark brown; size without scale 12 × 3mm. Hairs present in 4–5 rows on the anterior and the posterior margins, a few on the veins and on the membrane. Length 32–60 μm; density on margins 2000/mm², on membrane 500/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Pointed, thorny; 5–6 rows on the anterior margin (size 6–8 μm × 4–6 μm, density 7100/mm²), 2–4 rows on the posterior.

Micrasters: All over. Thin; nonasteroid (1–4 arms); size 4–6 μm × 4–6 μm, density 6600/mm².

Other species with *thin* micrasters are discussed below briefly.

34. *Nasutitermes beckeri* (Prashad & Sen-Sarma 1959, p. 8.) (figure 4 D–F). India: Neriamangalam (Western Ghats). Papillae small and weak (size 3 × 1.5μm); 5–6 rows on the anterior margin, 2–3 on the posterior. Micrasters thin, asteroid (5–8 arms); size 3–5 μm × 3–5 μm; density 9600–10100/mm².

35. *Nasutitermes brunneus* Snyder. (Snyder 1949, p. 269.) India: Ananmalai Hills, Tamil Nadu. Papillae small and thin on the anterior margin (4–5 × 0.5–1 μm), stouter on the posterior (6 × 1 μm). Micrasters thin; nonasteroid (3–6 arms); size 4–6 μm × 4–6 μm, density 7600/mm².

36. *Nasutitermes dunensis* [Chatterjee & Thakur 1969, *Bull. syst. Zool.*, Calcutta, **1** (2) p. 57]. India: Asarori forest near Dehra Dun (Uttar Pradesh). Micrasters thin; nonasteroid (3–7 arms); size 6–8 μm × 6–8 μm; density 6400–8000/mm².

37. *Nasutitermes ephratae* (Holmgren). (Snyder 1949, p. 275.) Central America: Guatemala. Papillae as in *N. corniger*. Micrasters thin; nonasteroid (4–6 arms); size 6–8 μm × 6–8 μm; density 8600/mm².

38. *Nasutitermes exitiosus* (Hill) (figure 4 G–I). (Snyder 1949, p. 276.) 4 miles N of Murraytown, South Australia. Papillae as in *N. corniger*. Micrasters thin; nonasteroid (3–6 arms); size 4–6 μm × 4–6 μm, density 5600–7600/mm².

39. *Nasutitermes fumigatus* (Brauer) (figure 4 J–L). (Snyder 1949, p. 277.) Australia: 13 miles SE of Grafton (New South Wales). Papillae as in *N. corniger*. Micrasters thin; with asteroid and nonasteroid shapes (5–8 arms); size 6–8 μm × 6–8 μm, density 8100/mm².

40. *Nasutitermes garoensis* Roonwal and Chhotani (1962, *Proc. natn. Inst. Sci. India* **B28**, p. 379). (figure 4 M–O). South Asia: Phuntsholing (Bhutan). Papillae long, thin, pointed (6–9 μm × 2–3 μm); 1–2 rows on the anterior margin, a row of smaller ones on the posterior. Micrasters thin, asteroid (5–6 arms); size 5–6 μm × 3–6 μm; density 6000–8800/mm².

41. *Nasutitermes graveolus* (Hill). (Snyder 1949, p. 278.) Australia. Papillae as in *N. corniger*. Micrasters thin, both nonasteroid and asteroid (4–7 arms); size 6–8 μm × 6–8 μm, density 7100/mm².

42. *Nasutitermes lacustris* (Bugnion). (Snyder 1949, p. 282.) South Asia: Sri

Lanka. Papillae as in *N. corniger*. Micrasters thin, nonasteroid (4–7 arms), size 4–6 μm × 4–6 μm, density 7600–8100/mm^2.

43. *Nasutitermes lambai* Verma and Thakur (1978, *J. Indian Acad. Wood Sci.* Bangalore, **9**, p. 50). India: Corbett National Park (NW Uttar Pradesh). Papillae as in *N. corniger*. Micrasters thin; both nonasteroid and asteroid (4–7 arms): size 6–8 μm × 6–8 μm, density 9100/mm^2.

44. *Nasutitermes longipennis* (Hill) (figure 4 P–R). (Snyder 1949, p. 284.) Australia. Papillae as in *N. corniger*, but in 1–2 rows. Micrasters thin; both nonasteroid and asteroid (4–7 arms); size 6–8 μm × 6–8 μm, density 8100–8600/mm^2.

45. *Nasutitermes luzonicus* (Oshima) (figure 4 S–U). (Snyder 1949, p. 284.) Southeast Asia: Novaliches (Rizal, Philippines). Papillae as in *N. corniger*. Micrasters thin; both asteroid and nonasteroid (4–8 arms); size 6–8 μm × 6–8 μm, density 8600–9200/mm^2.

46. *Nasutitermes magnus* (Froggatt). (Snyder 1949, p. 285.) Australia. Papillae as in *N.corniger*. Micrasters thin, nonasteroid (1–5 arms); size 4–6 μm × 2–6 μm, density 7600/mm^2.

47. *Nasutitermes matangensis matangensis* (Haviland). (Snyder 1949 p. 287; and Roonwal & Sen-Sarma 1956, *Indian J. agric. Sci.*, **26**.) Southeast Asia: Sarawak (Borneo). Papillae as in *N. corniger*. Micrasters thin; both asteroid and nonasteroid (5–7 arms); size 4–6 μm × 4–6 μm, density 9100/mm^2.

48. *Nasutitermes matangensis matangensiformis* (Haviland). (Snyder 1949, p. 286; and Roonwal & Sen-Sarma 1956, *Indian J. agric. Sci.* **26.**) Southeast Asia: Sarawak (Borneo). Papillae and micrasters as in *N. m. matangensis* above.

49. *Nasutitermes takasagoensis* (Oshima). (Snyder 1949, p. 298.) Southeast Asia: Botel Tobago Island (Formosa = Taiwan). Papillae as in *N. corniger*. Micrasters thin; nonasteroid (4–7 arms); size 6–8 μm × 6–8 μm, density 8600/mm^2.

(B) *Nasutitermes with thick micrasters*

50. *Nasutitermes dixoni* (Hill) (figure 4V–X; and plate 2). (Snyder 1949, p. 274.) Australia. Wings brownish, anterior veins darker; size without scale 12 × 4 mm. Numerous hairs present on margins in 2–5 rows, a few on membrane; length 40–60 μm; density, on margins, 500/mm^2. Micro-sculpturing consists of papillae and micrasters.

Papillae: Longish, pointed, thorny; 4–5 rows on the anterior margin (size 6–8 μm × 3–4 μm, density 7000/mm^2), 2–4 rows of smaller ones on the posterior.

Micrasters: All over; thick; mostly asteroid (5–8 arms); size 6–8 μm × 6–8 μm, density 6400–9000/mm^2.

Other species with thick micrasters are described below briefly.

