

Evolution and Systematic Significance of Wing Micro-sculpturing in Termites (Isoptera)

IX. Subfamily Termitinae of Family Termitidae

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(1) Of the Termitinae, 17 genera and 37 species from many parts of the world were studied: *Allognathotermes*, *Crenetermes*, *Megagnathotermes*, *Cubitermes*, *Lepidotermes*, *Noditermes*, *Orthotermes*, *Tuberculitermes*, *Angulitermes*, *Orthognathotermes*, *Crepititermes*, *Termes*, *Cavitermes*, *Promirotermes*, *Protocapritermes*, *Dicuspidermes* and *Pericapritermes*.

(2) Micro-sculpturing on both wing surfaces consists of a dense covering of four principal types of structures, viz., small, pointed, spiny papillae (all directed distally and found universally on the anterior and posterior wing margins), and the nondirectional micrasters, microsetae and thin rods of which only one is present in a species, most commonly the micrasters. Microsetae are present in *Tuberculitermes*, thin rods in *Megagnathotermes*, and micrasters in the remaining genera. Micrasters may be of either the nonasteroid (1-5 arms) or asteroid (5-8 arms) type; densities vary as 3510-11595/mm² and sizes as about 4-9 $\mu\text{m} \times 2-8 \mu\text{m}$.

(3) The evolutionary trends and the systematic significance of these structures are discussed. Micrasters reach their maximum development in the Termitinae. Micro-sculpturing is of considerable assistance in discriminating between the lower taxa (genera and species) but less so for the higher taxa (families and subfamilies).

Key Words: Termites, Wings, Micro-sculpturing, Isoptera, Termitidae, Termitinae

Introduction

In a series of recent studies (Roonwal et al. 1967-1980, vide References at the end) the occurrence of a dense covering of a variety of microscopic structures on the wing surfaces of several families and genera of

termites has been established. The present part deals with the large and widespread subfamily Termitinae of the family Termitidae. Apart from thorny papillae, micro-sculpturing here consists most usually of

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micrasters and occasionally of microsetae and thin rods. Their evolution and systematic significance are discussed.

We have followed the simpler subfamily classification of Snyder (1949) in preference to that of Sands (1972). For older species synonymies and taxonomic references are according to Snyder's world catalogue (1949); for the later species, the first reference and recent revisions are indicated.

Material and Methods

Winged imagoes from many parts of the world were examined, e.g., Africa, South and Southeast Asia, Central and South America, the West Indies and Australia. A total of 17 genera and 37 species, as follows, were available:— *Allognathotermes* (1 sp.), *Crenetermes* (1 sp.), *Megagnathotermes* (1 sp.), *Cubitermes* (1 sp.), *Lepidotermes* (1 sp.), *Noditermes* (3 spp.), *Orthotermes* (1 sp.), *Tuberculitermes* (1 sp.), *Angulitermes* (3 spp.), *Orthognathotermes* (2 spp.), *Crepiditermes* (1 sp.), *Termes* (9 spp.), *Cavitermes* (2 spp.), *Promirotermes* (3 spp.), *Protocapritermes* (1 sp.), *Dicuspiditermes* (3 spp.) and *Pericapritermes* (3 spp.).

The techniques used were as in the previous parts. Densities of micro-structures refer to the middle portion of wing on the dorsal surface.

Results

The various genera and species of the subfamily Termitinae are now discussed in some detail.

Genus (1) *Allognathotermes* Sjöstedt

This is a small Ethiopian genus of which a single species was available.

1. *Allognathotermes hypogaeus* Silvestri 1914 (figure 1 A) (Snyder 1949, p. 149)

Imagoes from West Africa: Adipodoume near Abidjan, Ivory Coast

Wings (without scale): 14×4 mm; transparent, colourless; two anterior veins dark brown, others paler. Hairs: 3–4 rows of short to long, thick hairs (length 30–80 μm) on anterior margin and front vein, a row on the second vein, and 2 rows of smaller hairs on posterior margin; membrane almost hairless.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 3–4 rows of very small, pointed papillae (1–2 μm × 1–2 μm) on anterior margin and a row of still smaller ones on posterior margin. *Micrasters*: Densely present all over, including veins; both nonasteroid (2–5 arms) and asteroid (5–8 arms) types present about equally; arranged in circles and spirals. Size 4–8 μm × 4–8 μm. Density 9420/mm².

Genus (2) *Crenetermes* Silvestri

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

1. *Crenetermes albotarsalis* (Sjöstedt 1897) (figures 1 B–D) (Snyder 1949, p. 153)
Imagoes from Central Africa: Chincoco, Congo (=Zaire)

Wings (without scale): 12×4 mm; transparent, colourless, veins pale brown. Hairs: 3–5 rows of 50–80 μm long hairs on anterior margin; a row of scattered hairs on posterior margin; membrane almost hairless.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: A row of pointed, spiky papillae (4 μm × 8 μm) on anterior margin and a row of similar but smaller ones on posterior margin. *Micrasters*: Wings, including veins, covered all over with micrasters arranged densely in circles and spirals; both asteroid (5–7 arms) and nonasteroid (1–4 arms) types

