

**COMPARATIVE LEAF ANATOMY  
OF THE ASIATIC MYRISTICACEAE**

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CONTENTS

Summary . . . . .	116
Introduction . . . . .	116
Materials and methods . . . . .	117
A survey of the leaf anatomical characters in the Asiatic <i>Myristicaceae</i> . . . . .	118
The indumentum . . . . .	118
The cuticle . . . . .	120
The unspecialized epidermal cells . . . . .	121
Some miscellaneous epidermal features . . . . .	122
The stomatal complex . . . . .	122
The hypodermis . . . . .	123
The mesophyll . . . . .	124
The midrib . . . . .	124
The veins . . . . .	125
The petiole . . . . .	126
Crystals . . . . .	126
Secretory structures . . . . .	127
Sclereids . . . . .	128
Generic descriptions . . . . .	128
Explanatory notes . . . . .	128
<i>Gymnacranthera</i> . . . . .	129
<i>Horsfieldia</i> . . . . .	131
<i>Knema</i> . . . . .	136
Hair types of <i>Knema</i> . . . . .	140
<i>Myristica</i> . . . . .	141
Value of the characters . . . . .	146
Taxonomic implications . . . . .	151
Introductory remarks . . . . .	151
Below the genus level . . . . .	151
<i>Gymnacranthera</i> . . . . .	151
<i>Horsfieldia</i> . . . . .	152
<i>Knema</i> . . . . .	153
A tentative phylogeny of the hair types in <i>Knema</i> . . . . .	155
<i>Myristica</i> . . . . .	156
On the genus level . . . . .	158
On the family level . . . . .	159
Remarks on ecology . . . . .	161
Keys . . . . .	162
Synoptical key to the Malesian species and varieties of <i>Gymnacranthera</i> . . . . .	162
Synoptical key to the groups of <i>Knema</i> species . . . . .	163
Acknowledgements . . . . .	164
References . . . . .	164

## SUMMARY

The leaf anatomy of *c.* 60 species of the four Asiatic genera of the *Myristicaceae* (*Gymnacranthera*, *Horsfieldia*, *Knema* and *Myristica*) is described in detail. *Myristicaceae* have characteristic, uniseriate hairs, the cells of which have arms. The number of arms per cell and the relative length of the arms are important characters to separate the Asiatic genera. The hairs of *Knema* can be classified further into different types. Many species of *Myristicaceae* have a layer of cutinaceous, alveolar material overlying the cuticle proper on the abaxial leaf surface. In angiosperms such a layer was hitherto only reported for *Winteraceae*. Guard cells are often embedded in the subsidiary cells. The paracytic stomatal complex in *Knema* and *Myristica* is sunken and overarched by typically arranged bordering cells, leaving a star-shaped opening in *Knema* and forming a ring in *Myristica*. The vascular system of the midrib is composed of an abaxial and adaxial collateral bundle (the latter is absent from *Gymnacranthera*), and there are always free phloem bundles in the centre.

The diagnostic and taxonomic value of these and many other varying leaf anatomical characters is analysed and discussed. Much of the leaf anatomical variation can be used for species grouping and identification, and the four genera can easily be separated on leaf anatomical characters (see table V, and synoptical keys at the end of this paper). Leaf anatomy lends little support to a close affinity of *Myristicaceae* with *Annonaceae* and *Canellaceae*, and although the family shows several typically Magnolialean characters (e.g. oil cells, paracytic stomata) leaf anatomy points to a fairly isolated position of the family within the order *Magnoliales*.

Many of the leaf anatomical characters of *Myristicaceae* are highly xeromorphic. This is discussed in relation to the markedly mesic ecology of the family.

## INTRODUCTION

In 1897 Warburg published his monograph of the *Myristicaceae*, in which he recognized 15 genera. In another publication (Warburg, 1895) he paid special attention to the remarkable hairs, present in this family. Sinclair worked towards a revision of the four Asiatic genera of the *Myristicaceae* for Flora Malesiana (Sinclair, 1958a and b, 1961, 1968, 1974 and 1975) and recognized 6 species in *Gymnacranthera*, 37 in *Knema*, 72 in *Myristica* and about 50 in *Horsfieldia*. When he died in 1968 his work remained unfinished. Since much new material has been collected and has become available the last several years, De Wilde (Rijksherbarium, Leiden) started a new revision of the Asiatic genera for Flora Malesiana, with *Knema* as the first genus (De Wilde, 1979), and recognized 83 species. Complementary to De Wilde's revision work it seemed worthwhile to explore the leaf anatomical diversity within the Asiatic *Myristicaceae*, since leaf anatomy can often add to our knowledge of taxonomic boundaries and patterns of natural affinity, and be of help in the identification of sterile specimens. The leaf anatomical literature on *Myristicaceae* is scarce. A short characterization can be found in Solereder (1899, 1908) and Metcalfe and Chalk (1950). Warburg's publication (1895) on the hairs has been mentioned before. Worsdell (1908) recorded strands of medullary phloem in the midrib and petiole of *Myristica fragrans*. Rao and Chin (1966) studied the foliar sclereids in some species of the family. Siddiqi and Wilson (1975c) and Armstrong (1975) included leaf anatomy in their studies of several species of *Knema* and *Horsfieldia* respectively.

This study comprises the leaf anatomy of *c.* 60 species, belonging to the four Asiatic genera, with an emphasis on *Knema*. In order to gain some impression of leaf anatomical variation within a species, two specimens of most species or varieties were studied. Of one species per genus five or ten specimens were studied.

## MATERIALS AND METHODS

The material was taken from dried specimens present in the Rijksherbarium, Leiden; only the material of *Knema korthalsii* came from the Kew Herbarium. To reduce the chance of misidentification, only material from specimens with flowers, identified by Sinclair, or in the case of *Knema*, material identified by De Wilde was taken. Fully developed leaves were selected, but the study of the indumentum sometimes required younger material, when the hairs had been shed from the older leaves. Permanent slides, mounted in Euparal, were made of transverse microtome sections of the central part of the lamina and both distal and basal end of the petiole and of free hand paradermal sections. The sections were stained with a safranin-haematoxylin mixture. For some specimens lignin tests were carried out with phloroglucinol and hydrochloric acid. Cuticular preparations of all specimens were made using equal volumes of hydrogen peroxyde 30% and glacial acetic acid. The cuticles were stained with Sudan IV and mounted in glycerin-jelly.

For scanning electron microscopy fragments of leaves were shaken ultrasonically for half an hour in warm ether, alcohol or chloroform or boiled in water, alcohol or ether and subsequently rinsed in fresh dissolvent in order to remove any wax. The leaf fragments were coated with gold.

Measurements and counts were carried out as follows: The width of the guard cell pairs at their widest part and the length from pole to pole were measured with a linear eye piece micrometer at  $\times 1000$  magnification in the free hand sections. Ten measurements were made per leaf. For the lamina thickness areas between the veins were measured, for the cuticle thickness the thickest parts of the cuticle between the veins were measured, the tips of the papillae excepted. For both characters at least 7 measurements were carried out per leaf. The number of basal parts of hairs on areas with a surface of half a field of vision at  $\times 400$  magnification ( $0.063 \text{ mm}^2$ ), distributed over the midrib and the lamina between midrib and leaf margin was counted; at least 7 counts per leaf for both midrib and areolae were made.

## Specimens studied.

*Gymnacranthera bancana* (Miq.) Sinclair var. *bancana*; Singapore: Sinclair 44045; var. *borneensis* (Warb.) Sinclair; Borneo: Bujang S 11044. — *G. contracta* Warb.; Borneo: Jacobs 5326, 5363; Haviland 134; Zehnder 9437; Anderson 9420; Galau S 14970; Ashton et al. SAN 17514; Kostermans 7241, 13696; Billiton: van Rossum 63. — *G. eugeniifolia* (A. DC.) Sinclair var. *eugeniifolia*; Sumatra: Rahmat si Boeea 8035; Malaya: Whitmore FRI 3908; var. *griffithii* (Warb.) Sinclair; Sumatra: Rahmat si Toroes 3944; Malaya: King's coll. 6622. — *G. forbesii* (King) Warb. var. *crassinervis* (Warb.) Sinclair; Borneo: Rosli 3393; Jacobs 5259; var. *forbesii*; Malaya: FRI 5749; King's coll. 6591. — *G. paniculata* (A. DC.) Warb. var. *paniculata*; Philippines: Miranda 18969; var. *zippeiana* (Miq.) Sinclair; Moluccas: bb 23779.

*Horsfieldia crassifolia* (Hook. f. & Th.) Warb.; Borneo: Sanusi b. Tahir S 12325; Sumatra: Theunissen 59. — *H. glabra* (Bl.) Warb.; Java: Jungkuhn 230. — *H. irya* (Gaertn.) Warb.; West New Guinea: van Royen 5101; Java: van Steenis 5274. — *H. iryagedhi* (Gaertn.) Warb.; cult. ex. — *H. macrocoma* (Miq.) Warb.; West New Guinea: Schram BW 2796; Philippines: Merrill 4031. — *H. parviflora* (Roxb.) Sinclair; Moluccas: Kostermans 767. — *H. sabulosa* Sinclair; Borneo: Sinclair & Kadim bin Tassim 10437. — *H. sylvestris* (Houtt.) Warb.; West New Guinea: Koster BW 4446; Schram BW 1839; van Royen 4510; Gjellerup 407; bb 30811; Moluccas: Robinson 235; Kostermans 1123; Kuswata & Soepadmo 3; Pleyte 379.

Superficially studied: *H. fulva* (King) Warb.; Malaya: Kochummen KEP 80627; *H. superba* (Hook. f. & Th.) Warb.; Singapore: Sinclair SFN 40047.

*Knema ashtonii* Sinclair var. *ashtonii*; Borneo: Sibat ak Luang S 22841; var. *cinnamomea* de Wilde; Borneo: Murthy & Ashton S 23314. — *K. attenuata* (Hook. f. & Th.) Warb.; India, Peninsular: Subramanian 1407. — *K. conferta* (King) Warb.; Singapore: Sinclair SFN 40046. — *K. curtisii* (King) Warb. var. *curtisii*; Borneo: Ashton BRUN 5587; Malaya: Whitmore FRI 12326. — *K. elmeri* Merr.; Borneo: Wood SAN A4139, Ashton S 18294. — *K. furfuracea* (Hook. f. & Th.) Warb.; Malaya: Kadim &

Mahmud 22. — *K. globularia* (Lamk.) Warb.; Thailand: Hansen & Smitinand 12308. — *K. hookeriana* (Wall. ex Hook. f. & Th.) Warb.; Sumatra: Lörzing 12207. — *K. intermedia* (Bl.) Warb.; Java: Dransfield 2488. — *K. korthalsii* Warb.; Philippines: Cenabra FB 29973. — *K. kunstleri* (King) Warb. ssp. *kunstleri*; Malaya: Kochummen FRI 2252. — *K. latifolia* Warb.; Borneo: Mikil SAN 31371. — *K. laurina* (Bl.) Warb. var. *laurina*; Malaya: Chew Wee Lek 143; Kochummen FRI 2431; Sumatra: de Wilde & de Wilde-Duyffes 14429; Borneo: Ampuria SAN 41273; Java: Ja. 2502. — *K. linguiformis* (Sinclair) de Wilde; Borneo: Ilias Paie S 27799. — *K. linifolia* (Roxb.) Warb.; India, Assam: Plants of Assam 6188. — *K. lunduensis* (Sinclair) de Wilde; Borneo: Chai S 18478. — *K. malayana* Warb.; Singapore: Sinclair SFN 40714. — *K. mandarahan* (Miq.) Warb.; Sumatra: van Steenis 10092. — *K. oblongata* Merr. ssp. *oblongata*; Borneo: Bakar SAN 24985; Chai S 34822. — *K. oblongifolia* (King) Warb.; Malaya: Chelliah KEP 98224; Whitmore FRI 0111. — *K. pallens* de Wilde; Borneo: Meijer 2533; Lantoh SAN 73312. — *K. percoriacea* Sinclair forma *sarawakensis* de Wilde; Borneo: Sibat ak Luang S 23645. — *K. plumulosa* Sinclair; Malaya: Carrick 1510. — *K. pseudolaurina* de Wilde; Malaya: Shah MS. 1403. — *K. psilantha* de Wilde; Borneo: Anderson S 14373; Othman bin Haron S 29064. — *K. pulchra* (Miq.) Warb.; Borneo: Kostermans 5103; Malaya: Corner SFN 29015. — *K. retusa* (King) Warb.; Malaya: Sinclair 9907, 9908. — *K. rubens* (Sinclair) de Wilde; Malaya: Shah MS. 1312. — *K. rufa* Warb.; Borneo: Asah anak Unyong S 13963. — *K. tenuinervia* de Wilde ssp. *setosa* de Wilde; Thailand: van Beusekom & Geesink c.s. 4747. — *K. tomentella* (Miq.) Warb.; Moluccas: de Vogel 4197.

*Myristica chrysophylla* Sinclair var. *entrecasteauxensis* Sinclair; New Guinea, Fergusson I.: Brass 25986; Normanby I.: Brass 25893. — *M. cinnamomea* King; Borneo: Wood SAN 15066; Singh SAN 24236. — *M. fatua* Houtt. var. *fatua*; Moluccas: Kuswata & Soepadmo 57; var. *papuaana* Markgraf; New Guinea: Koster BW 1016. — *M. fragrans* Houtt.; Philippines: Sulit 15023; Moluccas: de Vriese s.n.; Beguin 787. — *M. gigantea* King; Malaya: Scortechini s.n. — *M. globosa* Warb.; Papua New Guinea: Carr 12890. — *M. guatterifolia* A. DC.; Java: Kostermans UNESCO 7; Borneo: Sinanggul SAN 39995; Mikil SAN 30298; Elmer 20850; Aban Gibot SAN 32924; Agan b. Ambulah SAN 37177; Kostermans 4873; Corner BRUN 5365; Malaya: FRI 5056. — *M. lepidota* Bl.; West New Guinea: Lundquist 121 (=bb 32840). — *M. maingayi* Hook. f.; Malaya: Maingay 1289. — *M. maxima* Warb.; Sumatra: Thorenaar (Enderit) 55E1P624; Grashoff 908. — *M. sphaerosperma* A. C. Smith; West New Guinea: Brass & Versteegh 12547. — *M. subalulata* Miq.; East New Guinea: Floyd & Havel NGF 7446. — *M. villosa* Warb.; Borneo: Kostermans 6438; Wood SAN A4747.

#### A SURVEY OF THE LEAF ANATOMICAL CHARACTERS IN THE ASIATIC MYRISTICACEAE

##### The indumentum (figs. 1–3, photos 1–10, 19, 21, 25)

Hairs are present, at least in young leaves, on the adaxial and abaxial surface (in *Horsfieldia*, *Knema*, and in most species examined of *Myristica*) or only on the abaxial surface (in *Gymnacranthera* and some *Myristica* species), usually most frequent on the midrib on both sides in *Horsfieldia* and *Knema* and adaxially in *Myristica*, most frequent on the lamina in *Gymnacranthera* and abaxially in *Myristica*.

The indumentum appears very different per genus, but one can recognize a basic hair type: a sympodially branched, uniseriate trichome (Warburg, 1895). In other words, a hair is composed of one row of short to tall cells, having one or two arms each, one or two, rarely more cells nearest the epidermis, the so-called stalk cells, excepted. In *Gymnacranthera* and *Myristica* the cells have two arms, not of the same length in *Gymnacranthera*; the cells in *Horsfieldia* and *Knema* have one arm (fig. 2, 3; photo 4, 9). The arrangement of the arms may give a hair, as seen from above, the appearance of a stellate hair (e.g. photo 7). In *Horsfieldia* and *Knema*, the walls between the cells may be very oblique and the 'body' of each cell very small; this may obscure the uniseriate nature. The length of the hairs is variable. Short hairs, consisting of a few cells (most typical for *Gymnacranthera*) to extremely long hairs, consisting of numerous cells, which are sometimes filiform, with a length of about 250  $\mu\text{m}$  per cell in *Knema*, may occur. In *Knema* the species show a range of hair forms, which will be discussed separately. In older leaves the hairs have often been

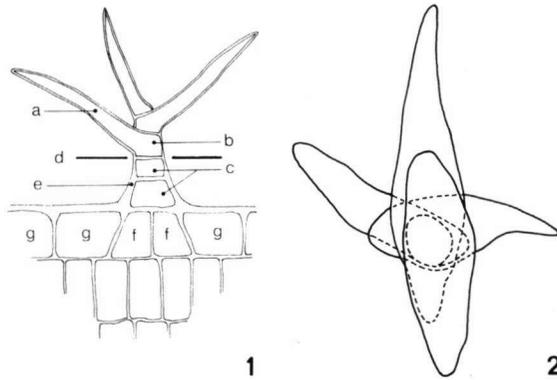


Fig. 1. Diagram of *Myristicaceae* hair. — a = arm; b = body; c = stalk cell; d = line separating the deciduous and persistent part of the hair; e = cutinized ring; f = basal cells (e and f form together the basal part of the hair); g = unspecialized epidermal cells. — Fig. 2. *Gymnacranthera contracta*. — Camera lucida drawing of hair in surface view showing unequal length of arms of hair cells,  $\times 400$ .

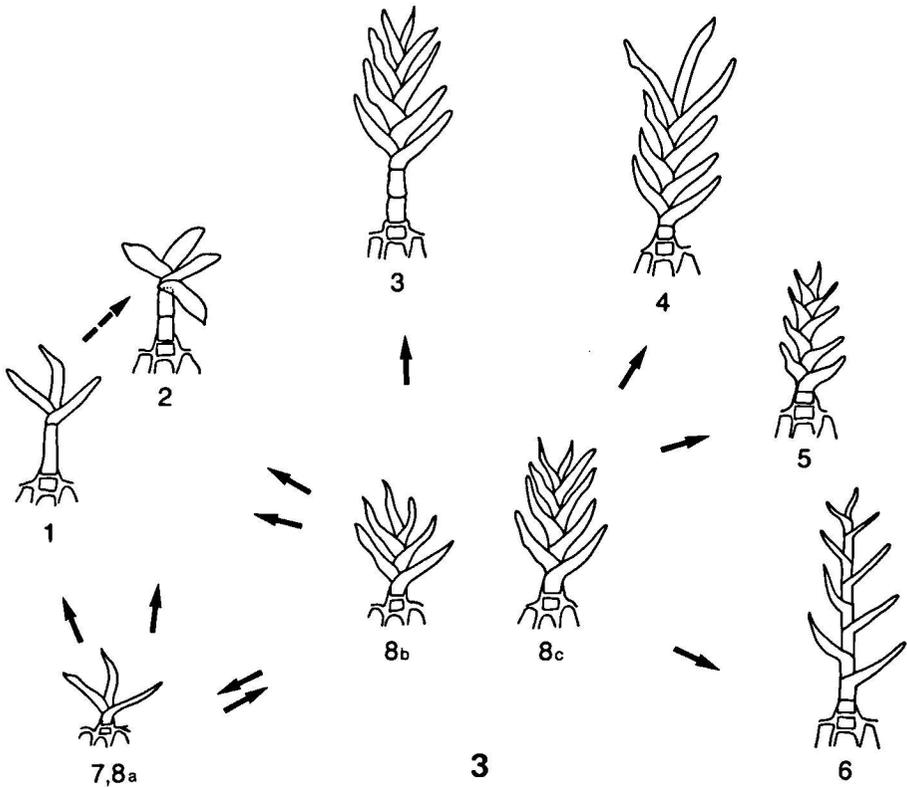


Fig. 3. Diagram of the different hair types in *Knema*. — Arrows indicate tentative phylogenetic derivations. See text for definitions of different types.

shed, but a basal part is always left: one or two stalk cells nearest the epidermis have strongly cutinized walls, as have the unspecialized epidermal cells. The upright walls of this most proximal part of the hair remain as a cutinized ring on the epidermis after the rest of the hair has been shed (fig. 1). Two to numerous (in *Horsfieldia* and *Knema*) mainly small cells, arranged in a characteristic circle or oval, subtend this cuticular wall (photo 21). Usually in *Gymnacranthera* and *Myristica* one small circular cell takes this position (photo 25 and fig. 1). These basal cells may be slightly sunken to elevated. Armstrong (1975) described 'circular' and 'oval patterns of epidermal cells' for *Horsfieldia*, but did not connect these patterns with the hairs.