51. *Nasutitermes ceylonicus* (Holmgren)(plate 2). (Snyder 1949, p. 270.) South Asia: Battaramull (Western Province, Sri Lanka). Hairs all over wing except on proximal third. Papillae as in *N. dixoni*. Micrasters thick, nonasteroid (3–6 arms); size 6–8 μm × 6–8 μm; density 6800–8100 mm^2.

52. *Nasutitermes kinoshitae* (Hozawa). (Snyder 1949, p. 282.) Southeast Asia: Kappanzan (Formosa=Taiwan). Papillae as in *N. dixoni*. Micrasters thick; asteroid (5–8 arms); size 6–8 μm × 6–8 μm; density 9100/mm^2.

53. *Nasutitermes marivalles* (Light & Wilson). (Snyder 1949, p. 286.) Southeast

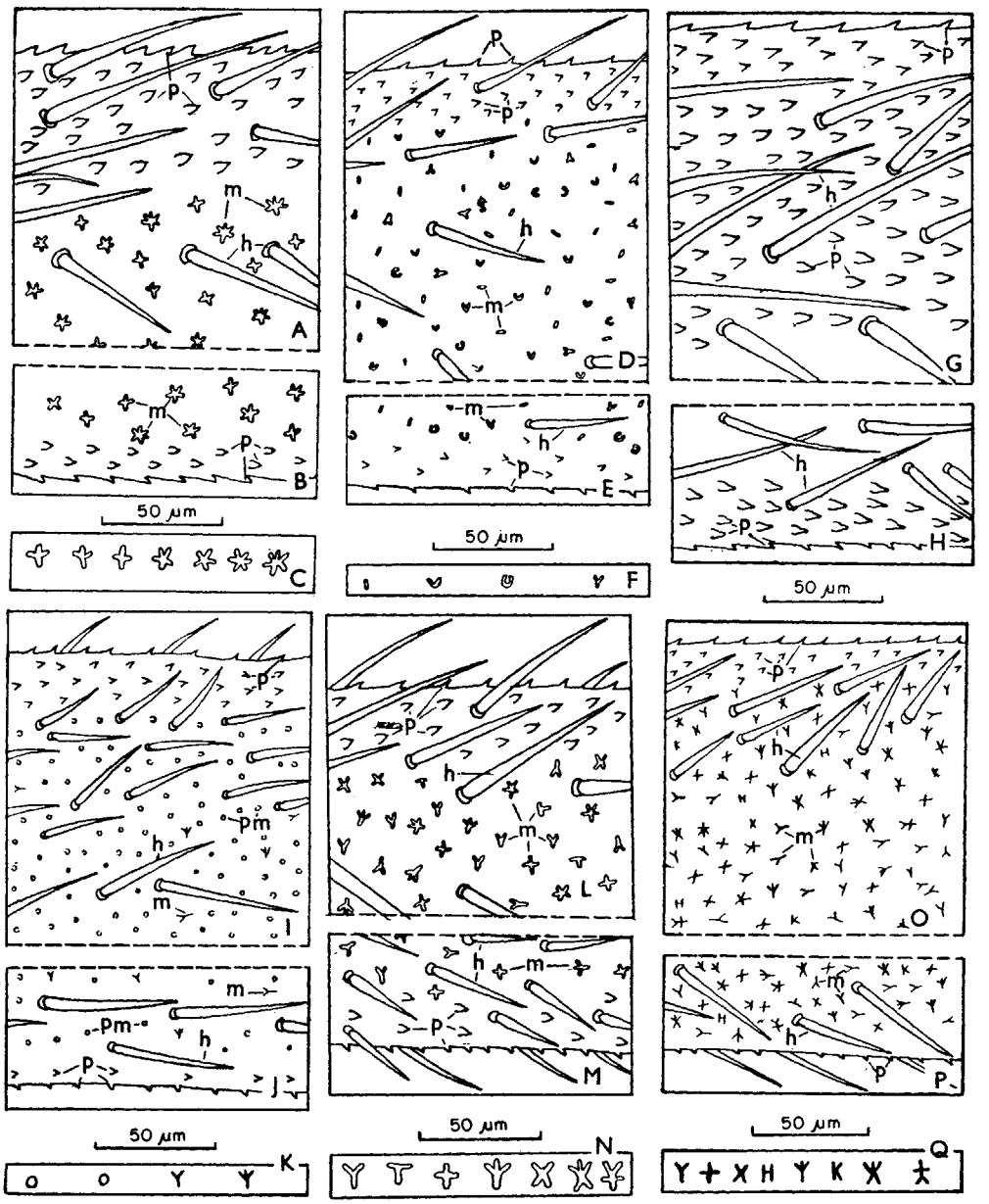

Figure 5 Portions of wing surfaces of some Nasutitermitinae, to show micro-sculpturing. **(A–C)** *Havilanditermes atripennis;* **(D–F)** *Labiotermes brevilabius;* **(G–H)** *Labiotermes labralis boreus;* **(I–K)** *Armitermes euamignathus;* **(L–N)** *Grallatotermes africanus;* **(O–Q)** *Occasitermes occasus; A, D, G, I, L, O,* anterior margins; *B, E, H, J, M, P,* posterior margins; *C, F, K, N, Q,* micrasters, in middle of wing, enlarged (also pimpules in K), (Lettering as in figure 1)

Asia: Mt. Marivalles (Bataan Province, Luzon, Phillipines). Papillae and micrasters as in *N. kinoshitae*.

54. *Nasutitermes mindanensis* (Light & Wilson). (Snyder 1949, p. 288.) Southeast Asia: Near Craan Point (Cotabato Province, Mindando, Phillipines). Papillae and micrasters as in *N. kinoshitae*, but micrasters denser (9100–9600/mm²).

55. *Nasutitermes parvonasutus* (Nowa). (Snyder 1949, p. 292.) Southeast Asia: (Formosa = Taiwan). Papillae and micrasters as in *N. kinoshitae*.

Genus (17) **Havilanditermes** Light

Of this small Oriental genus, a single species was available.

56. *Havilanditermes atripennis* (Haviland) (figure 5 A–C; and plate 2). (Snyder 1949, p. 301.) Southeast Asia: Sarawak (Borneo). Wings semi-transparent, brown, anterior veins darker; size without scale 13×4 mm. Hairs all over wing, including veins; length 60–80 μm, density 1000/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Short, pointed, thorny; 4–5 rows on the anterior margin 2–3 rows on the posterior. Density 6100/mm².

Micrasters: Thick type; present all over wing; both nonasteroid (4–5 arms) and asteroid (5–6 arms). Arranged in curves and circles, often with a central piece (plate 2, figure 7). Size 6–8 μm × 6–8 μm, density 7100/mm².

Genus (18) **Labiotermes** Holmgren

Of this small Neotropical genus, two species were available.

57. *Labiotermes brevilabius* Emerson and Banks (figure 5 D–F). (Emerson & Banks 196 5, *Am. Mus. Novitat.*, New York, No. 2208, p. 24.) South America: Novo Horizonte (Sao Paolo, Brazil). Wings pale brown, anterior veins darker; without scale 12×4 mm. Hairs all over; length 48–60 μm, density 1000/mm². Micro-sculpturing consisting of papillae and micrasters.

