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EPIDERMAL LEAF CHARACTERS OF THE MALESIAN ICACINACEAE*

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SUMMARY

The cuticular characters of the leaves of all Malesian species belonging to 25 genera of the Icacinaceae and those of *Pennantia* from Australia and New Zealand and some taxa from Continental Asia have been studied and are described in detail. Five stomatal types and nine different hair types are recorded for this part of the family. Haberlandt's interpretation of the slender papilla-like hairs of *Gonocaryum* as hydathodes is challenged. Penetrating asteroscleroids in the cuticular flanges of two *Stemonurus* species are reported for this family for the first time.

A synoptical key to the genera on the basis of cuticular characters only is given. The diagnostic and taxonomic value of the characters used is discussed.

Taxonomic implications of this study are the indication of a close relationship between Phytocreneae and Iodeae (all climbers), the isolated position of the genera *Platea* and *Gonocaryum*, and the impression that *Mappianthus* should be treated as a genus separate from *Iodes*.

The combined characters of indumentum and stomatal type do not show an absolute correlation with the levels of specialization found in wood- and nodal anatomy for this family by Bailey and Howard. The distribution of stomatal types over the genera, however, suggests that the paracytic and anomocytic types are primitive for Icacinaceae and that the cyclocytic and anisocytic types are more derived.

1. INTRODUCTION

The family Icacinaceae includes c. 56 genera with c. 300 species. Their distribution is predominantly tropical. SLEUMER (1971) revised part of the family for Flora Malesiana.

All species of the Malesian Icacinaceae and those of *Pennantia* from Australia and New Zealand were studied for leaf epidermal characters in cuticular preparations. Such a study seemed rewarding because of the great range of type of indumentum recorded for the family by HEINTZELMANN & HOWARD (1948) and because of the suspected range in stomatal types (cf. BAAS in SLEUMER, 1971).

It is hoped that the results of this study will be of some use for the identification of sterile material and of fossil leaf remains belonging to the Icacinaceae. A further aim of this study was to establish whether any relation could be found between leaf epidermal specialization and the specialization of the node and xylem, as suggested by BAILEY & HOWARD (1941).

The anatomical literature has been comprehensively summarized by SOLE-

* This paper reports the results of a post-graduate study by the first author under the supervision of the second. It is dedicated to Prof. Dr. W. K. H. KARSTENS who guided both authors on their initial steps in the field of general plant anatomy.

REDER (1899 & 1908), METCALFE & CHALK (1950), and BAAS in SLEUMER (1971). For the indumentum the paper by Heintzelmann and Howard is an essential starting point for the interpretation of the present study.

2. MATERIALS AND METHODS

For our study one leaf was taken from an herbarium-specimen for each of the 111 species belonging to the 26 genera examined. To gain some impression of variability within a species, 11 specimens of *Apodytes dimidiata* and 6 and 5 specimens of *Iodes cirrhosa* and *Platea latifolia*, respectively, were studied.

From each leaf an area from the middle, including midrib and leaf margin, was taken. All the material was boiled in water. Subsequently it was macerated at 60 °C in a mixture of equal volumes of 20 % hydrogen peroxide and concentrated glacial acetic acid, stained in a solution of Sudan IV in alcohol 70 %, and mounted in glycerin-jelly.

The specimens used are listed at the beginning of each specific description for small genera, after the generic description for the larger genera. Herbarium numbers are abbreviated as by SLEUMER (1969).

3. CHARACTERS USED IN THE DESCRIPTIONS AND THE KEY

3.1. The stomatal complex (*plate I, II* and *III* p.p.).

In the Icacinaceae stomata occur on the abaxial surface; only in *Pyrenacantha repanda* and *Miquelia reticulata* some stomata have been found on and near major and minor veins on the adaxial surface. The stomata are almost always randomly distributed, at least in the areolae. They rarely occur in groups.

For all species the length and width of the stomata were measured with an eye piece micrometer at $\times 1000$ magnification. For each species of the genera *Apodytes*, *Cantleya* and *Citronella* 25 stomata were measured, for the remaining species 10 stomata. Giant or water stomata, present in many species, were not included in these measurements. In the anatomical descriptions the range and average for each species is given.

For *Apodytes dimidiata*, 11 specimens of which were examined, the stomatal index (SALISBURY 1927) was calculated. For that purpose 25 areas of the lamina were examined in each specimen. In *A. dimidiata*, a rather variable species with a wide distribution in Malesia, Continental Asia and Africa, the stomatal indices varied between 7 and 21. Because of the great range in this species it did not seem useful to determine the stomatal indices for the remaining 110 species. Current research on Celastraceae and Winteraceae (JANSEN & BAAS, in the press, and BONGERS, in preparation) also indicates that the stomatal index may be extremely variable within a species. This invalidates claims by authors in the past that the stomatal index is a diagnostic character at the species level.

The terminology of VAN COTTHEM (1971) was used for the various stomatal types. In Malesian Icacinaceae the stomatal complex may be anisocytic,

anomocytic, cyclocytic, helicocytic, paracytic or of an intermediate type. Like van Cotthem we deviate from STACE (1965) in the definition of the cyclocytic type. Stomata with three subsidiary cells of equal size are regarded here as intermediate between anisocytic and cyclocytic. Stomata with subsidiary cells of the same size as the unspecialized cells, but with deviating cuticular characters, are treated as intermediate between anomocytic and cyclocytic. In such intermediate types the cells surrounding the guard cell pairs may have a cuticle which stains more deeply than the unspecialized cells, or have a striated or granular cuticle as contrasted with the smooth cuticle of the unspecialized cells. In the discussion and *fig. 27* reference is made to stomata with intermediate stomatal types; this may mean that actually intermediate stomatal types occur or that the genera in question show both types of stomata and are in this respect intermediate between the genera with each one clearly defined stomatal type only.

In all species the stomata possess outer stomatal ledges. In some species also inner stomatal ledges (*fig. 10*) and occasionally a peristomal rim (WILKINSON 1971) are present. In cuticular preparations of Icacinaceae leaves these inner stomatal ledges are only clearly visible if a stomatal flap (a cutinized part of the stomatal chamber) remains attached to them. In the descriptions and the synoptical key the presence of inner cuticular ledges therefore also implies the presence of these other cuticular remains, which are in fact more obvious than the inner stomatal ledges themselves. It is possible that inner ledges are present in some species where they remained unnoticed because of the absence of adhering cuticular material.

The presence of a T-shaped thickening or T-piece at the stomatal poles is very common in the Icacinaceae (see *fig. 8* and *9*). These polar T-pieces were only recorded when they were distinctly present, that is, when both the upright and the cross-piece were present together.

The subsidiary cells and neighbouring cells may be submersed or not. When possible the number of subsidiary cells was counted. Often the periclinal walls of these cells possess concentric or radiate cuticular striations of varying distinctness. Concentric cuticular striations if massive enough may intergrade with the presence of a peristomal rim (*fig. 9*).

3.2. The indumentum (*plate III* and *IV*)

Hairs are mostly confined to the abaxial surface, in some species even restricted to the midrib and veins on that surface and may be very scarce. For the different hair types the terminology of HEINTZELMANN & HOWARD (1948) was largely followed. Hairs in the Icacinaceae are mainly unicellular and of the following types: a. normal hairs, b. malpighiaceous hairs, c. globular hairs, d. uncinate hairs, e. clustered hairs, f. peltate-stellate hairs, g. glandular hairs, h. slender papilla-like hairs, and i. multicellular, uniseriate hairs (see *plate III* and *IV*).

Heintzelmann and Howard, moreover, distinguished thin-base and icacinaceous hairs. They defined a thin-base hair as "a long, tapering hair with a thick

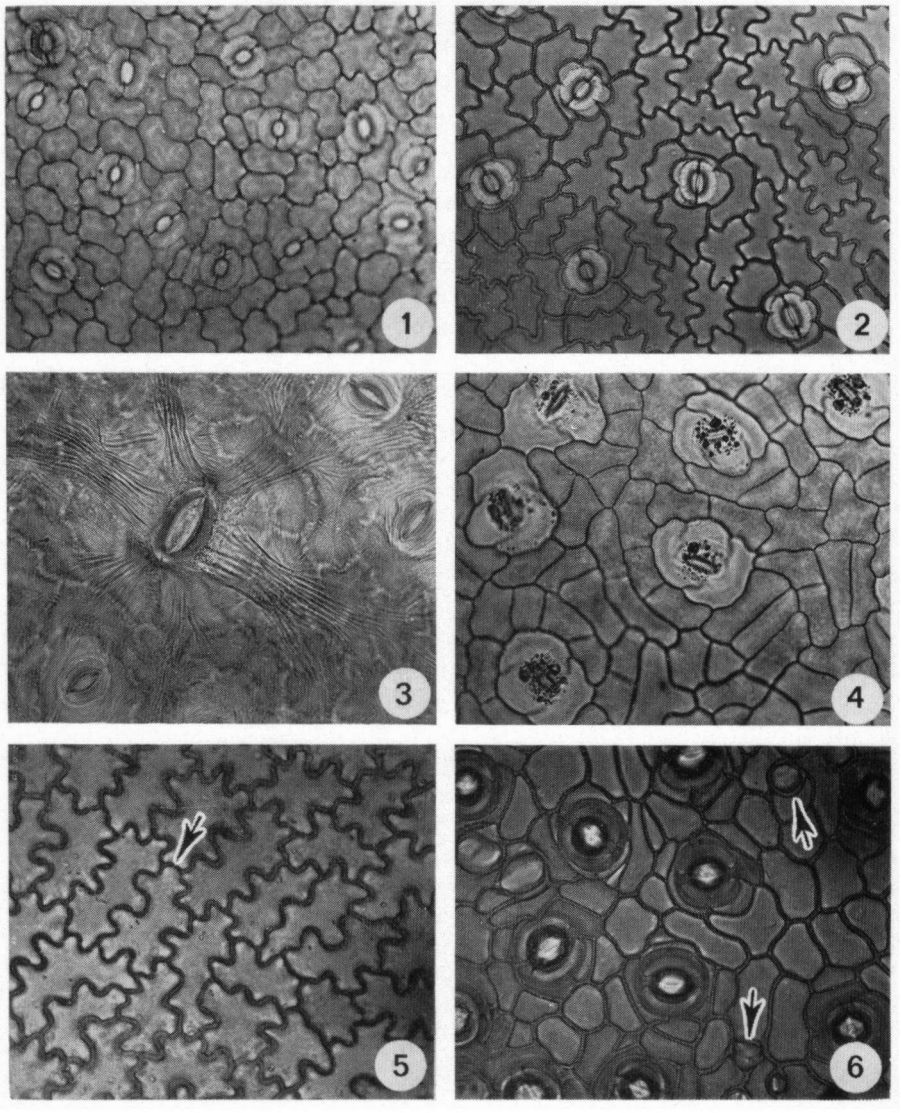


Plate I. Cuticular preparations, × 200.

Fig. 1. *Apodytes brachystylis*, anomocytic stomata; fig. 2. *Rhyticaryum elegans*, cyclocytic stomata with partly submersed subsidiary cells; fig. 3. *Gomphandra comosa*, water stoma surrounded by radiate cuticular striations; fig. 4. *Medusanthera laxiflora*, anisocytic stomata; fig. 5. *Rhyticaryum longifolium*, adaxial surface showing pitted anticlinal cuticular flanges (arrow); fig. 6. *Stemonurus grandifolius*, sites of penetration by asterosclereids indicated with arrows, stomata predominantly cyclocytic.