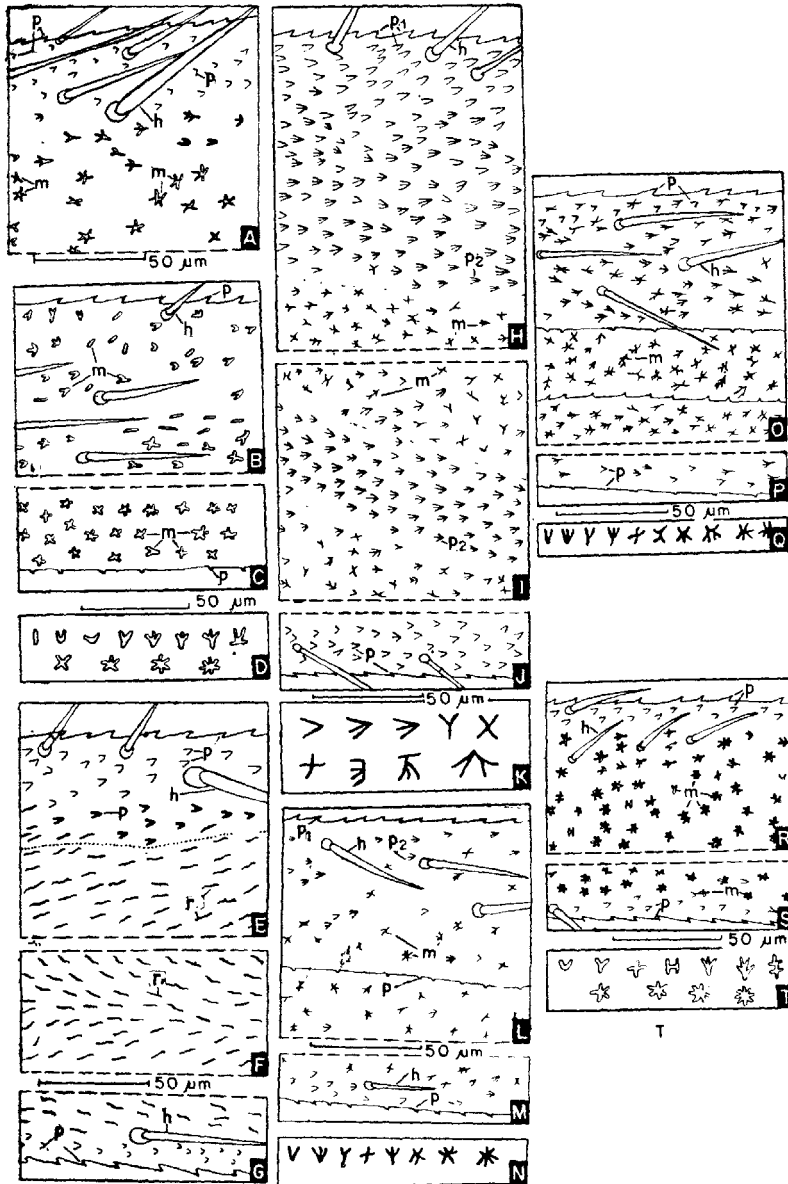


Figure 1 Wing micro-sculpturing in some Termitinae. Views of dorsal surface (the ventral surface is similar). A: *Allognathotermes hypogaeus*, forewing. Anterior margin; B-D: *Crenetermes albotarsalis*, hindwing. B, anterior margin; C, middle; D, micrasters enlarged and rearranged. E-G: *Megagnathotermes* sp., forewing. F, middle (note the thin, sinuous rods instead of micrasters). G, posterior margin. H-K: *Cubitermes breviceps*, forewing. H, anterior margin. I, middle. J, posterior margin. K, micrasters enlarged and rearranged. L-N: *Lepidotermes simplex*, forewing. L, anterior margin. M, posterior margin. N, micrasters enlarged and rearranged. O-Q: *Noditermes aburiensis*, forewing. O, anterior margin. P, posterior margin. Q, micrasters enlarged and rearranged. R-T: *Orthotermes mansuetus*, forewing. R, anterior margin. S, posterior margin. T, micrasters enlarged and rearranged.

h, hairs; m, micrasters; p, papillae (p1, simple type; p2, arrowhead type); r, thin rods.

present about equally. Size 4–6 μm \times 4–6 μm . Density 10870/mm².

Genus (3) *Megagnathotermes* Silvestri

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

1. *Megagnathotermes* sp. (figures 1 E–G)
Imagoes from Africa: Akisi near Ibba, Zandu District, Sudan

Wings (without scale): 17 \times 4.5 mm; transparent, colourless, veins dark brown. Hairs: 3–4 rows of 50–65 μm long hairs on anterior margin and a row on the distal half of posterior margin; distal parts of membrane having scattered hairs, rest hairless.

Wing micro-sculpturing: Consists of papillae and thin rods. *Papillae*: 3–4 rows of pointed papillae (4–5 μm \times 5–6 μm) on anterior margin, and below this, 2–3 rows of similar but thicker ones; 2–3 rows of smaller, pointed papillae on posterior margin. *Rods*: Wings covered densely with thin, sinuous rods (length 12–16 μm , density 8700/mm²) lying subhorizontally to obliquely. (They recall the cuticular rods of some Macrotermitinae, e.g., *Odontotermes*, etc., vide Roonwal & Chhotani 1967; and Roonwal et al. 1980, but the latter lie subvertically).

Genus (4) *Cubitermes* Wasmann

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

1. *Cubitermes breviceps* (Sjöstedt 1913) (figures 1 H–K) (Snyder 1949, p. 157)
Imagoes from East Africa; Iringa, Tanganyika (now Tanzania)

Wings (without scale): 14 \times 3.5 mm; transparent, colourless, veins brown. Hairs: 4–5 rows of 80–100 μm long hairs on front vein, a row on second vein, and 1–2 rows on

posterior margin; membrane almost hairless.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: Of two types: (i) Simple, thorny, pointed ones (*p1*): 6–7 rows on anterior margin (size 4–6 μm \times 3–4 μm), and 3–4 rows of similar but smaller ones on posterior margin. (ii) Like arrowheads, often with a central arm (*p2*), with sizes as above; several rows on posterior half of front vein and on other veins (sometimes mixed with micrasters). *Micrasters*: Small, thin ones all over except on veins (where arrowhead-type papillae are present), arranged in circles and spirals. All nonasteroid $\frac{2}{3}$ (2–5 arms) and of unusual shapes. Size 4–6 μm \times 4–6 μm . Density 8700/mm².

Genus (5) *Lepidotermes* Sjöstedt

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

1. *Lepidotermes simplex* (Holmgren 1913) (figures 1 L–N) (Snyder 1949, p. 166)
Imagoes from Africa: Pietermaritzburg, Natal, South Africa

Wings (without scale): 9 \times 2 mm; transparent, colourless, veins brown. Hairs: 2–3 rows of stiff hairs, 80–100 μm long, on front vein; a row of scattered ones on second vein; 1–2 rows of small hairs on posterior margin; and a few scattered ones on membrane.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: A row of small, pointed papillae (2–4 μm \times 3–5 μm) on anterior margin of wing and on posterior margin of front vein; also a row of similar but smaller ones on posterior wing margin. *Micrasters*: Thin micrasters all over, including veins; both asteroid (5–7 arms) and non-asteroid (2–5 arms) types present, mostly the latter. Size 4–6 μm \times 6–8 μm . Density 10870/mm².