Papillae: Small, pointed, thorny; 3–4 rows on the anterior margin (size 4–6 μm×4 μm, density 6100 mm²), 2–3 rows on the posterior.

Micrasters: Mostly on the proximal half of wing, only a few on the distal half. Thick; simple, nonasteroid (1–3 arms); small (2×2 μm); density 9100/mm².

58. *Labiotermes labralis boreus* (Emerson) (figure 5 G, H). (Snyder 1949, p. 334.) West Indies: North Range (Trinidad). Wings brown, anterior veins darker; size without scale 18×5 mm. Long hairs all over wing; length 85×100 μm, density 1000/mm². Micro-sculpturing consists of papillae *only;* 10–12 rows of pointed, thorny papillae on the anterior margin, 4–5 rows on the posterior. Some papillae, especially the middle ones, are nipple-shaped; size 6–8 μm×4–6 μm; density 9100/mm².

Genus (19) **Armitermes** Holmgren

Of this moderate-sized Neotropical genus, 5 species were available.

59. *Armitermes chargesi* Snyder. (Snyder 1949, p. 135.) Central America: Barro Colorado Island (Canal Zone, Panama). Wings brownish, anterior veins darker; without scale 10×4 mm. Hairs all over; length 50–70 μm, density 1500/mm². Micro-sculpturing consists of papillae and pimpules; micrasters apparently absent.

Papillae: Pointed, thorny; 3–4 rows on anterior margin (size 6–8 μm×4 μm,

density 6100/mm²); 1–2 rows of smaller ones on the posterior.

Pimpules: Minute, rounded; present on proximal half of wing, especially near suture; size 2 μm × 2 μm, density 7600/mm².

60. *Armitermes euamignathus* Silvestri (figure 5 I–K). [*A. euhamignathus* of authors. The correct original spelling is as given above.] (Snyder 1949, p. 335.) South America: Sao Paolo (Brazil). Wings and hairs generally as in *A. chargesi;* hair density 800/mm². Micro-sculpturing consists of papillae, pimpules and a few simple micrasters. Papillae and pimpules as in *A. chargesi.* A few simple, nonasteroid (3–4 arms) micrasters scattered all over.

61. *Armitermes holmgreni* Snyder (plate 3). (Snyder 1949, p. 336.) South America: Kartabo (Guyana). Wings (without scale 9.5 × 3 mm) and hairs generally as in *A. chargesi,* but the hairs more numerous (density 5100/mm²). Micro-sculpturing as in *A. chargesi,* with papillae and pimpules only.

62. *Armitermes neotenicus* Holmgren. (Snyder 1949, p. 337.) South America: "Noon Stop above Wanoceri, Courantyne" (Surinam, formerly Dutch Guiana). Wings (without scale 9.5 × 3 mm) and hairs as in *A. chargesi.* Micro-sculpturing consists of papillae, pimpules and simple micrasters. Papillae and pimpules generally as in *A. chargesi.* A few nonasteroid (rod-like, 1 armed) micrasters scattered all over wing.

63. *Armitermes parvidens* Emerson and Banks. (Emerson & Banks 1957, *Am. Mus. Novitat',* New York, No. 1841, p. 6.) South America: Mendes (Est. d. Rio, Brazil). Wings (without scale 15–16 mm × 4 mm) and hairs as in *A. chargesi,* but hairs fewer (density 500/mm²). Micro-sculpturing consists of papillae and pimpules. Papillae pointed; 8–9 rows on the anterior margin, and 2–3 on the posterior; size 6–8 μm × 4–6 μm, density 6100/mm². Pimpules present on proximal third of wing; size 2 μm × 2 μm; density low, 3000/mm². Micrasters apparently absent.

Genus (20) **Grallatotermes** Holmgren

Of this small Papuan, Oriental and Ethiopian genus, two species were available.

64. *Grallatotermes admirabilis* Light and Wilson. (Snyder 1949, p. 314.) Southeast Asia: Negros (Phillipines). Wings yellowish, anterior veins darker; size without scale 17 × 5 mm. Hairs on distal half of wing and on margins; length 40–60 μm; density low, 500/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Pointed, thorny; 3–4 rows on the anterior margin, 2–3 on the posterior; size 6–8 μm × 4–6 μm, density 5100/mm².

Micrasters: All over. Thick; asteroid (5–8 arms); nonasteroids absent. Size 8–10 μm × 8–10 μm, density 7100/mm².

65. *Grallatotermes africanus* Harris (figure 5 L–N). (Harris 1954, *Proc. R. ent. Soc. Lond.,* **B23**, p. 135.) East Africa: Ngomeni (Tanga District, Tanzania). Wings brown, anterior veins darker; without scale 17 × 5 mm. Hairs all over; length 48–64 μm, density 1000/mm². Micro-sculpturing consists of pointed papillae and micrasters. Papillae as in *G. admirabilis* but denser (6100/mm²). Micrasters all over; thick, nonasteroid (3–5 arms); size 4–6 μm × 4–6 μm, density 7100/mm².