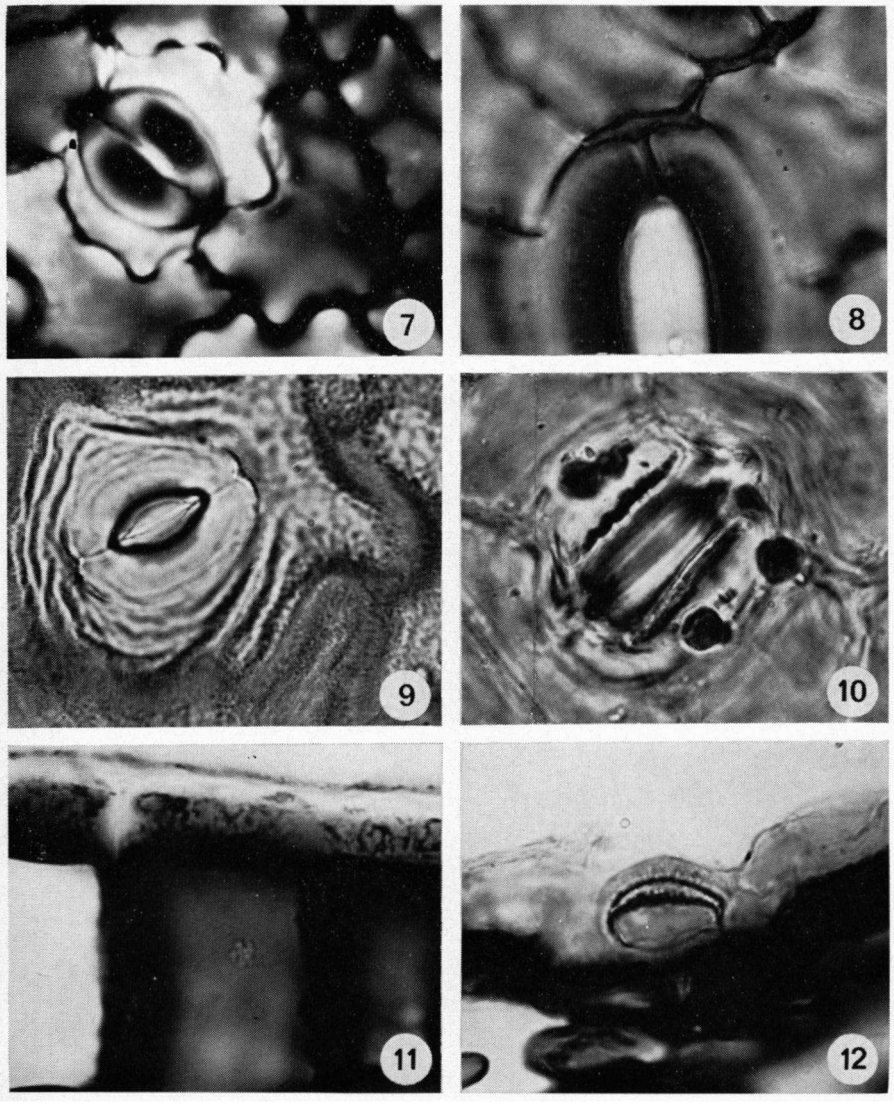


Plate II. Sections and cuticular preparations, × 900.

Fig. 7. *Pennantia cunninghamii*, paracytic stoma; fig. 8. *Gonocaryum gracile*, fragments of two stomata with conspicuous T-pieces; fig. 9. *Gomphandra coriacea*, stoma with very faint polar T-pieces surrounded by concentric cuticular striations, cuticle also granular; fig. 10. *Citronella latifolia*, stoma at low focus showing inner stomatal ledges; fig. 11. *Hartleya inopinata*, transverse section through upper epidermis, showing granular cuticular layer in between cuticle proper and outer epidermal cell wall; fig. 12. *Platea excelsa*, transverse section with unicellular glandular hair.

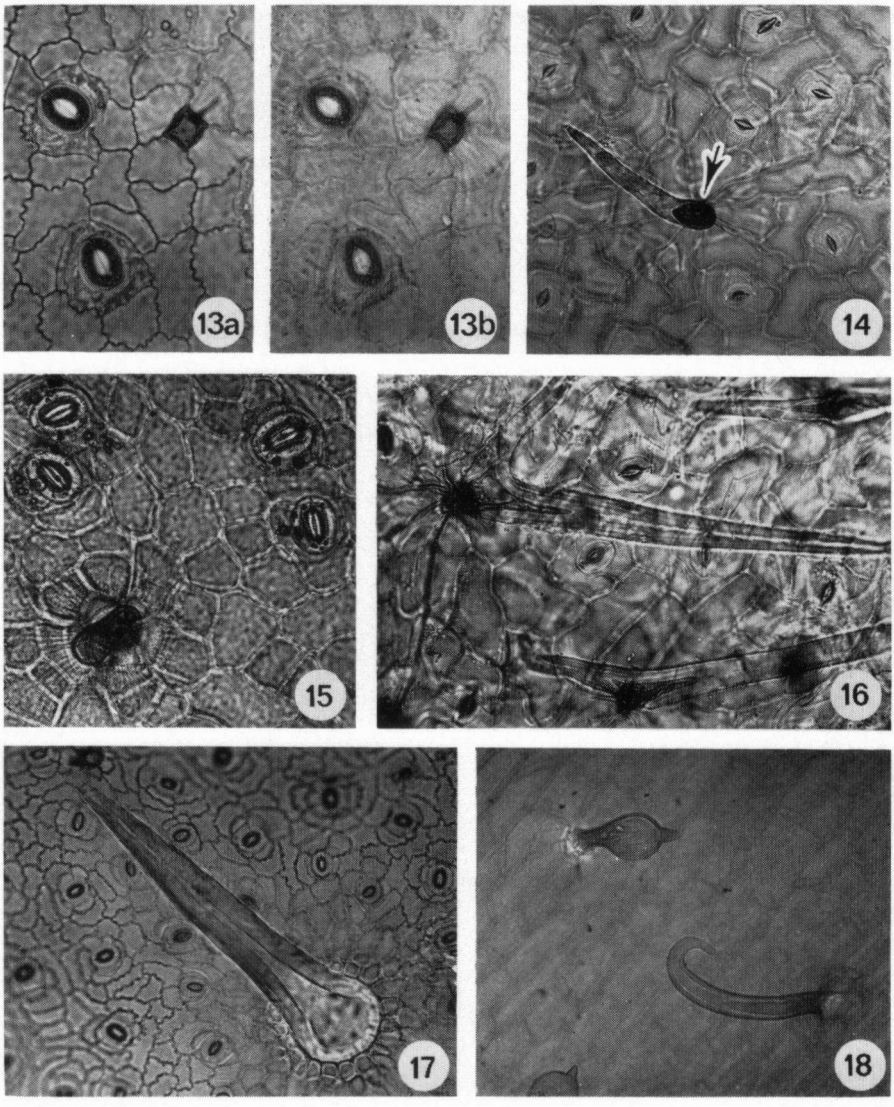


Plate III. Cuticular preparations, × 200.

Fig. 13. *Gonocaryum macrophyllum*, papilla-like hair at low (a) and high (b) focus, stomata cyclocytic with not or hardly submersed subsidiary cells; fig. 14. *Gomphandra fusiformis*, normal hair with thin-walled base and a second arm stub. Hair insertion indicated by arrow; fig. 15. *Citronella latifolia*, minute malpighiaceous hair; fig. 16. *Gomphandra papuana*, malpighiaceous hair with one well developed and one less developed arm. Hairs with a thick-walled body and a much restricted lumen; fig. 17. *Pyrenacantha repanda*, normal hair with a bulging basal part; fig. 18. *Miquelia celebica*, uncinate and globular hairs on midrib of abaxial surface.

wall and restricted lumen and a very thin-walled base". In the material examined by us we found many transitions between normal hairs with a normal wall thickness and without a restricted lumen and hairs with a thick-walled body and a thin-walled base and with a lumen which was restricted or not. Therefore we do not distinguish between normal and thin-base hairs, but between normal hairs with or without a thick-walled body and a thin-walled base.

The icacinaceous hairs found in 9 of the 26 genera are not so common as the name suggests. This hair type differs from a normal hair only by the presence of a second arm stub (see *fig. 14* and *25*). Furthermore we found gradual transitions between normal hairs and malpighiaceous hairs, namely a. normal hairs with a second arm stub, b. hairs with one well and one less developed arm – as in *Gomphandra papuana* (see *fig. 16* and *24*) – here called malpighiaceous hairs with one well developed arm, and c. hairs with two well developed arms, the real malpighiaceous hairs (see *fig. 23*). The real malpighiaceous hairs are sometimes very small, as in *Citronella* (see *fig. 15*). Malpighiaceous hairs may be either thin-walled or thick-walled with a very restricted lumen.

Because of the above mentioned transitions, which can only be separated arbitrarily, it does not seem useful to recognize an icacinaceous hair type. In the descriptions and the synoptical key this type is called a normal hair with a second arm stub.

Another character which the normal hairs may exhibit and which is very common in the Iodeae and Phytocreneae (except in *Mappianthus*), is the presence of a bulging basal part and numerous pits in the wall of that part (see *fig. 17*). Many normal hairs also possess cuticular markings of varying distinctness on the outer layer of the body (see *fig. 25*).

Uncinate hairs, hairs with a recurved tip (see *fig. 18* and *26*), only occur in the Iodeae and Phytocreneae. Uncinate hairs may also possess a bulging basal part.

Globular hairs are also very common in the lianoid genera (see *fig. 18* and *26*). They were always found in combination with other hair types.

Clustered hairs consist of groups of hairs fused at the base (see *fig. 19*). The central hair is sometimes several times as long and thick as the other hairs of the cluster and sometimes has verrucose cuticular markings on the outer layer of the body.

Peltate-stellate hairs only occur in *Platea* and consist of a group of cells fused over a considerable part of their body. They are appressed to the surface (see *fig. 19* and *20*).

In *Platea* we also found glandular hairs, noted before for *Platea excelsa* by SOLEREDER (1899) (see *fig. 12* and *19*). He called this hair type spherical, unicellular hairs. HEINTZELMANN & HOWARD (1948) did not find truly glandular hairs in their material. We agree with them when they say that the idea of some authors to consider the globular type as glandular is incorrect. However, the spherical hairs of *Platea* have a thick cuticle and a small space at the top between the wall and cuticle, filled with granular material (see *fig. 12*), which is very suggestive of a glandular nature.

The slender papilla-like hairs found only in *Gonocaryum* have been referred to as hydathodes by HABERLANDT (1894). They are unicellular structures with a broad basal cell part inserted between the unspecialized epidermal cells. From an excentric position in this cell a slender papilla-like structure protrudes *fig.13 a & b, 21* and *22*). Haberlandt noted the presence of water droplets on the upper and lower leaf surface in *Gonocaryum pyriforme* in the mornings and regarded these hairs as responsible for the guttation. To us it seems most unlikely that these slender structures can guttate water. It seems more likely that the giant water stomata also present in *Gonocaryum* serve as pathways for the guttation (cf. also ESAU 1964). The guttation from the upper as well as from the lower leaf surface noticed by Haberlandt remains unexplained, however, because water stomata are absent from the upper leaf surface in *Gonocaryum.*