Genus (6) *Noditermes* Sjöstedt

This is a small Ethiopian genus of which three species were available.

1. *Noditermes aburiensis* (Sjöstedt 1926) (figures 1 O-Q) (Snyder 1949, p. 169) Imagoes from West Africa: Aburi, "Gold Coast" (=Ghana)

Wings: Colourless, transparent, veins brown to pale brown. Hairs: 2-3 rows of 55-60 μm long hairs on anterior margin; rest of wing hairless.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 2-3 rows of fine, pale, pointed papillae (mixed with micrasters) on anterior margin (size 4-6 μm \times 4-8 μm), on hind margin of front vein and on front margin of second vein; also a row of minute, pointed ones on posterior margin. *Micrasters*: Thin micrasters all over. Both nonasteroid (2-5 arms) and asteroid (5-7 arms) types present, mostly the former. Size 4-6 μm \times 6-8 μm . Density 8700/mm².

2. *Noditermes cristifrons* (Wasmann 1911) (Snyder 1949, p. 170) Imagoes from West Africa: Bipindi, Cameroun
3. *Noditermes lamanianus* (Sjöstedt 1905) (Snyder 1949, p. 170) Imagoes from Central Africa: Mukimbungu [on R. Congo between Boma and Kinsasha], Congo (=Zaire)

In both the above species, wing micro-sculpturing consists of papillae and micrasters, nearly resembling *N. aburiensis* above.

Genus (7) *Orthotermes* Silvestri

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

1. *Orthotermes mansuetus* (Sjöstedt 1911) (figures 1R-T) (Snyder 1949, p. 173)

Imagoes from Central Africa: Mukimbungu [on R. Congo between Boma and Kinsasha] Congo (=Zaire)

Wings (without scale): 8 \times 1.5 mm; transparent, colourless, veins brown. Hairs: 2-4 rather dense rows of hairs (length 30-60 μm) on anterior margin and front vein, a row on second vein, and 1-2 rows on posterior margin.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 1-2 rows of pointed papillae (3-5 μm \times 2-4 μm) on anterior margin and similar rows of smaller ones on posterior margin. *Micrasters*: Membrane densely covered with thick, brown, hyaline micrasters; both nonasteroid (2-4 arms) and asteroid (5-8 arms) types present, mostly the latter. Size 6-8 μm \times 6-8 μm . Density 10870/mm².

Genus (8) *Tuberculitermes* Holmgren

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

1. *Tuberculitermes bycanistes* (Sjöstedt 1905) (figures 2A-C) (Snyder 1949, p. 174) Imagoes from Africa: Gell River Post, 70 miles from Bahr-el-Gabel, Sudan

Wings (without scale): 8 \times 2.5 mm; transparent, colourless, veins brown. Hairs: 4-5 dense rows of hairs (length 50-60 μm) on front vein, a row on second vein, and 2-3 rows on posterior margin especially in distal region.

Wing micro-sculpturing: Consists of papillae and microsetae. *Papillae*: 5-7 rows of small, pointed papillae (4-6 μm \times 3-4 μm) on anterior margin and 1-3 rows of similar but smaller ones on posterior margin. *Microsetae*: Various directed, thin, setae-like structures, present all over membrane. Length 8-16 μm , longer in middle of wing than elsewhere. Density 5800/mm².