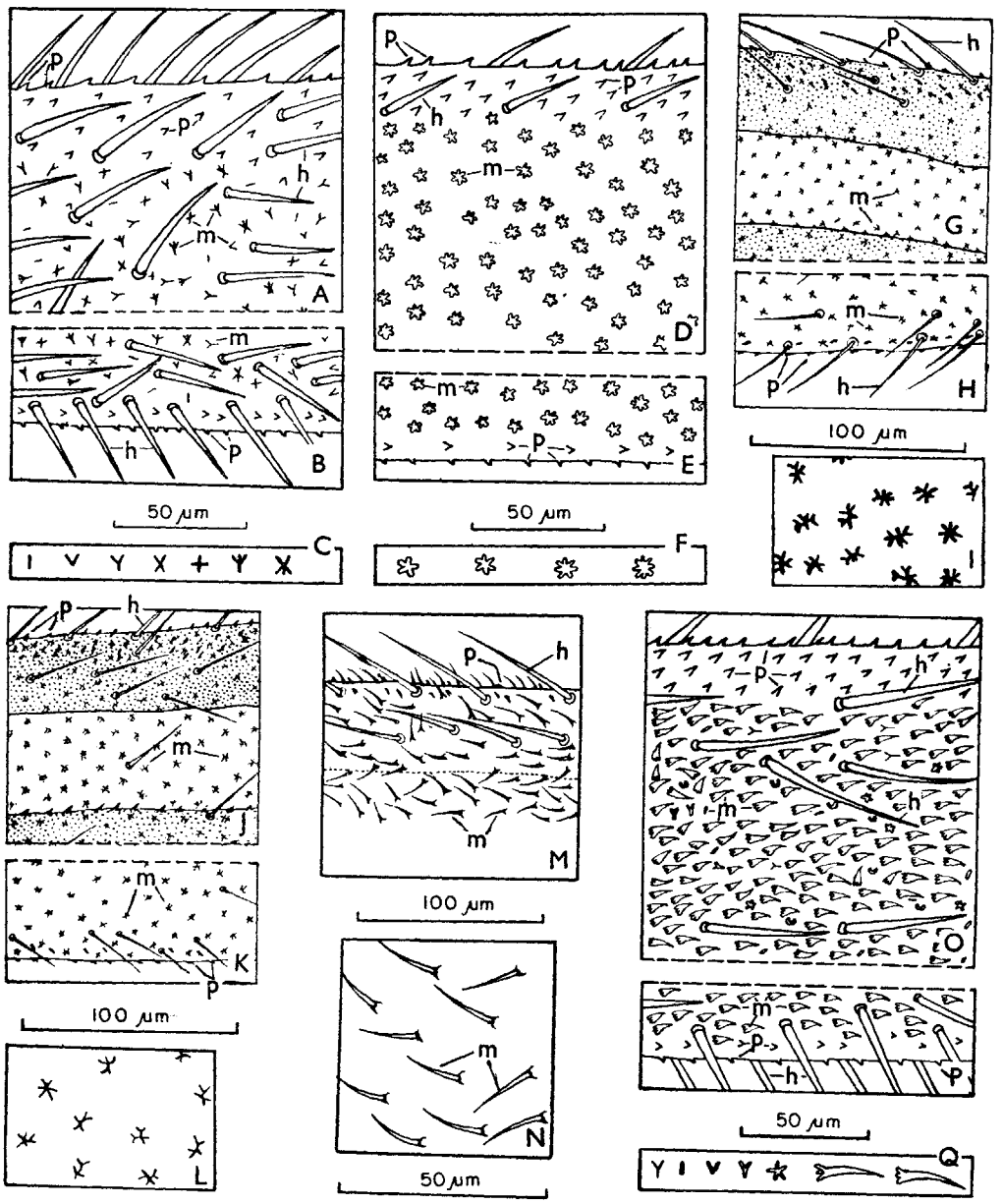

Figure 6 Portions of wing surfaces in some Nasutitermitinae, to show micro-sculpturing. **(A–C)** *Convexitermes clevelandi;* **(D–F)** *Subulitermes baileyi;* **(G–I)** *Subulitermes kirbyi;* **(J–L)** *Subulitermes parvellus;* **(M–N)** *Afrosubulitermes congoensis;* **(O–Q)** *Mimeutermes giffardi; A, D, G, J, M, O,* anterior margins; *B, E, H, K, P,* posterior margins; *C, F, I, L, N, Q,* micrasters, in middle of wing, enlarged. (Lettering as in figure 1)

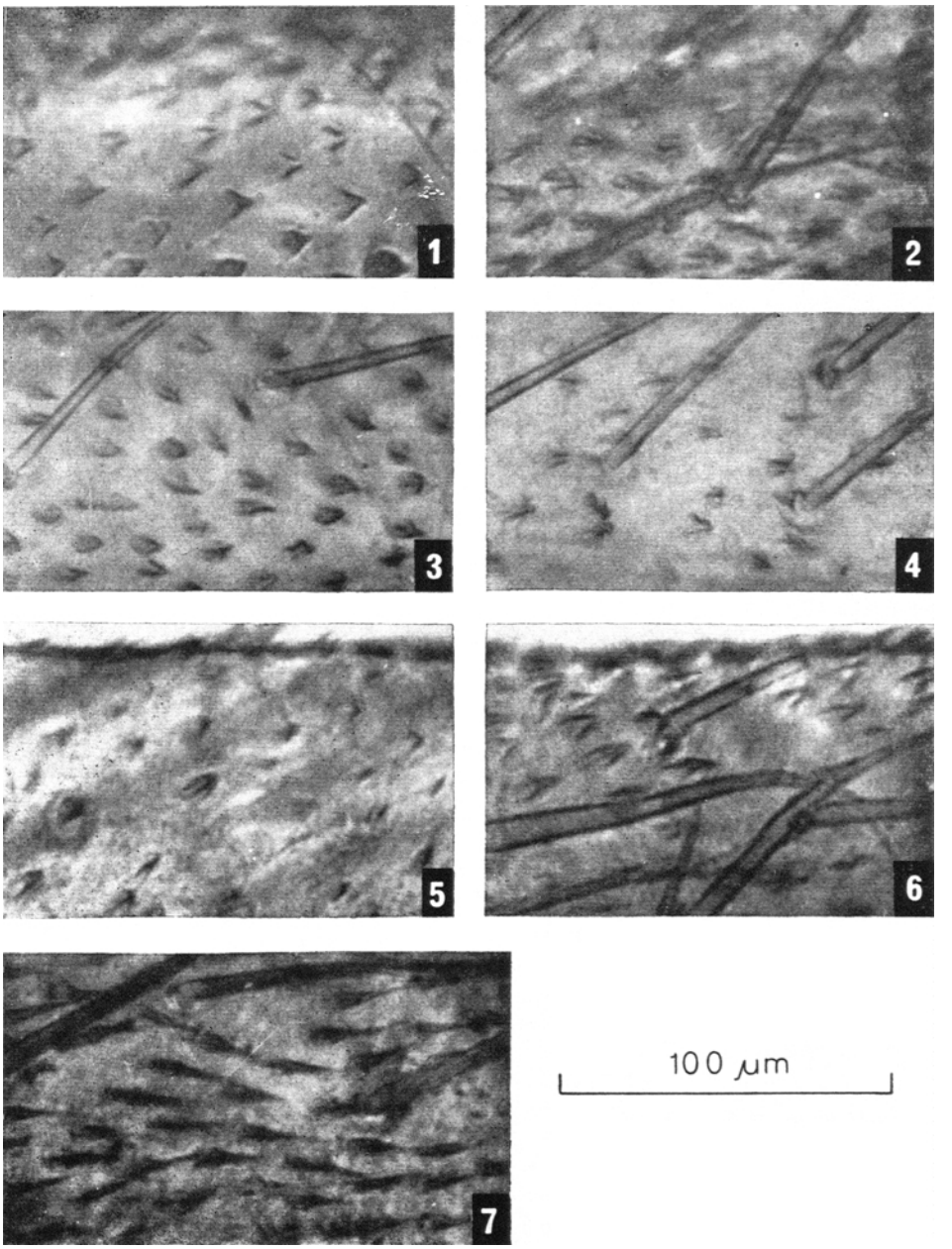

Plate 1 Photomicrographs of anterior margins of wings of Nasutitermitinae, to show papillae, micrasters and hairs; *1*, ***Syntermes molestus***, papillae; *2*, ***Nasutitermes matangensis matangensiformis***, papillae and hairs; *3*, ***Tumulitermes westraliensis***, papillae and hairs; *4*, ***Occasitermes occasus***, papillae and hairs; *5*, ***Tenuirostritermes tenuirostris***, papillae; *6*, ***Trinervitermes biformis***, papillae and hairs; *7*, ***Mimeutermes giffardi***, micrasters and hairs