Multicellular, uniseriate hairs have only been found in *Pennantia corymbosa.*

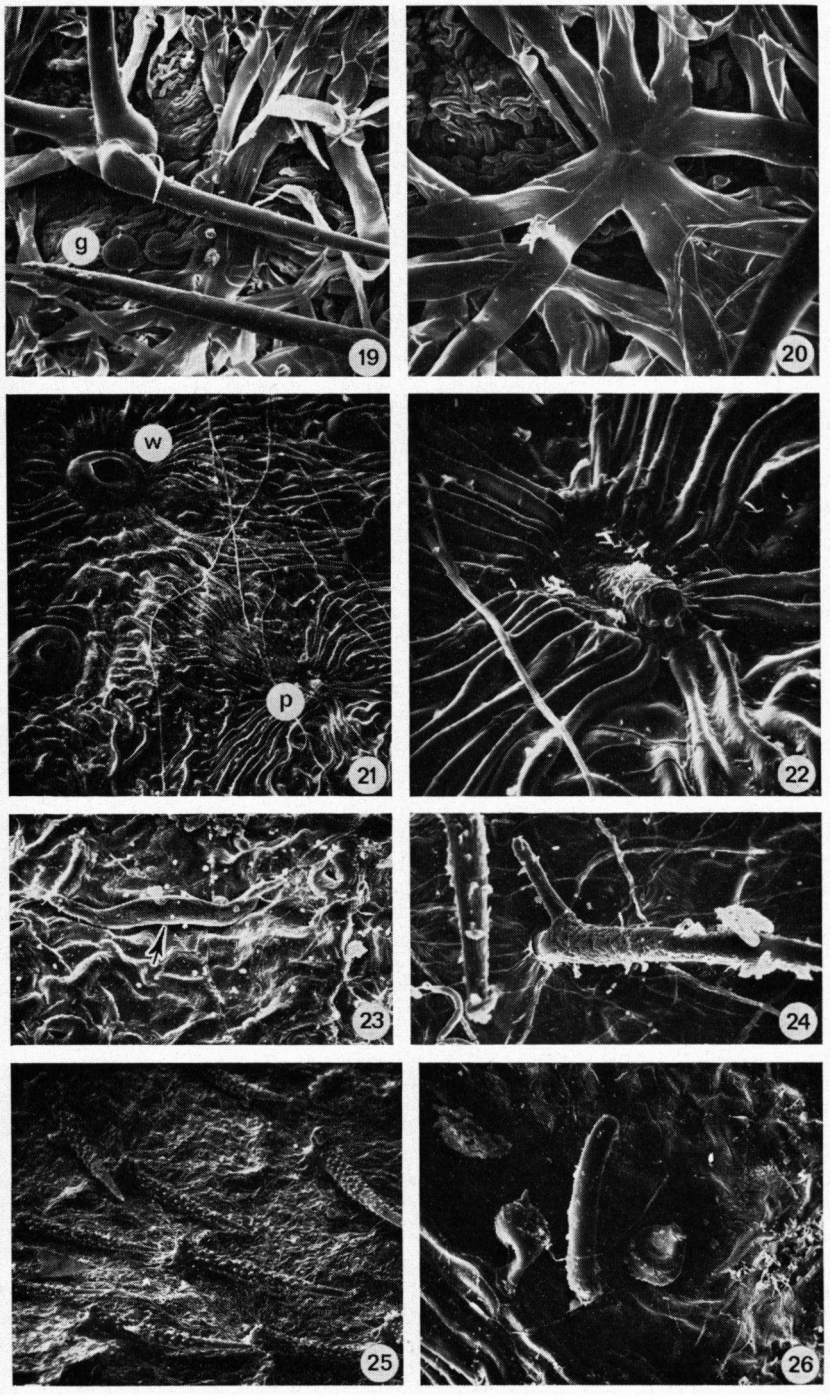
3.3. The unspecialized cells (*plate I* and *II* p.p.)

The anticlinal walls of the unspecialized cells on both surfaces may be straight, slightly curved, slightly sinuous, or sinuous. In some species unspecialized cells have sinuous walls with thin periclinal areas of cuticle in the loops. The anticlinal cuticular flanges, especially of cells overlying midrib and veins, are sometimes pitted, as in *Rhyticaryum longifolium* (see *fig. 5*). The cuticle overlying the anticlinal and periclinal walls may be smooth, granular, or striated. The granular nature is due to the structure of the cuticular layer underneath the cuticle, as in *Hartleya inopinata* (see *fig. 11*).

In two species of *Stemonurus* the epidermal pattern is modified by the intrusion of asterosclereids between the cuticular flanges of the cuticle (*fig. 6*). Presumably this penetration develops through intrusive growth. FOSTER (1947, 1955) recorded similar structures for *Boronia serrulata* (Rutaceae) and *Mouriria huberi* (Melastomataceae). It is noteworthy that in *S. grandifolius* the anticlinal cuticular flanges of the unspecialized cells are pitted, but that the flanges surrounding the arms of the asterosclereids are not.

Plate IV. Scanning electron photomicrographs.

Fig. 19. *Platea bullata*, detail of clustered hair, peltate-stellate hairs and glandular hairs (g), × 250; fig. 20. ibid. detail of peltate-stellate hair. Note striated cuticle of underlying epidermis, × 500; fig. 21. *Gonocaryum gracile*, papilla-like hair (p) and water stoma (w), both surrounded by conspicuous radiate cuticular striations, × 250; fig. 22. ibid., detail of papilla-like hair, × 1000; fig. 23. *Gomphandra montana*, malpighiaceous hair with two well developed arms. Hair insertion indicated by arrow, × 250; fig. 24. *Gomphandra papuana*, malpighiaceous hair with one well developed and one less developed arm, × 250; fig. 25. *Natsiatum herpeticum*, normal hairs with a second arm stub and verrucose cuticular markings, × 85; fig. 26. *Miquelia celebica*, uncinate and globular hairs on vein. Uncinate hair viewed on convex side of curved apex, × 250. Some of the leaf surfaces with fungal hyphae.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3.4. The veins

Venation patterns were not examined in this study. Only the prominence of veins in cuticular preparations was recorded. In this paper prominence of veins means that the epidermal cells overlying the minor veins are arranged differently (usually in rows) from the epidermal cells in the areolae. Prominent minor veins are particularly common in the lianoid genera.

4. ANATOMICAL DESCRIPTIONS

1. **APODYTES** E. Meyer ex Arn. (*fig. 1*)
Stomata randomly distributed or irregularly grouped, anomocytic; guard cells with more or less conspicuous outer stomatal ledges and polar T-pieces of varying distinctness. *Indumentum* consisting of normal hairs mostly confined to midrib and major veins, with septate lumen and a smooth or slightly verrucose outer layer of the body. *Unspecialized cells* of adaxial and abaxial surface with straight or curved, rarely with slightly sinuous walls, mostly without cuticular striations; anticlinal walls of adaxial and abaxial cells mostly with pitted cuticular flanges. *Minor veins* not prominent.

1. **A. brachystylis** F. v. M. (*fig. 1*)
Material studied. Queensland: *Kajewski 1380.*
Stomata 27–29–32 μm long, 23–27–30 μm wide. *Indumentum*: hairs confined to abaxial surface, with one septum each, and verrucose cuticular markings on the body. *Unspecialized cells* of the adaxial and abaxial surface with slightly sinuous walls.

2. **A. dimidiata** E. Meyer ex Arn.
Material studied: Borneo: *Clemens 40872*; Java: *Den Berger 605, Kostermans c.s. UNESCO 289*; Cambodja: *Pierre 583*; Madagascar: *Lam 6048*; Natal: *Rudatis 227* and *786*; Philippines: *B.S. 24941*; S. Africa: *Wylle s.n.*; Thailand: *R. F. D. 3616, Larsen 504.*
Stomata 27–29–35 μm long, 20–24–29 μm wide; average length 27–30 μm, average width 22–26 μm; Rudatis 786 and Wylle s.n. with more or less conspicuous grouping of the stomata (epidermal cells surrounding the guard cells here also with different staining properties for Sudan IV). *Indumentum*: hairs on abaxial and adaxial surface with one or more septa and with or without verrucose cuticular markings on the body. *Unspecialized cells* of adaxial and abaxial surface with straight to slightly sinuous walls, sometimes with cuticular striations on the epidermal cells surrounding the stomata and on the cells overlying the midrib.

2. **CANTLEYA** Ridl.

1. **C. corniculata** (Becc.) Howard
Material studied. Sumatra: *Grashoff F.R.I. 36E, 664.*
Stomata 27–31–35 μm long, 21–24–28 μm wide, cyclocytic, with 3 to 5 partly submersed subsidiary cells; guard cells with conspicuous outer stomatal ledges and small polar T-pieces; subsidiary cells with striations over the locally thin cuticle. *Indumentum* consisting of normal hairs, confined to abaxial surface and midrib of adaxial surface, with a thick-walled body and a thin-walled base. *Unspecialized* cells on adaxial surface with straight walls, on the abaxial surface with curved walls and with faint cuticular striations. *Minor veins* not prominent.

3. **CITRONELLA** D. Don (*fig. 10* and *15*)
Stomata paracytic; guard cells with conspicuous outer and inner stomatal ledges and without polar T-pieces, mostly with a strongly cutinized stomatal chamber; subsidiary cells partly

submersed, one of them often subdivided perpendicular to the pore, in some species with cuticular striations. *Indumentum* consisting of small malpighiaceous hairs on both surfaces of the whole lamina and on the midrib, rarely absent from the midrib; indumentum rarely also consisting of normal hairs confined to midrib of abaxial surface. *Unspecialized cells* of abaxial and adaxial surface with straight or curved, rarely with slightly sinuous walls; cuticle often striated and granular over periclinal walls; anticlinal walls sometimes seemingly interrupted due to coarse granular structure of cuticle overlying these walls. *Minor veins* not prominent.

1. **C. latifolia** (Merr.) Howard (*fig. 10* and *15*)
Material studied. Philippines: *B.S. 24557.*
Stomata 32–39–42 μm long, 24–28–31 μm wide; subsidiary cells obscured by concentric cuticular striations. *Indumentum* consisting of small malpighiaceous hairs only. *Unspecialized cells* of adaxial and abaxial surface with straight to slightly curved walls; cuticle striated and granular over periclinal walls on abaxial side and granular on adaxial side; anticlinal walls of cells on both sides seemingly interrupted due to coarsely granular structure of the cuticle.

2. **C. lucidula** (Sleum.) Howard
Material studied. New Caledonia: *sine nomine 9550.*
Stomata 32–38–40 μm long, 25–27–30 μm wide; subsidiary cells without cuticular striations. *Indumentum* consisting of small malpighiaceous and a few normal hairs with a second arm stub. *Unspecialized cells* of adaxial surface with straight walls, of abaxial side with slightly curved walls, with faint cuticular striations on cells overlying the midrib; anticlinal walls of these cells seemingly interrupted due to granular structure of cuticle overlying these walls.

3. **C. samoensis** (A. Gray) Howard
Material studied. Solomon Isl.: *BSIP 1983.*
Stomata 33–36–40 μm long, 24–27–30 μm wide; subsidiary cells with faint concentric cuticular striations. *Indumentum* consisting of small malpighiaceous hairs only. *Unspecialized cells* of adaxial surface with curved walls, of abaxial side with slightly sinuous walls; with faint cuticular striations on abaxial surface and on cells overlying the midrib on adaxial side; cuticle granular over periclinal walls on both sides; anticlinal walls not interrupted.

4. **C. suavolens** (Bl.) Howard
Material studied. New Guinea: *NGF 17332.*
Stomata 28–32–37 μm long, 23–27–30 μm wide, without cuticular striations. *Indumentum* consisting of small malpighiaceous hairs only, absent from midrib. *Unspecialized cells* of adaxial and abaxial surface with straight to curved walls, with faint cuticular striations on the epidermal cells overlying the midrib, with a granular cuticle over periclinal walls on abaxial side, without interruption of anticlinal walls.

4. **CODIOCARPUS** Howard
Stomata grouped, anisocytic to cyclocytic, with 3 to 5 hardly submersed subsidiary cells; guard cells with conspicuous outer stomatal ledges, rather distinct polar T-pieces and with a peristomal rim around the guard cells; subsidiary cells rarely or often divided so that two rings of subsidiary cells are present, with different staining properties for Sudan IV from unspecialized cells, and with cuticular striations. *Indumentum* consisting of small normal hairs over the whole lamina and on the midrib of both sides, with or without a second arm stub. *Unspecialized cells* of adaxial surface with straight walls, of the abaxial surface with straight to curved walls and with cuticular striations on the cells on the whole lamina or especially on cells surrounding hairs. *Minor veins* not prominent.

1. **C. andamanicus** (Kurz) Howard
Material studied. S. Andaman: *King's coll. s.n.*
Stomata 24–27–28 μm long, 20–24–27 μm wide; subsidiary cells often subdivided. *Indumentum*:

hairs with or without a second arm stub. *Unspecialized cells* with cuticular striations, especially on the cells surrounding the hairs of abaxial surface.

2. **C. merrittii** (Merr.) Howard
Material studied. Philippines: *PNH 91272.*
Stomata 24–27–29 μm long, 21–24–25 μm wide; subsidiary cells rarely subdivided. *Indumentum*: hairs mostly with a second arm stub. *Unspecialized cells* with cuticular striations on the cells: of the whole abaxial surface.

5. **GASTROLEPIS** Van Tiegh.