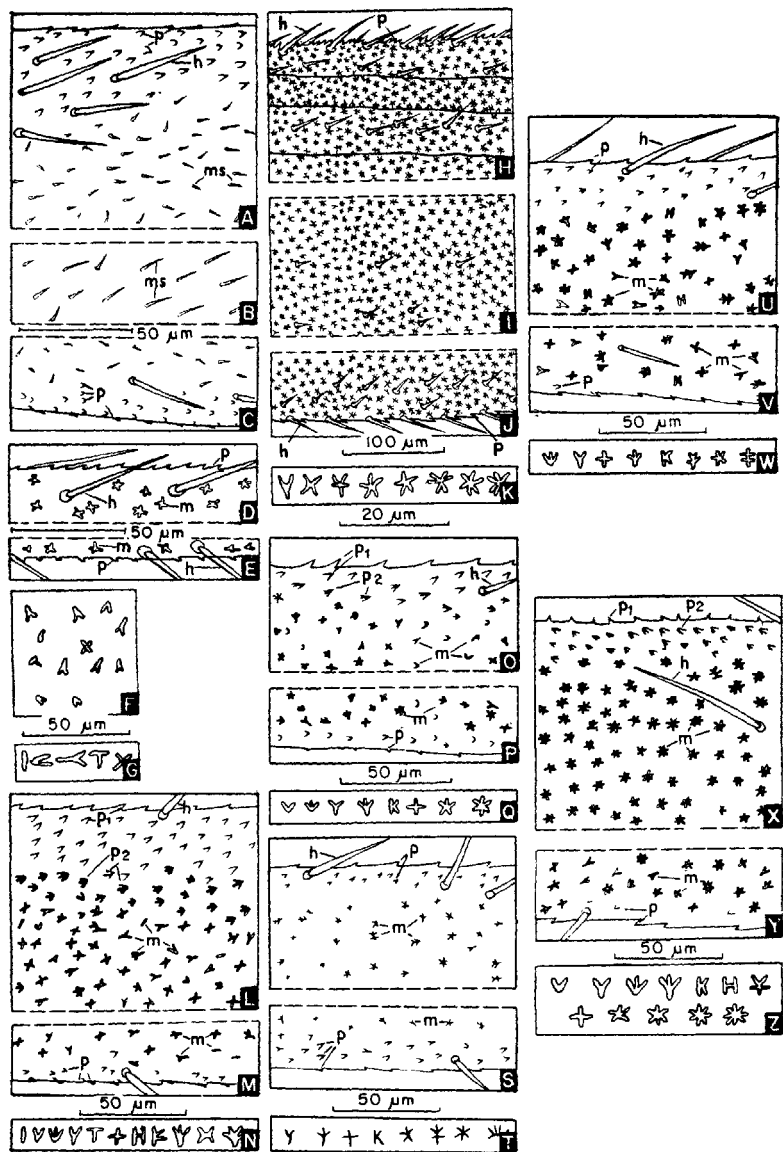


Figure 2 Wing micro-sculpturing in some Termitinae. Views of dorsal surface (the ventral surface is similar). *A-C*: *Tuberculitermes bycanistes*, forewing. *A*, anterior margin. *B*, middle (note the microsetae instead of micrasters) *C*, posterior margin. *D-E*: *Angulitermes akhorisainensis*, forewing. *D*, anterior margin. *E*, posterior margin. *F-G*: *A. dehraensis*, hindwing. *F*, middle. *G*, micrasters enlarged and rearranged. *H-K*: *A. jodhpurensis*, forewing. *H*, anterior margin. *I*, middle. *J*, posterior margin. *K*, micrasters enlarged and rearranged. *L-N*: *Orthognathotermes aduncus*, forewing. *L*, anterior margin. *M*, posterior margin. *N*, micrasters enlarged and rearranged. *O-Q*: *Crepitiitermes verruculosus*, forewing. *O*, anterior margin, *P*, posterior margin. *Q*, micrasters enlarged and rearranged. *R-T*: *Termes cheeli*, forewing. *R*, anterior margin. *S*, posterior margin. *T*, micrasters enlarged and rearranged. *U-W*: *T. fatalis*, forewing. *U*, anterior margin. *V*, posterior margin. *W*, micrasters enlarged and rearranged. *X-Z*: *T. fur*, forewing. *X*, anterior margin. *Y*, posterior margin. *Z*, micrasters enlarged and rearranged.

h, hairs, m, micrasters; ms, microsetae; p, papillae (p1, simple type; p2, arrowhead type).

Genus (9) *Angulitermes* Sjöstedt

This is a small Oriental and Ethiopian genus of which three species were available.

1. *Angulitermes akhorisainensis* Chatterjee & Thakur 1964 (figures 2D, E) (Chatterjee and Thakur 1964, *J. Bombay nat. Hist. Soc.*, **61**, p. 348) Imagoes from South Asia (India): Tehri Garhwal, Uttar Pradesh

Wings pale yellow, transparent. Hairs: 3-4 rows of hairs (length 60-80 μm) on anterior margin and first vein, 1 row on the second vein and 1-3 rows of smaller ones on posterior margin; a few hairs on the membrane.

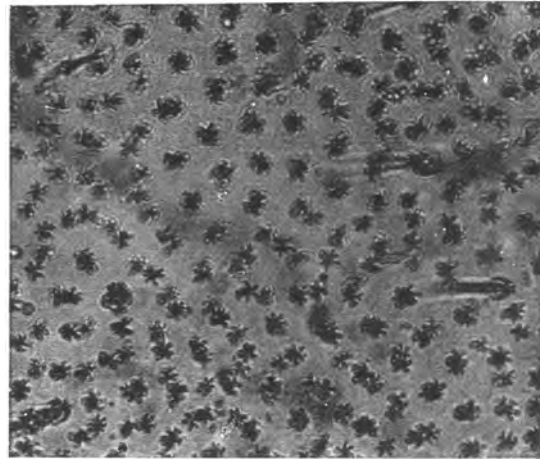
Wing micro-sculpturing: Consists of papillae and micrasters: *Papillae*: A row of pointed ones (4 $\mu\text{m} \times 5 \mu\text{m}$) on anterior margin and a row of similar but smaller ones on posterior margin. *Micrasters*: Densely cover the membrane. Both non-asteroid (5-6 arms) and asteroid (6-8 arms) types present, mostly the latter. Size 5-9 $\mu\text{m} \times 5-8 \mu\text{m}$. Density 5535-5805/mm². (Also see Roonwal et al. 1974).

2. *Angulitermes dehraensis* (Gardner 1945) (figures 2F, G) (Snyder 1949, p. 179, *Termes dehraensis*.) Imagoes from India

Papillae probably present as in *A. akhorisainensis* above, but not examined. Nonasteroid micrasters (1-4 arms) present all over; size 5-8 $\mu\text{m} \times 3-8 \mu\text{m}$; density 3510/mm². (Also see Roonwal et al. 1974).

3. *Angulitermes jodhpurensis* Roonwal & Verma 1976 (figures 2H-K and 3) (Roonwal and Verma, *Entomol. mon. Mag., Lond.* **112**, p. 5) Imagoes from South Asia (India): Jodhpur, Rajasthan

Wings (with scale): 8 \times 1.5 mm; colourless, transparent; veins brown, with wide strips on either side of them pale brown. Hairs: A row of 60-90 μm long hairs on the two anterior veins; 1-3 rows of smaller hairs



50 μm

Figure 3 *Angulitermes jodhpurensis*. Photomicrograph of dorsal surface of forewing, to show micrasters.

(30 μm long) on posterior margin; and a few small, scattered ones on membrane.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: A row of brown, closely packed, very small, pointed papillae on anterior margin (1 $\mu\text{m} \times 0.5 \mu\text{m}$) and a row of still smaller, paler and scattered ones on posterior margin. *Micrasters*: Nonasteroid (2-6 arms), and asteroid (5-7 arms) types present all over, mostly the latter. Size 5-8 $\mu\text{m} \times 3-8 \mu\text{m}$. Density 7315-8100/mm².

Genus (10) *Orthognathotermes* Holmgren

Of this small Neotropical genus, two species were available.

1. *Orthognathotermes aduncus* Emerson 1949 (figures 2L-N) (Snyder 1949, p. 176) Imagoes from South America: Kartabo, Guyana

Wings (without scale): 11 \times 3.5 mm; transparent, colourless, veins brown. Hairs: 3-4

rows of hairs (60–80 μm long) on anterior vein, a row on second vein and 2–3 rows on posterior margin; several scattered hairs all over membrane.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: Of two types: (i) Simple, pointed papillae (4–6 μm \times 4 μm): 3–5 rows on anterior margin and 2 rows of similar but smaller ones on posterior margin; (ii) Arrowhead type (thicker and slightly larger): 2–3 rows on anterior vein below the simple papillae. *Micrasters*: Thick ones all over. Only the nonasteroid (1–5 arms) type present. Size 6–8 μm \times 2–8 μm . Density 7250/mm².