The hair index as a measure of hair density may be very variable in leaves of one specimen or even in one leaf (Stace, 1965), and is therefore of little taxonomic use. The number of hairs (in fact remaining basal parts of the hairs) per surface unit is also variable, but it is more easy to determine and gives nevertheless a rough impression of the difference in hair density, provided that fully developed leaves are studied. It is of course essential to know whether hairs have persisted in fully developed leaves or not. When necessary this has been checked by studying the leaves at low power magnification with a dissecting microscope because the absence of hairs from anatomical slides may be due to microtechnical artefacts.

#### The cuticle (photos 11–18, 21, 28)

After boiling in water, alcohol or ether, or shaking in warm chloroform, a structured layer, overlying the cuticle proper remains on the abaxial side in many species. An identical structure, referred to as alveolar material, has been recorded for the *Winteraceae* by Bailey and Nast (1944), and was thoroughly studied by Bongers (1973). In the Asiatic *Myristicaceae* this material is absent in most of the species examined of *Horsfieldia* and in some *Myristica* species. When present the material usually covers the whole epidermis except the guard cells, and the cells overlying the midrib, the major veins and the leaf margin, (photo 28), but in *Knema intermedia* and *Knema plumulosa* it is only conspicuously present on the cells bordering on the subsidiary cells of the stomata (photo 12); in *Horsfieldia sylvestris* it is only slightly present on the subsidiary cells. The sunken subsidiary cells in *Knema* and *Myristica* usually do not have alveolar material (see under 'The stomatal complex').

One leaf of a species of both *Gymnacranthera* and *Knema* has been boiled in a 9:1 mixture of acetic acid anhydride and sulfuric acid. The alveolar material was resistant to this coarse treatment (used in palynology) and moreover stained positively with Sudan IV. From the resistance to organic solvents and to this acetolysis it was concluded that the composition is cutinaceous.

The alveolar material in *Gymnacranthera* and *Knema* is composed of a dense reticulum of irregularly structured erect plates (photo 11), in *Myristica* it is more variable in appearance: species with plates occur (photo 13), but species with rod-like structures (photo 14) or warts (photo 15) are also present in this genus. An irregular, porous layer is present on the abaxial surface in *Horsfieldia iryagedhi* (photo 16). See Koster and Baas (in the press) for a more elaborate description of the alveolar material in the Asiatic *Myristicaceae*.

Besides the alveolar material, there may be other types of sculpturing of the cuticle (but not as a layer overlying the cuticle proper). Striations (fine ridges) are present in some species, most conspicuously abaxially in *Horsfieldia crassifolia* (photo 21) and *Horsfieldia sylvestris*, faintly adaxially in some *Knema* species.

Grooves corresponding with the anticlinal walls of the epidermal cells are rarely present in *Horsfieldia*, *Knema* and *Myristica* (photo 17). Adaxial convex sculpturings of the cuticle are present in *Knema rufa* (photo 18). It should be noted that one can only clearly distinguish ridges, grooves and other sculpturings with the scanning electron microscope. However, not all specimens have been examined this way adaxially. Moreover, alveolar material, when present on the abaxial surface, may obscure other sculpturings of the cuticle.

The cuticular layer (sensu Stace, 1965) may appear granular in the light microscope or smooth. The alveolar material, when present, obscures this feature in surface view. In this case it must be examined in the transverse sections.

Wax, although an important feature, has not been considered in this study, because of the ephemeral nature of this material.

The cuticle thickness, exclusive of the alveolar material, varies between 2–18  $\mu\text{m}$  adaxially and 1–11  $\mu\text{m}$  abaxially. The thickness per species is fairly constant, although a difference between two specimens of one species (*Gymnacranthera contracta*, abaxially) of 9  $\mu\text{m}$  has been found to occur.

#### The unspecialized epidermal cells (photos 13, 16, 20, 22, 30, 34)

The unspecialized epidermal cells are polygonal in surface view. The cells overlying the midrib and the major veins are square to rectangular, with the long axis parallel or in some cells perpendicular to the course of the veins. Adaxially they usually tend to be polygonal rather than rectangular. Venation patterns have not been studied. Only the prominence of minor veins has been recorded (that is when the course of the vein is perceptible in the macerations in the pattern of the overlying epidermal cells). In *Gymnacranthera*, *Horsfieldia* and *Myristica* the minor veins are slightly visible in the epidermal cell pattern of the abaxial epidermis only; in *Knema* they are prominent abaxially and faintly visible adaxially.

In the macerations the cuticular flanges on the adaxial surface are usually more or less sinuous at high focus and straight to slightly curved at lower focus (photo 22); on the midrib and the major veins they are less sinuous. Thin areas of cuticle of varying conspicuousness are present in the loops of the undulations. This character is very striking in *Gymnacranthera* (photos 22, 30), where even on the midrib and the major veins prominent thin areas are present. In some transverse sections these areas indeed proved to be thin areas of the cuticle only: the outer wall has the same thickness all over. On the abaxial surface the cuticular flanges are mostly more or less straight, in some species of *Gymnacranthera* and *Horsfieldia* they are slightly sinuous. In these species thin areas of the cuticle may be present, but inconspicuously so. Pitting of the cuticular flanges (cf. Bongers, 1973) is present in nearly all specimens, but in low frequencies and inconspicuous, least inconspicuous on the midrib, the major veins and the leaf margin, where the flanges are most straight.

In transverse sections the adaxial unspecialized epidermal cells are usually square to rectangular, on the midrib they are often dome-shaped (not in *Gymnacranthera*). The abaxial unspecialized epidermal cells are usually more or less dome-shaped (photo 34). The cuticle of these cells is slightly thickened on the top of the dome. For the measurements of the cuticle thickness these thickened parts have been taken.

Abaxial papillae occur in many species of *Knema* (most striking in *Knema conferta* and *Knema linifolia*), in *Horsfieldia iryagedhi* and in *Myristica gigantea*

and *Myristica maingayi* (photos 13, 16, 20). In the species mentioned of *Horsfieldia* and *Knema*, where the papillae may be considered as extreme forms of dome-shaped cells, the thickness of the cuticle of one single cell does not vary strongly, whereas in the *Myristica* species mentioned the epidermal cells have a strongly thickened cuticle on the top of the papillae (photo 20).

#### Some miscellaneous epidermal features (photos 28—31)

Often and in species distributed over all the four genera epidermal cells are present with a very thin cuticle or with a thin cuticle or a hole in only the centre of the cell surface (photo 28). These cells are usually relatively small, about circular in shape and surrounded by more or less radially oriented epidermal cells. They may occur on the adaxial as well as the abaxial surface, mostly on the midrib, the major veins and along the leaf margin. In transverse sections the cells appear as large empty idioblasts in the epidermis, sunken and to a large extent situated in the mesophyll (photo 29). The outer wall has a restricted surface (in this case the cell is pear-shaped) or is partly covered by the surrounding epidermal cells. In view of these properties, the cells are probably secretory.

In many macerations areas are present of several cells, not sharply delimited, staining less deeply and with relatively thin cuticular flanges (photo 30). From transverse sections it appears that druses are connected with this feature. The large crystalliferous idioblasts are adjacent to epidermal cells, which are flattened, having a relatively thin cuticle and narrow and short cuticular flanges (photo 31). The areas mentioned are present in *Myristica* adaxially, in *Gymnacranthera* and *Horsfieldia* adaxially and abaxially, and they are absent in *Knema*.

Cork warts are present in each specimen examined, but usually in small numbers. Since they are irregularly distributed and shaped, their origin is probably traumatic. However, *Horsfieldia glabra*, *Horsfieldia sabulosa*, *Knema conferta* and *Knema kunstleri* abound in more or less circular structures, identical to regular cork warts. These structures are most frequent on the abaxial surface, having a regular distribution, in the *Knema* species mostly on and along the midrib and the veins. De Wilde refers to these cork warts (De Wilde, 1979) and uses them as a lens character to separate a group of species from others. In *Horsfieldia glabra* groups of basal cells of hairs are probably the origin of most of the cork warts. This species loses its hairs early in the leaf ontogeny, but basal parts remain. In the fully developed leaves on the adaxial surface the groups of basal cells are large and consist of numerous small cells; sometimes a transition to a cork wart is recognizable. On the abaxial surface relatively small basal parts of hairs are rarely present, whereas cork warts abound. Perhaps the basal cells become subdivided in the course of the leaf development and finally the walls of these cells are suberized. Why this suberization frequently occurs on the abaxial surface only is not understood. Moreover there is some evidence that a cork wart is developed from a stomatal complex. Sometimes the outlines of a guard cell pair (or a part of it) are recognizable in a cork wart.

#### The stomatal complex (photos 13, 23—27)

Stomata are confined to the abaxial epidermis; however, in *Gymnacranthera bancana* var. *borneensis* a very small number is also present in the adaxial epidermis. They are randomly distributed, abundant on the areolae, scanty on the midrib, the veins and along the leaf margin. If they are present here, the stomatal complex shows abnormalities.

Several authors have pointed out that the stomatal index may be extremely variable within a species (Bongers, 1973; Jansen & Baas, 1973; Van Staveren & Baas, 1973). Stomatal indices have therefore not been determined in this study.

The stomatal type of the species examined is paracytic (photo 27). The dimensions of the guard cell pairs range from 8 to 21  $\mu\text{m}$  for the width and from 15 to 39  $\mu\text{m}$  for the length. The genera have a different size range (in *Myristica* relatively long stomata and in *Gymnacranthera* and *Knema* relatively short stomata are present), but a large overlap occurs. The variation in one single leaf can be up to 8 and 12  $\mu\text{m}$  for the width and length respectively. However, the average values show fairly little variation in a genus. Therefore, the data for the stomatal sizes per specimen are not given in tables. Giant or water stomata have been recorded for some specimens of *Gymnacranthera contracta* and *Gymnacranthera forbesii* var. *forbesii* only.

The guard cells are often embedded in the subsidiary cells, most conspicuously in *Gymnacranthera* and *Knema*; here, in a section perpendicular to the pore, the subsidiary cells fully enclose the guard cells, the poral sides excepted (photo 24). In *Gymnacranthera* such sections also show pointed, sometimes protruding subsidiary cells, whereas the unspecialized epidermal cells are lowly dome-shaped or square to rectangular. Outer stomatal ledges are fairly well developed in some species of *Horsfieldia* only.

A peculiar character is formed by the cells surrounding the stomatal complex in *Knema* and *Myristica*. In the cuticular macerations and the free hand sections of the *Knema* species the stomatal complex itself is difficult to observe, lying on a lower level than the other epidermal cells. A star-shaped opening, left by 4 to 6 epidermal cells overarched the stomatal complex, indicates the position of the stoma (photo 23). The transverse sections show the strongly sunken stomatal complex with a thin cuticle, overarched by more or less horizontally directed papillae of the bordering epidermal cells (photo 24); these nipple-shaped papillae give the star its characteristic form. Siddiqi and Wilson (1975c) proposed that the 'star-shaped structure' is formed by hypodermal cells. This appears to be incorrect. In *Myristica* the sunken stomatal complex is partly overarched by more or less upright papillae of the 4 to 11 bordering epidermal cells (photo 26). In surface view these papillae, varying in height per species, form a ring above the stomatal complex (photo 13, 25). As stated elsewhere, the unspecialized epidermal cells in most species are without papillae.

### The hypodermis (photo 32)

An adaxial hypodermis as a continuous layer of translucent cells, distinct from the epidermis, has been recorded for some *Horsfieldia* and *Myristica* species. In some *Knema* species and specimens of *Myristica guatteriifolia* the hypodermis is only locally developed, especially near the midrib and the major veins, and intergrades with the palisade parenchyma.

In *Horsfieldia* some cells of the hypodermis have periclinal division walls. In this genus swollen cells with thin walls occur in the hypodermis, or few-layered groups of these cells are adjacent to the adaxial and sometimes to the abaxial epidermis, in elevations of the leaf surface (photo 32), and/or are present in the periphery of the ground tissue of the midrib and the petiole, where these cells in *Knema* and *Myristica* also occur, sometimes probably of traumatic origin.

An inconspicuous *abaxial* hypodermis is present in some *Knema* species and in *Myristica sphaerosperma*.

### The mesophyll

The mesophyll is virtually always dorsiventral, with mostly two to three, sometimes up to four adaxial layers of palisade parenchyma, the most abaxial layer intergrades with the spongy tissue. *Horsfieldia sabulosa* has an isobilateral leaf. The cells of the palisade parenchyma have a different length to width ratio per layer and per species, in a range from one to five.

Strong birefringence of cell walls (secondary walls in a few leaves demonstrated to be lignified; i.e. sclerified cells) occurs in the mesophyll in a whole range of possibilities. Either the cells of only the abaxial layers of the spongy tissue have birefringent walls (in some species of *Gymnacranthera* and *Knema*) or the whole spongy tissue is interspersed to variable extents with such cells (in some species of *Gymnacranthera*, *Knema* and *Myristica*) or even the palisade parenchyma cells have thick, strongly birefringent walls, supplied with large pits (in *Knema mandarahan* and *Knema pallens*). There are also species without cells with strongly birefringent walls in the mesophyll (particularly in *Horsfieldia*). In the leaf margin the cells, adjacent to the epidermis, often have sclerified walls.

**Note:** Most *Horsfieldia* species have brittle leaves; the dried leaves break soon, and for the transverse sections the cell walls cannot be made to expand completely in domestic bleach or are damaged in the sectioning process. This caused the transverse sections to be of bad quality and made the study of anatomical characters difficult. In consequence, the lamina thickness and the thickness of midrib to thickness of lamina ratio have to be taken with some reservation (and not in *Horsfieldia* specimens only, because of the variation in swelling behaviour in domestic bleach).

### The midrib (figs. 4—7)

The midrib of the species studied is fine to robust; criteria for these characters are: ratio thickness of midrib/thickness of lamina 3 and less: fine; ratio 6 and more: robust. The midrib is abaxially prominently raised, and adaxially raised in *Horsfieldia*, *Knema* and *Myristica* as well (in some *Horsfieldia* and *Myristica* species there is only a raised central ridge adaxially), but in *Gymnacranthera* and some *Horsfieldia* species the midrib is more or less flat to concave on the adaxial surface.

The vascular system is quite remarkable. Generally there is a more or less straight adaxial bundle and an arc-shaped abaxial bundle, sometimes joined together. The phloem is arranged in separate strands, often in two layers. One to numerous phloem bundles are interspersed in the ground tissue between the main bundles, often accompanied by xylem elements (fig. 4); these centrally situated phloem bundles have been mentioned before by Worsdell (1908) for *Myristica fragrans*, by Siddiqi and Wilson (1975c) for *Knema* species and by Armstrong (1975) for *Horsfieldia* species. This type of vascular system is present in *Horsfieldia*, *Knema* and *Myristica*. In some *Knema* species there is a complete collateral bundle in the pith (fig. 5); in some *Horsfieldia* and *Myristica* specimens the adaxial bundle is strongly interrupted, or there are several small bundles (fig. 6). In *Gymnacranthera* the adaxial bundle is absent, but phloem bundles occur in the centre of the midrib as described above (fig. 7). The whole vascular system is surrounded by groups of sclerenchyma fibres, which often are associated with peripheral phloem groups (figs. 4—7); fibre groups also occur in the centre of the midrib, associated with and often even in the centre of the phloem bundles (figs. 4—7).



Figs. 4–9. Vascular patterns in midrib and petiole. Camera lucida drawings. 4, 6, 7, and 9:  $\times 40$ ; 5 and 8:  $\times 16$ . — 4. *Knema laurina*, midrib. — 5. *Knema lunduensis*, midrib. — 6. *Horsfieldia glabra*, midrib. — 7. *Gymnacranthera contracta*, midrib. — 8. *Knema linifolia*, distal part of petiole. — 9. *Myristica lepidota*, basal part of petiole. — Lines: xylem; black: sclerenchyma; white: phloem.

The ground tissue is from centre to periphery parenchymatous to collenchymatous, often interspersed to various extent with cells with sclerified walls, especially in *Gymnacranthera* and *Knema*, in the former mostly abaxially; in these genera there are often several layers of these cells at the periphery of the midrib. Often the collenchyma or the sclerified cells appear as a locally developed one- to several-layered hypodermis on the adaxial side of the midrib. In specimens of *Gymnacranthera* and *Myristica*, rarely in *Knema*, adaxial chlorenchyma is continuous in the midrib, situated abaxially of the collenchyma or the layers of sclerified cells, if present.

#### The veins (photos 33, 34)

The major veins are adaxially either slightly depressed (not in *Gymnacranthera*), or flat or raised; abaxially they are always raised.

The veins are supplied with collateral bundles and sclerenchyma fibres; the major veins may have a more complex vascular system, intermediate between that of midrib and minor veins. *Gymnacranthera*, *Horsfieldia* and *Myristica* have sclerenchyma caps at the adaxial and abaxial side of the bundle (little developed in *Gymnacranthera*). In *Knema* the two well-developed sclerenchyma caps are connected by one more or less continuous row of fibres at each side, thus constituting a sclerenchymatous bundle sheath. A usually poorly differentiated parenchymatous bundle sheath surrounds the bundle and the sclerenchyma. In a number of *Knema* species there is a fairly well-developed parenchymatous bundle sheath, which may be continuous to either the adaxial or the abaxial epidermis or to both (photo 33); the cells of these bundle sheath extensions adjacent to the adaxial or abaxial epidermis often have birefringent walls and are probably lignified. Apart from these vertically transcurrent veins, the veins are usually embedded in the mesophyll.

Another character recorded for *Knema* only has to be mentioned: structures, in outline, position, and distribution not unlike the vein bundles, consisting of sclerenchyma fibres only; sometimes only one row or a few fibres may be present at these places in the transverse section (photo 34). These structures may be considered homologous with minor veins.

#### The petiole (figs. 8, 9)

The vascular system of the distal end of the petiole is comparable with the vascular system of the midrib, but often the abaxial and (in *Horsfieldia*, *Knema* and *Myristica*) the adaxial part consists of more bundles, mostly up to three large bundles for the abaxial part (fig. 8). Generally the vascular system of the basal end of the petiole consists of three more or less arc-shaped collateral bundles, also with free phloem bundles adaxially, giving the appearance of bicollateral bundles (fig. 9); the sclerenchyma is usually confined for the greater part to the abaxial sides. Sometimes small collateral bundles have been found (not in *Gymnacranthera*), close and adaxial to the main bundles. Most probably these transverse sections were not from the extreme basal end of the petiole.

Brachy- to astroclereids are often interspersed in the ground tissue of the petiole.

#### Crystals (photo 31, fig. 10)

Crystals show a large diversity in the leaves studied. Large druses (i.e. in enlarged idioblasts, photo 31, fig. 10g), mentioned before under 'Some miscellaneous epidermal features', have frequently been found in the mesophyll of most species, but in *Knema* and *Myristica* their occurrence is restricted to the palisade parenchyma. Small druses (fig. 10h) may occur in the ordinary parenchyma cells of the mesophyll and the ground tissue of the midrib and in epidermal cells; these druses have not been found in *Gymnacranthera*.