1. **G. austro-caledonica** (Baill.) v. Tieghem ex Engl.
Material studied. New Caledonia: *Lam 7207.*
Stomata 41–44–47 μm long, 30–35–39 μm wide, cyclocytic, with 4 to 7 hardly submersed subsidiary cells; guard cells with conspicuous outer stomatal ledges and faint polar T-pieces. *Indumentum* consisting of malpighiaceous hairs with one well developed arm, noted on both sides of lamina. *Unspecialized cells* on adaxial and abaxial surface with straight walls; those of the adaxial surface with thick walls rounded at the cell corners; cells on both sides with a finely granular cuticle. *Minor veins* not prominent.

6. **GOMPHANDRA** Wall. ex Lindl. (*fig. 3, 9, 14, 16, 23* and *24*, see also *table I*)
Stomata anisocytic, occasionally tending to be helicocytic, with 3 (4) not or hardly submersed subsidiary cells; guard cells with conspicuous outer stomatal ledges, with or without small polar T-pieces, with faint to rather distinct cuticular striations in more or less concentric circles giving the impression of cuticular rims; subsidiary cells of some species with concentric or radiate cuticular striations of varying distinctness, with a smooth or finely granular cuticle in the others. *Indumentum* in 24 species consisting of normal hairs, in 11 species with a second arm stub, in 16 species with a thick-walled body and a thin-walled base; in 4 species indumentum consisting of malpighiaceous hairs with one or two well developed arms. Hairs mostly confined to abaxial surface, abundant in *G. subrostrata, G. tomentella, G. velutina, G. papuana,* and *G. montana. Unspecialized cells* of adaxial surface with straight to curved walls, rarely with sinuous walls; of abaxial surface with curved to sinuous walls, rarely with straight to slightly curved walls; in some species with thin areas of cuticle in loops of sinuous walls (*G. luzoniensis, G. lysipetala, G. mappioides*, and *G. simalurensis*); most species on both sides with cells with granular and sometimes striated cuticle over periclinal walls; anticlinal walls of these cells often seemingly interrupted due to a finely to coarsely granular cuticle overlying these walls. *Minor veins* not prominent. *Cork warts* abundant in *G. quadrifida* and *G. subrostrata*, rare to absent in remaining species.

Material studied
1. *G. apoensis* (Elm.) Merr. Philippines: *PNH 13584*; 2. *G. australiana* F.v.M. New Guinea: *Lam 554*; 3. *G. capitulata* (Jungh. & de Vriese) Becc. Sumatra: *Loerzing 7009 p.p.*; 4. *G. comosa* King. South Andamans: *King's coll. 1890*; 5. *G. coriacea* Wight. India: *Wight K.D. 433*; 6. *G. cumingiana* (Miers.) F.-Vill. Borneo: *Hallier 2814*; 7. *G. donnaniensis* (Gagnep.) Sleum. Indo-China: *Poilane 23467*; 8. *G. flavicarpa* (Elm.) Merr. Philippines: *PNH 13511*; 9. *G. fuliginea* (Elm.) Merr. Philippines: *Elmer 8620*; 10. *G. fusiformis* Sleum. Sumatra: *Meyer 4066*; 11. *G. javanica* (Bl.) Valet. Java: *Kostermans 6205*; 12. *G. luzoniensis* (Merr.) Merr. Philippines: *F.B. 711*; 13. *G. lysipetala* Stapf. Borneo: *Clemens 29394*; 14. *G. mappioides* Valet. Celebes: *Koorders 18354*; 15. *G. montana* (Schellenb.) Sleum. New Guinea: *Carr 14501*; 16. *G. oblongifolia* Merr. Philippines: *PNH 38543*; 17. *G. oligantha* Sleum. Philippines: *Elmer 12508*; 18. *G. papuana* (Becc.) Sleum. New Guinea: *NGF 31689*; 19. *G. parviflora* (Bl.) Valet. Sumatra: *Korthals 882b*; 20. *G. pseudojavanica* Sleum. Simalur Isl.: *Achmad 64*; 21. *G. quadrifida* (Bl.) Sleum. Sumatra: *Iboet 561*; 22. *G. sawiensis* (Birnie) Sleum. New Guinea: *Gjellerup 608*; 23. *G. schoepfiifolia* Sleum. New Guinea: *Carr 13617*; 24. *G. simalurensis* Sleum. Simalur Isl.: *Achmad 1534*; 25. *G. subrostrata* Merr. Sumatra: *Loerzing 6685*; 26. *G. tetrandra* (Wall. in

Table I. Quantitative and qualitative epidermal leaf characters of *Gomphandra*.

species	stomata sizes in µm		cuticular striations on subsidiary cells	polar T-pieces	normal hairs	hairs with second arm stub	hairs with thick-walled body and restricted lumen	malpighiaceous hairs	adaxial surface glabrous	undulation of anticlinal walls		thin areas of cuticle in loops of walls	cuticle smooth
	length	width								ad	ab		
1. *G. apoensis*	20–22–24	11–14–15	–	–	+	–	+	–	+	–	±	–	±
2. *G. australiana*	20–22–24	16–19–20	–	–	+	+	–	–	+	–	±	–	±
3. *G. capitulata*	20–24–27	13–17–20	–	–	+	+	–	–	+	–	±	–	±
4. *G. comosa*	35–38–44	27–30–32	conc.	+	+	+	+	–	–	±	+	–	+
5. *G. coriacea*	25–28–30	19–21–23	conc.	+	+	+	+	–	–	±	+	–	+
6. *G. cumingiana*	21–24–27	13–15–17	–	–	+	+	–	–	–	–	±	–	±
7. *G. donnaniensis*	25–27–29	20–23–25	conc.	+	+	+	+	–	–	±	+	–	+
8. *G. flavicarpa*	22–24–30	14–17–21	–	–	+	+	–	–	–	–	±	–	±
9. *G. fuliginea*	29–33–35	21–25–30	conc./rad.	–	+	+	+	–	–	±	+	–	+
10. *G. fusiformis*	20–21–23	13–15–16	–	–	+	+	–	–	–	–	±	–	±
11. *G. javanica*	21–23–28	16–18–21	–	–	+	+	–	–	–	–	±	–	±
12. *G. luzoniensis*	23–28–31	16–23–26	conc./rad.	+	+	+	+	–	–	±	+	–	+
13. *G. lysipetala*	21–22–24	17–18–22	conc.	+	+	+	+	–	–	±	+	–	+
14. *G. mappioides*	20–23–28	15–16–18	–	–	+	+	–	–	+	–	±	–	±
15. *G. montana*	30–31–32	25–26–30	conc.	+	–	–	+	+2	–	+	+	–	+
16. *G. oblongifolia*	18–22–25	13–15–18	–	–	+	+	–	–	+	–	±	–	±
17. *G. oligantha*	24–26–28	15–19–20	conc.	+	+	+	+	–	+	–	±	–	±
18. *G. papuana*	23–25–27	16–17–19	–	+	–	–	+	+1	–	–	±	–	+
19. *G. parviflora*	22–23–24	18–19–21	–	–	+	–	+	–	+	–	±	–	+
20. *G. pseudojavanica*	21–23–26	13–16–18	–	+	+	+	–	–	–	–	±	–	±
21. *G. quadrifida*	24–26–29	16–19–21	–	+	+	–	+	–	–	–	±	–	+
22. *G. sawiensis*	18–20–22	13–15–16	conc.	–	–	–	+	+2	–	–	±	–	±
23. *G. schoepfiifolia*	21–23–26	13–15–16	conc.	+	–	–	+	+2	–	–	±	–	+
24. *G. simalurensis*	31–33–38	26–27–29	–	–	+	–	–	–	–	–	±	–	±
25. *G. subrostrata*	22–23–25	14–17–18	conc.	±/–	+	–	+	–	+	–	±	–	+
26. *G. tetrandra*	21–27–32	19–20–24	–	–	+	–	+	–	–	–	±	–	+
27. *G. tomentella*	18–21–23	15–16–17	–	+	+	–	–	–	–	–	±	–	+
28. *G. velutina*	21–23–25	16–17–18	conc.	–	+	–	±	–	–	–	–	–	–

Explanation of abbreviations in tables.
ad = adaxial; ab = abaxial; conc. = concentric; rad. = radiate. Undulation of anticlinal walls: + = slightly sinuous to sinuous, ± = curved, – = straight to slightly curved; in other columns: + = present, ± = infrequent or not pronounced, – = absent; + 1 and + 2 = with one or two well developed arms, respectively.

Roxb.) Sleum. Indo-China: *HCPM 2727*; 27. *G. tomentella* (Kurz.) Mast. in Hook. Burma: *Kurz 813*; 28. *G. velutina* Sleum. Celebes: *Kjellberg 2683.*

7. **GONOCARYUM** Miq. (*fig. 8, 13, 21,* and *22,* see also *table II*)
Stomata intermediate between anomocytic and cyclocytic, with 3 to 7 not or hardly submersed neighbouring or subsidiary cells; guard cells with very massive outer stomatal ledges, with or without faint to distinct polar T-pieces; subsidiary cells mostly with cuticular striations of varying distinctness, in more or less concentric circles giving the impression of cuticular rims, in *G. macrophyllum* and *G. lobbianum* with an irregularly granular cuticle, staining more deeply with Sudan IV than unspecialized cells except in *G. calleryanum. Indumentum* on both sides consisting of papilla-like hairs. A few normal hairs noted in *G. calleryanum, G. gracile,* and *G. impressinervium. Unspecialized cells* of adaxial surface with straight to slightly curved walls, of abaxial surface with slightly curved to sinuous walls with shallow loops; anticlinal walls of cells overlying the midrib on adaxial or abaxial surface often with pitted cuticular flanges; periclinal and anticlinal walls of cells of one or both surfaces often with cuticular striations of varying distinctness, occasionally also faintly granular. *Minor veins* mostly prominent.

Material studied
1. *G. calleryanum* (Baill.) Becc. Borneo: *Kostermans 4664*; 2. *G. cognatum* Elm. Philippines: *PNH 6252*; 3. *G. gracile* Miq. Sumatra: *Meijer 6765*; 4. *G. impressinervium* Sleum. Borneo: *Endert 2443*; 5. *G. litorale* (Bl.) Sleum. Celebes: *Cel IV/184*; 6. *G. lobbianum* (Miers.) Kurz. Siam: *Put 894*; 7. *G. macrophyllum* (Bl.) Sleum. Sumatra: *sine nomine*; 8. *G. minus* Sleum. Borneo: *Sibat S 24582.*

8. **HARTLEYA** Sleum. (*fig. 11*)

1. **H. inopinata** Sleum.
Material studied. New Guinea: *Hartley 11836.*
Stomata 31–36–41 μm long, 29–33–37 μm wide, cyclocytic, with 4 to 7 partly submersed

Table II. Quantitative and qualitative epidermal leaf characters of *Gonocaryum.*

species	stomata sizes in μm		polar T-pieces	cuticular rim	undulation of anticlinal walls		cuticle striated (s) and/or granular (g)		pitted cuticular flanges	minor veins prominent
	length	width			ad	ab	ad	ab		
1. *G. calleryanum*	40–42–44	31–34–36	±/−	+	−	±	−	s ±	ab	+
2. *G. cognatum*	41–43–44	33–36–39	±	+	−	−	s ±	s ±	ad	±
3. *G. gracile*	47–50–55	33–36–38	+	±	−	±	s/g ±	s/g ±	ab	+
4. *G. impressinervium*	31–33–35	25–26–28	±/−	−	−	±	−	−	−	+
5. *G. litorale*	36–40–42	27–29–31	+	+	−	−	−	s ±	ab	+
6. *G. lobbianum*	32–34–37	25–28–31	−	−	−	−	g ±	g ±	ad+ab	±/−
7. *G. macrophyllum*	33–34–35	28–29–31	−	−	−	+	g ±	g ±	−	+
8. *G. minus*	45–48–52	32–35–39	+/±	+	−	−	s ±	s +	ab	+

subsidiary cells; guard cells with outer stomatal ledges and without polar T-pieces; subsidiary cells with a granular cuticle over periclinal walls. *Indumentum* absent. *Unspecialized cells* of both surfaces with straight to very slightly curved walls and with a granular cuticle over periclinal walls (see *fig. 11*). *Minor veins* not prominent.