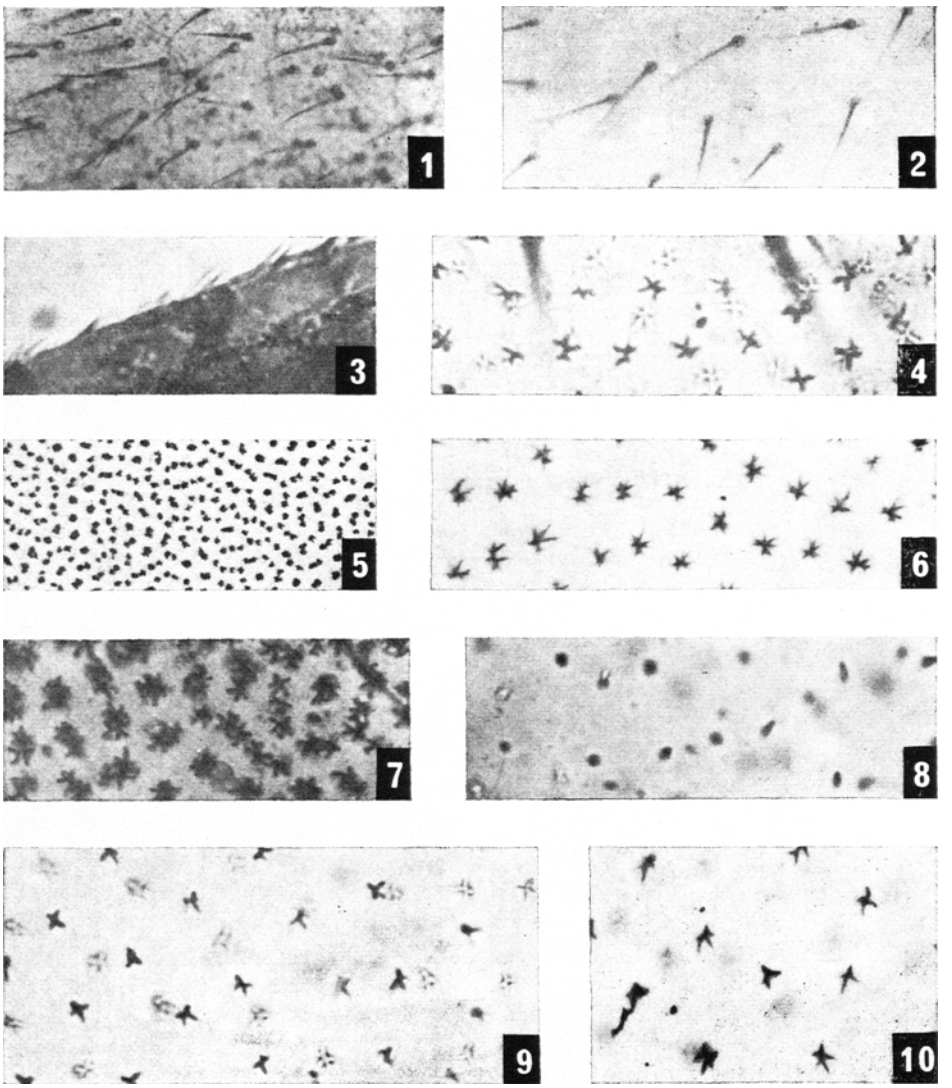

Plate 2 Photomicrographs of wings of Nasutitermitinae, to show micro-sculpturing. (All in middle of wing, except where otherwise stated.); *1*, *Syntermes territus*, hairs; *2*, *Cornitermes pugnax*, hairs; *3*, *Nasutitermes ceylonicus*, anterior margin; papillae; *4*, Ditto, microasters; *5*, *N. dixoni*, microasters; *6*, Ditto, same, enlarged; *7*, *Havilanditermes atripennis*, microasters; *8*, *Tumulitermes hastalis*, pimpules and 1-armed microasters; *9*, *T. westraliensis*, microasters; *10*. *Occasitermes occasus*. microasters