A second crystal type of frequent occurrence is represented by more or less spindle-shaped, usually minute, particles, grouped in cells of the mesophyll and the ground tissue of the midrib (fig. 10a). They are most abundant in the parenchymatous bundle sheath of the veins. Most probably these are the acicular crystals mentioned by Metcalfe and Chalk (1950). In some *Knema* and *Myristica* specimens they have been found in epidermal cells as well, but here the possibility exists that the spindle-shaped particles are fragments of small druses, especially when druses are also present in the epidermis. Relatively large spindle- to needle-

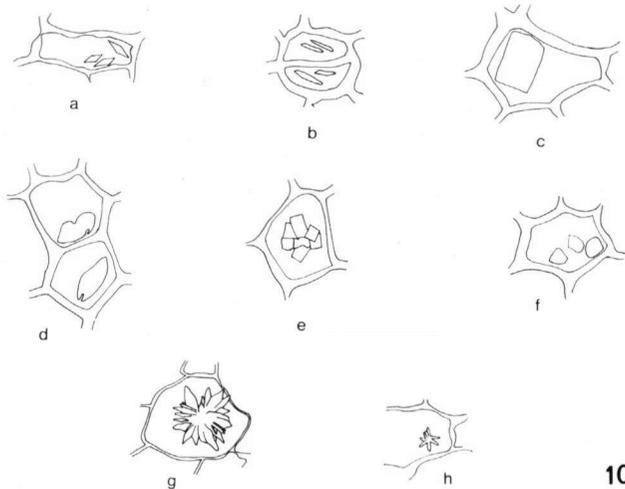


Fig. 10. Crystal types. Camera lucida drawings, all  $\times 630$ . — a. spindle-shaped crystals in parenchyma cell of bundle sheath (*Knema hookeriana*). — b. spindle- to needle-shaped crystals in basal cells of a hair (*Myristica fatua* var. *fatua*). — c. flattened prismatic crystal in abaxial epidermal cell (*Myristica fragrans*). — d. flattened crystals with rounded (corroded?) edges in abaxial epidermal cells (*Myristica fragrans*). — e. clustered crystals in abaxial epidermal cells (*Myristica fragrans*). — f. irregular, small crystals in abaxial epidermal cell (*Knema hookeriana*). — g. big druse in mesophyll idioblast (*Knema hookeriana*). — h. small druse in ordinary cell of spongy tissue (*Knema hookeriana*).

shaped crystals occur in epidermal cells of some *Myristica* specimens, especially in the basal cells of hairs (fig. 10b).

Flattened, more or less prismatic crystals occur in epidermal cells in *Gymnacranthera bancana* var. *bancana* and several *Myristica* species or, in some specimens of *Knema*, in the cells of the parenchymatous bundle sheath, mostly solitary (fig. 10c).

Irregular small crystals, usually with rounded edges, grouped, sometimes clustered, occur in abaxial epidermal cells in *Knema hookeriana* (fig. 10f). Some species of *Myristica* have also peculiar crystals in the epidermal cells: flattened crystals with four to six rounded edges; if more than one in a cell, they are usually smaller than the solitary ones. Often they have a corroded appearance, which makes, together with the rounded edges, a composition of calcium oxalate doubtful (fig. 10d). Further study would be necessary to determine the exact nature of these crystals.

Druse-like clustered crystals occur in *Myristica fragrans*, but unlike druses composed of relatively few, large, irregularly shaped particles (fig. 10e). Intermediate forms have been found of clustered crystals, crystals with rounded edges and prismatic crystals. The different types of crystals in *Myristica fragrans* have been reported to enable sex distinction of seedlings by Nayar et al. (1977).

### Secretory structures (photos 34, 35)

The large, more or less spherical oil cells, as mentioned in the older literature, have been found in the mesophyll and the ground tissue of the midrib in most of the

specimens studied, usually in great frequencies (photo 34); also in *Gymnacranthera*, contrary to Warburg's remark (1895), that they are probably absent in this genus. There are indications (colour and staining properties) that in some cases the contents of these cells are tannin-like or (in *Horsfieldia iryagedhi*) even mucilaginous. West (1969) also recorded tannin-like substances instead of oil in the large idioblasts of some *Myristicaceae*, and for some *Annonaceae* he noted mucilage cells instead of oil cells occurring in mutually related species. The empty idioblasts in the epidermis have been described under 'Some miscellaneous epidermal features'; probably their distribution is irregular and not constant per species.

The presence of tanniferous sacs, also mentioned in the literature, could not be unambiguously confirmed in this study. On the whole it is impossible to identify cell contents strictly in a study like this, because of the staining technique followed and the fact, that all leaves studied were dried herbarium specimens. However, somewhat peculiar structures occur in some specimens of *Knema* and *Myristica*: fairly thick-walled cells, adaxially and abaxially of the sclerenchyma caps of the vein bundles (photo 34), sometimes 'branching' towards the adaxial epidermis, sometimes even protruding in the epidermal layer (photo 35); these structures must be the so-called tanniferous sacs, which are situated in the veins according to Metcalfe and Chalk (1950) and Armstrong (1975). The latter describes '...tanniferous tubules... adaxial to the vascular traces...' for some *Horsfieldia* species. In the *Horsfieldia* specimens examined in this study, these structures have not been clearly observed.

#### Sclereids (photos 36—38)

Sclereids are often present in varying amounts as brachy- to astrosclereids (rarely in *Knema* and *Myristica* as brachysclereids only) in the ground tissue of the midrib, mostly abaxially; sometimes they are clustered (photo 37).

Filiform, rarely branched sclereids have been recorded for *Gymnacranthera*, where they frequently occur in the ground tissue of the midrib, most frequent adaxially, and in the mesophyll, with a high frequency in the spongy tissue as well (photo 38), which is in contrast with the findings of Rao and Chin (1966).

Astrosclereids have been found abundantly in two *Horsfieldia* species, superficially examined: *Horsfieldia fulva* and *Horsfieldia superba*. This is in accordance with the finding for *Horsfieldia superba* of Rao and Chin (1966) and Armstrong (1975).

Infrequent, thick filiform, branched sclereids are present in some *Knema* species; they are abundant in *Knema percoriacea*, extending from the sclerenchymatous bundle sheaths of the veins mostly to the epidermis (photo 36).

### GENERIC DESCRIPTIONS

#### Explanatory notes

The generic leaf anatomical descriptions are very detailed. If relevant and expedient individual species or specimens are mentioned in the descriptions. For several characters the infrageneric variation is presented in tables and referred to as such in the descriptions. For some variable characters of limited or without diagnostic value only the generic range is given without further specification. The adopted procedure makes individual specific descriptions superfluous.

**GYMNACRANTHERA** WARB. — figs. 2, 7; Photos 22, 27, 30, 31, 37, 38; figs. 2, 7; table I

6 species; 5 species studied.

**In surface view:** *Hairs* present (table I), confined to abaxial surface, least frequent on the midrib, uniseriate, composed of flattened cells with mostly 2 arms, the stalk cells (up to 4) excepted. Arms of the same cell usually not of the same length, spread out horizontally; arms of the whole hair parallel to each other to in decussate arrangement (fig. 2). Arms with thin walls. Basal cells mostly 1, sometimes up to 6, arranged in a circle or oval, surrounded by more or less radially oriented epidermal cells and subtending a cutinized ring after shedding of the hair. *Cuticle* adaxially nearly smooth to granular, abaxially with alveolar material as a reticulum of erect plates, which is absent on midrib, major veins and leaf margin. *Unspecialized epidermal cells* polygonal, adaxially with sinuous anticlinal walls at high focus and straight to slightly curved anticlinal walls at lower focus and with conspicuous thin areas of cuticle between anticlinal wall undulations (photo 22). Abaxial epidermal cells with faintly sinuous anticlinal walls at high focus and inconspicuous thin areas of cuticle, or with straight to slightly curved anticlinal walls, but on midrib, major veins and leaf margin with prominent thin areas of cuticle along anticlinal walls. *G. bancana* adaxially as well as abaxially without conspicuously sinuous anticlinal walls. Abaxial cells overlying *midrib and major veins* arranged in rows, rectangular to square with the long axis parallel or perpendicular to the course of the veins; corresponding adaxial cells also arranged in rows but tending to be polygonal rather than rectangular. Pitting of cuticular flanges usually present, most conspicuous on abaxial surface. *Minor veins* slightly visible in epidermal cell pattern of abaxial epidermis only. *Stomata* confined to abaxial epidermis, in *G. bancana* var. *borneensis* scarcely present in adaxial epidermis near midrib; stomata abundant in areolae, scanty and aberrant or absent on midrib, major veins and leaf margin, paracytic. Guard cell pairs  $15-26 \times 10-19 \mu\text{m}$ , average values  $18-23 \times 12-16 \mu\text{m}$ , length to width ratio 1.0–2.3, average values 1.2–1.9. Polar T-pieces absent or inconspicuous. Giant or water stomata rarely present (in *G. contracta*, Zehnder 9437 and *G. forbesii* var. *forbesii*, King's coll. 6591). *Cork warts* variously present, usually infrequent, probably of traumatic origin. *Small cells with a thin cuticle* in the centre of the cell surface, probably secretory cells, sometimes present in the adaxial and/or abaxial epidermis, surrounded by radially oriented epidermal cells.

**In transverse section:** *Lamina* dorsiventral, 130–410  $\mu\text{m}$  thick (table I). Adaxial *cuticle* 5–18  $\mu\text{m}$  thick, abaxial cuticle 2–11  $\mu\text{m}$  thick (table I), usually with a granular cuticular layer, *G. bancana* excepted. *Unspecialized epidermal cells* square to rectangular, usually flattened, sometimes erect, abaxially often slightly dome-shaped, of about the same size as the adaxial epidermal cells, sometimes lower; epidermal cells overlying midrib on adaxial surface often erect, on abaxial surface usually small and erect, sometimes dome-shaped. Outer periclinal wall complex of adaxial epidermal cells with indentations on the lumen side, corresponding with thin areas of cuticle as seen in surface view; outer periclinal wall complex of abaxial epidermal cells flat to mostly slightly convex, sometimes slightly indented on the lumen side. *Stomata* and subsidiary cells slightly sunken; guard cells embedded in subsidiary cells; stomatal ledges absent. Subsidiary cells pointed, sometimes protruding above the surrounding epidermal cells. *Hypodermis* as a continuous

Table I. Some leaf anatomical characters of *Gymnacranthera* species

Sizes in  $\mu\text{m}$ ; ++ = abundant; + = present;  $\pm$  = scarce;  $\pm$  = very scarce; ? = character not observed because of poor preparation or other reasons; ad. = adaxial; ab. = abaxial.

Species and specimens studied	Thickness of lamina	Thickness of cuticle		Number of basal parts of hairs/0.1 mm <sup>2</sup> in the areolae	Sclerified parenchyma cells in ground tissue of midrib		Sclerified parenchyma cells in leaf margin
		ad.	ab.		ad.	ab.	
<i>G. bancana</i> var. <i>bancana</i>	260	14	8	30	—	+	+
<i>G. bancana</i> var. <i>borneensis</i>	410	18	10	50	$\pm$	+	+
<i>G. contracta</i>							
Jacobs 5363	200	5	6	15	—	+	$\pm$
Zehnder 9437	310	10	8	15	—	+	—
SAN 17514	270	11	7	5	$\pm$	+	?
Kostermans 13696	220	5	2	15	$\pm$	+	—
Anderson 9420	260	7	6	5	$\pm$	+	—
Haviland 134	300	8	8	15	—	+	—
Kostermans 7241	260	10	8	15	—	+	$\pm$
Galau 14970	350	11	11	15	—	+	—
Jacobs 5326	240	5	5	10	—	+	$\pm$
van Rossum 63	210	6	2	15	$\pm$	+	$\pm$
<i>G. eugeniifolia</i> var. <i>eugeniifolia</i>							
FRI 3908	250	8	5	5	$\pm$	+	++
Rahmat si Boeea 8035	260	8	6	5	$\pm$	+	++
<i>G. eugeniifolia</i> var. <i>griffithii</i>							
Rahmat si Toroes 3944	200	8	4	10	$\pm$	++	++
King's coll. 6622	240	9	5	5	$\pm$	++	$\pm$
<i>G. forbesii</i> var. <i>crassinervis</i>							
Jacobs 5259	180	5	5	20	—	+	?
Rosli 3393	190	5	2	15	?	+	++
<i>G. forbesii</i> var. <i>forbesii</i>							
FRI 5749	210	5	2	20	—	++	$\pm$
King's coll. 6591	220	6	2	20	—	+	?
<i>G. paniculata</i> var. <i>paniculata</i>	130	5	2	15	—	+	—
<i>G. paniculata</i> var. <i>zippeliana</i>	210	7	5	15	—	+	+

layer absent. *Mesophyll* composed of 2–3 adaxial layers of palisade parenchyma cells, which are square to 3 times, sometimes up to 4 times as long as wide, and fairly loose spongy tissue. Abaxial layers of spongy tissue sometimes sclerified, most conspicuously so in *G. eugeniifolia*, locally present in *G. forbesii* var. *crassinervis*, *Rosli 3393*, rarely some cells in the centre of the spongy tissue sclerified. Leaf margin either with sclerified parenchyma cells, often adjacent to the epidermis (table I), or supplied with collenchyma. *Midrib* fine to intermediate, in *G. bancana* var. *bancana* robust, adaxially approximately flat to shallowly concave, abaxially prominently raised, supplied with an abaxial arc-shaped bundle with the phloem in separate groups in 2 layers and with several to numerous phloem bundles situated adaxially

of the collateral bundle, rarely accompanied by some xylem elements (fig. 7). Groups of sclerenchyma fibres present abaxially of the collateral bundle, associated with peripheral phloem groups, and in the centre, associated with, and often even in the centre of, the adaxial phloem bundles. Ground tissue from centre to periphery parenchymatous to collenchymatous, interspersed with sclerified parenchyma cells, which are abundantly present abaxially of the vascular system and between the central phloem groups, and scarcely present to absent near the adaxial epidermis (table I); often the collenchyma or the sclerified cells as a locally developed hypodermis on the adaxial side. Ground tissue also interspersed with brachy- to astrosclereids; adaxial chlorenchyma continuous in the midrib (not in *G. bancana*), situated abaxially of the collenchyma or the sclerified parenchyma cells. Major veins adaxially flat to slightly raised (in *G. eugeniifolia* var. *eugeniifolia* never raised), abaxially raised. Veins with collateral bundles, embedded in mesophyll, supplied with small sclerenchyma caps abaxially and usually a few sclerenchyma fibres adaxially (veins in *G. paniculata* with very little sclerenchyma), surrounded by a mostly poorly differentiated parenchymatous bundle sheath. *Petiole* with vascular system at the distal end similar to that of midrib, but with interruptions in the xylem, at the basal end with 3 more or less arc-shaped collateral bundles, also with free phloem bundles adaxially. Groups of sclerenchyma fibres at the basal end mostly confined to the abaxial side of the bundles. Ground tissue abundantly interspersed with brachy- to astrosclereids. *Crystals* usually frequent as large druses in mesophyll idioblasts, mostly adjacent to epidermal cells (in *G. eugeniifolia* var. *griffithii* only abaxially) which then may be extremely flattened and have a thin cuticle and thin and short cuticular flanges, also visible in cuticular macerations as areas of several less deeply staining cells. Minute, more or less spindle-shaped crystals usually present, grouped in cells in spongy tissue, sometimes especially in the parenchymatous bundle sheaths, rarely in palisade parenchyma, sometimes in ground tissue of midrib. Minute, more or less prismatic crystals present in *G. bancana* var. *bancana*, grouped in abaxial epidermal cells. Large, more or less spherical *oil cells* invariably present, frequent to scarce, usually in spongy tissue and/or in ground tissue of midrib. Empty idioblasts with a thin cuticle, probably secretory, sometimes present in the epidermis. *Sclereids* usually present as sometimes clustered brachy- to astrosclereids in the ground tissue of the midrib (photo 37), sometimes of the major veins, abaxially; filiform, rarely branched sclereids frequently present in the mesophyll and the ground tissue of the midrib, most numerous adaxially (photo 38).

#### HORSFIELDIA WILLD. — Photos 16, 21, 32; fig. 6; table II

C. 50 species; 8 species studied, 2 species superficially examined.

**I n s u r f a c e v i e w:** *Hairs* present on adaxial and abaxial surface of young leaves, in older leaves mainly shed, especially in *H. glabra* and *H. sabulosa*, but usually some hairs persistent on abaxial surface, in particular on the midrib. Hairs uniseriate, composed of cells with one arm (cells with arms 2–11, mostly 3–6 per hair, usually on midrib the hairs longer than elsewhere), the 1–3 stalk cells excepted. Arms extended upwards in different directions, as in stellate hairs. Cell walls between cells with arms very oblique, arms with thin walls but in *H. sylvestris* robust hairs with thick walls also present. Basal cells adaxially 1–13, mostly 4 or 8,

Table II. Some leaf anatomical characters of *Horsfieldia* species

For legend see also table I. <1 = between 0 and 1; >1 = between 1 and 1.5; s = sinuous; (h) = at high focus; st = straight to slightly curved; c.st = only sinuous at very high focus.

Species and specimens studied	Thickness of lamina		Thickness of cuticle		Number of basal parts of hairs/0.1 mm <sup>2</sup> in the areolae		Number of basal cells per hair (most common numbers only)		Anticlinal walls		Thin areas of cuticle	Xylem in pith of midrib	Some epidermal cells, adjacent to druse idioblasts, extremely flattened	Spindle-shaped crystals	Brachy- to astrosclereids in ground tissue of midrib	Swollen cells, adjacent to the epidermis
	ad.	ab.	ad.	ab.	ad.	ab.	ad.	ab.	ad.	ab.						
<i>H. crassifolia</i>	200	8	6	3	10	8	2	s(h)	st	st	—	+	—	+	+	—
Theunissen 59 SAR 12325	490	9	9	2.5	10	8	2	c.st	st	st	—	+	—	+	+	—
<i>H. glabra</i>	250	2	1	<1	<1*	16-43**	*	s(h)	s(h)	s(h)	±	+	—	+	+	—
Jungkuhn 230 Ibid.	280	3	1	<1	<1*	18-31**	*	s(h)	s	s	±	+	—	+	+	—
<i>H. irya</i>	220	4	3	<1	1.5	4,6,8	4	st	s	s	—	+	—	+	+	+
van Royen 5101 van Steenis 5274	210	3	1	1	1.5	4	2	st	s	s	—	—	—	+	+	—
<i>H. iryagedhi</i>	310	6	5	<1	1.5	2	2	st	st	st	—	—	+	—	+	—
<i>H. macrocoma</i>	110	4	3	?	?	?	?	s(h)	s(h)	s(h)	±	—	+	+	+	—
Merrill 4031 BW 2796	170	3	3	1.5	1.5	3	2	s(h)	s(h)	s(h)	±	+	+	—	—	—
<i>H. parviflora</i>	250	5	3	>1	1.5	2,4	2	s	s	s	+	—	+	+	+	—
<i>H. sabulosa</i>	460	13	10	1	>1	4,6	8	st	st	st	—	—	—	+	+	—

Species and specimens studied

H. sylvestris	240	5	4	<1	5	4	2	c.st	s	-	-	+
BW 4446	160	4	2	1	3	4,8	2	st	s	-	-	-
van Royen 4510	240	5	4	1	15	4	1	c.st	s	-	-	+
bb 30811	200	2	2	<1	3	4	2	s(h)	s	-	-	+
Gjellerup 407	270	6	5	<1	10	4	1	c.st	s	-	-	+
BW 1839	180	6	3	<1	3	4	2	st	s	-	-	+
Robinson 235	280	7	5	1.5	5	5,6,7	2	s(h)	s	-	-	+
Kostermans 1123	270	4	4	1.5	10	4,8	1,2	s(h)	s	-	-	+
Kuswata & Soepadmo 3	310	7	5	1.5	5	4	2	c.st	s	-	-	+
Pleyte 379												-

\* Hardly comparable with other species, because of transformation of many basal parts into cork warts.