9. **IODES** Bl. (see also *table III*)
Stomata cyclocytic, with 3 to 5 partly to almost completely submersed, in cuticular preparations often hardly distinguishable, subsidiary cells; guard cells with rather distinct outer stomatal ledges, without polar T-pieces. *Indumentum* consisting of normal, uncinate, and globular hairs; normal hairs present in all species, confined to abaxial surface and on midrib and veins of adaxial surface, sometimes of two distinct sizes, with verrucose cuticular markings on the outer layer of the body (except in *I. velutina* var. *subvillosa* and on small normal hairs of *I. yatesii* var. *yatesii*), with pits in bulging basal wall. Uncinate hairs present in 5 species, often with pits in bulging basal wall, without verrucose cuticular markings. A type intermediate between small normal and uncinate hairs in *I. ovalis*. Globular hairs present in 3 species, also confined to midrib and veins of both sides. *Unspecialized cells* of adaxial surface with straight to sinuous walls, of abaxial surface with straight to slightly sinuous walls; anticlinal walls of cells of adaxial surface with pitted cuticular flanges in 3 species; cells of both sides often with a finely to coarsely granular cuticle overlying anticlinal walls and with cuticular striations of varying distinctness. *Minor veins* strikingly prominent.

Material studied
1. *I. cirrhosa* Turcz. Celebes: *Teijsmann H. B. 12624*; Java: *Van Steenis 12717* and *12717a*; Malay Peninsula: *Sinclair 9875*; Sumatra: *Maradjo 253*; Thailand: *Hansen & Smitinand 12985*;

Table III. Quantitative and qualitative epidermal leaf characters of *Iodes*.

species	stomata sizes in μm		hairs			undulation of anticlinal walls		pitted cuticular flanges
	length	width	normal	uncinate	globular	ad	ab	
1. *I. cirrhosa* Teijsmann 12624	20–21–23	15–17–18	+	−	+	+	+	+
van Steenis 12717	17–20–21	15–18–20	+	−	+	−	±	−
id. 12717a	16–19–21	13–16–18	+	−	+	−	−	−
Sinclair 9875	19–22–26	18–20–21	+	−	+	±	?	+
Maradjo 253	21–23–25	17–20–21	+	−	+	±	±	±
Hansen 12985	20–22–26	16–18–20	+	−	+	−	±	±
2. *I. ovalis* Bakh. v.d. Brink 5709	18–19–20	14–16–17	+	O	+	+	+	−
Loerzing 5533	20–22–24	16–19–21	+	O	+	+	+	−
3. *I. philippinensis*	16–21–25	17–19–21	+	+	−	−	±	−
4. *I. reticulata*	15–18–20	13–16–18	+	+	−	−	−	±
5. *I. seguinii*	19–21–23	19–21–23	+	+	−	±	+	−
6. *I. velutina* var. *subvillosa*	17–20–21	16–18–20	+	+	−	+	−	−
7. *I. vitiginea* var. *vitiginea*	18–21–25	14–17–19	+	−	+	+	−	−
8. *I. yatesii* var. *yatesii*	17–18–20	13–16–18	+	+	−	±	+	+

O = intermediate type between normal and uncinate hair.

2. *I. ovalis* Bl. Java: *Bakhuizen v.d. Brink 5709*; Sumatra: *Loerzing 5533*; 3. *I. philippinensis* Merr. Borneo: *Cuadra A 2342*; 4. *I. reticulata* King. Malay Peninsula: *King's coll. 6687*; 5. *I. seguinii* (Lévl.) Rehd. Indo-China: *W. T. Tsang 29923*; 6. *I. velutina* King. var. *subvillosa* Sleum. Sumatra: *Ajoeb 164*; 7. *I. vitiginea* (Hance) Hemsl. var. *vitiginea*. Thailand: *Kerr 21351*; 8. *I. yatesii* Merr. var. *yatesii*. Sumatra: *Buwalda 6908*.

10. MAPPIANTHUS Hand.-Mazz.
Stomata cyclocytic, with 4 to 6 almost completely submersed subsidiary cells; guard cells with outer stomatal ledges and without polar T-pieces; subsidiary cells with a finely granular cuticle over periclinal and anticlinal walls, staining more deeply with Sudan IV than cuticle of unspecialized cells and guard cells. *Indumentum* consisting of normal hairs, confined to midrib and veins of both surfaces. *Unspecialized cells* of adaxial and abaxial surface with straight to sinuous walls. *Minor veins* prominent.

1. **M. hookerianus** (Baill.) Sleum.
Material studied. Sumatra: *Korthals 652*.
Stomata 24–26–30 μm long, 21–24–26 μm wide. *Unspecialized cells* of adaxial and abaxial surface with straight to slightly curved walls.

2. **M. iodoides** Hand.-Mazz.
Material studied. China: *Steward & Cheo 1093*.
Stomata 26–28–31 μm long, 22–25–27 μm wide. *Unspecialized cells* of adaxial and abaxial surface with slightly curved to sinuous walls; thin areas of cuticle present in loops of anticlinal walls of adaxial epidermis.

11. MEDUSANTHERA Seem. (*fig. 4*)
Stomata anisocytic, with 3 hardly or not submersed subsidiary cells; guard cells with rather distinct outer stomatal ledges, without polar T-pieces; subsidiary cells mostly with a finely granular cuticle, in *M. laxiflora* occasionally with concentric or radiate cuticular striations. *Indumentum* consisting of normal hairs rarely with a very minute second arm stub, with a very thick-walled body and a thin-walled base, possibly articulate; mostly leaving a papilla-like stub after being shed, mostly confined to abaxial surface. Adaxial surface without hairs or hair bases, except for *M. gracilis*. *Unspecialized cells* of both sides with straight to slightly curved walls, in *M. gracilis* with slightly sinuous to sinuous walls; cells of both surfaces often with a granular cuticle, those surrounding hairs or hair bases often with a striated cuticle. *Minor veins* not prominent.

1. **M. gracilis** (King) Sleum.
Material studied. Malay Peninsula: *FRI 3428*.
Stomata 32–35–40 μm long, 27–29–31 μm wide. *Indumentum* present on both sides. *Unspecialized cells* of adaxial surface with curved to sinuous walls, of abaxial surface with sinuous walls.

2. **M. laxiflora** (Miers.) Howard (*fig. 4*)
Material studied. Moluccas: *Atasrip 71*.
Stomata 30–33–36 μm long, 27–30–31 μm wide; subsidiary cells occasionally with faint radiate or concentric cuticular striations. *Unspecialized cells* overlying major veins on adaxial surface with faint cuticular striations.

3. **M. samoensis** (Reinecke) Howard
Material studied. Samoa: *Reinecke 104*.
Stomata 27–34–37 μm long, 22–26–28 μm wide.

4. **M. vitiensis** Seem.
Material studied. Fiji: *Smith 6159.*
Stomata 34–35–38 μm long, 30–31–34 μm wide.

12. MERRILLIODENDRON Kaneh.

1. **M. megacarpum** (Hemsl.) Sleum.
Material studied. New Britain: *NGF 32614.*
Stomata 24–26–29 μm long, 22–25–28 μm wide, cyclocytic, with 4 to 6 almost completely submersed subsidiary cells; guard cells with conspicuous outer and faint inner stomatal ledges and with polar T-pieces. *Indumentum* of both surfaces consisting of normal hairs with a second arm stub. *Unspecialized cells* of both surfaces with straight to slightly curved walls; anticlinal walls of cells on adaxial side overlying midrib and veins with pitted cuticular flanges. *Minor veins* not prominent.

13. MIQUELIA Meisn. (*fig. 18* and *26*)
Stomata confined to abaxial surface, in *M. reticulata* also present in low numbers on major and minor veins of adaxial surface, cyclocytic, with 4 to 5 partly submersed subsidiary cells; guard cells with conspicuous outer stomatal ledges and without polar T-pieces. *Indumentum* consisting of normal, uncinate and globular hairs; normal hairs infrequent, with pits in mostly bulging basal walls, with very fine cuticular markings on the outer layer of the body; all types of hairs mostly confined to abaxial surface. Adaxial surface mostly with some hair bases only. *Unspecialized cells* of adaxial and abaxial surface with curved to sinuous walls: in *M. caudata* with coarsely granular anticlinal cuticular flanges; cells of abaxial surface with a finely granular cuticle. *Minor veins* prominent.

1. **M. caudata** King
Material studied. Malay Peninsula: *Shah & Sidek 1168.*
Stomata 29–33–36 μm long, 22–26–29 μm wide. *Unspecialized cells* of adaxial surface with coarsely granular anticlinal cuticular flanges.

2. **M. celebica** Bl. (*fig. 18* and *26*)
Material studied. Celebes: *Forsten s.n.*
Stomata 29–32–37 μm long, 24–26–28 μm wide. *Indumentum*: uncinate and globular hairs confined to abaxial surface; normal hairs infrequently present on both surfaces.

3. **M. kleinii** Meisn.
Material studied. India: *sine nomine 1447.*
Stomata 26–29–31 μm long, 22–24–28 μm wide. *Indumentum* very scanty. Hair bases absent from adaxial surface.

4. **M. reticulata** Merr.
Material studied. Philippines: *B.S. 43303.*
Stomata 28–31–34 μm long, 22–24–26 μm wide, a few present on and near the veins on adaxial surface.

14. NATSIATUM Buch.-Ham. (*fig. 25*)

1. **N. herpeticum** Ham.
Material studied. India: *Griffith 828.*
Stomata 19–21–24 μm long, 16–18–20 μm wide, intermediate between anomocytic and cyclocytic, with partly submersed neighbouring cells; guard cells with distinct outer stomatal ledges and without polar T-pieces. *Indumentum* consisting of many normal hairs, with or without a

second arm stub and with a verrucose outer layer of the body, with pits in bulging basal wall, also consisting of malpighiaceous hairs with one well developed arm; both types of hairs present on both surfaces. *Unspecialized cells* of adaxial surface with slightly curved walls, of abaxial surface with slightly sinuous walls; cells of abaxial surface with granular cuticle over anticlinal walls. *Minor veins* prominent.

15. NOTHAPODYTES Bl.

Stomata intermediate between anomocytic and cyclocytic; guard cells with more or less conspicuous outer stomatal ledges and with or without very faint polar T-pieces, with faint cuticular strations parallel to the pore in *N. foetida*. *Indumentum* consisting of some normal hairs, with or without a second arm stub, mostly confined to midrib and major veins of both surfaces. *Unspecialized cells* of adaxial surface with sinuous walls, of abaxial surface with slightly curved to slightly sinuous walls; cell sin *N. foetida* with striated cuticle confined to neighbouring* cells; in *N. montana* and *N. pittosporoides* with granular cuticle. *Minor veins* mostly prominent in *N. foetida* and *N. pittosporoides*, most veins not prominent in *N. montana*.

1. **N. foetida** (Wight) Sleum.

Material studied. Philippines: *Edaño 3778*.

Stomata 36–41–45 μm long, 25–28–30 μm wide; guard cells with faint cuticular rims. *Indumentum:* normal hairs with a small second arm stub. *Unspecialized cells* of adaxial surface with many cuticular striations over periclinal and anticlinal walls; of abaxial surface especially neighbouring cells with striated cuticle. *Minor veins* mostly prominent.

2. **N. montana** Bl.

Material studied. Java: *Kostermans & Kuswata 53*.

Stomata 25–27–30 μm long, 21–22–25 μm wide. *Indumentum*: normal hairs with a distinct indication of a second arm stub. *Unspecialized cells* of both surfaces with finely granular cuticle over periclinal and anticlinal walls. *Minor veins* not prominent.

3. **N. pittosporoides** (Oliv.) Sleum.

Material studied. China: *Fan & Li 179*.

Stomata 36–40–45 μm long, 26–30–31 μm wide. *Indumentum*: normal hairs without a second arm stub. *Unspecialized cells* of both surfaces with very finely granular cuticle over periclinal and anticlinal walls. *Minor veins* mostly prominent.