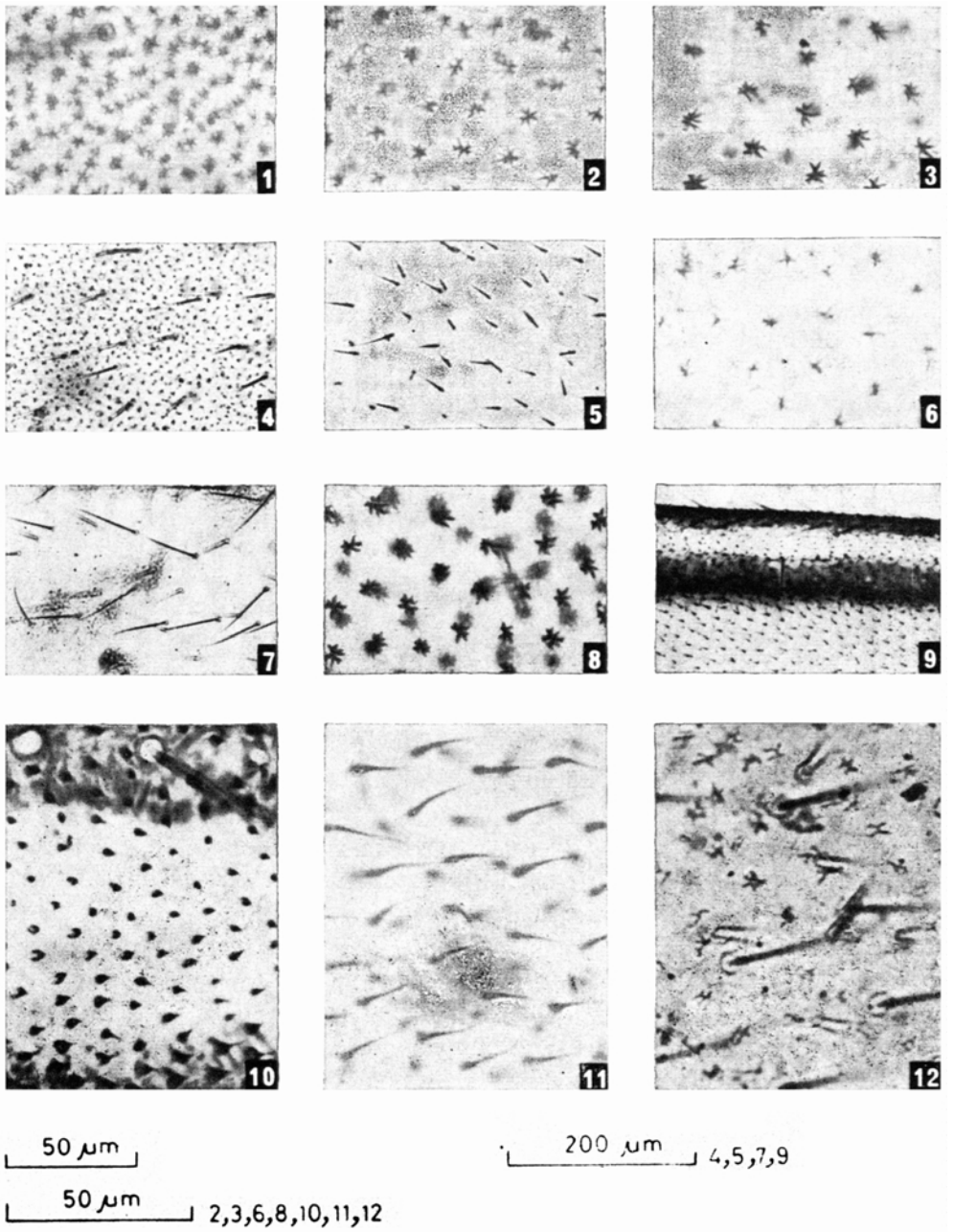

Plate 3 Photomicrographs of wings of Nasutitermitinae, to show micro-sculpturing. (All from middle of wing, except where otherwise stated.) *1*, ***Bulbitermes constrictiformis***, micrasters; *2*, ***Velocitermes barrocolaradensis***, micrasters; *3*, ***Constrictotermes cavifrons***, micrasters; *4*, ***Hospitalitermes monoceros***, proximal part; micrasters and hairs; *5*, Ditto, distal part; hairs only; *6*, ***Trinervitermes biformis***, micrasters; *7*, ***Armitermes holmgreni***, hairs; *8*, ***Subulitermes kirbyi***, micrasters; *9*, ***Afrosubulitermes congoensis***, near anterior margin; papillae, micrasters and hairs; *10*, Ditto, proximal part; micrasters (small types); *11*, Ditto, distal part; micraster (long, curved type); *12*, ***Convexitermes cleveland***, micrasters and hairs

Genus (21) **Occasitermes** Holmgren

Of this small Australian genus, a single species was available.

66. *Occasitermes occasus* (Silvestri) (figure 5 O–Q; and plates 1 and 2). (Snyder 1949, p. 304.) Western Australia. Wings transparent, colourless, veins brown; without scale 10×2.5 mm. Several thin hairs on margins (length 35–50 μm, density 1000/mm²), a few scattered ones elsewhere. Micro-sculpturing consists of papillae and micrasters.

Papillae: 2–3 rows of small, pointed papillae on the anterior margin (size 3–4 μm×1–2 μm, density 5000/mm²), a single row of smaller ones on the posterior.

Micrasters: Present all over. Thin, nonasteroid (3–5 arms). Size 4–6 μm× 4–6 μm, density 5600–9000/mm².

Genus (22) **Convexitermes** Holmgren

Of this small Neotropical genus, 4 species were available.

67. *Convexitermes clevelandi* (Snyder) (figure 6 A–C, and plate 3). (Snyder 1949, p. 342.) Central America: Barro Colorado Island (Canal Zone, Panama). Wings brown, anterior veins darker; without scale 6.5×2.5 mm. Numerous hairs all over; length 64–72 μm, density 1500/mm². Micro-sculpturing consists of papillae and micrasters.

Papillae: Small, pointed, thorny, 3–4 rows on the anterior margin (size 3 μm× 3 μm, density 5600/mm²), 1–2 rows of smaller ones on the posterior.

Micrasters: Present all over. Thin, nonasteroid (1–5 arms). Size 3–4 μm× 2–3 μm; density 5200–6100/mm².

68. *Convexitermes kartaboensis* (Emerson). (Snyder 1949, p. 343.) South America: Kartabo (Guyana). Wings (size without scale 8×2 mm) and hairs as in *C. clevelandi*. Micro-sculpturing consists of papillae and micrasters. Papillae as in *C. clevelandi*. Micrasters all over; thin, nonasteroid (3–6 arms); size 4×4 μm, density 7100/mm².

69. *Convexitermes manni* (Emerson). (Snyder 1949, p. 343.) South America: Kartabo (Guyana). Wings (size without scale 7.5×2 mm) and hairs generally as in *C. clevelandi*. Papillae and micrasters as in *C. kartaboensis*.

70. *Convexitermes mazaruniensis* (Emerson). (Snyder 1949, p. 343.) South America: Kartabo (Guyana). Wings (size without scale 6.5×2 mm) and hairs generally as in *C. clevelandi*. Micro-sculpturing consists of papillae and micrasters. Papillae and micrasters as in *C. clevelandi*, but micrasters of *thick* type; nonasteroid (1–5 arms); size 4× 4μm, density 7600/mm².

Genus (23) **Subulitermes** Holmgren

Of this moderate-sized, widespread genus, 7 species were available.

71. *Subulitermes baileyi* (Emerson) (figure 6 D–F). (Snyder 1949, p. 339.) South America: Kartabo (Guyana). Wings brown, anterior veins darker; without scale 6×2 mm. A few hairs (length 30–40 μm, density 500/mm) on distal half of wing and on margins; almost absent elsewhere. Micro-sculpturing consists of papillae and micrasters.

Papillae: Pointed, thorny; 3–4 rows on the anterior margin (size 4×3 μm, density 5100/mm²), 1–2 rows of smaller ones on the posterior.

Micrasters: All over; thick, asteroid (5–8 arms); size 6–8 μm×6–8 μm, density 9100/mm².

72. *Subulitermes greavesi* (Hill). (Snyder 1949, p. 339.) Australia: Gadgarra (North Queensland). Wings (8×2 mm), hairs and micro-sculpturing generally as in *S. baileyi*, with small differences of density, etc.; micrasters density 7600/mm².

73. *Subulitermes kirbyi* (Snyder) (figure 6 G–I; and plate 3). (Snyder 1949, p. 340.) Central America: Barro Colorado Island (Canal Zone, Panama). Wings without scale 6.5×2 mm), hairs (density 1000/mm²) and micro-sculpturing (with papillae and micrasters) generally as in *S. baileyi*. Micrasters thick and multi-armed (5–8), but shapes are mostly irregular and nonasteroid (only a few are asteroid); density 8400–8800/mm².

74. *Subulitermes longinotus* Emerson. (?MS name) (Listed in Mathur & Thapa 1962, p. 99.) West Indies. St. Joseph (Trinidad). Wings (without scale 6×2 mm), hairs (density 1000/mm²) and micro-sculpturing generally as in *S. baileyi*. Micraster density 8100/mm².

75. *Subulitermes microcosma* (Silvestri) (Snyder 1949, p. 340.) South America: Cuyoba (Motto Grosso, Brazil). Wings without scale 6.5×2 mm) as in *S. baileyi*, but hairs present all over (length 32–40 μm, density 500/mm²). Papillae as in *S. baileyi*. Micrasters all over, but *thin;* nonasteroid (1–5 arms); size 4–6 μm× 4–6 μm, density 6600/mm².