\*\* Full range.

abaxially 1–15, mostly 1 or 2 (table II), in *H. glabra* adaxially 16–43, abaxially most of the groups of basal cells probably changed into cork warts. Basal cells arranged in a circle or oval, surrounded by more or less radially oriented epidermal cells and subtending a cutinized ring after shedding of the hair. Usually most basal parts of hairs per surface unit (table II) on the midrib. In *H. crassifolia* abaxially 2 or more basal parts often joined together. *Cuticle* faintly to conspicuously granular, but in *H. glabra* smooth abaxially. Alveolar material obviously present in *H. iryaghedhi* only, then absent on midrib, major veins and leaf margin, irregularly structured and distributed (photo 16). Cuticular striations present in *H. crassifolia* abaxially and faintly adaxially, and sometimes in *H. sylvestris* faintly abaxially. *Unspecialized epidermal cells* polygonal; anticlinal walls straight to slightly curved or sinuous, at least at high focus (table II), sometimes with inconspicuous thin areas of cuticle between anticlinal wall undulations (table II); when walls sinuous, some division walls are straight. Cuticular flanges in a few specimens very thin, but then some thickened. Abaxial epidermal cells with papillae in *H. iryaghedhi*. Abaxial cells overlying *midrib and major veins* arranged in rows, rectangular to square with the long axis parallel or perpendicular to the course of the veins; corresponding adaxial cells also arranged in rows but tending to be polygonal rather than rectangular. Pitting of cuticular flanges present, but inconspicuous. *Minor veins* slightly visible in epidermal cell pattern of abaxial epidermis only. *Stomata* confined to abaxial epidermis, abundant in areolae, scanty and aberrant or absent on midrib, major veins and leaf margin, paracytic. Subsidiary cells with prominent cuticular striations perpendicular to the stomatal pore in *H. crassifolia* and *H. sylvestris* (photo 21), sometimes faintly so in *H. glabra*; cuticle on subsidiary cells relatively thin and, when striations are absent, less granular than elsewhere. Guard cell pairs 20–35 × 8–19 μm, average values 25–32 × 10–17 μm, length to width ratio 1.2–3.3, average values 1.6–2.8; in *H. parviflora* and *H. sabulosa* the guard cell pairs are relatively wide: 15–19 μm. Outer stomatal ledges present, sometimes inconspicuous. Polar T-pieces absent or inconspicuous. *Cork warts* variously present, probably of traumatic origin, but in *H. glabra* and to a less extent in *H. sabulosa* frequent on the abaxial surface, regularly distributed and circular, probably developed from modified basal parts of hairs and from stomatal complexes. *Small cells with a thin cuticle*, sometimes in the centre of the cell surface only, probably secretory, sometimes present in the adaxial and/or abaxial epidermis, surrounded by radially oriented epidermal cells, most frequent in *H. glabra* and *H. sabulosa*.

In transverse section: *Lamina* dorsiventral or, in *H. sabulosa*, isobilateral, 110–490 μm thick (table II). Adaxial *cuticle* 2–13 μm thick, abaxial cuticle 1–10 μm thick (table II), in *H. crassifolia* and usually in *H. sylvestris* with grooves above anticlinal walls of epidermal cells. *Unspecialized epidermal cells* square to rectangular, usually flattened, abaxially sometimes slightly to conspicuously dome-shaped, higher to lower than the adaxial epidermal cells; epidermal cells overlying midrib often dome-shaped and/or erect, on abaxial side usually small. Outer periclinal wall complex of epidermal cells more or less flat, sometimes with shallow indentations on the lumen side, corresponding with thin areas of cuticle as seen in surface view. Abaxial epidermis with papillae in *H. iryaghedhi*; papillae absent on midrib, major veins and leaf margin. *Stomatal complex* sunken (in *H. iryaghedhi* and slightly in *H. crassifolia* and *H. sylvestris* p.p.) or not; guard cells partly embedded in subsidiary cells, but hardly so in *H. glabra*

and *H. macrocoma*; outer and inner stomatal ledges probably often present. *Hypodermis* as a continuous layer often present (absent in *H. crassifolia*, *Theunissen 59*, *H. glabra* and *H. sabulosa*), consisting of one adaxial layer of square to flattened rectangular translucent cells, lower to higher, sometimes broader than adjacent epidermal cells, sometimes with periclinal division walls. *Mesophyll* composed of 2–3, in *H. crassifolia*, *H. irya*, *Van Royen 5101* and *H. sabulosa* 3–4 adaxial layers of palisade parenchyma cells (in *H. sabulosa* some abaxial palisade layers are also present), which are square to 4 times, sometimes up to 5 times as long as wide, and fairly loose or (in *H. sylvestris*) more or less compact spongy tissue. Leaf margin either with sclerified parenchyma cells, usually adjacent to the epidermis, or supplied with collenchyma. *Midrib* fine to robust, adaxially raised (sometimes only a raised central ridge present) or, in *H. parviflora* and *H. sabulosa*, concave, abaxially prominently raised, supplied with a more or less straight adaxial bundle, interrupted in *H. glabra*, or with 2 small adaxial bundles in *H. parviflora*, and an arc-shaped abaxial bundle, rarely joined together with the adaxial bundle; with the phloem in small separate groups, usually only abaxially in 2 layers, and with several to numerous phloem bundles in the pith, often accompanied by xylem groups (table II; fig. 6). Groups of sclerenchyma fibres present, surrounding the vascular system, associated with peripheral phloem groups, and sclerenchyma fibres present in the pith, associated with and often even in the centre of the phloem bundles. Ground tissue from centre to periphery parenchymatous to collenchymatous, sometimes with the collenchyma as a locally developed hypodermis on the adaxial side; ground tissue sometimes, mostly abaxially, interspersed with some sclerified parenchyma cells which are usually present in the pith, and often interspersed with brachy- to astrosclereids. Major *veins* adaxially slightly depressed to slightly raised, abaxially raised. Veins with collateral bundles, embedded in mesophyll, supplied with sclerenchyma caps, sometimes only with a few fibres, and surrounded by a usually poorly differentiated parenchymatous bundle sheath. *Petiole* with vascular system at the distal end similar to that of midrib, at the basal end with 3 arc-shaped collateral bundles, also with free phloem bundles adaxially, sometimes with small collateral bundles close and adaxial to the main bundles. Groups of sclerenchyma fibres at the basal end mostly confined to the abaxial side of the main bundles. Ground tissue interspersed with brachy- to astrosclereids. *Crystals* frequent as large druses in mesophyll idioblasts, mostly close to the adaxial and abaxial epidermis, often adjacent to epidermal cells, which may be extremely flattened and have a thin cuticle and thin and short cuticular flanges (table II), also visible in cuticular macerations as areas of several less deeply staining cells; a few, mainly small druses often present in the ground tissue of the midrib. Minute, more or less spindle-shaped crystals frequent to scarce, grouped in cells in the mesophyll, most frequently in the spongy tissue, sometimes especially in the parenchymatous bundle sheath, and in the ground tissue of the midrib (table II). Large, more or less spherical *oil cells* usually abundant in the mesophyll and the ground tissue of the midrib, often in the pith. Empty idioblasts with a thin cuticle, probably secretory, sometimes present in the epidermis, most frequent in *H. glabra* and *H. sabulosa*. *Sclereids* often present, sometimes abundantly, as sometimes clustered brachy- to astrosclereids in peripheral ground tissue of the midrib (table II), usually abaxially, rarely also in the pith (in *H. parviflora* and *H. sylvestris*, *bb 30811*), sometimes in the ground tissue of the major veins, abaxially (in *H. crassifolia*, *H. glabra* and *H. sabulosa*), and sclereids abundantly present as astrosclereids in the superficially examined *H. fulva*

and *H. superba*, at least in the mesophyll. *Swollen cells* with thin walls often present, solitary or in groups in the hypodermis, if present, or rarely adjacent to the abaxial epidermis (table II), sometimes in elevations of the leaf surface (photo 32), and/or in the periphery of the ground tissue of the midrib.

**KNEMA LOUR.** — Photos 1—8, 11, 12, 18, 23, 24, 28, 29, 33—36; figs. 3—5, 8, 10; table III

83 species; 31 species studied.

**I n s u r f a c e v i e w:** *Hairs* present on adaxial and abaxial surface, in older leaves often shed (table III), especially adaxially, but usually some hairs persistent on midrib and major veins. Hairs uniseriate, composed of cells with one arm (cells with arms one to many; sometimes on the midrib the hairs longer than elsewhere), the 1–3 (on midrib sometimes up to 4) stalk cells excepted; when hairs are extremely long (as in *K. hookeriana*) the most distal cells do not have arms. Arms extended upwards in different directions, as in stellate hairs. Cell walls between cells with arms very oblique, especially on the midrib, where the arms may be relatively short; arms with thin to thick walls. Hairs varying in structure (table III, photos 1–8, fig. 3, see also classification of types below). Basal cells adaxially 1–14, mostly 1–11, abaxially 1–8, mostly 1–4 (table III), arranged in a circle or oval, surrounded by more or less radially oriented epidermal cells and subtending a cutinized ring after shedding of the hair. Most basal parts of hairs per surface unit (table III) on the midrib. *Cuticle* adaxially almost smooth to granular, abaxially with alveolar material as a reticulum of erect, usually lobed plates, which is absent on midrib, major veins and leaf margin; the alveolar material in *K. intermedia* and *K. plumulosa* is mainly restricted to cells bordering stomatal complexes. Cuticular striations and grooves corresponding with anticlinal walls of epidermal cells rarely present adaxially; adaxial cuticle with convex sculpturings in *K. rufa* (photo 18). *Unspecialized epidermal cells* polygonal, adaxially with sinuous anticlinal walls at (very) high focus and straight to slightly curved anticlinal walls at lower focus and with thin, sometimes very inconspicuous areas of cuticle between anticlinal wall undulations; anticlinal walls on midrib less sinuous, sometimes straight. Abaxial epidermal cells with straight to slightly curved anticlinal walls, and often with papillae. Abaxial cells overlying *midrib and major veins* arranged in rows, rectangular to square with the long axis parallel or perpendicular to the course of the veins; corresponding adaxial cells also arranged in rows but tending to be polygonal rather than rectangular. Pitting of cuticular flanges present, but inconspicuous. *Minor veins* prominent in epidermal cell pattern of abaxial epidermis, slightly visible or not in epidermal cell pattern of adaxial epidermis. *Stomata* confined to abaxial epidermis, abundant in areolae, scanty and aberrant or absent on midrib, major veins and leaf margin, paracytic. Stomatal complex overarched by more or less horizontally directed nipple-shaped papillae of the 4–6 bordering epidermal cells; the papillae leave a star-shaped opening above the stomatal complex (photo 23). Guard cell pairs 17–30 × 8–16 μm, average values 20–27 × 9–14 μm, length to width ratio 1.3–2.8, average values 1.7–2.4; in *K. oblongifolia* FRI0111, the guard cell pairs are relatively long: 26–30 μm; in *K. lunduensis* some guard cell pairs are relatively wide: 10–16 μm. Polar T-pieces sometimes present, usually inconspicuous. *Cork warts* variously present, usually infrequent, probably of traumatic origin, but in *K. conferta* and *K. kunstleri* abundant, especially abaxially,

and regularly distributed, mostly on veins and along the midrib, and circular, partly developed from stomatal complexes. *Small cells with a thin cuticle*, sometimes in the centre of the cell surface only, probably secretory, occasionally present in adaxial and/or abaxial epidermis of most leaves, especially on and along midrib, veins and leaf margin, often surrounded by radially oriented epidermal cells.

In transverse section: *Lamina* dorsiventral, 80–300  $\mu\text{m}$  thick (table III). Adaxial *cuticle* 2–17  $\mu\text{m}$  thick, abaxial cuticle 1–9  $\mu\text{m}$  thick (table III), often with a granular cuticular layer. *Unspecialized epidermal cells* adaxially square to rectangular, sometimes erect, abaxially slightly to conspicuously dome-shaped, higher to lower than adaxial epidermal cells; epidermal cells overlying midrib usually erect, on adaxial side often dome-shaped, on abaxial side usually small. Outer periclinal wall complex of adaxial epidermal cells with more or less shallow indentations on the lumen side, corresponding with thin areas of cuticle as seen in surface view. Abaxial epidermis often with papillae, most striking in *K. conferta* and *K. linifolia*; papillae absent on midrib, major veins and leaf margin. *Stomatal complex* sunken; bordering epidermal cells with more or less horizontally directed papillae. Subsidiary cells with a thin cuticle, without alveolar material; guard cells embedded in subsidiary cells; inner and/or outer stomatal ledges sometimes present, inconspicuous. *Hypodermis* sometimes present, consisting of one adaxial layer (sometimes of one inconspicuous abaxial layer) of flattened rectangular, translucent cells, as high as or lower than adjacent epidermal cells, adaxially never as a continuous layer but locally developed, sometimes only near the midrib and the major veins, and sometimes intergrading with the palisade parenchyma. *Mesophyll* composed of 2–3, sometimes up to 4, or 3–4 adaxial layers of palisade parenchyma cells, which are square (or even slightly flattened) to scarcely longer than wide (in *K. curtisii* and *K. linguiformis*) or to 3 times, sometimes up to 5 times (in *K. pallens* and *K. percoriacea*) as long as wide, and fairly loose to (in *K. curtisii*, BRUN 5587, *K. laurina*, *K. oblongifolia* and *K. pseudolaurina*) more or less compact spongy tissue; cells of spongy tissue occasionally sclerified, sometimes only the abaxial layers sclerified (table III); in *K. mandarahan* and *K. pallens* many cells of palisade and spongy tissue have thick lignified walls supplied with large pits. Leaf margin often with sclerified parenchyma cells (table III), usually adjacent to the epidermis, or supplied with collenchyma. *Midrib* of intermediate size to (very) robust, adaxially raised, sometimes prominently so, abaxially prominently raised, supplied with a straight to arc-shaped adaxial bundle, interrupted in *K. ashtonii* var. *ashtonii* and *K. kunstleri*, and an arc-shaped abaxial bundle, rarely joined together with the adaxial bundle; with the phloem in separate groups, usually in 2 layers, especially abaxially, and with one to numerous phloem bundles in the pith, often accompanied by xylem groups (table III; fig. 4); sometimes 1 or 2 large, more or less straight to arc-shaped xylem bundles, oriented as the main abaxial bundle, are present in the pith (table III; fig. 5). Groups of sclerenchyma fibres present surrounding the vascular system, associated with peripheral phloem groups, and sclerenchyma fibres present in the pith, associated with and often even in the centre of the phloem bundles. Ground tissue from centre to periphery parenchymatous to collenchymatous, usually interspersed with sclerified parenchyma cells, especially at the periphery, often abundant (table III) and also present in the pith; often the collenchyma or the sclerified cells as a locally developed hypodermis on the adaxial side; ground tissue also often interspersed with brachy- or (mostly) brachy- to

Table III. Some leaf anatomical characters of *Knema* species

For legend see also tables I and II. a = abaxial layers; 1 = large bundles.

Species and specimens studied	Thickness of lamina		Thickness of cuticle		Number of basal parts of hairs/0.1 mm <sup>2</sup> in the areolae		Number of basal cells per hair (most common numbers only)		Adult leaves covered with hairs abaxially	Hair type (see text)	Sclerified parenchyma cells in spongy tissue	Sclerified parenchyma cells in leaf margin	Xylem in pith of midrib	Sclerified parenchyma cells in peripheral ground tissue of midrib	Brachy- to astrosclereids in ground tissue of midrib
	ad.	ab.	ad.	ab.	ad.	ab.	ad.	ab.							
<i>K. ashtonii</i> var. <i>ashtonii</i>	170	6	2	3	15	2	1	1	—	8a	±	±	+	+	—
<i>K. ashtonii</i> var. <i>cinnamomea</i>	140	6	2	5	40	2,4	1	1	++	2	±	±	+1	+	—
<i>K. attenuata</i>	140	6	3	3	5	2	1	1	+	7+8b	—	±	+	+	—
<i>K. conferta</i>	230	9	4	3	3	4	2	2	+	8a	±	—	—	—	—
<i>K. curtisii</i> var. <i>curtisii</i>	90	4	3	3	5	2	1	1	?	8b	—	—	—	±	+
BRUN 5587	120	6	4	1.5	3	4	2	2	—	?	—	—	—	±	+
FRI 12326															
<i>K. elmeri</i>	120	4	2	5	20	2	1	1	?	8b	—	—	—	+	—
SAN A4139	110	4	2	5	30	2	1	1	++	8b	—	±	—	+	—
S 18294															
<i>K. furfuracea</i>	230	12	9	1.5	3	2	2	2	—	3	+	+	+	+	—
<i>K. globularia</i>	160	5	2	1.5	3	4	2	2	±	7	—	±	—	±	—
<i>K. hookeriana</i>	140	12	8	3	3	2	2	2	—	3	+	—	+1	—	—
<i>K. intermedia</i>	180	9	3	3	5	2	2	2	—	6	—	—	+	+	+
<i>K. korthalsii</i>	160	7	2	3	10	4	2	2	±	3+7+8c	—	—	+	+	+
<i>K. kunstleri</i> ssp. <i>kunstleri</i>	220	13	6	3	10	2	1	1	±	7	+	+	+	+	—
<i>K. latifolia</i>	120	4	3	<1	3	8,9	1	1	±	7	—	+	—	±	—



astrosclereids (table III); adaxial chlorenchyma rarely continuous in the midrib, then situated abaxially of the collenchyma. Major veins adaxially slightly depressed to raised, abaxially prominently raised. Veins with collateral bundles, supplied with a sclerenchymatous bundle sheath, one-layered on the lateral sides, of several cell layers on the adaxial and abaxial sides, and surrounded by a sometimes poorly differentiated parenchymatous bundle sheath, embedded in mesophyll to vertically transcurrent to the adaxial and/or abaxial epidermis through bundle sheath extensions, which are sometimes sclerified adjacent to the epidermis. Minor veins often entirely composed of sclerenchyma fibres in small, few- to many-celled bundles or vertical rows (the latter condition especially in *K. laurina*, *K. oblongata*, *K. percoriacea* and *K. pseudolaurina*). Petiole with vascular system at the distal end similar to that of midrib, often with interruptions in the xylem, at the basal end with 3 more or less arc-shaped collateral bundles, also with free phloem bundles adaxially, sometimes with small, collateral bundles between the main bundles, and with more or less small collateral bundles close to and adaxially from the main bundles. Groups of sclerenchyma fibres at the basal end mostly confined to the abaxial side of the main bundles. Ground tissue usually abundantly interspersed with brachy- to astrosclereids. Crystals usually frequent as small to large druses (when large in idioblasts) in the mesophyll, often also present in the ground tissue of the midrib, in the palisade parenchyma most frequent and large; (very) small druses often also present in epidermal cells. Usually minute, more or less spindle-shaped crystals frequent to scarce, grouped in cells in the mesophyll (most frequent in the parenchymatous bundle sheath), and in the ground tissue of the midrib, rarely also present in epidermal cells. Flattened, more or less prismatic crystals sometimes present in cells of the parenchymatous bundle sheath, usually solitary. Irregular small crystals, usually with rounded edges, grouped, sometimes clustered, present in abaxial epidermal cells of *K. hookeriana* (fig. 10f). Large, more or less spherical oil cells usually present, sometimes abundant, in mesophyll and/or in peripheral ground tissue of the midrib, in *K. elmeri*, *K. kunstleri* and *K. retusa*, Sinclair 9908, also in the pith. Empty idioblasts with a thin cuticle, probably secretory, sometimes present in the epidermis (photo 29). More or less thick-walled cells, probably tanniferous sacs, often present adaxially and abaxially of the sclerenchymatous bundle sheaths of the veins, sometimes 'branching' towards the adaxial epidermis, sometimes even protruding in the epidermal layer (photos 34, 35). Sclereids often present, sometimes abundant, as brachysclereids (in *K. curtisii* var. *curtisii*, FRI 12326) or as sometimes clustered brachy- to astrosclereids in peripheral ground tissue of the midrib, mostly abaxially, in some specimens of *K. laurina* also in the pith, in *K. oblongata* S. 34822 also in the ground tissue of the major veins (table III). Thick filiform, branched sclereids sometimes present, abundant in *K. percoriacea*, extending through the chlorenchyma from the sclerenchymatous bundle sheaths of the veins to the, mostly adaxial epidermis (photo 36).