2. *Orthognathotermes wheeleri* (Snyder 1923) (Snyder 1949, p. 177) Imagoes from Central America: La Jagua Hunting Club, 6 miles SE of Pacora River, Panama

Wings (without scale): 11 \times 4 mm; transparent, colourless, veins brown. Hairs: 3–4 rows on anterior vein (60–80 μm long), a row on second vein and 2–3 rows on posterior margin; also a few scattered ones on membrane in distal region.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: A row of spiny, pointed papillae (6–7 μm \times 4 μm) on anterior margin and a row of similar but smaller ones on posterior margin. *Micrasters*: Thin, brown ones all over; only the nonasteroid (1–5 arms, mostly 3–4) type present. Size 6–8 μm \times 6–8 μm . Density 7250/mm².

Genus (11) *Crepititermes* Emerson

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

1. *Crepititermes verruculosus* (Emerson 1925) (figures 20–Q) (Snyder 1949, p. 177) Imagoes from the West Indies: North Range, Trinidad

Wings (without scale): 6 \times 1.5 mm; transparent, colourless, veins brown. Hairs: A row of stout hairs (40–50 μm long) on anterior and posterior margins; rest of wing hairless.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 3–4 rows of large, pointed, spiny papillae (4–6 μm \times 4 μm) on anterior margin, the front rows of simple type (*p1*) and the rest like arrowheads (*p2*); and 2–3 rows of smaller, simple papillae on posterior margin. *Micrasters*: Thick, brown ones all over. Both non-asteroid (2–5 arms) and asteroid (5–6 arms) types present, mostly the former. Size 4–6 μm \times 4–5 μm . Density 10870/mm².

Genus (12) *Termes* Linnaeus

This is a large, widespread genus of which nine species were available from the Oriental, Ethiopian, Neotropical and Australian regions.

1. *Termes cheeli* (Mjoeberg 1920) (figures 2R–T) (Snyder 1949, p. 179) Imagoes from Australia

Wings (without scale): 7 \times 2 mm; transparent, colourless, veins pale brownish yellow. Hairs: 2–3 rows of 40–50 μm long hairs on front vein, a row on second vein, and a row of smaller ones on posterior margin; a few scattered hairs on distal half of membrane.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 2–3 rows of small, pointed papillae on anterior and posterior margins; size 3–4 μm \times 2–3 μm . *Micrasters*: Membrane covered all over with small, thin micrasters. Mostly nonasteroid (2–5 arms) and a few asteroid (5 arms) types present. Size 4–6 μm \times 3–4 μm . Density 8700/mm².

2. *Termes comis* Haviland 1898 (Snyder

1949, p. 179) Imagoes from South Asia: Singapore

Mirco-sculpturing by means of papillae and micrasters almost as in *T. cheeli*, but micrasters thinner and the asteroid and non-asteroid types equally numerous.

3. *Termes fatalis* Linnaeus 1758 (figures 2U-W) (Snyder 1949, p. 180) Imagoes from South America: Kartabo, Guyana

Wings (without scale): 8×2.5 mm; transparent, colourless, veins pale brown. Hairs: 4-5 rows of hairs (60-80 μ m long) on anterior margin, a row on posterior margin and most veins, and several scattered ones on membrane especially on the distal half.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 4-5 rows of dark brown, pointed, spiny papillae (4-6 μ m \times 3-4 μ m) on anterior half of front vein, and a row of similar but smaller, paler and scattered ones on posterior margin. *Micrasters*: Thick ones present all over. Both asteroid (5-6 arms) and non-asteroid (3-5 arms) types present, mostly latter. The Size 6-8 μ m \times 6-8 μ m. Density 8700/mm².

4. *Termes fur* (Silvestri 1901) (figures 2X-Z) (Snyder 1949, p. 180) Imagoes from South America: Sao Domingo, Matto Grosso, Brazil

Wings (without scale): 10×3 mm; transparent, colourless, veins brown. Hairs: 4-5 rows of numerous hairs (length 40-60 μ m) on anterior vein, a row of scattered ones on second vein and on posterior margin; membrane hairless.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: Of two types: (i) Simple pointed ones: A row on anterior margin (size 4-6 μ m \times 3-4 μ m) and 1-2 rows of similar but smaller ones on posterior margin; (ii) Arrowhead type (with a middle arm in many): 2-3 rows on front

vein below the simpler papillae. *Micrasters*: Thick, brown ones all over, arranged in circles and spirals. Both asteroid (5-8 arms) and nonasteroid (3-5 arms) types present. Size 6-8 μ m \times 6-8 μ m. Density 7250/mm².

5. *Termes hispaniole* (Banks 1918) (Snyder 1949, p. 181) Imagoes from Central America: Galeta Is., Canal Zone, Panama
6. *Termes hospes* (Sjostedt 1900) (Snyder 1949, p. 181) Imagoes from Central Africa: "Region of Stanleyville, Belgian Congo" (= Region of Kisangani, Zaire)
7. *Termes kraepelini* (Silvestri 1909) (Snyder 1949, p. 182) Imagoes from Australia

In the above three species, micro-sculpturing is by means of papillae and micrasters, nearly as in *T. fur* above.

8. *Termes medioculatus* Emerson 1949 (Snyder 1949, p. 183) Imagoes from South America: Kartabo, Guyana

Micro-sculpturing with papillae and micrasters nearly as in *T. fur* above, but nonasteroid micrasters more numerous than asteroid ones.

9. *Termes rostratus* Haviland 1898 (Snyder 1949, p. 186) Imagoes from South-east Asia: Sumatra (Indonesia)

Micro-sculpturing consists of papillae and micrasters. *Papillae*: Of two types: (i) Simple, pointed ones: 1-2 rows on anterior margin and similar but smaller ones on posterior margin. (ii) Arrowhead type: 5-6 rows on anterior margin below the rows of simple ones. *Micrasters*: As in *T. fatalis* above.

Genus (13) *Cavitermes* Emerson

Of this small Neotropical genus, two species were available.