76. *Subulitermes parvellus* (Silvestri) (figure 6 J–L). (Snyder 1949, p. 341.) South America: Kartabo (Guyana). Wings (without scale 6×1.5 mm) yellowish, anterior veins darker. Hairs on distal half and on margins; length 30–44 μm, density 1000/mm². Papillae as in *S. baileyi*. Micrasters thin, nonasteroid (1–5 arms): size 4–6 μm×2–6 μm; density 6000–7100/mm².

77. *Subulitermes snyderi* (Emerson). (Snyder 1949, p. 342.) South America: Kartabo (Guyana). Wings (without scale 6×1.5 mm) as in *S. baileyi*, but with hairs (length 48–60μm, density 1000–1500/mm²) all over wing and denser. Papillae as in *S. baileyi* Micrasters all over; thin, nonasteroid (4–6 arms); size 4–6 μm×4–6 μm, density 8600–9100/mm².

Genus (24) **Afrosubulitermes** Emerson

Of this small Ethiopian genus, a single species was available.

78. *Afrosubulitermes congoensis* Emerson (figure 6 M, N; and plate 3). (Emerson 1960, *Am. Mus. Novitat.*, New York, No. 1987 p. 9.) West Africa: Adipodoume near Abidjan (Ivory Coast). Wings small (without scale 4.5× 1 mm), colourless, anterior veins pale brown. Hairs: 1–2 rows of long hairs (140–210 μm) on anterior vein and a row all around margin; none on membrane. Micro-sculpturing consists of papillae and simple, 1-armed micrasters.

Papillae: Small, pointed, thorny; 1–2 rows on the front margin of anterior vein; a row on posterior wing margin. Size 3–4 μm×2–3 μm.

Micrasters: Entire wing covered with a peculiar *new type* of slightly curved, pointed, 1-armed micraster with an incurved base. The micrasters are long (17–23 μm×2.5–3 μm) on the distal part of wing (plate 3, figure 11) and short (6×6 μm to 2×3 μm) on the proximal part (plate 3, figure 10). Density 4400/mm². (Cf. nearly similar micrasters in *Mimeutermes giffardi*, vide infra.

Genus (25) **Mimeutermes** Silvestri

Of this small Ethiopian genus, a single species was available.

79. *Mimeutermes giffardi* (Silvestri) (figure 6 O–Q; and plate 1). (Snyder 1949, p. 338.) West Africa: Adipodoume near Abidjan (Ivory Coast). Wings brownish, anterior veins darker; without scale 8×2.5 mm. Hairs: 5–6 rows on the anterior margin and 4-5 on the posterior; a row on all veins, and a few scattered ones on rest of the membrane. Mirco-sculpturing consists of papillae and two types of micrasters (including a peculiar *new* pointed type).

Papillae: Pointed, thorny; 3–4 rows on the anterior margin, 2–3 on the posterior. Size 6–8 μm×4 μm; density 7100/mm².

Micrasters: Two types of nonasteroid ones present all over: (a) the small, standard ones (1–5 arms); are few and scattered. (b) A long, peculiar, 1-armed type with a long, thick, pointed, slightly curved arm and a tripod-like base; size 14–16 μm×1.5—2 μm; are numerous all over, density 6100/mm². (The second type of micraster resembles the somewhat similar ones in *Afrosubulitermes congoensis*, vide supra).

Discussion

Types of Structures

Hairs (not strictly a part of micro-sculpturing) are generally present on the margins, veins and membrane of wings sometimes in considerable abundance (densities 1000–5100/mm²), at others fewer, and in a few cases almost absent. Hair length ranges from c. 35–90 μm (sometimes much longer, 140–210 μm, *Afrosubulitermes)*, the marginal hairs being generally longer than the rest.

Micro-sculpturing in the Nasutitermitinae consists of three types of structures, viz. papillae, pimpules and micrasters, which are characterised as follows:

Papillae: They are always present in the Nasutitermitinae (and indeed constitute a universal feature of the wings of the order Isoptera, where they were first described by Roonwal & Rathore 1978). They are always directed distally and are localised in distribution, being confined, in one to several rows, to the anterior and posterior wing margins in densities from 5000–9100/mm². Their shape is most often pointed and thorny, but in a few cases (*Syntermes* and *Rotunditermes*) they are mostly nipple-shaped, forming a *new type*. Sizes vary from small to large (3×1.5 μm to 8–10×6–8 μm). Those on the anterior margin are generally larger than those on the posterior, but in a few cases the reverse occurs (e. g., *Rotunditermes rotundiceps*, *Nasutitermes brunneus*). Usually papillae are present simultaneously with either pimpules or micrasters or both, but in some species papillae alone occur (*Syntermes territus* and *Labiotermes labralis boreus)*.

Pimpules: They are minute (usually 1–2 μm×1–2 μm; rarely larger, 3–7 μm ×2–4 μm, as in *Hospitalitermes)*, non-directional, glassy. refractile, colourless and rounded (rarely slightly pointed, as in *Tumulitermes*) bodies which are scattered all over the wing, sometimes in considerable density (3000–7600/mm²). (Pimpules were first described by Roonwal & Rathore 1978, in the Kalotermitidae and Hodotermitidae, and are a mark of primitiveness.) In the Nasutitermitinae they occur in the primitive genera (*Syntermes*, *Procornitermes*, *Cornitermes* and *Rhynchotermes*, where micrasters are absent), but occasionally occur along with micrasters *(Hospitalitermes*, *Tumulitermes*, *Armitermes)*. Sometimes, in the same genus, they are present in some species and absent in others (*Syntermes*, *Tumulitermes*).

Micrasters: They are small (2 μm × 2 μm to 6–8 μm × 6–8 μm; rarely larger, 14–23 μm × 1.5–3 μm, as in *Afrosubulitermes* and *Mimeutermes*), non-directional bodies† with various shapes from rod-like (1-armed) to 8-armed asteroids, the more common shapes being I, V, Y, T, K, H, + and*. In some species they are thin and stringy, in others thick and glassy. When present, they occur densely all over the wing (4400-10100/mm²) and are arranged in curves and circles, often with a central piece (see plates 2 and 3).

Micrasters are absent in the primitive genera *(Syntermes, Procornitermes, Cornitermes* and *Rhynchotermes)*, and just begin to appear, as simple, 2- to 4-armed nonasteroid structures in *Hospitalitermes* (table 1). Both asteroid and nonasteroid shapes may be present, together or alone. In the same genus, some species have thick micrasters, others thin; and further, micrasters may be either present or absent *(Labiotermes, Armitermes)*. On the whole, the presence of micrasters, especially of the more elaborate asteroid type, is a mark of higher evolution.

A *new type* of nonasteroid, 1-armed micraster is described in two genera: *Afrosubulitermes* and *Mimeutermes*. These micrasters are slightly curved, rather long (14–23 μm), hair-like and pointed, with a broad base (1.5–3 μm). In *Afrosubulitermes congoensis* they are gently curved and the base is incurved; further, they are long in the distal half of the wing and short (2–6 μm) in the proximal half. In *Mimeutermes giffardi* also they are gently curved, but the base is tripod-like; and, in addition, there occurs here the standard type of micrasters (nonasteroid, with 1–5 arms) also. [The new type recalls the somewhat similar but much small micrasters (3–6 μm × 1.5–3 μm) in two species of the Rhinotermitidae, viz. *Coptotermes michaelseni* and *C. testaceus*, vide Roonwal, Verma & Thakur 1979b, pp 345–347 and 352.]