#### Hair types of *Knema*

For a detailed study of the morphology of the hairs, transverse and paradermal sections and preparations of individual hairs for light microscopy, as well as surface views obtained with the S.E.M. have been used. Unfortunately the hairs are often damaged during the microtechnical process, so that for certain leaves only S.E.M. photographs were left for the study of the hairs. The entire tomentum has also been studied at low power magnification with a dissecting microscope. In fully developed

leaves the hairs are often shed, in that case (very) young leaves have been studied.

The morphological diversity of the hairs of *Knema* have been classified using such characters as type of stalk cells, relative size of the body of the cells with arms, total size, cell wall thickness etc.

Hairs on the midrib and the major veins are usually different from those on the remaining part of the leaf. They are longer, more compact (which means: the cells with arms have very short bodies) and have relatively short arms. These hairs, rarely present on other places of the leaf, have not been taken into account in this classification.

The photos and drawings (photos 1–8, fig. 3) should be considered as an indispensable part of the descriptions of hair types. In some way the classification is also a key. If a hair does not fit type 1, then try type 2 etc.

#### CLASSIFICATION OF HAIRS ON AREOLAE AND MINOR VEINS OF KNEMA LEAVES.

##### A. One or more stalk cells distinctly longer than wide:

- Type 1. Long stalk cells one or two; part with arms short and compact; arms with thick walls. See photo 1, fig. 3.
- Type 2. Long stalk cells up to three; part with arms short and compact; arms with thin walls. See fig. 3.
- Type 3. Long stalk cells one or two; part with arms (very) long; arms long (in particular in the proximal region), with thin to thick walls. See photo 2, fig. 3.

##### B. Stalk cells not longer than wide:

- Type 4. Hairs long; arms at the distal end longer than in the more proximal regions; arms with thick walls. See fig. 3.
- Type 5. Hairs long; arms fairly short, very broad near the body, with a pointed tip, and with fairly thin walls. See photo 3, fig. 3.
- Type 6. Hairs long; body of cells long (the distance between the arms is considerable); arms thin, with fairly thin to thick walls. See photo 4, fig. 3.

Hairs short to long; body of cells small; arms (fairly) long, at the distal end relatively short, with thin to thick walls:

- Type 7. Hairs very short and small (diameter in surface view 100  $\mu\text{m}$  and less); arms with thin to thick walls. See photo 5, fig. 3.
- Type 8a. Hairs short; diameter in surface view 65–250  $\mu\text{m}$ . When hairs with a diameter of 100  $\mu\text{m}$  and less are present (see type 7), hairs with a diameter of more than 100  $\mu\text{m}$  also occur. Arms with thick walls. See photo 6, fig. 3.
  - c. Hairs long; arms with thick walls. See photo 8, fig. 3.
  - b. Hairs with a length between the lengths of hairs of type 8a and c; arms with fairly thin to thick walls. See photo 7, fig. 3.

**Note:** The subdivision of type 8 is difficult; some species show a gradual transition from one subtype to another. Therefore it is useless to give precise lengths. Still this subdivision may help to identify a specimen in the case of obviously short or long hairs.

#### MYRISTICA L. — Photos 9, 10, 13–15, 17, 19, 20, 25, 26; figs. 9, 10; table IV

C. 72 species; 13 species studied.

**In surface view:** *Hairs* present, sometimes confined to abaxial surface (table IV), in older leaves on adaxial surface almost always, on abaxial surface sometimes shed (table IV), uniseriate, composed of flattened cells with 2 arms, the 1 or 2 (on midrib and major veins often more) stalk cells excepted. Arms of a single cell of about equal length, spread out horizontally, and at angles with arms of adjoining

Table IV. Some leaf anatomical characters of *Myristica* species

For legends see also tables I—III. sc = sclerified parenchyma cells; b = brachysclereids; a = astroclereids.  
 For crystal types only: r = crystals with rounded edges; p = prismatic crystals; c = clustered crystals; d = druses; s = spindle-shaped crystals;  
 n = spindle- to needle-shaped crystals; h = in basal cells of hairs only. Intermediate forms hyphenated. Types of infrequent occurrence  
 between brackets.

Species and specimens studied	Thickness of lamina		Thickness of cuticle		Alveolar material		Number of basal parts of hairs/0.1 mm <sup>2</sup> on the lamina		Adult leaves covered with hairs abaxially		Papillae on cells, bordering the stomatal complex		Number of epidermal cells, bordering the stomatal complex		Continuous hypodermis		Xylem in pith of midrib		Sclerified cells in peripheral ground tissue of midrib		Crystals in adaxial epidermal cells		Crystals in abaxial epidermal cells		Spindle-shaped crystals in mesophyll		
	ad.	ab.	ad.	ab.	ad.	ab.	ad.	ab.	+	-	+	-	5-8	6-9	+	-	sc-b	-	+	-	s,n	r	+	-	+	-	
<i>M. chrysophylla</i>	230	9	6	+	1	5	-	-	+	5-8	-	+	5-8	-	+	sc-b	-	+	-	+	s,n	r	+	+	+	-	+
Brass 25986	310	12	6	+	1	15	-	-	+	6-9	-	+	6-9	-	-	-	-	-	-	-	s,n	r-p	+	+	+	-	-
<i>M. cinnamomea</i>	140	8	6	-	-	40	++	++	++	6-10	-	++	6-10	-	-	sc,b-a	-	-	-	-	-	-	-	-	-	-	-
SAN 15066	230	8	4	-	-	30	++	++	++	5-9	-	++	5-9	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SAN 24236	200	4	2	+	5	15	++	++	+	6-10	+	+	6-10	+	-	-	-	-	-	-	s,n,h	p,s	-	-	-	-	-
<i>M. fatua</i> var. <i>fatua</i>	210	5	3	-	15	50	++	++	-	4-6	+	-	4-6	+	-	b-a	-	-	-	-	s,n,h	p,s	+	+	+	-	-
<i>M. fatua</i> var. <i>papuana</i>																											
<i>M. fragrans</i>	260	6	3	+	-	15	-	-	±	6-10	-	±	6-10	-	-	-	-	-	-	-	-	(p)-c	+	+	+	-	-
Sulit 15023	190	7	3	+	-	15	-	-	±	6-9	-	±	6-9	-	-	-	-	-	-	-	-	r-p-c	-	-	-	-	-
de Vriese s.n.	220	8	3	+	5	3	-	-	±	6-9	-	±	6-9	-	-	-	-	-	-	-	-	r-p-c	+	+	+	-	-
Beguain 787	230	8	5	+	1.5	3	-	-	±	6-10	-	±	6-10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. gigantea</i>	240	4	3	+	-	25	+	+	+	6-8	+	+	6-8	+	-	sc-b-a	-	-	-	-	(s)	p,s,n	+	+	+	-	-
<i>M. globosa</i>																											

Species and specimens studied

<i>M. guatterifolia</i>	270	9	5	5	3	45	++	-	4-7	-	(p),d,(s)	-	+
Kostermans UNESCO 7	190	9	5	5	5	40	++	+/-	4-7	-	-	-	+
Sinanegul 39995	220	10	5	10	50	50	++	-	5-8	-	d,(s)	-	-
Mihil 30298	190	9	6	5	50	50	++	-	5-8	-	(p),d,(s)	-	-
Elmer 20850	260	11	8	3	45	45	++	+	4-7	+	d,(s)	s*	+
BRUN 5365	290	10	11	3	50	50	++	+	5-8	-	-	-	+
SAN 32924	310	9	9	5	50	50	++	-	4-8	-	(s)	-	+
Ambulah 37177	260	11	8	5	50	50	++	-	4-7	-	d,(s)	-	+
Kostermans 4873	310	10	5	1.5	40	40	++	-	4-8	-	(p),d,(s)	s	+
FRI 5056	180	4	3	3	20	20	-	-	6-11	-	s,h	(p),s	++
<i>M. lepidota</i>	200	7	5	1.5	3	3	-	-	6-9	-	-	-	-
<i>M. maingayi</i>													
<i>M. maxima</i>													
Thorenaar 55 E1P 624	170	7	4	1	10	10	+	-	4-8	-	-	-	-
Grashoff 908	200	7	4	1.5	10	10	+	?	5-8	-	-	-	-
<i>M. sphaerosperma</i>	320	11	6	5	15	15	+	+	7-11	+	(p),d	d	+
<i>M. subulata</i>	220	7	3	5	15	15	+	+	6-10	+	s,n	r,p	++
<i>M. villosa</i>													
Kostermans 6438	280	9	5	10	30	30	++	-	4-6	+	-	-	-
SAN A4747	350	8	7	5	35	35	++	-	4-6	+	-	-	+

\* very minute; \*\* probably of traumatic origin.

cells. Arms with thin walls (photo 9). Hairs on midrib usually taller than elsewhere. In *M. villosa* some hairs extremely long, with body of cells with oblique walls and with short, almost parallel, thick-walled arms (photo 10); these hairs are also present in some other species, but on bud scales etc., not on leaves. Basal cells 1–4, arranged in a circle or oval, sometimes with 3–4 in a row; mostly 1 or, in *M. fatua*, *M. lepidota* and *M. maxima* on adaxial surface mostly 2; basal cells surrounded by more or less radially oriented epidermal cells and subtending a cutinized ring after shedding of the hair; basal parts on abaxial surface, if composed of one cell usually very small, especially in *M. villosa*. Basal parts of hairs adaxially, if present, most frequent on the midrib, abaxially most frequent in the areolae. *Cuticle* almost smooth to granular, abaxially often with alveolar material (table IV) of variable appearance (photos 13–15), sometimes as a reticulum of erect plates; alveolar material absent on midrib, major veins and leaf margin. Very shallow grooves corresponding with anticlinal walls of epidermal cells present adaxially in *M. gigantea* and *M. maingayi*. *Unspecialized epidermal cells* polygonal, adaxially with sinuous anticlinal walls at (very) high focus and straight to slightly curved anticlinal walls at lower focus and usually with, sometimes very inconspicuous, thin areas of cuticle between anticlinal wall undulations; cells with straight division walls especially common in *M. fragrans*. Abaxial epidermal cells with straight to slightly curved anticlinal walls and with papillae in *M. gigantea* and *M. maingayi*. Adaxial epidermal cells often smaller than abaxial epidermal cells. Abaxial cells overlying *midrib and major veins* arranged in rows, rectangular to square with the long axis parallel or perpendicular to the course of the veins; corresponding adaxial cells also arranged in rows but tending to be polygonal rather than rectangular. Pitting of cuticular flanges usually present, but inconspicuous. *Minor veins* slightly visible in epidermal cell pattern of abaxial epidermis only. *Stomata* confined to abaxial epidermis, abundant in areolae, scanty and aberrant or absent on midrib, major veins and leaf margin, paracytic. Stomatal complex partly overarched by a ring of 4–11 bordering epidermal cells with or without papillae (table IV, photos 13, 15, 25). Guard cell pairs 21–39 × 8–21 μm, average values 26–34 × 11–18 μm, length to width ratio 1.3–3.4, average values 1.6–2.8; in *M. sphaerosperma* the guard cell pairs are relatively long: 27–39 μm. Polar T-pieces sometimes present, usually inconspicuous. *Cork warts* variously present, usually infrequent, probably of traumatic origin. *Small cells with a thin cuticle*, sometimes in the centre of the cell surface only, probably secretory, sometimes present in the adaxial and/or abaxial epidermis, especially on and along the midrib, the veins and the leaf margin, surrounded by radially oriented epidermal cells.

In transverse section: *Lamina* dorsiventral, 140–350 μm thick (table IV). Adaxial *cuticle* 4–12 μm thick, abaxial cuticle 2–11 μm thick (table IV), often with a granular cuticular layer. *Unspecialized epidermal cells* adaxially square to rectangular, often erect, rarely dome-shaped, abaxially dome-shaped to square to rectangular, erect to flattened, higher to lower than adaxial epidermal cells; epidermal cells overlying midrib on abaxial surface often small. Outer periclinal wall complex of adaxial epidermal cells with more or less shallow indentations on the lumen side, corresponding with thin areas of cuticle as seen in surface view. Abaxial epidermis in *M. gigantea* and *M. maingayi* with papillae with a strongly thickened cuticle on the tips; papillae absent on midrib, major veins and leaf margin. Basal cells of hairs abaxially of about the same height as the unspecialized epidermal cells, but higher in *M. cinnamomea*, *M. guatteriifolia* and *M. villosa* (photo 19).

*Stomatal complex* sunken; bordering epidermal cells often with more or less upright papillae of varying conspicuousness (table IV); a small sunken cell, separating the stomatal complex on one or both lateral sides of the bordering epidermal cells often present (photo 26). Subsidiary cells, sometimes slender, with a thin cuticle, without alveolar material; guard cells more or less embedded in subsidiary cells; inner and/or outer stomatal ledges sometimes present, inconspicuous. *Hypodermis* as a continuous layer sometimes present (table IV), consisting of one adaxial layer (in *M. sphaerosperma* also one abaxial layer) of square to flattened rectangular, translucent cells, usually broader and lower, rarely higher than adjacent epidermal cells, in some specimens of *M. guatteriifolia* only locally developed, especially near the midrib and major veins, and sometimes intergrading with the palisade parenchyma. *Mesophyll* composed of 2–3, in *M. guatteriifolia*, *M. sphaerosperma* and *M. villosa* 3–4 adaxial layers of palisade parenchyma cells, which are square to 4 times, sometimes up to 5 times as long as wide, and fairly loose spongy tissue; cells of spongy tissue occasionally sclerified, frequently so in *M. villosa*. Leaf margin usually supplied with collenchyma, sometimes with some sclerified parenchyma cells adjacent to the epidermis. *Midrib* usually of intermediate size to robust, rarely fine, adaxially raised, sometimes only a raised central ridge present, abaxially prominently raised, supplied with a more or less straight, sometimes interrupted adaxial bundle and an arc-shaped abaxial bundle, with the phloem in separate groups, often in 2 layers, especially abaxially, and with 2–9 phloem bundles in the pith, sometimes accompanied with xylem groups (table IV, as in fig. 4). Groups of sclerenchyma fibres present, surrounding the vascular system, associated with peripheral phloem groups, and in the pith, associated with and often even in the centre of the phloem bundles. Ground tissue from centre to periphery parenchymatous to collenchymatous, often with the collenchyma as a locally developed hypodermis on the adaxial side; ground tissue sometimes interspersed with sclerified parenchyma cells (table IV), which are usually present in the pith, and sometimes interspersed with brachysclereids and/or brachy- to astrosclereids (table IV); adaxial chlorenchyma sometimes continuous in the midrib, situated abaxially of the collenchyma. Major *veins* adaxially slightly depressed to slightly raised, abaxially raised. Veins with collateral bundles, mostly embedded in mesophyll, supplied with sclerenchyma caps and surrounded by an often poorly differentiated parenchymatous bundle sheath, sometimes tending to be vertically transcurrent through bundle sheath extensions, especially in *M. lepidota*. *Petiole* with vascular system at the distal end similar to that of midrib, sometimes with interruptions in the xylem, at the basal end with 3 more or less arc-shaped collateral bundles, also with free phloem bundles adaxially, sometimes with small collateral bundles close to and adaxially from the main bundles. Groups of sclerenchyma fibres at the basal end mostly confined to the abaxial side of the main bundles. Ground tissue usually abundantly interspersed with brachy- to astrosclereids. *Crystals* usually frequent as large druses (in *M. villosa* they are small) in idioblasts in the palisade parenchyma, often adjacent to adaxial epidermal cells, which then may be flattened and have a thin cuticle and thin and short cuticular flanges, also visible in cuticular macerations as areas of several, less deeply staining cells; small druses sometimes present in epidermal cells (table IV) and/or in parenchyma cells of the mesophyll and the ground tissue of the midrib. Minute, more or less spindle-shaped crystals, grouped in cells in the mesophyll, most frequent in the spongy tissue, especially in the parenchymatous bundle sheath, and in the ground tissue of the midrib, sometimes

also present in epidermal cells, where they may be larger and spindle- to needle-shaped, especially in basal cells of hairs adaxially (table IV). Flattened, more or less prismatic crystals sometimes present in epidermal cells, mostly solitary (table IV). Flattened crystals with 4–6 rounded edges, often with a corroded appearance (fig. 10d) sometimes in epidermal cells, mostly solitary, when grouped smaller in size. Clustered crystals, composed of relatively few, large, irregularly shaped particles (fig. 10e) present in abaxial epidermal cells of *M. fragrans*. Sometimes intermediate forms occur of prismatic and clustered crystals and crystals with rounded edges. Large, more or less spherical *oil cells* usually present, sometimes abundant, in mesophyll and in peripheral ground tissue of the midrib; in *M. guatteriifolia*, *M. maxima* and *M. villosa* also in the pith. Empty idioblasts with a thin cuticle, probably secretory, sometimes present in the epidermis. More or less thick-walled cells, probably tanniferous sacs, occur adaxially and abaxially of the sclerenchyma caps of the vein bundles, sometimes 'branching' towards the adaxial epidermis, sometimes even protruding into the epidermal layer. *Sclereids* present in a few specimens only, sometimes abundant, as brachysclereids and/or as sometimes clustered brachy- to astrosclereids in peripheral ground tissue of the midrib, usually abaxially, in *M. maxima* in the pith, in *M. sphaerosperma* also in ground tissue of the major veins (table IV).

#### VALUE OF THE CHARACTERS

In the generic descriptions and in the tables a very great number of characters has been recorded. It is essential to analyse which of these characters are constant for a species (or variety) or for a genus and which are not; in other words: which characters have diagnostic value for a species (or variety), or even for a genus. This is also important for the determination of patterns of relationship on the species and genus level. For most of the characters the determination of the constancy for a species (or variety) is possible to a limited extent because many species (and, for *Gymnacranthera*, varieties) are represented by two or more specimens in this study.

The characters are listed following their constancy for species or genera.

In the first list those characters are mentioned, which are *not* constant for a species.

#### List 1

Pitting of cuticular flanges	Number of layers of phloem groups in the collateral bundles of the midrib
Presence of polar T-pieces	Number of phloem bundles in the pith of the midrib
Shape of abaxial epidermal cells in transverse section (papillae excepted)	Presence of locally developed hypodermis in the midrib
Presence of stomatal ledges	Frequency of druses
Degree of prominence of the midrib adaxially*)	Frequency of oil cells
Presence of interruptions in the adaxial bundle of the midrib*)	Presence of tanniferous sacs

\*) Does not apply for *Gymnacranthera*.

The characters, mentioned in list 1 do not have any diagnostic or taxonomic value.

The next characters are applicable to one or two genera only, and are not constant for the species (or varieties).

#### List 2

Basal cells of hairs in a row ( <i>Myristica</i> )	Minor veins slightly prominent in the adaxial epidermis or not ( <i>Knema</i> )
Difference in size of adaxial and abaxial epidermal cells ( <i>Myristica</i> )	Presence of periclinal division walls in the hypodermis ( <i>Horsfieldia</i> )
Presence of stomata in the adaxial epidermis ( <i>Gymnacranthera</i> )	Connection of adaxial and abaxial bundles in the midrib ( <i>Horsfieldia</i> , <i>Knema</i> )
Presence of giant or water stomata ( <i>Gymnacranthera</i> )	Degree of vertically transcurrence of the veins ( <i>Knema</i> , <i>Myristica</i> )

The characters of list 2 do not have diagnostic or taxonomic value on the species level either, but on the genus level they may have some indicative circumstantial value, especially the two latter features and the 'prominence of the minor veins', because of their frequent occurrence within the genera concerned.

The characters of list 3 are applicable to each genus and are not constant for most of the species, but for a few species (or varieties) they are. When the latter applies to one or two genera especially, these genera are mentioned.

#### List 3

Cuticular layer granular or not ( <i>Gymnacranthera</i> , <i>Horsfieldia</i> )	Presence of xylem in the pith of the midrib ( <i>Myristica</i> )
Sizes of guard cell pairs ( <i>Gymnacranthera</i> , <i>Horsfieldia</i> )	Continuity of chlorenchyma in the midrib
Frequency of secretory cells ( <i>Horsfieldia</i> )	Shape of veins adaxially ( <i>Gymnacranthera</i> )
Length/width ratio of palisade parenchyma cells ( <i>Knema</i> ).	Size of druses ( <i>Myristica</i> )
Relative size of midrib	Position of brachy- to astroscleireids in the midrib and major veins ( <i>Myristica</i> )

These characters have some (very little) diagnostic and taxonomic value on the species or variety level in some particular genera.