16. PHYTOCRENE Wall. (see also *table IV*)

Stomata cyclocytic, with 3 to 5 partly to almost completely submersed subsidiary cells; guard cells with faint to rather distinct outer stomatal ledges and with or without minute polar T-pieces (stomata not visible in cuticular preparations of *P. borneensis*, *P. bracteata*, and *P. macrophylla* due to the abundance of hairs over areolae). *Indumentum* consisting of normal, uncinate, globular, and clustered hairs; normal and globular hairs present in all species; normal hairs mainly on abaxial surface, occasionally on adaxial surface, globular hairs on midrib and veins only; normal hairs with verrucose cuticular markings on the body and with pits in bulging basal wall. Uncinate hairs present in 3 species, clustered hairs present in 5 species; both types of hairs confined to midrib and veins of abaxial surface; central hair of clustered hairs several times as long and thick as the other hairs of the cluster, with verrucose cuticular markings on the body. *Unspecialized cells* of adaxial surface in 4 species with straight to slightly curved walls, in 5 species with slightly sinuous walls; cells of abaxial surface with

* One may also call the neighbouring cells of *N. foetida* subsidiary cells because they deviate from the other epidermal cells by a stronger cuticular striation. Because of this deviation the stomatal complex in *Nothapodytes* has been classified as intermediate between anomocytic and cyclocytic.

curved to sinuous walls, rarely with straight to slightly curved walls; in the 3 above mentioned species unspecialized cells in areolae not visible due to the abundance of hairs (anticlinal walls of cells of abaxial surface overlying veins mainly straight in these densely hairy species); cells of abaxial surface often with a finely granular cuticle overlying anticlinal walls; anticlinal walls of cells overlying midrib and veins with pitted cuticular flanges in 4 species. *Minor veins* strikingly prominent.

Material studied
1. *P. anomala* Merr. Borneo: *B.S. 1840*; 2. *P. borneensis* Becc. Borneo: *Teijsmann H.B. 8459*; 3. *P. bracteata* Wall. Malay Peninsula: *Maingay 2715* (= K.D. 377); 4. *P. hirsuta* Bl. Celebes: *Rant 905*; 5. *P. interrupta* Sleum. New Guinea: *Carr 12612*; 6. *P. macrophylla* (Bl.) Bl. var. *macrophylla*. Sumatra: *Teijsmann s.n.*; 7. *P. oblonga* Wall. Malay Peninsula: *Phyt. Surv. Fed. Malaya 1759*; 8. *P. palmata* Wall. Malay Peninsula: *King's coll. 2226*; 9. *P. racemosa* Sleum. Borneo: *S 22325 Murthy & Ashton.*

17. PITTOSPOROPSIS Craib

1. P. kerrii Craib

Material studied. Thailand: *Garrett 138.*
Stomata 20–23–25 μm long, 17–20–21 μm wide, cyclocytic, with about 5 partly submersed subsidiary cells; guard cells with outer stomatal ledges and without polar T-pieces. *Indumentum* consisting of malpighiaceous hairs with one or two well developed arms, confined to midrib of both sides. *Unspecialized cells* of adaxial and abaxial surface with sinuous walls; cells of adaxial surface with a granular cuticle. *Minor veins* not prominent.

18. PLATEA Bl. (*fig. 12, 19* and *20*)

*Stomata** cyclocytic, with 4 to 5 partly submersed subsidiary cells and with a well developed peristomal rim; guard cells with conspicuous outer stomatal ledges, probably in all species

Table IV. Quantitative and qualitative epidermal leaf characters of *Phytocrene.*

species	stomata sizes in μm		hairs				undulation of anticlinal walls		pitted cuticular flanges
	length	width	uncinate	globular	clustered	normal	ad	ab	
1. *P. anomala*	23–26–30	18–20–22	+	+	−	+	−	+	−
2. *P. borneensis*	?	?	−	+	+	+	−	?	+
3. *P. bracteata*	?	?	−	+	+	+	−	?	+
4. *P. hirsuta*	18–20–22	15–16–17	−	+	+	+	+	−	−
5. *P. interrupta*	26–30–33	24–27–30	+	+	−	+	+	±	+
6. *P. macrophylla*	?	?	+	+	+	+	−	?	+
7. *P. oblonga*	19–21–23	17–19–21	−	+	−	+	+	+	−
8. *P. palmata*	21–24–27	19–20–21	−	+	−	+	+	+	−
9. *P. racemosa*	22–25–28	17–20–22	−	+	+	+	+	+	−

* Length and width of stomata were only measured in *P. sclerophylla.* In the remaining species the guard cells are obscured by a peristomal rim.

with faint polar T-pieces, often not visible due to the peristomal rim overlying the guard cells. *Indumentum* in all species consisting of peltate-stellate and sessile, unicellular glandular hairs; in *P. bullata* and *P. latifolia* also consisting of clustered hairs. Glandular hairs with a thick cuticle and at the top with a small space between the wall and cuticle, filled with granular material. Peltate-stellate and glandular hairs present on abaxial surface and usually also on major and minor veins of adaxial surface; clustered hairs, if present, confined to abaxial surface. *Unspecialized cells* of adaxial and abaxial surface with straight to slightly curved walls; adaxial cells with or without a coarsely granular, rarely with a striated cuticle, abaxial cells mostly with conspicuous cuticular striations. *Minor veins* prominent.

1. **P. bullata** Sleum. (*fig. 19* and *20*)

Material studied. Borneo: *S 19638 P.S. Ashton.*
Indumentum consisting of peltate-stellate, glandular and clustered hairs. *Unspecialized cells* of both sides with conspicuous cuticular striations.

2. **P. excelsa** Bl. var. **excelsa** (*fig. 12*)

Material studied. Java: *Dakkus 166.*
Indumentum consisting of peltate-stellate and glandular hairs. *Unspecialized cells* of adaxial surface with a coarsely granular cuticle, cells overlying veins with faint cuticular striations; abaxial cells with conspicuous cuticular striations.

3. **P. latifolia** Bl.
Material studied. Borneo: *sine nomine*; China: *F.C. How 73310*; Malay Peninsula: *Sinclair 40618*; Philippines: *Sulit 21597*; Sumatra: *Kostermans 267.*
Indumentum consisting of peltate-stellate, glandular and clustered hairs. *Unspecialized cells* of adaxial surface with a coarsely granular and/or striated cuticle; abaxial cells with conspicuous cuticular striations.

4. **P. sclerophylla** Sleum.
Material studied. Borneo: *Chew 8026.*
Stomata 28–32–37 μm long, 29–33–39 μm wide. *Indumentum* consisting of peltate-stellate and glandular hairs. *Unspecialized cells* of both sides without cuticular striations.

19 **POLYPORANDRA** Becc.

1. **P. scandens** Becc.
Material studied. New Guinea: *Docters van Leeuwen 10613.*
Stomata 19–21–23 μm long, 17–18–20 μm wide, cyclocytic, with a variable number of partly or almost completely submersed subsidiary cells; guard cells with outer stomatal ledges and without polar T-pieces. *Indumentum* consisting of normal hairs with a coarsely verrucose outer layer of the body and with pits in bulging basal walls, besides also consisting of globular hairs. Both types of hairs confined to abaxial surface. *Unspecialized cells* of adaxial and abaxial surface with slightly curved walls. *Minor veins* prominent.

20. **PSEUDOBOTRYS** Moeser
Stomata predominantly paracytic, sometimes also anomocytic; guard cells with conspicuous outer stomatal ledges and with well developed polar T-pieces. *Indumentum* consisting of normal hairs with a thick-walled body and a thin-walled base, confined to abaxial surface. *Unspecialized cells* of adaxial and abaxial surface with straight to slightly curved walls; cells of abaxial surface with a striated and finely granular cuticle, those of adaxial surface with a finely granular cuticle. *Minor veins* not prominent.

1. **P. cauliflora** (Pulle) Sleum.
Material studied. New Guinea: *Docters van Leeuwen 9307.*
Stomata 24–27–29 μm long, 21–23–26 μm wide, ranging from paracytic to anomocytic.

2. **P. dorae** Moeser
Material studied. New Guinea: *Carr 12760.*
Stomata 27–29–31 μm long, 26–28–30 μm wide, almost exclusively paracytic.

21. PYRENACANTHA Wight (*fig. 17*)

1. **P. repanda** (Merr.) Merr.
Material studied. Philippines: *Elmer 17359.*
Stomata mainly confined to abaxial surface, a few also present on major and minor veins of adaxial surface, 17–19–21 μm long, 13–15–16 μm wide, cyclocytic, with 3 to 6 partly submersed subsidiary cells; guard cells with conspicuous outer stomatal ledges and without polar T-pieces. *Indumentum* confined to abaxial surface, consisting of normal hairs with cuticular markings on the broad body and with pits in bulging basal wall, besides consisting of globular and of uncinate hairs, the latter especially on midrib and major veins. Adaxial surface without hairs or hair bases. *Unspecialized cells* of adaxial surface with strongly sinuous walls with thin areas of cuticle in loops; wave-length and amplitude of sinuses small. Abaxial cells with slightly curved to slightly sinuous walls; cells on both surfaces with very finely granular cuticle over periclinal walls and a coarsely granular cuticle over anticlinal walls. *Minor veins* prominent.

22. RHYTICARYUM Becc. (*fig. 2* and *5*, see also *table V*)

Stomata cyclocytic, with 4 to 6 partly, in *R. oxycarpum* almost completely submersed subsidiary cells; guard cells with rather conspicuous outer stomatal ledges, in *R. longifolium* with coarsely granular material, with small polar T-pieces in 6 species and mostly with a finely granular cuticle. *Indumentum:* in 6 species only some hair bases noted on adaxial or abaxial side; in *R.*

Table V. Quantitative and qualitative epidermal leaf characters of *Rhyticaryum.*

species	stomata sizes in μm		polar T-pieces	undulation of anticlinal walls		cuticle				pitted cuticular flanges
						adaxial		abaxial		
	length	width		ad	ab	granular	striated	granular	striated	
1. *R. elegans*	27–29–32	24–26–28	+	+	+	−	+	−	−	ad+ab
2. *R. fasciculatum*	22–24–28	21–22–24	+	+	+	±	±	−	−	ad
3. *R. longifolium*	37–40–45	31–35–39	+	+	+	+	−	±	±	ad+ab
4. *R. macrocarpum*	26–28–29	23–25–28	−	+	−	+	−	+	−	−
5. *R. novoguineense*	26–29–31	23–27–28	+	+	+	±	±	−	−	ad+ab
6. *R. oleraceum*	26–29–32	22–24–26	+	−	−	−	−	±	−	−
7. *R. oxycarpum*	25–30–31	25–27–28	+	±	+	±	±	±	−	ab
8. *R. racemosum*	25–26–28	22–24–26	±	+	+	−	−	±	−	ad

oleraceum and *R. racemosum* indumentum consisting of normal hairs with a second arm stub. *Unspecialized cells* in 6 species on both sides with sinuous walls, in the remaining species with slightly curved to slightly sinuous walls; anticlinal walls of cells on adaxial and /or abaxial surface in 6 species with pitted cuticular flanges. Adaxial and abaxial cells with granular, striated or smooth cuticle. *Minor veins* not prominent.

Material studied
1. *R. elegans* Schellenb. New Guinea: *BW 13351*; 2. *R. fasciculatum* Becc. New Guinea: *Tuyama 1085*; 3. *R. longifolium* K. Sch. & Laut. New Guinea: *Clemens 1028*; 4. *R. macrocarpum* Becc. New Guinea: *BW 11366*; 5. *R. novoguineense* (Warb.) Sleum. New Guinea: *NGF 8386*; 6. *R. oleraceum* Becc. Moluccas: *Kornassi 503*; 7. *R. oxycarpum* K. Sch. & Laut. New Guinea: *Ledermann s.n.*; 8. *R. racemosum* Becc. New Guinea: *Van Royen 3129*.