Evolutionary Trends (table 1)

The Nasutitermitinae is a large and complicated subfamily where it is difficult to unravel phylogenetic order. The generic phylogeny reveals several trends such as conservation, and regressive, parallel and convergent evolution, etc., and it is not possible to arrange the genera in a single linear series. Starting with the most primitive genus, *Syntermes*, we have arranged the genera studied by us into the following groups and subgroups, largely as adopted in Sen-Sarma's (1968) phytogenetic review (on the basis mainly of the imago-worker mandibles); the probable evolution of wing micro-sculpturing in the Nasutitermitinae is then viewed against this background:

(A) Most Primitive Genus: *Syntermes*

(B) Procornitermes Group:

(i) Primitive Genera Subgroup: *Procornitermes, Cornitermes, Rhynchotermes.*

(ii) Hospitalitermes Subgroup: *Hospitalitermes, Lacessititermes, Thailanditermes, Bulbitermes.*

(iii) Constrictotermes Subgroup: *Constrictotermes, Tenuirostritermes, Velocitermes, Diversitermes.*

† They were first described in detail, in the Amitermitinae and Termitinae, by Roonwal, Verma and Rathore, 1974, who grouped them into two main categories, viz. nonasteroids (1–5 arms) and asteroids (5–8 arms). These categories are broadly followed here. Occasionally, though multi-armed (5–8), they may have irregular, nonasteroid shapes in some Nasutitermitinae.

Table 1 *Summary of wing micro-sculpturing in some Nasutitermitinae (Isoptera)*

Genera	Papillae		Pimpules	Micrasters		Hairs (on wing-membrane)	Remarks
	Nipple-like	Pointed & thorny		Non-asteroid	Asteroid		
1	2	3	4	5	6	7	8
1. *Syntermes*	+ (mostly)	+ (a few)	±	—	—	+	Hairs dense. Pimpules present or absent
2. *Procornitermes*	—	+	+	—	—	+	Hairs dense
3. *Cornitermes*	—	+	+	—	—	+	Hairs moderately dense
4. *Rhynchotermes*	—	+	+	—	—	±	Hairs present in some, absent in others
5. *Hospitalitermes*	—	+	+	+	—	+	Hairs moderately dense
6. *Lacessititermes*	—	+	—	+	+	+	Hairs dense
7. *Thailanditermes*	—	+	—	+	+	+	Hairs dense
8. *Bulbitermes*	—	+	—	+	+	+	Hairs dense
9. *Constrictotermes*	—	+	—	+	+	+	Hairs few
10. *Tenuirostritermes*	—	+	—	+	—	+	Hairs dense
11. *Velocitermes*	—	+	—	—	+	+	Hairs dense
12. *Diversitermes*	—	+	—	±	+	+	Hairs dense
13. *Trinervitermes*	—	+	—	+	—	+	Hairs dense
14. *Tumulitermes*	—	+	±	+	—	+	Hairs few to many. Pimpules present in some species, absent in most
15. *Rotunditermes*	+ (mostly)	+ (some)	—	+	—	+	Hairs dense
16. *Nasutitermes*	—	+	—	+	+	+	Hair density moderate to high
17. *Havilanditermes*	—	+	—	+	+	+	Hairs dense

18.	*Labiotermes*	—	+	—	±	—	+	Hairs dense. Micrasters simple, present or absent
19.	*Armitermes*	—	+	—	±	—	+	Hair density moderate to very high Micrasters simple, present or absent
20.	*Grallatotermes*	—	+	—	+	+	+	Hair density low to high
21.	*Occasitermes*	—	+	—	+	—	+	Hairs especially on margins
22.	*Convexitermes*	—	+	—	+	—	+	Hairs dense
23.	*Subulitermes*	—	+	—	+	+	+	Hairs all over wing or localised (distal part); density low to high
24.	*Afrosubulitermes*	—	+	—	+	—	+	Hairs localised (on margins and veins). Micraster of a new type (1-armed, pointed)
25.	*Mimeutermes*	—	+	—	+	—	+	Hairs localised. Micrasters of 2 types (standard, nonasteroid, 1-5 arms; and larger, pointed, 1-armed, nearly as in *Afrosubulitermes*)

+, present; —absent; ± present or absent

(iv) Nasutitermes Subgroup: *Trinervitermes, Tumulitermes, Rotunditermes, Nasutitermes, Havilanditermes.*

(C) *Paracornitermes Group:*

(i) Labiotermes-Armitermes Subgroup: *Labiotermes, Armitermes, Grallatotermes Occasitermes, Convexitermes.*

(ii) Curvitermes-Subulitermes Subgroup: *Subulitermes, Afrosubulitermes, Mimeutermes.*

The primitive genera *(Syntermes, Procornitermes, Cornitermes, Rhynchotermes)* are characterised by the presence of pimpules and the absence of micrasters, both features being marks of primitiveness*. In a few others, pimpules appear sporadically, either with or without micrasters *(Hospitalitermes, Tumulitermes, Armitermes)*. In the Procornitermes Group, micrasters first appear in the relatively primitive genus *Hospitalitermes* (micrasters simple, nonasteroid) and then continue thereafter. In the Paracornitermes Group, they first appear as simple, nonasteroid structures in the relatively primitive genera *Labiotermes* and *Armitermes*, and continue thereafter. The more evolved (asteroid) type of micrasters are found in the higher genera, either with or without the simple ones.

Thus, on the whole, the evolution of micro-sculpturing follows the general phylogenetic trends as established on the basis of other characters. Parallel evolution is a special feature of this trend, and it is not possible, to discern a sole linear evolutionary arrangement.

Systematic significance

Although in the higher systematic categories, e.g. genera, general evolutionary trends are clearly seen, differences in micro-sculpturing which are of taxonomic value are best evident at the lower levels (species and subspecies) in such features as the type, shape, sizes and densities of structures like hairs, papillae, pimpules and micrasters. A few examples will suffice. Thus, pimpules are present in *Syntermes molestus* but absent in *S. territus;* again they are present in *Tumulitermes hastalis* but absent in other species of the genus. Hairs densely cover the wings in *Rhynchotermes perarmatus* but are absent in *R. nasutissimus*. Micrasters are present in *Labiotermes brevilabius* but absent in *L. labralis boreus;* again, they are present in *Armitermes euamignathus* and *A. neotenicus* but absent in *A. chargesi, A. holmgreni* and *A. parvidens*.

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* In the primitive families Mastotermitidae and Kalotermitidae pimpules are present and micrasters absent (Roonwal & Rathore 1978; Roonwal, Verma & Thakur 1979a)

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