1. *Cavitermes tuberosus* (Emerson 1925) (figures 4A-C) (Snyder 1949, p. 187) Imagoes from the West Indies: Guaico Fores, Trinidad

Wings (without scale): 7×2 mm; transparent, colourless, veins dark brown. Hairs: 4-5 rows of hairs (length 60-80 μ m) on front vein, and a row each on other veins and on posterior margin; several hairs scattered all over membrane especially in distal half.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 1-3 rows of spiny, pointed papillae (4-6 μ m \times 3-4 μ m) on anterior margin and 1-2 rows of smaller ones on posterior margin. *Micrasters*: Thick ones present all over. Both nonasteroid (2-6 arms) and asteroid (5-7 arms) types present, mostly the latter. Size 6-8 μ m \times 6-8 μ m. Density 8700/mm².

2. *Cavitermes* sp. (figures 4D, E) Imagoes from South America: Lassance, Minas Gerais, Brazil. Wings rather hairy especially on anterior vein; hairs 60-80 μ m long.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 1-2 rows of pointed, spiny papillae on anterior margin (size 3-5 μ m \times 3-4 μ m) and a row of similar but longer ones on posterior margin. *Micrasters*: Small, thin ones all over. Both nonasteroid (2-6 arms) and asteroid (5-6 arms) types present, mostly the former. Size 4-6 μ m \times 4-6 μ m; density 7250/mm².

Genus (14) *Promirotermes* Silvestri

Of this small Ethiopian genus, three species were available.

1. *Promirotermes gracilipes* Schmitz 1917 (Snyder 1949, p. 188) Imagoes from Africa: "Stanleyville, Belgian Congo" (=Kisangani, Zaire)

Wing micro-sculpturing: Generally as in *P. holmgreni* below, with papillae and micrasters. Both asteroid and nonasteroid micrasters present, mostly the former; size 4-6 μ \times 4-6 μ m; density 10870/mm².

2. *Promirotermes holmgreni* (Silvestri 1912) (figures 4F-H) (Snyder 1949, p. 188) Imagoes from West Africa: Accra, "Gold Coast" (=Ghana)

Wings (without scale): 9×2.5 mm; transparent, colourless, veins pale brown. Hairs: 3-4 rows on anterior vein (length 60-80 μ m), a scattered row on second and other veins; a few scattered hairs near margins of wing membrane in distal half.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 1-3 rows of small, pointed papillae (4-6 μ m \times 4 μ m) on anterior margin and a row of similar but smaller ones on posterior margin. *Micrasters*: Thin and colourless, present all over. Both nonasteroid (3-4 arms) and asteroid (5-6 arms) types present, mostly the latter. Size 6-8 μ m \times 6-7 μ m. Density 10870/mm².

3. *Promirotermes* sp. Imagoes from East Africa: Close to Kamir River near Nairobi, Kenya

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 2 rows of large, dark brown, pointed, spiny papillae (4-8 μ m \times 4 μ m) on anterior margin and a row of similar but smaller and paler ones on posterior margin. *Micrasters*: Generally as in *P. holmgreni* above, but smaller. Size 4-6 μ m \times 4-6 μ m. Density 10870/mm².

Genus (15) *Protocapritermes* Holmgren

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

1. *Protocapritermes krisiformis* (Froggatt 1897) (figures 4I-K) (Snyder 1949, p. 188) Imagoes from Australia