In the following list those characters are mentioned, which are usually applicable to each genus, and which are constant for most of the species (or varieties), but not for all species. The latter species may be thought to show a 'tendency' for these characters, without them having become fixed in the speciation process (through either acquisition or gradual loss).

## List 4

Number of basal parts of hairs per surface unit	Degree of sclerification of the central spongy tissue
Degree of covering of the adult leaves by the hairs	Leaf margin sclerified or not
Presence of grooves in the cuticle	Degree of sclerification of the peripheral ground tissue of the midrib
Anticlinal walls of epidermal cells sinuous or not	Epidermal cells flattened, when druse idioblasts are adjacent to epidermis, or not
Thin areas of cuticle present or not	Frequency of spindle-shaped and prismatic crystals
Thickness of the lamina	Presence of oil cells in the pith of the midrib
Thickness of the cuticle	Frequency of brachy- to astroclereids
Number of layers of palisade parenchyma cells	

The characters of list 4 have diagnostic and taxonomic value on the species level; the characters are not very strong, however: most of them can possibly be influenced by ecological factors, and some of them may be age-dependent in the persistent *Myristicaceae* leaves.

In list 5 characters are mentioned, applicable to one or two genera only, which are constant for most of the species. The species, for which a character is inconstant, are thought to show a tendency for that character.

## List 5

Presence of cuticular striations ( <i>Horsfieldia</i> , <i>Knema</i> )	Presence of large xylem bundles in the pith of the midrib ( <i>Knema</i> )
Number of cells, bordering the stomatal complex (forming the 'ring'; <i>Myristica</i> )	Minor veins as rows or as small bundles of sclerenchyma fibres ( <i>Knema</i> )
Stomata on the level of the epidermis or slightly sunken ( <i>Horsfieldia</i> )	Presence of peculiar crystals in the epidermal cells ( <i>Myristica</i> , <i>Knema</i> )
Presence of a continuous hypodermis ( <i>Horsfieldia</i> , <i>Myristica</i> ; the locally developed hypodermis in <i>Knema</i> and <i>Myristica</i> is highly inconstant)	Presence of relatively thick filiform sclereids ( <i>Knema</i> *)
Spongy tissue compact or not ( <i>Horsfieldia</i> , <i>Knema</i> )	Presence of swollen cells in the subepidermal layer ( <i>Horsfieldia</i> )
Abaxial layers of spongy tissue sclerified or not ( <i>Gymnacranthera</i> , <i>Knema</i> )	

These characters also have some diagnostic and taxonomic value on the species level, but only in certain genera. The value is low on the genus level.

\*) The thin filiform sclereids in *Gymnacranthera* are not meant here.

The following characters are applicable to one or two genera only, and are constant for the species, but not for the genera in question.

*List 6*

Type of hairs with cells with one arm ( <i>Horsfieldia</i> , <i>Knema</i> )	Presence of many regular cork warts ( <i>Horsfieldia</i> , <i>Knema</i> )
Basal parts of hairs often joined or not ( <i>Horsfieldia</i> )	Upright papillae of cells, bordering the stomatal complex, conspicuous or not ( <i>Myristica</i> )
Basal parts of hairs, when composed of one cell, very small or not ( <i>Myristica</i> )	Palisade parenchyma sclerified and with large pits or not ( <i>Knema</i> )
Basal cells of hairs higher than the unspecialized epidermal cells or not ( <i>Myristica</i> )	Major veins with very little sclerenchyma or with caps ( <i>Gymnocranthera</i> )

The characters of list 6 have diagnostic and taxonomic value on the species level in certain genera; on the genus level the value is low.

The next few characters are applicable to each genus and are constant for the species and for most of the genera. The genus for which the character is inconstant is mentioned.

*List 7*

Basal parts of hairs on adaxial surface present or not ( <i>Myristica</i> )	Degree of being embedded of the guard cells in the subsidiary cells ( <i>Horsfieldia</i> )
Alveolar material obviously present or not ( <i>Horsfieldia</i> and <i>Myristica</i> )	Stomata sunken below the level of the epidermis or not ( <i>Horsfieldia</i> )
	Midrib adaxially raised or not ( <i>Horsfieldia</i> )

These characters have diagnostic and taxonomic value on the species level for the genera, for which the characters are inconstant; the characters also have diagnostic and taxonomic value on the genus level, but this value is not of the same degree for each genus.

In the following list those characters are mentioned, which are applicable to and constant for each genus, but are inconstant for the family.

*List 8*

Basal parts of hairs most or least frequent on the midrib abaxially	Structure of stomatal complex, the bordering cells included
Arms of hairs one or two per cell, and, in the latter case, of the same size or not	Major veins with sclerenchyma sheaths or caps (and the size of the caps)
	Position of big druses in the mesophyll

The characters of list 8 have diagnostic and taxonomic value on the genus level.

In the last list some characters are mentioned, which are applicable to one genus only, and which are constant for that genus.

*List 9*

Adaxial vascular bundle in the midrib absent ( <i>Gymnacranthera</i> )	Filiform, rarely branched sclereids present in the mesophyll and the ground tissue of the midrib
Phloem groups of collateral bundles in midrib small ( <i>Horsfieldia</i> )	( <i>Gymnacranthera</i> )

These characters have diagnostic and taxonomic value on the genus level.

The classification of characters, as outlined above, is not strict. When more specimens per species and more species would have been studied, it is likely that more characters would appear to be inconstant on the different levels. It may be noted that as far as characters of general occurrence throughout the evergreen Dicotyledons are concerned, the above analysis confirms the limitations and possibilities for taxonomic purposes as proposed in earlier studies in the Rijksherbarium on representatives of widely different families such as *Aquifoliaceae* (Baas, 1975), *Celastraceae* (Jansen & Baas, 1973; Den Hartog-Van Ter Tholen & Baas, 1978), *Crypteroniaceae* (Van Vliet & Baas, 1975), *Guttiferae* (Baas, 1970), *Icacinaceae* (Van Staveren & Baas, 1973) and *Winteraceae* (Bongers, 1973; Vink, 1977).

Some important characters such as epidermal papillae (in species of *Horsfieldia*, *Knema* and *Myristica*), the type and distribution of the alveolar material (variable in *Myristica* and *Knema* respectively), and the occurrence of astroscleroids in *Horsfieldia* have not been included in the foregoing lists.

Papillae have been recorded in species of which unfortunately only one specimen has been studied, so the constancy for the species is unknown. The very conspicuous papillae in *Myristica*, however, occur in *M. gigantea* and *M. maingayi*, species regarded by Sinclair (1968) as closely related, whereas the other *Myristica* species examined have at most dome-shaped unspecialized epidermal cells. This gives reasons to suppose, that the papillae are constant for these species. In *Knema* things are different: the full range of slightly dome-shaped cells to papillae occur in this genus; moreover the papillae do not have such pronounced shapes as in *Myristica*. These facts make the constancy of this character in *Knema* doubtful. The constancy for *Horsfieldia iryaghedhi* is unknown. In *Cratoxylum* (*Guttiferae*, Baas, 1970) papillae are not constant for *C. formosum*, but they were regarded as possibly reflecting a further differentiation of the (sub)species into taxa of lower rank.

The type of the alveolar material (a character variable in *Myristica*) can be thoroughly studied with scanning electron microscopy only; however, with the S.E.M. only one specimen per species has been examined. Therefore the constancy of this character for a species is uncertain. The distribution of the alveolar material over the leaf is a character variable in *Knema*. The presence of the material is mainly restricted to the cells, bordering the stomatal complexes in *K. intermedia* and *K. plumulosa*, represented in this study by one specimen each; De Wilde (1979) has placed these species in one series. This suggests a constancy of this character for these species. In *Winteraceae* (Bongers, 1973) the distribution and the type of the alveolar material is variable in some species.

Astrosclereids have been recorded for two species only: *Horsfieldia fulva* and *H. superba*; only one specimen per species has been studied. These species are, according to Sinclair (1958) closely related. Therefore this character is expected to be constant for these species. The character 'number of basal cells of the hairs' (not mentioned in the lists either) is difficult, as far as the constancy is concerned: The highest numbers of basal cells per hair have been counted in *Horsfieldia* and *Knema* species, but in these genera species with small numbers also occur. Specimens of one species in *Knema* have either a high number or a small number of basal cells, whereas this character is inconstant for *Horsfieldia* species. The numbers, most frequently found on a leaf are constant for *Gymnacranthera* and *Myristica* species, inconstant for *Horsfieldia* species and reflect some trend for *Knema* species.

The constancy of the convex sculpturings of the cuticle in *Knema rufa* is simply unknown, because it is the only specimen examined of this species, while the feature has not been observed in other species.

The feature 'isobilateral leaf' (recorded for *Horsfieldia sabulosa*) will be discussed elsewhere.

#### TAXONOMIC IMPLICATIONS

##### Introductory remarks

In the following discussions, suggestions about natural affinity will be only based on an evaluation of the shared and distinguishing leaf anatomical characters of species, genera and families. With our present stage of knowledge of systematic leaf anatomy, this phenetic approach is more feasible than an attempt towards applying cladistic methods (cf. Bremer & Wanntorp's plea, 1978, for phylogenetic systematics in the sense of Hennig). This is mainly because there is no way of telling whether certain character states should be considered derived or ancestral. The hair types in *Knema* are perhaps an exception to this, and their possible phylogenetic significance will be further explored.

In view of the limitations of the research materials, the taxonomic suggestions can only be tentative.

##### Below the genus level

##### **Gymnacranthera**

This genus is fairly homogeneous: the species differ only in a few characters. In this context *G. bancana* may be regarded as taking a more or less isolated position because of some, mostly epidermal features: a relatively large number of basal parts of hairs per surface unit, cuticular layer not granular, a relatively thick adaxial cuticle, anticlinal walls of unspecialized epidermal cells not conspicuously sinuous and the chlorenchyma not continuous in the midrib. *G. eugeniifolia* can be recognized by the high degree of sclerification of the spongy tissue, the peripheral ground tissue of the midrib, and the parenchyma cells of the leaf margin. These features are sometimes also present in *G. forbesii*, but to a less extent. One specimen of *G. forbesii* var. *forbesii* and a few specimens of *G. contracta* are very similar.

These findings are partly in agreement with Sinclair (1958a, b); he regarded *G. bancana* as the most distinct species, and the remaining species as very close to each other, especially *G. eugeniifolia* and *G. forbesii*.

Where all Malesian species and their varieties have been examined, it seems useful to give a key to enable identification on leaf anatomical characters. A synoptical key to the Malesian species and varieites of *Gymnacranthera* is given at the end of this paper. All species and varieties, except *G. contracta* and *G. forbesii* var. *forbesii*, can be separated leaf anatomically.

### Horsfieldia

It is possible to distinguish most species examined of *Horsfieldia* anatomically: on epidermal features *H. crassifolia* (relatively numerous basal parts of hairs per surface unit adaxially and basal parts often joined together on the abaxial surface), *H. glabra* (basal parts of hairs composed of many cells adaxially and abaxial cuticle smooth) and *H. iryagedhi* (alveolar material clearly present, abaxial epidermis papillose and stomatal complex distinctly sunken); *H. sylvestris* too has some, for *Horsfieldia* unique features (hairs often robust and spongy tissue more or less compact); *H. sabulosa* as only species has isobilateral mesophyll. Other characters are distributed over the species in a more or less reticulate pattern, but there are species, which have relatively many important characters in common:

*H. crassifolia* and *H. sylvestris* share the presence of cuticular striations and grooves, the slightly sunken stomatal complex with the subsidiary cells with prominent cuticular striations and the relatively many basal parts of hairs per surface unit abaxially; all epidermal characters, not recorded for the other *Horsfieldia* species examined.

*H. crassifolia* and *H. sabulosa* also have some (in our view unimportant) features in common, as the relatively thick cuticle and lamina.

*H. sabulosa* and *H. glabra* share another set of characters; the most important (and unique for *Horsfieldia*) are epidermal: hairs completely absent from the lamina of adult leaves, many regular cork warts abaxially and many secretory cells in the epidermis.

*H. fulva* and *H. superba* (species not examined on the characters mentioned above) both have many astrosclereids in the mesophyll, a character not recorded for the other *Horsfieldia* species.

To compare the results, outlined above, with the classification of *Horsfieldia*, made by Sinclair (1958a, 1974, 1975), this classification is given here, as far as the species examined leaf anatomically are concerned. The more closely related species, according to Sinclair, are placed on one line.

#### Section Bivalves

*H. crassifolia*, *H. irya*  
*H. parviflora*  
*H. sylvestris*

#### Section Trivalves

*H. fulva*, *H. superba*  
*H. glabra*  
*H. iryagedhi*  
*H. macrocoma*  
*H. sabulosa*

The close relationship between *H. fulva* and *H. superba* is supported by this study. A special relationship between *H. crassifolia* and *H. sylvestris*, and between *H. glabra* and *H. sabulosa*, as suggested by this study, has not been recognized by Sinclair; the species of the pairs mentioned were, however, placed in the same section by Sinclair. Our results do not support a special relationship between *H. crassifolia* and *H. irya*. Also the division into the sections does not appear from the leaf anatomy. *H. iryagedhi* is a species with a deviating inflorescence (Sinclair,

1975). Although it has some important leaf anatomical characters, not recorded for the other *Horsfieldia* species, the majority of the characters is in the range of *Horsfieldia*.

No key to the species of *Horsfieldia* is given, because of the small number of species examined.

### Knema

Only a few of the *Knema* species examined can individually be recognized on the basis of leaf anatomical characters: *K. ashtonii* var. *cinnamomea*, *K. korthalsii* and *K. laurina* have unique hair types or a unique combination of types, *K. hookeriana* has peculiar crystals in the abaxial epidermis, *K. percoriacea* has many sclereids in the mesophyll and *K. rufa* has a sculptured, adaxial cuticle.

Some other species share one, or a couple of, for *Knema* unique features (which may point to a special relationship), for instance: *K. intermedia* and *K. plumulosa* (the distribution of the alveolar material and hair type 6); *K. conferta* and *K. kunstleri* (many regular cork warts); *K. mandarahan* and *K. pallens* (sclerified mesophyll with large pits); *K. linifolia* and *K. tenuinervia* (hair type 4); and *K. lunduensis* and *K. psilantha* (hair type 5).

Most other more or less constant characters are distributed in a reticulate pattern over the species: each character gives another classification of the species. But when these characters (c. 20, largely from lists 3–6 of the previous chapter) are listed in a diagram with compartments for each possible species pair there appear to be species with many features in common, which may point to a close relationship, whereas other combinations share none or few features. In this way groups of species have been formed: (The roman numbers behind the species refer to the series of De Wilde's classification).

<b>Group 1</b>		<b>Group 2</b>		<b>Group 3</b>	
<i>K. curtisii</i>	VI	<i>K. ashtonii</i>	II	<i>K. malayana</i>	XI
<i>K. latifolia</i>	V	<i>K. attenuata</i>	X	<i>K. oblongifolia</i>	I
<i>K. linguiformis</i>	VI	<i>K. elmeri</i>	II	<i>K. rubens</i>	XI
		<i>K. globularia</i>	IV		
		<i>K. laurina</i>	I		
		<i>K. oblongata</i>	IV		
		<i>K. pseudolaurina</i>	I		
		<i>K. pulchra</i>	IV		
		<i>K. retusa</i>	II		
		<i>K. tomentella</i>	X		
<b>Group 4</b>		<b>Group 5</b>		<b>Group 6</b>	
<i>K. intermedia</i>	IX	<i>K. conferta</i>	XII	<i>K. furfuracea</i>	III
<i>K. korthalsii</i>	IX	<i>K. kunstleri</i>	XII	<i>K. hookeriana</i>	III
<i>K. plumulosa</i>	IX			<i>K. linifolia</i>	I
				<i>K. lunduensis</i>	III
				<i>K. mandarahan</i>	IV
				<i>K. pallens</i>	III
				<i>K. percoriacea</i>	III
				<i>K. psilantha</i>	III
				<i>K. rufa</i>	IV
				<i>K. tenuinervia</i>	IV

The first group contains species which have the characters: hair type 7, 8a or 8b, lamina thin ( $\leq 120 \mu\text{m}$ ), adaxial cuticle less than  $10 \mu\text{m}$  thick, abaxial cuticle less than  $5 \mu\text{m}$  thick, adult leaves not conspicuously covered with hairs, spongy tissue and leaf margin not sclerified, midrib weakly sclerified. In *K. curtisii* and *K. linguiformis* the palisade parenchyma cells are scarcely longer than wide, a unique feature in *Knema*.

The second group contains species, linked to each other in a reticulate pattern. This group exhibits the following features: hair type 1, 2, 7, 8a or 8b, thickness of lamina usually intermediate ( $> 120 \mu\text{m}$ ,  $< 200 \mu\text{m}$ ), adaxial cuticle  $< 10 \mu\text{m}$ , abaxial cuticle  $< 5 \mu\text{m}$ , adult leaves usually covered with hairs, spongy tissue and leaf margin weakly sclerified or not, midrib usually moderately sclerified. Other important characters, shared by species of this group are: relatively numerous basal parts of hairs per surface unit abaxially, spongy tissue compact, anastomosing veins as rows of sclerenchyma fibres, large xylem bundles in the pith of the midrib and oil cells present in the pith of the midrib. *K. elmeri* and *K. retusa* in particular appear similar. The second group shares some characters with species of the first group.

The third group contains species which have the characters: hair type 7 and/or 8b, thickness of lamina usually intermediate, adaxial and abaxial cuticle  $\leq 5 \mu\text{m}$ , adult leaves not conspicuously covered with hairs, spongy tissue sclerified, leaf margin not sclerified and midrib moderately sclerified. This group shares some characters with species of the second group; *K. oblongifolia* and *K. laurina* in particular have certain common features, such as the compact spongy tissue.

The fourth group contains species, which exhibit the features: hair type 3, 6, 7 and/or 8c, thickness of lamina intermediate, adaxial cuticle  $< 10 \mu\text{m}$ , abaxial cuticle  $< 5 \mu\text{m}$ , adult leaves not conspicuously covered with hairs, spongy tissue and leaf margin not sclerified, midrib (moderately) sclerified.

The fifth group is rather heterogeneous and contains species which have the characters: hair type 7 or 8a, lamina thick ( $\geq 200 \mu\text{m}$ ), adaxial cuticle  $> 5 \mu\text{m}$ , abaxial cuticle  $4 - 6 \mu\text{m}$  thick, adult leaves covered with hairs or not, spongy tissue weakly sclerified, leaf margin sclerified or not, midrib moderately sclerified. This group, *K. kunstleri* in particular, shares some characters with species of the third and the sixth group, such as the sclerification of the abaxial layers of the spongy tissue.

The sixth group contains species, linked to each other in a reticulate pattern, and which have the characters: hair types 3, 4, 5 or 8c, lamina intermediate to thick, adaxial cuticle usually  $> 5 \mu\text{m}$ , adult leaves not covered with hairs, spongy tissue (strongly) sclerified, leaf margin usually sclerified, midrib (moderately) sclerified. Other important characters, shared by species of this group are: sclerification of the abaxial layers of the spongy tissue and large xylem bundles in the pith of the midrib. *K. furfuracea*, *K. hookeriana*, *K. pallens* and *K. percoriacea* in particular are similar; in *K. pallens* and *K. percoriacea* the palisade parenchyma cells are up to five times as long as wide, a unique feature in *Knema*. *K. linifolia* and *K. rufa* also have many characters in common. Some species of this group share some characters with species of the fourth group, especially with *K. korthalsii*.

The results outlined above are compared below with the classification proposed by De Wilde (1979), as far as species, examined in this study are concerned. Species of series VII and VIII were not studied by us. The number behind each species name refers to the leaf anatomical group.