23. SARCOSTIGMA W. & A.

Stomata mainly confined to abaxial surface, cyclocytic, with 4 to 5 partly submersed subsidiary cells; guard cells with conspicuous outer stomatal ledges and with faint to rather distinct, small polar T-pieces. *Indumentum*: only hair bases and a few normal hairs with minute second arm stubs noted. *Unspecialized cells* of adaxial surface with straight walls, of abaxial surface with straight to slightly curved walls; cells on both sides with distinctly striated cuticle. *Minor veins* prominent.

1. **S. kleinii** W. & A.
Material studied. Java: *Zollinger 228*.
Stomata confined to abaxial surface, 23–25–28 μm long, 21–23–25 μm wide.

2. **S. paniculata** Pierre
Material studied. Borneo: *SAN 39985*.
Stomata mainly confined to abaxial surface, a few also present on and near midrib of adaxial surface, 24–27–28 μm long, 24–25–26 μm wide.

Table VI. Quantitative and qualitative epidermal leaf characters of *Stemonurus*.

species	stomata sizes in μm		peristomal rim distinct	stomata predominantly anisocytic	stomata predominantly cyclocytic
	length	width			
1. *S. ammui*	30–32–35	29–31–33	+	−	+
2. *S. celebicus*	34–38–42	27–29–34	+	+	−
3. *S. gitingensis*	35–37–42	33–34–35	−	±	±
4. *S. grandifolius*	40–45–47	40–45–50	+	−	+
5. *S. malaccensis*	32–35–37	29–31–33	+	±	±
6. *S. monticolus*	35–37–39	33–36–38	+	+	−
7. *S. perobtusus*	33–35–37	25–27–30	+	+	−
8. *S. scorpioides*	25–28–30	26–29–30	−	±	±
9. *S. secundiflorus*	28–31–32	26–27–29	+	+	−
10. *S. umbellatus*	33–36–37	27–30–32	−	+	−

24. STEMONURUS Bl. (*fig. 6*, see also *table VI*)
Stomata anisocytic to cyclocytic, with 3 to 4 partly submersed subsidiary cells, with a distinct peristomal rim in 7 species; guard cells with rather distinct outer stomatal ledges and with thick polar T-pieces. *Indumentum* in *S. secundiflorus* var. *secundiflorus* and *S. umbellatus* consisting of malpighiaceous hairs confined to abaxial surface, in the remaining species indumentum absent or only evident through hair bases, noted on adaxial and/or abaxial surface. *Unspecialized cells* of both sides with straight to slightly curved walls; in *S. celebicus*, *S. perobtusus*, and *S. umbellatus* abaxial cells with curved to slightly sinuous walls; cells of both surfaces with a finely to coarsely granular cuticle; abaxial cuticle moreover often with faint striations, in *S. secundiflorus* var. *secundiflorus* with distinct striations. Anticlinal walls in *S. grandifolius* and *S. scorpioides* with pitted cuticular flanges. In *S. grandifolius* and *S. umbellatus* on abaxial side with penetration of asterosclereids between unspecialized cells (see *fig. 6*) giving the impression of rounded epidermal cells. *Minor veins* not prominent. *Corkwarts* abundant on adaxial side in *S. malaccensis* and on abaxial side in *S. umbellatus*, rare to absent in the remaining species.

Material studied
1. *S. ammui* (Kaneh.) Sleum. New Guinea: *NGF 2027*; 2. *S. celebicus* Valet. in Koord. Celebes: *Cel II/339*; 3. *S. gitingensis* (Elm.) Sleum. Philippines: *Elmer 12277*; 4. *S. grandifolius* Becc. Borneo: *SAN 16782*; 5. *S. malaccensis* (Mast.) Sleum. Thailand: *Swanakoses 292*; 6. *S. monticolus* (Schellenb.) Sleum. New Guinea: *bb. 25059*; 7. *S. perobtusus* (Gagnep.) Sleum. Indo-China: *Pierre 2838*; 8. *S. scorpioides* Becc. Borneo: *SAN 24315*; 9. *S. secundiflorus* Bl. var. *secundiflorus*. Sumatra: *Thorenaar T. 33*; 10. *S. umbellatus* Becc. Borneo: *S 8641*.

25. WHITMOREA Sleum.

1. **W. grandiflora** Sleum.
Material studied. Solomon Isl.: *Schodde (& Craven) 3629*.
Stomata 40–41–45 μm long, 33–35–37 μm wide, anisocytic to cyclocytic, with 3 to 4 hardly submersed subsidiary cells; guard cells with rather distinct outer and inner stomatal ledges and without polar T-pieces. *Indumentum* consisting of normal hairs with a thick-walled body and a thin-walled base on abaxial surface. Adaxial surface without hairs or hair bases. *Unspecialized cells* of adaxial surface with straight walls, of abaxial surface with slightly curved walls; cells of both surfaces with a finely granular cuticle over periclinal walls. *Minor veins* not prominent.

26. PENNANTIA Forst.
Stomata paracytic; guard cells with conspicuous outer stomatal ledges and with rather distinct polar T-pieces. *Indumentum* consisting of normal hairs; in *P. corymbosa* also of multicellular, uniseriate hairs with rounded apex; both hair types mainly confined to major and minor veins of abaxial surface. *Unspecialized cells* of adaxial and abaxial surface with curved to sinuous walls, with coarsely granular cuticle. *Minor veins* prominent.

1. **P. corymbosa** Forst.
Material studied. Three Kings Isl.: *Baylis 22875* (= *Plectomirtha baylisiana*); New Zealand: *Baylis s.n.*
Stomata 25–26–28 μm long, 16–19–20 μm wide. *Indumentum* consisting of normal hairs and multicellular, uniseriate hairs.

2. **P. cunninghamii** Miers.
Material studied. New South Wales: *Nat. Herb. 11151*.
Stomata 21–23–25 μm long, 16–18–19 μm wide. *Indumentum* only consisting of normal hairs.

5. SYNOPTICAL KEY TO THE GENERA OF MALESIAN ICACINACEAE

From the foregoing descriptive part a great diversity in leaf epidermal structure has become apparent. This diversity makes it possible to characterize genera by epidermal characters and consequently to identify most of them using these characters only. Since many genera also show a considerable range of variation amongst their species, we chose the synoptical key for this purpose. LEENHOUTS (1966) discussed the advantages of this type of key.

At present it is of course only possible to use the key when one is certain of dealing with leaf material belonging to the family Icacinaceae. In several cases the specific descriptions will be helpful in narrowing down the possibilities to a species or a group of species, though one has to be cautious and be aware of the fact that virtually all the descriptions are based on one leaf only.

Dr. Sleumer kindly selected 10 leaf fragments of herbarium material to try out the key. We were able to identify 8 of these satisfactorily down to the genus. In the case of *Medusanthera* and *Gomphandra* we were unable to distinguish between the two genera.

In the key an underlined number for a genus means that the genus shows several alternative types of the structure in question. A genus number between brackets implies that the genus exhibits an intermediate stomatal type.

1. *Apodytes*, 2. *Cantleya*, 3. *Citronella*, 4. *Codiocarpus*, 5. *Gastrolepis*, 6. *Gomphandra*, 7. *Gonocaryum*, 8. *Hartleya*, 9. *Iodes*, 10. *Mappianthus*, 11. *Medusanthera*, 12. *Merrilliodendron*, 13. *Miquelia*, 14. *Natsiatum*, 15. *Nothapodytes*, 16. *Phytocrene*, 17. *Pittosporopsis*, 18. *Platea*, 19. *Polyporandra*, 20. *Pseudobotrys*, 21. *Pyrenacantha*, 22. *Rhyticaryum*, 23. *Sarcostigma*, 24. *Stemonurus*, 25. *Whitmorea*, 26. *Pennantia*.

1. Stomatal types:
   anomocytic 1 (7) (14) (15) 20
   paracytic 3 20 26
   cyclocytic 2 (4) 5 (7) 8 9 10 12 13 (14) (15) 16 17 18 19 21 22 23 (24) (25)
   anisocytic (4) 6 11 (24) (25)
   helicocytic 6

2. Guard cells:
   a. with inner stomatal ledges 3 12 25
   b. without inner stomatal ledges 1 2 4 5 6 7 8 9 10 11 13 14 15 16 17 18 19 20 21 22 23 24 26

3. Guard cells:
   a. with polar T-pieces 1 2 4 5 6 7 12 15 16 20 22 23 24 26
   b. without polar T-pieces 3 6 7 8 9 10 11 13 14 15 16 17 18 19 21 22 25

4. Guard cells:
   a. with a distinct peristomal rim 4 18 24
   b. without a distinct peristomal rim 1 2 3 5 6 7 8 9 10 11 12 13 14 15 16 17 19 20 21 22 23 24 25 26

5. Subsidiary cells:
   a. not to hardly submersed 4 5 6
   b. partly to almost completely submersed 2 3 9 10 12 13 14 15 16 17 18 19 21 22 23 24

6. Average length of stomata:
   a. 10–20 μm 9 21
   b. 20–30 μm 1 4 6 9 10 12 13 14 15 16 17 18 19 20 22 23 24 26
   c. 30–40 μm 2 3 6 7 8 11 13 15 18 22 24
   d. 40–50 μm 5 7 15 24 25

7. Average width of stomata:
   a. 10–20 μm 6 9 14 16 17 19 21 26
   b. 20–30 μm 1 3 4 6 7 9 10 11 12 13 15 16 18 20 22 23 24
   c. 30–40 μm 2 5 7 8 11 18 22 24 25
   d. 40–50 μm 24

8. Hairs or hair bases:
   a. absent on both sides 7 8 24
   b. present on adaxial and/or abaxial side 1 2 3 4 5 6 7 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25

9. Indumentum consisting of:
   a. normal hairs 1 2 3 4 6 7 9 10 11 12 13 14 15 16 19 20 21 22 23 25 26
   b. malpighiaceous hairs 3 5 6 14 17 24
   c. globular hairs 9 13 16 19 21
   d. uncinate hairs 9 13 16 21
   e. clustered hairs 16 18
   f. peltate-stellate hairs 18
   g. glandular hairs 18
   h. papilla-like hairs 7
   i. multicellular, uniseriate hairs 26

10. Normal hairs:
    a. with a bulging basal part 9 13 14 16 19 21
    b. without a bulging basal part 1 2 3 4 6 7 10 11 12 15 20 22 23 25 26

11. Normal hairs:
    a. with a second arm stub 3 4 6 11 12 14 15 22 23
    b. without a second arm stub 1 2 4 6 7 9 10 11 13 14 15 16 19 20 21 22 25 26

12. Normal hairs:
    a. with a thick-walled body and a thin-walled base 2 6 11 20 25
    b. without a thick-walled body and a thin-walled base 1 3 4 6 7 9 10 12 13 14 15 16 19 21 22 23 26

13. Normal hairs:
    a. with cuticular markings on the outer layer of their body 1 9 13 14 16 19 21
    b. without cuticular markings 1 2 3 4 6 7 10 11 12 15 20 22 23 25 26

14. Anticlinal cell walls:
    a. with pitted cuticular flanges at least on midrib and veins 1 7 9 12 16 22 24
    b. without pitted cuticular flanges 1 2 3 4 5 6 7 8 9 10 11 13 14 15 16 17 18 19 20 21 22 23 24 25 26

15. Minor veins:
    a. prominent 7 9 10 13 14 15 16 18 19 21 23 26
    b. not prominent 1 2 3 4 5 6 7 8 11 12 15 17 20 22 24 25.

6. DISCUSSIONS

6.1. The value of the characters used

The characters used in the descriptions and the synoptical key are not all of the same taxonomic and diagnostic value. Some may be very variable, such as pitting of the cuticular flanges, undulation of the anticlinal walls and also the type of granulation and/or striation of the cuticle (see pp. 336, 343 & 348). In, e.g., *Apodytes dimidiata*, 12 specimens of which were examined, the anticlinal walls varied from straight (Rudatis 786) to sinuous (B.S. 24941). Some genera, however, exhibit a rather constant kind of striation and/or granulation in their cuticle. In other genera such characters may be restricted to part of the species only.