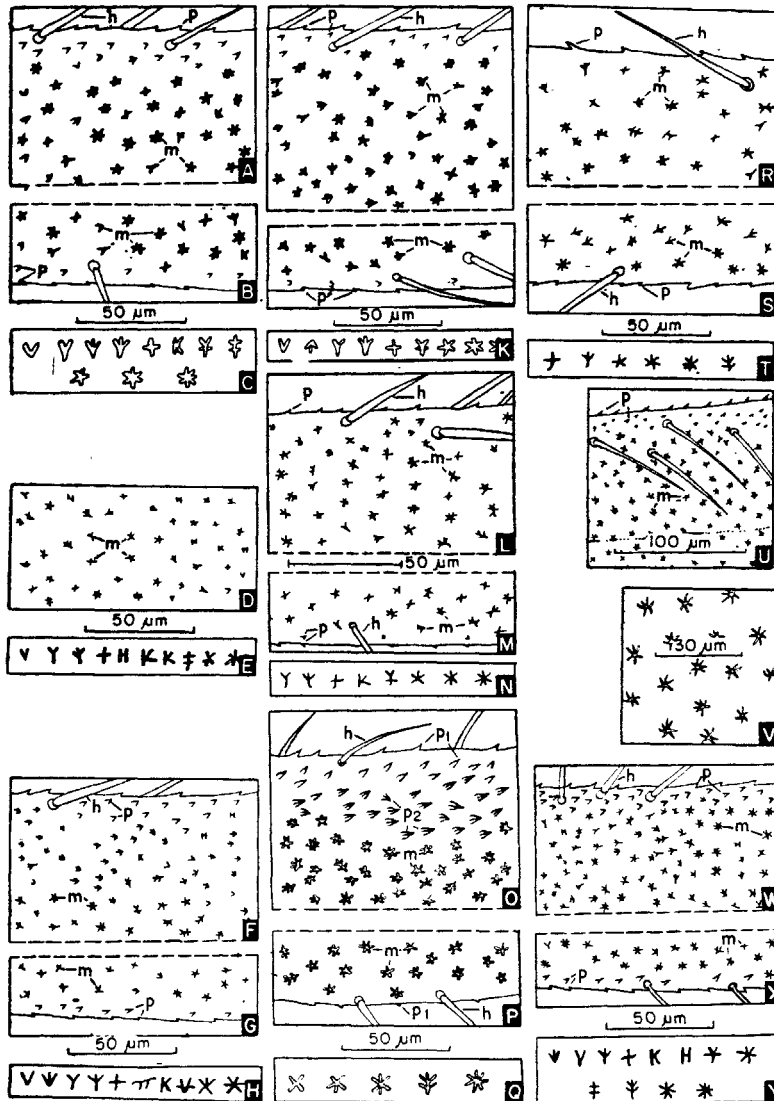


Figure 4 Wing micro-sculpturing in some Termitinae. Views of dorsal surface (the ventral surface is similar). A-C: *Cavitermes tuberosus*, forewing. A, anterior margin. B, posterior margin. C, micrasters enlarged and rearranged. D-E: *Cavitermes* sp., forewing. D, micrasters in middle of wing. E, same, enlarged and rearranged. F-H: *Promirotermes holmgreni*, hindwing. F, anterior margin. G, posterior margin. H, micrasters enlarged and rearranged. I-K: *Protocapritermes krisiformis*, hindwing. I, anterior margin. J, posterior margin. K, micrasters enlarged and rearranged. L-N: *Dicuspiditermes laetus*, forewing. L, anterior margin. M, posterior margin. N, micrasters enlarged and rearranged. O-Q: *D. nemorosus* forewing. O, anterior margin. P, posterior margin. Q, micrasters enlarged and rearranged. R-T: *D. obtusus*, forewing. R, anterior margin. S, posterior margin. T, micrasters enlarged and rearranged. U-V: *Pericapritermes dunensis*, forewing. U, anterior margin. V, micrasters enlarged. W-Y: *P. semarangi*, forewing. W, anterior margin. X, posterior margin. Y, micrasters enlarged and rearranged.

h, hairs; m, micrasters; p, papillae (p1. simple type; p2, arrowhead type).

Wings (without scale): 9×2.5 mm; transparent, colourless, veins brown. Hairs: 4-5 rows on front vein, a row on second and other veins, and 1-2 rows on posterior margin; several also scattered all over membrane especially in distal half.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 2-3 rows of brown, pointed, spiny papillae ($3-4 \mu\text{m} \times 3 \mu\text{m}$) on anterior margin and a row of similar but smaller and colourless ones on posterior margin. *Micrasters*: Thick ones all over, arranged in circles and spirals. Both nonasteroid (2-6 arms) and asteroid (5-7 arms) types present, mostly the latter. Size $4-6 \mu\text{m} \times 4-6 \mu\text{m}$. Density 8700/mm².

Genus (16) *Dicuspiditermes* Krishna

This is a small oriental genus of which three species were available from India, Burma and Borneo.

1. *Dicuspiditermes laetus* (Silvestri 1914) (figures 4L-N) [Sny. *Capritermes garthwaitei* Gardner] (Snyder 1949, p. 195, *Capritermes laetus*; Krishna 1968, p. 290, *D. laetus*) Imagoes from South Asia: Maymyo, Burma

Wings (without scale): 9×2 mm; transparent, colourless, front veins brown. Hairs: 3-4 rows of 50-60 μm long hairs on front vein, a row of smaller ones near posterior margin and a few scattered ones on membrane.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: A row of small, pointed, thorny papillae ($3-4 \mu\text{m} \times 2-3 \mu\text{m}$) on anterior margin and a row of similar but smaller ones on posterior margin. *Micrasters*: Thin, pale ones all over. Both nonasteroid (3-6 arms) and asteroid (5-7 arms) types present, mostly

the latter. Size $6-8 \mu\text{m} \times 6-8 \mu\text{m}$. Density 7300/mm².

2. *Dicuspiditermes nemorosus* (Haviland 1898) (figures 4O-Q) (Snyder 1949, p. 195, *Capritermes nemorosus*) Imagoes from Southeast Asia: Sandakan, north Borneo (Malaysia)

Wings (without scale): 9×2 mm; transparent, membrane pale yellow, veins dark brown. Hairs: 3-4 rows of hairs (45-55 μm long) on front vein and a row of smaller, scattered ones on second vein and near posterior margin; membrane hairless.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: Of two types: (i) 2-3 rows of large, dark brown, pointed, thorny papillae (*p1*) on anterior margin ($6-8 \mu\text{m} \times 3-4 \mu\text{m}$), and a row of similar but smaller and scattered ones on posterior margin. (ii) On front vein, below ordinary papillae, 3-4 rows of arrowhead type (*p2*), of same size. *Micrasters*: Membrane covered densely with thick, brown micrasters arranged in circles and spirals. Mostly asteroid (5-8 arms) and a few nonasteroid (4 arms) types present. Size $6-7 \mu\text{m} \times 6-8 \mu\text{m}$. Density 10600/mm².

3. *Dicuspiditermes obtusus* (Silvestri 1923) (figures 4R-T) (Snyder 1949, p. 192, *Capritermes obtusus*) Imagoes from South Asia (India): Barkuda Is., Chilka Lake, Orissa

Wings (without scale): 9×2 mm; transparent, pale, yellow, veins brown. Hairs: 2-3 rows of thin, 60-80 μm long hairs on front vein, 1-2 rows of smaller ones near posterior margin and a few scattered ones on membrane.

Wing micro-sculpturing: As in *D. laetus* above. *Papillae* $4-6 \mu\text{m} \times 2-3 \mu\text{m}$. *Micrasters* thin; size $4-6 \mu\text{m} \times 4-6 \mu\text{m}$; density 8300/mm².

Genus (17) *Pericapritermes* Silvestri

This is a moderate-sized, widespread genus of which three species were available from Asia and Africa.

1. *Pericapritermes dunensis* (Roonwal & Sen-Sarma 1960) (figures 4U-V) (Roonwal and Sen-Sarma 1960, p. 28, *Capritermes dunensis*; Krishna 1968, p. 294, and Roonwal & Chhotani, 1977, p. 64, *P. dunensis*) Imagoes from South Asia: Bhutan

Wings (without scale): 13 × 3 mm; brownish due to numerous brown micrasters; anterior veins brown, rest colourless. Hairs: 3-4 rows of hairs (length 70-80 μm) on anterior margin and front vein, a row on the next vein and a few on posterior margin and other veins; membrane with a few scattered hairs.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 3-4 rows of pointed, thorny papillae (4-6 μm × 1-2 μm) on anterior margin and a row of minute ones (3-4 μm × 0.5-1 μm) on posterior margin. *Micrasters*: Numerous brown, asteroid micrasters (5-7 arms) present all over. Size 4-5 μm × 5-8 μm. Density 5200-5600/mm². (Micrasters were first recorded by Roonwal and Chhotani, 1977, pp. 65-66: "Wing-membrane brownish, fairly densely covered with numerous 5 to 7-armed micrasters").