<b>I: Series Laurinae</b>	<b>II: Series Sericeae</b>	<b>III: Series Lamellariae</b>
<i>K. linifolia</i> 6	<i>K. elmeri</i> 2	<i>K. hookeriana</i> 6
<i>K. oblongifolia</i> 3	<i>K. retusa</i> 2	<i>K. furfuracea</i> 6
<i>K. pseudolaurina</i> 2	<i>K. ashtonii</i> 2	<i>K. pallens</i> 6
<i>K. laurina</i> 2		<i>K. psilantha</i> 6
		<i>K. percoriacea</i> 6
		<i>K. lunduensis</i> 6
<b>IV: Series Obovoideae</b>	<b>V: Series Latifoliae</b>	<b>IX: Series Mamillatae</b>
<i>K. pulchra</i> 2	<i>K. latifolia</i> 1	<i>K. plumulosa</i> 4
<i>K. oblongata</i> 2		<i>K. intermedia</i> 4
<i>K. mandarahan</i> 6	<b>VI: Series Curtisianae</b>	<i>K. korthalsii</i> 4
<i>K. tenuinervia</i> 6	<i>K. linguiformis</i> 1	
<i>K. rufa</i> 6	<i>K. curtisii</i> 1	
<i>K. globularia</i> 2		
<b>X: Series Glomeratae</b>	<b>XI: Series Glaucae</b>	<b>XII: Series Punctatae</b>
<i>K. tomentella</i> 2	<i>K. rubens</i> 3	<i>K. kunstleri</i> 5
<i>K. attenuata</i> 2	<i>K. malayana</i> 3	<i>K. conferta</i> 5

The classification based on leaf anatomical characters generally supports De Wilde's classification. Some differences and particular resemblances will be discussed, with reference to notes by De Wilde (1979). The classification of Sinclair (1958a, 1961) will also be cited, if this is relevant.

De Wilde placed *K. linifolia* in series I, albeit in an isolated position, whereas leaf anatomically this species goes together with *K. rufa* and *K. tenuinervia*. In a note De Wilde describes a resemblance between *K. linifolia* and *K. tenuinervia*.

*K. globularia*, *K. oblongata* and *K. pulchra* were placed in series IV (according to De Wilde a heterogeneous series) whereas in leaf anatomical aspects these species have much in common with *K. laurina*, *K. retusa*, *K. tomentella* and other species of the leaf anatomical group 2. De Wilde considered *K. globularia* as having close affinities with his series X and XI, and resembling *K. curtisii* in the vegetative parts, which is supported by this study. Sinclair has placed *K. globularia* (and *K. oblongata*) together with *K. laurina*, *K. oblongifolia* and *K. attenuata* in one group, a classification close to the leaf anatomical one. According to De Wilde, *K. oblongifolia* has characters in common with *K. rubens*, in the same manner as in leaf anatomy.

De Wilde created a series for *K. latifolia*, considering series VI as related which is in accordance with this study.

Not half the number of species of *Knema*, included by De Wilde (1979) has been examined in this study. Therefore it is useless to give a key to the species. A key to the leaf anatomical groups, however, may help to restrict the possibilities. In view of the parallelism of the classifications based on macromorphological and leaf anatomical characters, there is a chance that the species, not examined in this study, regarded by De Wilde as related to a species, examined leaf anatomically, fits the group of the species examined. For example, it may be hoped that *K. lamellaria* de Wilde (from De Wilde's series III) fits the leaf anatomical group 6. A synoptical key to the groups of *Knema* is given at the end of this paper.

#### A tentative phylogeny of the hair types in *Knema*

The indumentum of *Knema* can be classified in types with (very) long hairs (type 3, 4, 5, 6 and 8c) and types with shorter hairs (fig. 3). Leaves with long hairs loose

these hairs when they come to the adult stage, whereas leaves with shorter hairs usually retain them (at least partially).

Between type 8a and 7 (short hairs) there is no sharp distinction. On leaves with hairs of type 8a small hairs also occur. The classification into these types is artificial and made for identification purposes. Hair type 8b and c may be regarded as the least specialized types, having no peculiar structures. The long hairs with special structures (as long stalk cells, long arms at the distal end etc., types with a relatively rare occurrence) then may have been derived from type 8 (b and) c. There are no arguments to propose evolution lines between the types 3, 4, 5 and 6. The other hairs with long stalk cells (type 1 and 2, recorded for one species each) may also have been derived from type 8b (and c) through specialization (long stalk cells) and reduction of the part with arms. Other possible derivations of these types are indicated in fig. 3.

The types with short hairs (7 and 8a) may have been derived from the types 8b (and c) through reduction; another possibility is that these short hairs without peculiar structures are the 'forerunners' of type 8b and c (the types 7 and 8a are very common!). The types 1 and 2 may also have been derived from the types 7 and 8a through extension of the stalk cells.

The phylogeny of the hair types, as proposed here, is outlined in fig. 3. Only uniquely derived characters should be used for the determination of relationships between taxa (Bremer & Wanntorp, 1978). The presumably most derived hair types are 1, 2, 3, 4, 5 and 6. Type 1 and 2 are represented by one species (or variety) each (*K. laurina* and *K. ashtonii* var. *cinnamomea*, respectively). *K. furfuracea*, *K. hookeriana*, *K. korthalsii*, *K. pallens* and *K. percoriacea* have hairs belonging to type 3 and are, according to De Wilde (1979), closely related, *K. korthalsii* excepted. The latter species, however, has hairs belonging to three types. *K. linifolia* and *K. tenuinervia* both have hairs belonging to type 4; these species have been discussed before. *K. lunduensis* and *K. psilantha* both have hairs belonging to type 5 and have been placed in one series by De Wilde. *K. intermedia* and *K. plumulosa* both have hairs belonging to type 6 and are in De Wilde's series IX, together with *K. korthalsii*. It is remarkable that the species with the derived hair types with long hairs all are in the leaf anatomical groups 4 and 6. The remaining species of group 6, *K. mandarahan* and *K. rufa*, also have long hairs, but without a particular structure (type 8c, the putative, ancestral form of the hair types just mentioned), like one of the hair types of *K. korthalsii* (of group 4). These three species moreover are the only ones with type 8c. This supports the natural character of these leaf anatomical groups and their mutual relationship.

The species of group 1, 2, 3 and 5 have shorter hairs, belonging to different types, within group 2 the derived hair types 1 and 2. Hair type 7 and 8a occur (together with type 8b) in different groups, which may be an argument for the primitive nature of these types.

### Myristica

The species examined of *Myristica* are fairly distinct anatomically. Some species have some, for *Myristica* unique features, e.g. *M. villosa* (remarkable hairs on the leaves, basal cells of hairs, if solitary, very small; spongy tissue sclerified and druses in mesophyll not large) and *M. sphaerosperma* (guard cell pairs relatively long, abaxial hypodermis present, sclereids in major veins and druses in the abaxial

epidermis); *M. fragrans*, as only species, has clustered crystals in the abaxial epidermis.

*M. gigantea* and *M. maingayi* are very similar and have some rare features in common (as grooves in the adaxial cuticle and a papillose abaxial epidermis).

Most other more or less constant characters are distributed over the species in a reticulate pattern. The characters in question are often epidermal: presence of hairs on adult leaves, number of basal parts of hairs per surface unit, thickness of the cuticle, papillae on cells bordering the stomatal complex, presence of crystals in the epidermal cells etc. As non-epidermal characters the presence of a hypodermis, the sclerification of the peripheral ground tissue of the midrib, and the frequency of the spindle-shaped crystals in the mesophyll have to be mentioned. When these characters (c. 25, largely from lists 3–7 of the previous chapter) are listed in a diagram, as done for *Knema*, it appears that some species have many features in common, whereas others share none or few features. Of the former species each pair has its own 'character complement'; nevertheless groups of species can be formed. Not each character involved will be mentioned in the discussion of the groups, but only those which are more or less characteristic for the groups.

*M. chrysophylla*, *M. fatua*, *M. globosa*, *M. lepidota*, and *M. subalulata* have many common features, in particular: *M. chrysophylla* and *M. lepidota*; *M. fatua* and *M. lepidota*; *M. fatua* and *M. globosa*; *M. globosa* and *M. lepidota*; and *M. globosa* and *M. subalulata*. The crystals in particular are important for this group of species. *M. fragrans* has many features in common with species of this group, and again the crystals play an important role. *M. sphaerosperma* shares a couple of mainly epidermal characters with *M. chrysophylla*.

*M. cinnamomea*, *M. guatteriifolia*, and *M. villosa* have many common features; those concerning the hairs (such as basal cells higher than unspecialized epidermal cells, basal parts of hairs/0.1 mm<sup>2</sup> abaxially 30 or more and many hairs present on adult leaves) are the most striking. The two latter features have also been found in *M. fatua*. *M. cinnamomea* and *M. maxima* have also some, mainly epidermal features in common.

It is interesting to compare these results with Sinclair's revision (1958a; 1968). Sinclair too has struggled with the reticulate distribution of the characters over the species and the series. His classification is given here, as far as the species, examined in this study are concerned.

#### Section I: *Myristica*

1: series **Maximae**

*M. maxima*

4: series **Maingayae**

*M. gigantea*

*M. maingayi*

7: series **Cinnamomeae**

*M. cinnamomea*

8: series **Littorales**

*M. guatteriifolia*

9: series **Fragrantes**

*M. fragrans*

#### Section II: *Fatua*

10: series **Fuscae**

*M. sphaerosperma*

*M. chrysophylla*

11: series **Fatuae**

*M. lepidota*

*M. fatua*

*M. villosa*

14: series **Cimiciferae**

*M. globosa*

15: series **Subalulatae**

*M. subalulata*

The presence of *M. gigantea* and *M. maingayi* in one series is strongly supported by this study. The close relationship of *M. sphaerosperma* and *M. chrysophylla* has also some leaf anatomical support. *M. sphaerosperma* has nevertheless some deviating characters; in ecological respect too this species deviates from *M. chrysophylla*: it is a mountain species. The series 11 needs some comment: *M. fatua* and *M. lepidota* have many common anatomical characters, but *M. villosa* takes a somewhat distinct position, while this species has more features in common with *M. cinnamomea* and *M. guatterifolia* (species of section I) than with species of section II. Although Sinclair stated that the vegetative features (of *M. villosa*) alone will distinguish this species from *M. fatua*, he has placed these species together in one series. Sinclair has given his ideas about relationships within the sections and series in notes; so he regarded series 9 as a distinct series, differing from the others in section I in many ways, while *M. fragrans* has leaves somewhat similar to those of *M. globosa* and *M. lepidota*; this is in agreement with the present results.

Apart from the case of *M. fragrans* and *M. villosa*, the division into the two sections is supported by this study, to some extent.

According to Sinclair series 7 is close to series 8, series 10 is nearest to series 11, *M. lepidota* has resemblances to *M. globosa* and *M. globosa* is also similar to *M. subalulata* in many ways; all these remarks are supported by this study. The two varieties examined of *M. fatua* are rather different, which is in agreement with the macromorphological characters.

No key to the species of *Myristica* is given, because of the small number of species examined.

### On the genus level

The Asiatic genera of the *Myristicaceae* are leaf anatomically distinct. The characters are summarized in table V. Each genus has some, for the Asiatic *Myristicaceae*, unique features.

This applies in particular to *Gymnacranthera*. The important characters are: hairs with cells with two arms of different length, subsidiary cells of stomata protruding, midrib adaxially approximately flat to shallowly concave, adaxial vascular bundle in the midrib absent, major veins with (very) small sclerenchyma caps and filiform, rarely branched sclereids present in the mesophyll.

*Horsfieldia* is the least distinctive; the only character, constant for the genus and unique for the Asiatic part of the family is the small size of the phloem groups in the midrib.

*Knema* has as unique characters the 'star-shaped stomatal structure' and the sclerenchyma sheaths in the major veins.

For *Myristica* the unique characters are: hairs with cells with two arms of equal length and the 'ring' of bordering cells (with more or less conspicuous, upright papillae) above the stomatal complex.

Of the characters, applicable to each genus, those concerning the hairs separate the genera in two groups: 1) *Gymnacranthera* and *Myristica* and 2) *Horsfieldia* and *Knema*. Regarding the other characters, there appear to be no reasons for such a grouping. According to Sinclair (1958a) the four genera are close to each other; furthermore he arranged them in a series of increasing advancement: first *Myristica*, *Horsfieldia* with *Gymnacranthera* close to it and *Knema* last. This view is not supported by this study; leaf anatomy provides no motives to indicate one genus as the most primitive and another as the most advanced.

**Table V. Differential leaf anatomical characters of *Gymnacranthera*, *Horsfieldia*, *Knema* and *Myristica***

+ = present; - = absent; -/+ = in some species absent, in others present

	<i>Gymnacranthera</i>	<i>Horsfieldia</i>	<i>Knema</i>	<i>Myristica</i>
<b>Important characters occurring in more than one genus:</b>				
Basal parts of hairs on adaxial surface	-	+	+	-/+
Most basal parts of hairs per surface unit on abaxial side of the midrib	-	+	+	-
More than 6 basal cells per basal part of hair	-	(-) +	-/+	-
Number of arms per hair cell	2	1	1	2
Alveolar material	+	(+) -	+	-/+
Stomata distinctly sunken	-	(+) -	+	+
Large druses in spongy tissue	+	+	-	-
<b>Important characters occurring in single genera only:</b>				
Arms of hair cells of different length	+	-	-	-
Arms of hair cells of equal length	-	-	-	+
Subsidiary cells of stomata dome-shaped	+	-	-	-
Star-shaped stomatal structure	-	-	+	-
Ring of bordering cells above stomatal complex	-	-	-	+
Midrib adaxially approximately flat (to shallowly concave)	+	-	-	-
Adaxial vascular bundle in midrib absent	+	-	-	-
Phloem groups in midrib small	-	+	-	-
Major veins with small sclerenchyma caps	+	-	-	-
Major veins with sclerenchyma sheaths	-	-	+	-
Thin, filiform, rarely branched sclereids	+	-	-	-
<b>Characters, recorded for one genus and not constant for that genus:</b>				
Prominence of minor veins in the epidermis	-	-	±	-
Large xylem bundles in the pith of the midrib	-	-	±	-
Anastomosing veins, composed of sclerenchyma fibres	-	-	±	-
Swollen cells in the subepidermal layer	-	±	-	-

Garrat (1933) and Armstrong & Wilson (1980) recorded some deviating wood characters for *Horsfieldia*; Ehrendorfer et al. (1968) found a deviating chromosome number in *Horsfieldia* species; Armstrong and Wilson (1978) regarded the anatomy of the flowers of *Horsfieldia* as somewhat different from those of the other genera. The results, presented here, do not support a distinct position for *Horsfieldia*; only *Gymnacranthera* is leaf anatomically somewhat isolated. A grouping of certain genera cannot be supported with the present results.

Table V can be used as a synoptical key to the four genera.

### On the family level

In the more recent literature the *Annonaceae* and the *Canellaceae* have been mentioned as the closest allies of the *Myristicaceae*. The *Canellaceae* in particular have been regarded as the family most closely related, based on the anatomy of the androecium (Wilson, 1966; Wilson & Maculans, 1967), the anatomy of the young stem and node (Wilson, 1965; Siddiqi & Wilson, 1975a) and the structure of the pollen (Siddiqi & Wilson, 1975b). Based on pollen morphology the *Annonaceae*

have also been mentioned as the family, most strongly allied with the *Myristicaceae* (Joshi, 1946). Sinclair (1958a) also advocated this relationship, based on macromorphological characters. In order to compare the leaf anatomy of the three families, a short general survey of characters of each family is indispensable.

To complete the survey of the *Myristicaceae*, leaves of specimens of the African species (*Brochoneura acuminata*, *Coelocaryon cuneatum*, *Pycnanthus angolensis*, *Scyphocephalum ochocoa*, and *Staudtia gabonensis*) and the American species (*Compsonera ulei*, *Dialyanthera lehmanni*, *Iryanthera ulei*, *Osteophloeum platyspermum*, *Virola calophylla*, *V. lorentensis* and *V. pavonis*) have been examined. The anatomy does not deviate from that of the Asiatic genera in the characters mentioned here. The variation in the presence of the alveolar material and in the vascular system of the midrib, found in the Asiatic *Myristicaceae*, has also been found in the African as well as in the American genera. The morphology of the hairs recently described by Bernardi and Spichinger (1980) for some American genera, shows a similar variation as in the Asiatic genera. These similarities give us confidence that the leaf anatomical characteristic of the family given below is fairly comprehensive. The implications on the genus level; i.e. the possibility that some genera have their closest relatives on other continents, would require a more detailed study of African and American material, and is beyond the scope of this study.

The characteristics of the *Myristicaceae* are: *Hairs uniseriate, with cells with arms; when hairs have been shed, basal parts remain visible. Alveolar material mostly present. Stomata usually only abaxially present, paracytic; guard cells more or less embedded in the subsidiary cells. Leaf usually dorsiventral. Midrib with an arc-shaped collateral bundle, often with a more or less straight collateral bundle adaxially, the phloem in separate groups, often in two layers; always with free phloem bundles in the centre, sometimes accompanied by xylem groups. Veins with collateral bundles, with sclerenchyma caps or sheaths. Petiole with mostly three collateral bundles at the basal end, also with free phloem bundles adaxially. Crystals mainly as large to small druses and spindle-shaped particles in the mesophyll, the ground tissue of the midrib and sometimes in the epidermis. Oil cells present in the mesophyll and the ground tissue of the midrib; secretory cells present in the epidermis. Tanniferous sacs often present in the veins. Sclereids as brachy- to astrosclereids in the ground tissue of the midrib, sometimes also in the mesophyll as filiform, rarely branched elements.*

Of the *Canellaceae*, the leaf anatomy of a number of species (*Canella alba*, *Capsicodendron dinisii*, *cinnamodendron corticosum*, *C. macranthum*, *Cinnamosma fragrans*, *C. madagascariensis*, and *Warburgia mannii*) has been examined to complement the scanty data in the literature. The characteristics are: Hairs not recorded. Alveolar material absent. Stomata only abaxially present, paracytic to bicyclocytic; guard cells not embedded. Leaf dorsiventral. Midrib with an arc-shaped collateral bundle, the phloem apparently not in groups. Veins with collateral bundles, with sclerenchyma caps. Petiole with three collateral bundles at the basal end. Crystals as large to small druses and sometimes as spindle-shaped particles in the mesophyll and sometimes in the epidermis. Oil cells present in the mesophyll and the ground tissue of the midrib; secretory cells sometimes present in the epidermis. Tanniferous sacs absent. Sclereids usually absent.

Most of the characters, also present in the *Myristicaceae* (stomata only abaxially,

paracytic; leaf dorsiventral; collateral vein bundles with sclerenchyma; petiole with three bundles; crystals as druses and spindle-shaped particles; secretory cells present) have a wide distribution among the Dicotyledons (Metcalf & Chalk, 1950). Important characters, present in the *Myristicaceae* (as the peculiar hairs, the alveolar material, the guard cells embedded in the subsidiary cells, the phloem bundles in the pith of the midrib and the tanniniferous sacs) are absent in the *Canellaceae*. Therefore, a close relationship between these families can hardly be supported.

The characteristics of the *Annonaceae*, concerning the leaf anatomy, are, according to Jovet-Ast (1942), Metcalfe and Chalk (1950), West (1969) and Blunden et al. (1973): Hairs, if present, simple, stellate or peltate. Alveolar material not recorded. Stomata usually only abaxially present, paracytic; guard cells not embedded. Leaf sometimes isobilateral, mostly dorsiventral. Midrib with an arc-shaped collateral bundle, sometimes the arc consisted of several small bundles, or vascular system more complex, with an adaxial, abaxial and a medullary part (not with free phloem bundles in the centre); the phloem often in large groups (not in several layers). Veins with collateral bundles, with sclerenchyma caps or sheaths. Petiole with mostly three vascular strands at the basal end. Crystals as small to large druses and prismatic particles in the mesophyll, the ground tissue of the midrib and especially in the epidermis. Oil cells or mucilage cells and cavities present in the mesophyll and the ground tissue of the midrib; oil cells sometimes in the abaxial epidermis. Tanniniferous sacs absent. Sclereids sometimes present as brachysclereids or as brachy- to astrosclereids or as thin, branched, filiform sclereids in the mesophyll and/or the ground tissue of the midrib.