The presence or absence of distinct inner stomatal ledges with adhering cuticular flaps and of a peristomal rim was usually found to be constant for a genus. This mostly also applies to stomatal types and hair types, though exceptions exist (see underlined figures in synoptical key). The absence of certain hair types in mature leaves of some species of a genus may be due to the fact that these hairs are shed easily (e.g. normal hairs with a thick-walled body and a thin-walled base). Therefore, character 9 of the synoptical key should only be used when positive.

The great taxonomic and diagnostic value of hair types is clearly demonstrated in *Gonocaryum*, *Platea* and *Pennantia corymbosa*. These taxa can be easily recognized by their indumentum only, and *Gonocaryum* and *Platea* occupy rather isolated positions within the family because of the slender papilla-like hairs in the former genus and the complex indumentum of glandular, peltate-stellate and clustered hairs in the latter. In large genera like *Gomphandra* a more detailed study of more material on the species level might prove useful (cf. *table I*).

6.2. Taxonomic implications

ENGLER (1896) and SLEUMER (1942 and personal information) distinguished four tribes within the Icacinaceae:

Icacineae (*Apodytes* I, *Cantleya* II, *Citronella* I, *Codiocarpus* II, *Gastrolepis* II, *Gomphandra* II, *Gonocaryum* II, *Hartleya* II, *Medusanthera* II, *Merrilliodendron* III, *Nothapodytes* III, *Pennantia* I, *Pittosporopsis* I, *Platea* I, *Pseudobotrys* I, *Rhyticaryum* III, *Stenonurus* II and *Whitmorea* II).

Iodeae (*Iodes* III, *Mappianthus* III, *Natsiatum* III and *Polyporandra* III).

Sarcostigmateae (*Sarcostigma* III).

Phytocreneae (*Miquelia* III, *Phytocrene* III and *Pyrenacantha* III).

In his more recent revision of the Malesian Icacinaceae, SLEUMER (1971) refrained from subdividing the family into tribes because of unsatisfactory correlation of the macromorphological characters with anatomical data.

The roman figures following each genus name in the above enumeration represent the three levels of specialization in Icacinaceae as recognized by BAILEY & HOWARD (1941), who based themselves on wood anatomy and nodal

anatomy. Group I is characterized by scalariform vessel perforations and trilacunar nodes; Groups II by a mixture of scalariform and simple vessel perforations and trilacunar nodes, and group III has simple vessel perforations and unilacunar nodes.

CALLEN-LOBREAU (1973, in the press) also distinguishes three levels of specialization for the family as based on pollen morphological characters. These three levels coincide with those of Bailey and Howard for wood and node.

The present results on leaf epidermal features are suitable for comparison with the subdivisions of the family as outlined above.

The Iodeae and Phytocreneae resemble each other strongly in leaf epidermal features. Globular and uncinate hairs are restricted to these tribes. The normal hairs usually have a bulging basal part. All genera show cyclocytic stomata with partly to almost completely submersed subsidiary cells. Only *Natsiatum* has a stomatal type intermediate between cyclocytic and anomocytic. The stomata are usually small; polar T-pieces are very unusual. The veins are always prominent. The leaf epidermal resemblance between these two tribes is not an isolated phenomenon. All representatives of the Iodeae and the Phytocreneae are lianas, their wood anatomical features have many points in common, and pollen-morphologically they appear to be quite close as well (Callen-Lobreau, personal communication).

Mappianthus, belonging to the Iodeae and kept apart from *Iodes* by Sleumer in 1969, was reduced by him to *Iodes* in 1971. We have retained the generic name here because there is no indication of a close affinity in leaf epidermal features. Particularly the indumentum and the stomatal dimensions are strikingly different in the two "genera". *Iodes* possesses normal hairs with a bulging basal part, uncinate hairs, and globular hairs, whilst *Mappianthus* only has normal hairs without a bulging basal part. Stomatal size in *Iodes* averages 18–23 × 16–20 μm, in *Mappianthus* 26–28 × 24–25 μm. The characters shared by the two taxa: cyclocytic stomata, absence of polar T-pieces and striking prominence of the minor veins are ubiquitous throughout the Iodeae and the Phytocreneae and therefore do not support the reduction of *Mappianthus* to *Iodes*. Madame Callen-Lobreau (in the press) also kindly informed us that the pollen of *Mappianthus* is different from that of *Iodes*.

Sarcostigma (the only genus of Engler's Sarcostigmateae) is of climbing habit like the Iodeae and the Phytocreneae. Leaf anatomically, however, there is not so much resemblance between *Sarcostigma* and the other lianas. In *Sarcostigma* the indumentum consists of normal hairs with a second arm stub. This is very unusual for the Iodeae and the Phytocreneae (except for *Natsiatum*), where the hairs show cuticular markings (except for *Mappianthus*), whereas in *Sarcostigma* they are smooth. Polar T-pieces are present in *Sarcostigma*, absent from the other lianas. Epidermal anatomy therefore in a way supports Engler's view of regarding *Sarcostigma* as a rather isolated genus.

The remaining Icacinaceae, all belonging to the Icacineae, are rather heterogeneous in leaf epidermal characters. This apparently also applies to secondary xylem, node, and pollen features, because the genera may be on all levels of

specialization in Bailey and Howard's and Callen-Lobreau's classification. Using leaf epidermal characters only it is impossible to recognize a clear pattern of relationship within the Icacineae. There is, moreover, no obvious correlation with pollen or wood anatomical characters. We therefore restrict ourselves to the discussion of some genera in which the leaf anatomical evidence seems more straightforward.

Most species of *Gomphandra* cannot be distinguished from those of *Medusanthera* (see descriptions and synoptical key), which points to a close relationship between the two genera, even more so because they are the only ones with anisocytic stomata.

Platea and *Gonocaryum* both occupy rather isolated positions within the family because of their unusual indumentum (see p. 354).

As for the other genera, one might speculate about their mutual affinities using the stomatal type as a guiding character (see also *fig. 27*). Without due consideration of other characters this would be very hazardous indeed, and since no absolute correlation with other epidermal, wood, node and pollen characters could be established, we refrain from further speculation here.

6.3. The stomatal type and level of specialization

In *fig. 27* the distribution of the stomatal types over the genera and the level of specialization according to BAILEY & HOWARD (1941) and CALLEN-LOBREAU (in the press) of the genera is summarized. For the interpretation of intermediate types see p. 331, and 346. The diagram shows the lack of absolute correlation of specialization level in wood, node and pollen with stomatal type. Level I houses genera with paracytic, anomocytic, cyclocytic and intermediate stomatal types. The genera in level II may have anisocytic, cyclocytic or intermediate stomatal types, and the genera of level III have the cyclocytic or an intermediate type of stomata. In spite of this lack of an absolute correlation however, there is a strong tendency of the cyclocytic stomata to be restricted to the most specialized genera and of the anisocytic and two intermediate types to occur in genera at the intermediate specialization level II. The paracytic and anomocytic types, together with their intermediate, are wholly restricted to genera belonging to the most primitive group I. It thus becomes likely that in the Icacinaceae the paracytic and anomocytic stomatal types represent a primitive condition and that the cyclocytic and anisocytic stomata are more derived.

For other plant groups several authors have also claimed the anomocytic or paracytic stomata to be primitive. ROHWEDER, SCHLUMPF & KRATTINGER (1971) assume that the anomocytic type is a starting point for many specialization series. GUYOT (1966) and GORENFLOT (1971) regard anomocytic stomata as primitive for the Umbelliferae and Saxifragaceae, respectively. Other authors, however, assume that the paracytic stoma is basic to the other types in the angiosperms, because this type occurs in a number of so-called primitive families (BARANOVA 1972). For the Icacinaceae we also advance the hypothesis that paracytic stomata are more primitive than anomocytic ones. It is obvious that

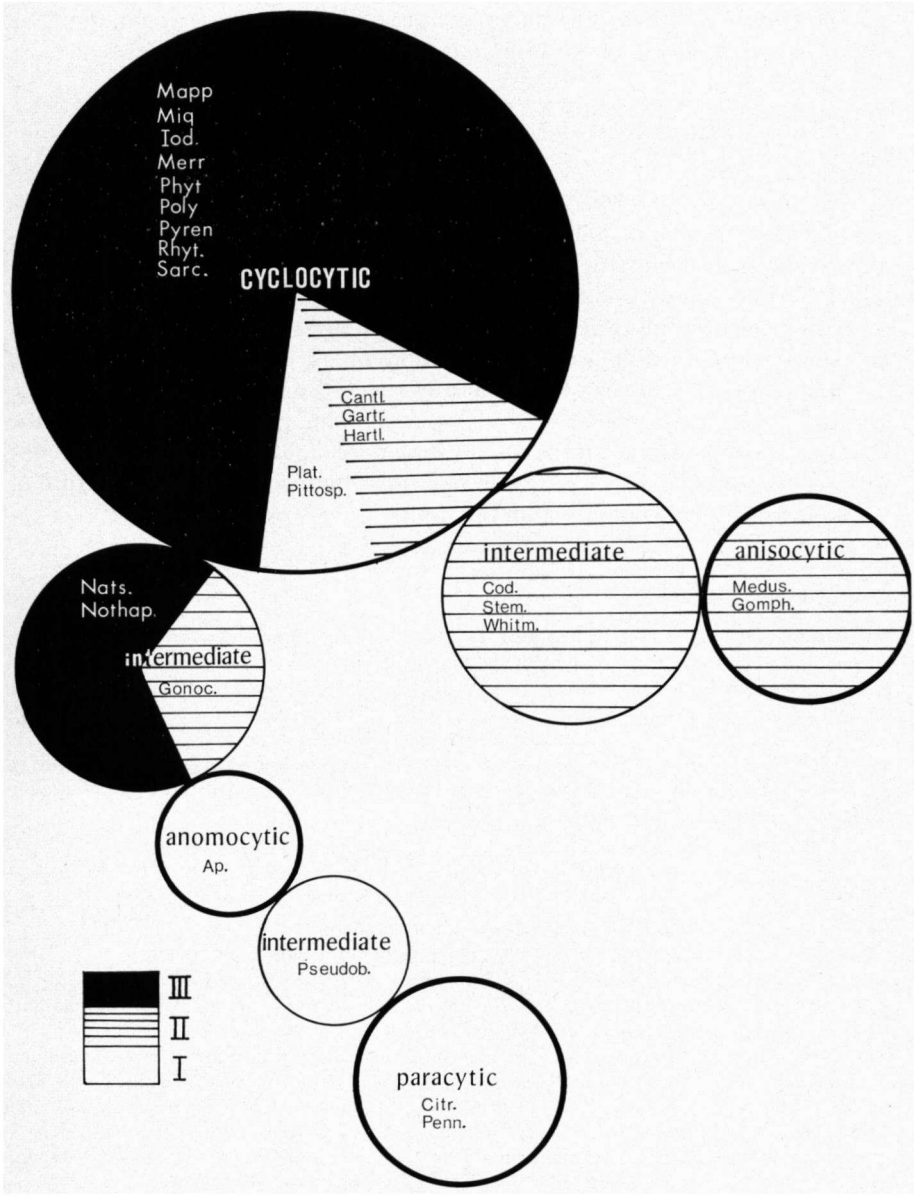

Fig. 27. Stomatal types and level of specialization in wood and node according to Bailey and Howard. See also the text. The circle with genera having anisocytic stomata also includes the species with helicocytic stomata. Generic names abbreviated.

ontogenetic studies should be undertaken to get a better understanding of the trends of specialization in the stomatal apparatus of the Icacinaceae.

7. GENERAL CONCLUSIONS

Epidermal diversity in the Malesian Icacinaceae can be profitably employed for the identification of genera. In some instances the epidermal characters provide straightforward indications of affinities, but the occurrence of intermediate types in most structures considered renders it impossible to subdivide this part of the family into tribes or other suprageneric taxa. This is in fact not surprising for a family where other characters like type of vessel perforation and general wood histology also show a more or less continuous variation. We therefore support Sleumer's view that any subdivision of the family would be artificial. An equally detailed study of the remaining genera and species of the Icacinaceae from Africa and America should be undertaken in order to test some of the ideas advanced here and to gain a more comprehensive picture of the huge range of variation within the family.

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