2. *Pericapritermes semarangi* (Holmgren 1913) (figures 4W-Y) (Syn. *Capritermes sumatrensis* John.) (Snyder 1949, p. 197, *Capritermes semarangi*; Krishna 1968, p. 294, *P. semarangi*) Imagoes from Southeast Asia: "Buitenzorg" (=Bogor), Java (Indonesia)

Wings (without scale): 7 × 1.5 mm; transparent, colourless, veins brown. Hairs: 1-3 rows of 50-60 μm long hairs on anterior margin, and a row on posterior margin; membrane almost hairless.

Wing micro-sculpturing: Consists of papillae and micrasters. *Papillae*: 4-5 rows of pointed, thorny papillae (6-8 μm × 4-8 μm) on anterior margin and a row of similar but smaller ones on posterior margin. *Micrasters*: Numerous thin, colourless ones all over. Both nonasteroid (3-5 arms) and asteroid (5-8 arms) types present, mostly the latter. Size 6-8 μm × 6-8 μm. Density 11595/mm².

3. *Pericapritermes silvestrianus* (Emerson 1928) (Snyder 1949, p. 199) Imagoes from West Africa: Mesurado, Liberia

Wings and micro-sculpturing generally as in *P. semarangi*. *Papillae* 4-6 μm × 4 μm. *Micrasters* of thin type, mostly nonasteroid and a few asteroid; size 6-8 μm × 6-8 μm; density 8700/mm².

Discussion and Conclusions

Four principal types of micro-structures are encountered in the Termitinae and are present on both upper and lower surfaces of wing membranes in large numbers (micrasters may reach a density of over 11000/mm²). These types are: papillae, micrasters, microsetae and thin rods (table 1). *Papillae* are pointed and spiny (sometimes like arrowheads) and are always directed distally; they are present in *all* species and are generally confined to the anterior and posterior wing margins. The remaining three types are nondirectional, and only one of them (most commonly the micrasters) is present in a species. Microsetae are present in *Tuberculitermes*, and thin, sinuous rods (recalling similar rods in some Macrotermitinae, viz., *Odontotermes*, etc.) in *Megagnathotermes*. In all other genera studied, micrasters are present; they are both of the nonasteroid (1-5 arms) and asteroid (5-8 arms) types (vide Roonwal, Verma & Rathore 1974, for classification of types).

Table 1 Summary of types of wing micro-sculpturing in the subfamily Termitinae (of family Termitidae)

Genera	Papillae (directed distally)			Short, thick, strai- ght rods	Micrasters		Mic- ro- setae	Thin sinu- ous rods (short to long)	Remarks
	Fin- ger sha- ped	Poin- ted and spiny	Arr- ow- head type		Non- aste- roid	Aste- roid-			
1. <i>Allognathotermes</i>	-	+	-	-	+	+	-	-	-
2. <i>Crenetermes</i>	-	+	-	-	+	+	-	-	-
3. <i>Megagnathotermes</i>	-	+	-	-	-	-	-	+	*Recall similar rods in some Macrotermitinae (<i>Odontotermes</i> , etc.)
4. <i>Cubitermes</i>	-	+	+	-	+	-	-	-	Papillae also present on veins. Micrs thin and of unusual shapes
5. <i>Lepidotermes</i>	-	+	-	-	+	+	-	-	Micrs thin
6. <i>Noditermes</i>	-	+	-	-	+	+	-	-	Micrs thin
7. <i>Orthotermes</i>	-	+	-	-	+	+	-	-	Micrs thick
8. <i>Tuberculitermes</i>	-	+	-	-	-	-	+	-	-
9. <i>Angulitermes</i>	-	+	-	-	+	+	-	-	Micrs thick
10. <i>Orthognathotermes</i>	-	+	+	-	+	-	-	-	Micrs thick
11. <i>Crepititermes</i>	-	+	+	-	+	+	-	-	Micrs thick
12. <i>Termes</i>	-	+	+	-	+	+	-	-	Micrs thin or thick
13. <i>Cavitermes</i>	-	+	-	-	+	+	-	-	Micrs think or thick
14. <i>Promirotermes</i>	-	+	-	-	+	+	-	-	Micrs thin
15. <i>Protocapritermes</i>	-	+	-	-	+	+	-	-	Micrs thick
16. <i>Dicuspiditermes</i>	-	+	+	-	+	+	-	-	Micrs thin or thick
17. <i>Pericapritermes</i>	-	+	-	-	+	+	-	-	Micrs thin

- absent; + present
Micrs = Micrasters

Evolutionary Trends

Compared to the Amitermitinae (with the simple, nonasteroid, 2- to 5- armed micrasters in most genera except the highly evolved ones, e.g., *Microcerotermes*), the Tetmitinae are more evolved and possess both nonasteroid and asteroid (5-8 arms) micrasters in most cases. The allied, highly evolved subfamily Macrotermitinae is characterised by the presence of either microsetae, pimpules or rods and by the almost complete absence of micrasters (Roonwal et al. 1980 and unpublished data).

Thus in the Isoptera as a whole, apart from the papillae (which are present univer-

sally), only tubercles and pimpules are present in the primitive families Kalotermitidae and most of the Hodotermitidae. Micrasters first appear in the subfamily Stolotermitinae (of the family Hodotermitidae, vide Roonwal et al. 1979a) and then again in some members of the intermediate family Rhinotermitidae (Roonwal et al. 1979b). They are present in the Amitermitinae mostly in simple forms, and attain their greatest development in the Termitinae. They are present irregularly in the Nasutitermitinae but virtually disappear in the Macrotermitinae where they are replaced by either microsetae or thin, sinuous rods, and occasionally by pimpules.

Systematic Significance

Different genera and species are characterised by the shape, size and disposition of the papillae. Among other micro-structures, some genera have rods or microsetae, while others have micrasters, the latter having their own characteristic shapes, categories and densities in allied species, as for example in *Dicuspidermes*. In *D. laetus* and *D. obtusus* the micrasters are thin, pale and moderately dense (7300–8300/mm²), while in *D. nemorosus* they are thick, brown and very dense (10600/mm²). These differences are even more clearly apparent at a glance in the illustrations than in descriptions, and are especially helpful where other structures

fail to provide clear differentiating characters between allied forms.

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