The resemblances between the *Annonaceae* and the *Myristicaceae* are more or less the same as those between the *Canellaceae* and the *Myristicaceae*. The *Annonaceae* too lack important characters, present in the *Myristicaceae* and vice versa (the hairs are very different, for instance). Some characters show only a superficial resemblance, as the medullary bundles, the phloem groups and the filiform sclereids. Therefore suffice it to say that there are no indications of a close relationship between the *Annonaceae* and the *Myristicaceae*.

Also Nair (1972), studying the morphology of the flowers in particular, did not see a close relationship between the *Myristicaceae* and the *Annonaceae* or the *Canellaceae* (among other families). A comparison with other families of the *Magnoliales* (taken in the broad sense of Cronquist, 1968) does not yield other candidates for close affinity with the *Myristicaceae*. Yet *Myristicaceae* clearly belong to this order through their leaf anatomical features like oil cells and paracytic stomata. The alveolar material of the *Winteraceae* (Bongers, 1973) and the embedded guard cells in the subsidiary cells of the *Lauraceae* provide additional circumstantial evidence of links with individual families of the *Magnoliales*. It is through the sympodially branched hairs and the separate phloem groups of the vascular system of petiole and midrib, that *Myristicaceae* take an isolated position within the order.

#### REMARKS ON ECOLOGY

The majority of the *Myristicaceae* are confined to the lowland tropical rain forests (Sinclair, 1958a), a very humid habitat. Therefore it is surprising to find so

many xeromorphic characters in most species. A thick cuticle, sclerified mesophyll and ground tissue of the midrib, a dense tomentum on the abaxial surface of the adult leaves, sunken stomata, overarched by papillae of the bordering cells and alveolar material (characters, usually constant for the species) may be regarded as features, restricting the transpiration (Burström & Odhnoff, 1963, Koster & Baas, in the press). These characters do not occur in all species (*Horsfieldia* species in particular lack these features), whereas the ecological circumstances of the species are apparently not different. Some xeromorphic characters perhaps are relics; i.e. adaptations to conditions to which the ancestors of the *Myristicaceae* were subjected, quite different from those of the present habitat. (cf. Doyle, 1978, for an interesting hypothesis on the early ecological differentiation of angiosperms passing through a semi-arid phase). The markedly xeromorphic and presumably primitive, vasselles *Winteraceae*, now occupying mesic habitats might call for a similar relic hypothesis for explaining the leaf anatomical features.)

The dense tomentum on adult leaves (in agreement with many basal parts of hairs per surface unit on the areolae), the alveolar material and the high papillae on the cells bordering the stomatal complexes are characters, not constant for *Myristica*. They appear to replace each other to some extent. The three characters are never present together on the same leaf, but at least one of them is.

Another xeromorphic character is the isobilateral leaf (Esau, 1960), only recorded for *Horsfieldia sabulosa*; this species has, according to Sinclair (1974), leaves in several rows, whereas most other *Myristicaceae* have the leaves in a more or less distichous arrangement. This fact, however, cannot serve as an explanation (if there is any) for the isobilateral leaf. The position of the leaves with regard to the sun (an important factor) appears to be not different from that of the other *Myristicaceae* (De Wilde, personal communication).

In conclusion, the *Myristicaceae* provide another example of a plant group which seems to defy all generalizations on the adaptability of various leaf anatomical features to the prevailing ecological conditions (cf. Baas, 1975, for a similar situation in the genus *Ilex*). The hypothesis of an earlier adaptive significance of the xeromorphic features in *Myristicaceae* stretches the limits of functional interpretation and speculation. It leaves the question unanswered why at present not even a small portion of the family grows in semi-arid habitats. However, it is equally difficult to visualize the development and retention of so many xeromorphic characters, if they were at all stages in evolution totally meaningless for survival. Physiological research on the actual role of the anatomical structures concerned in the water household and gas exchange in these and other tropical rain forest plants is badly needed to enable more fruitful discussions on ecological and functional leaf anatomy.

SYNOPTICAL KEY TO THE MALESIAN SPECIES AND VARIETIES OF  
GYMNACRANTHERA (p.p. = pro parte)

- a: Number of basal parts of hairs on the areolae and minor veins / 0.1 mm<sup>2</sup>  
abaxially (average values of about five counts):
- |          |   |
|----------|---|
| 2 – 11:  | <b>G. contracta</b> p.p., <b>G. eugeniifolia</b>                    |
| 14 – 22: | <b>G. contracta</b> p.p., <b>G. forbesii</b> , <b>G. paniculata</b> |
| 28 – 55: | <b>G. bancana</b>   |

- b: Thickness of lamina in  $\mu\text{m}$  (This character has to be used with some reservation; when other leaves than examined here are studied, overlaps are quite possible)
- < 200: **G. forbesii** var. **crassinervis**; **G. paniculata** var. **paniculata**
  - $\geq 200$ , < 400: **G. bancana** var. **bancana**; **G. contracta**; **G. eugeniifolia**; **G. forbesii** var. **forbesii**; **G. paniculata** var. **zippeliana**
  - > 400: **G. bancana** var. **borneensis**
- c: Thickness of adaxial cuticle in  $\mu\text{m}$ :
- $\leq 7$ : **G. contracta** p.p., **G. forbesii**; **G. paniculata**
  - > 7, < 12: **G. contracta** p.p., **G. eugeniifolia**
  - > 12: **G. bancana**
- d: Abaxial layers of spongy tissue sclerified, at least locally:  
**G. eugeniifolia**; **G. forbesii** var. **crassinervis** p.p.
- Abaxial layers of spongy tissue not sclerified:  
**G. bancana**, **G. contracta**, **G. forbesii** var. **crassinervis** p.p., **G. forbesii** var. **forbesii**, **G. paniculata**
- e: Major veins with well developed sclerenchyma caps:  
**G. bancana**, **G. contracta**, **G. eugeniifolia**, **G. forbesii**
- Major veins with little sclerenchyma:  
**G. paniculata**
- f: Druse idioblasts bordering on the abaxial epidermis only:  
**G. eugeniifolia** var. **griffithii**
- Druse idioblasts bordering on the abaxial and adaxial epidermis:  
**G. bancana**, **G. contracta**, **G. eugeniifolia** var. **eugeniifolia**, **G. forbesii**, **G. paniculata**
- g: Minute, prismatic crystals present in the abaxial epidermis:  
**G. bancana** var. **bancana**
- Minute, prismatic crystals absent:  
**G. bancana** var. **borneensis**, **G. contracta**, **G. eugeniifolia**, **G. forbesii**, **G. paniculata**

SYNOPTICAL KEY TO THE GROUPS OF KNEMA SPECIES  
(the groups are specified on p. 153) (p.p. = pro parte)

- a: Adult leaves densely covered with hairs abaxially:  
2 p.p., 5 p.p.
- Adult leaves not (or very sparsely) covered with hairs:  
1, 2 p.p., 3, 4, 5 p.p., 6
- b: Hair type (see page 141):
- 1: 2 p.p.
  - 2: 2 p.p.
  - 3: 4 p.p., 6 p.p.
  - 4: 6 p.p.
  - 5: 6 p.p.
  - 6: 4 p.p.
  - 7: 1 p.p., 2 p.p., 3 p.p., 4 p.p., 5 p.p.
  - 8a: 1 p.p., 2 p.p., 5 p.p.
  - 8b: 1 p.p., 2 p.p., 3
  - 8c: 4 p.p., 6 p.p.
- c: Number of basal parts of hairs on the areolae and minor veins /  $0.1 \text{ mm}^2$  abaxially (average values of about five counts):
- < 12: 1, 2 p.p., 3 p.p., 4, 5, 6
  - > 12: 2 p.p., 3 p.p.

- d: Thickness of lamina in  $\mu\text{m}$  (This character has to be used with some reservation; when other leaves than examined here are studied, overlaps are quite possible):  
 $\leq 120$ : 1, 2 p.p., 3 p.p.  
 $> 120, < 200$ : 2 p.p., 3 p.p., 4, 6 p.p.  
 $\geq 200$ : 2 p.p., 5, 6 p.p.
- e: Thickness of adaxial cuticle in  $\mu\text{m}$ :  
 $\leq 5$ : 1 p.p., 2 p.p., 3, 4 p.p., 6 p.p.  
 $> 5, < 10$ : 1 p.p., 2 p.p., 4 p.p., 5 p.p., 6 p.p.  
 $\geq 10$ : 5 p.p., 6 p.p.
- f: Thickness of abaxial cuticle in  $\mu\text{m}$ :  
 $< 5$ : 1, 2, 3, 4, 5 p.p., 6 p.p.  
 $\geq 5$ : 5 p.p., 6 p.p.
- g: Spongy tissue obviously sclerified:  
 2 p.p., 3, 5 p.p., 6  
 Spongy tissue not (obviously) sclerified:  
 1, 2 p.p., 4, 5 p.p.
- h: Leaf margin sclerified:  
 2 p.p., 5 p.p., 6 p.p.  
 Leaf margin not sclerified:  
 1, 2 p.p., 3, 4, 5 p.p., 6 p.p.
- i: Peripheral ground tissue of midrib strongly sclerified:  
 2 p.p., 3, 4, 5, 6  
 Peripheral ground tissue of midrib weakly sclerified or not:  
 1, 2 p.p.
- j: Xylem bundles in pith of midrib large (see fig. 5):  
 2 p.p., 6 p.p.  
 Xylem bundles in pith of midrib not large or absent:  
 1, 2 p.p., 3, 4, 5, 6 p.p.
- k: Regular cork warts abundantly present:  
 5  
 Regular cork warts absent:  
 1, 2, 3, 4, 6

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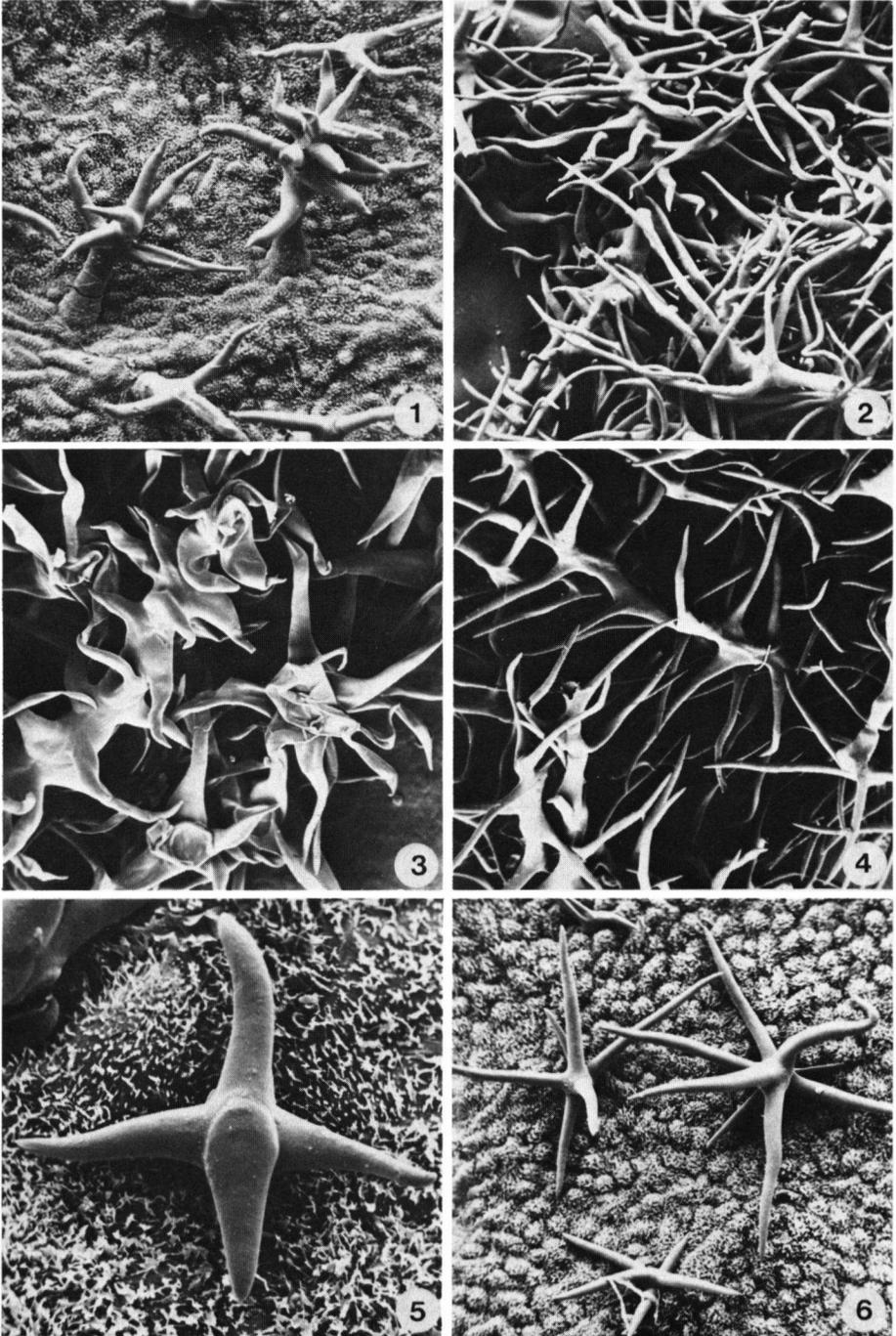
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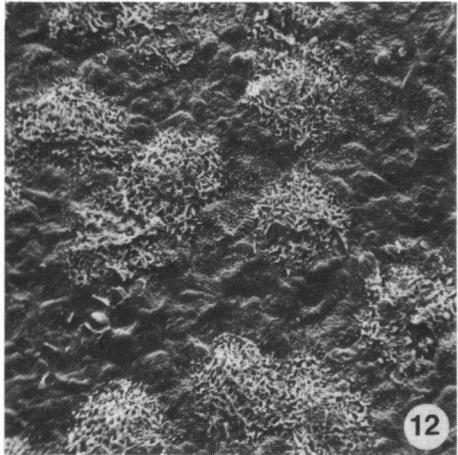
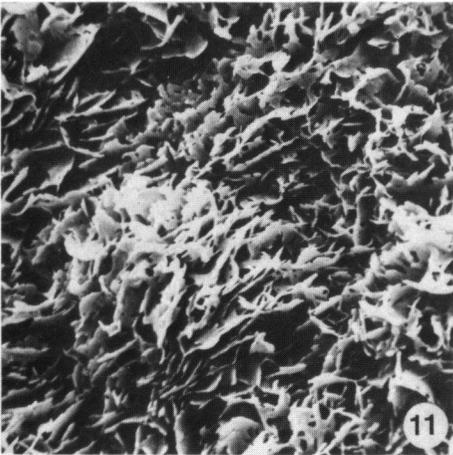
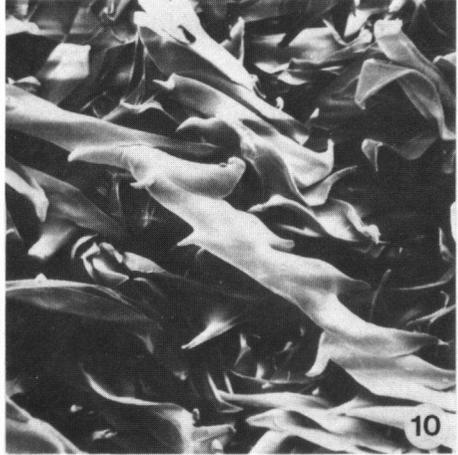
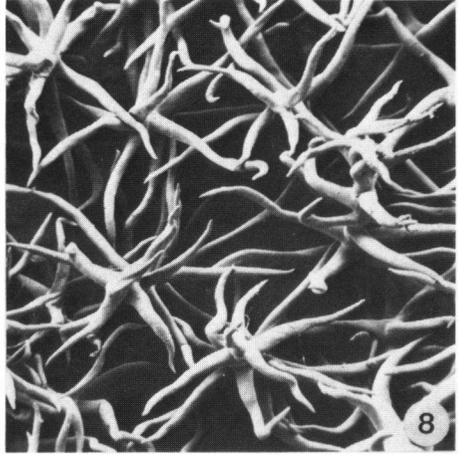
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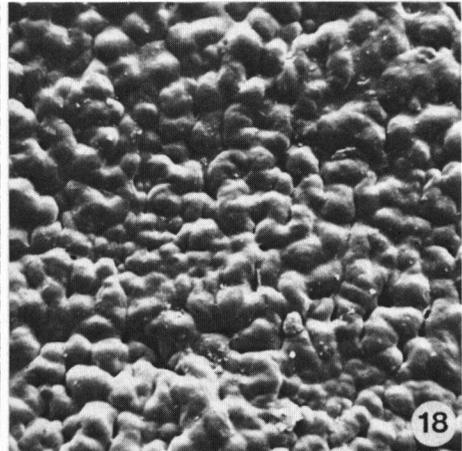
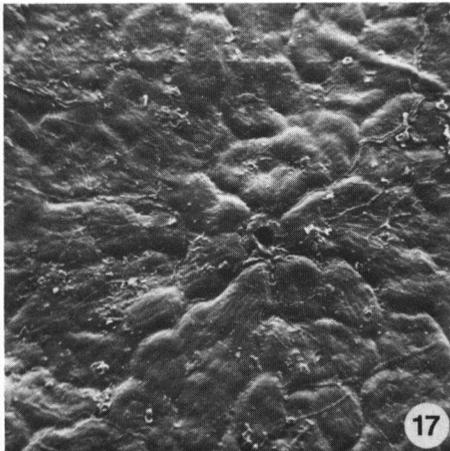
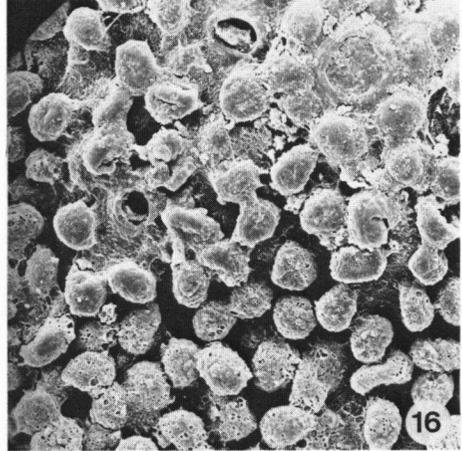
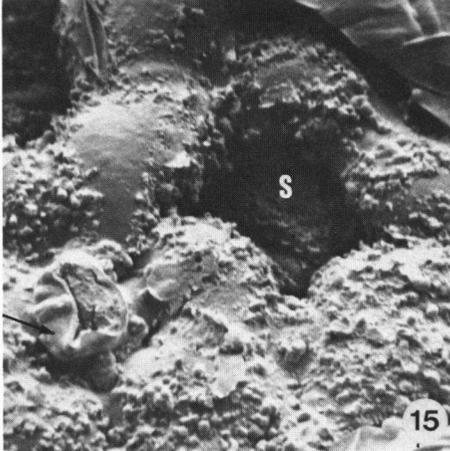
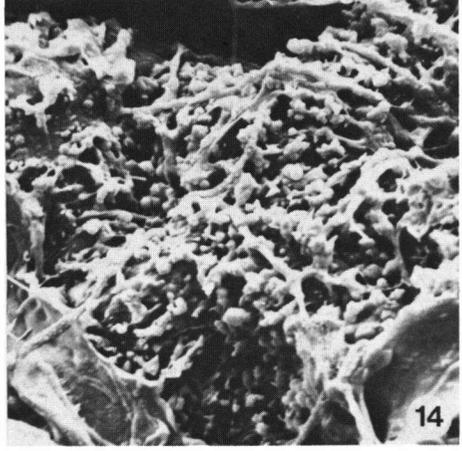
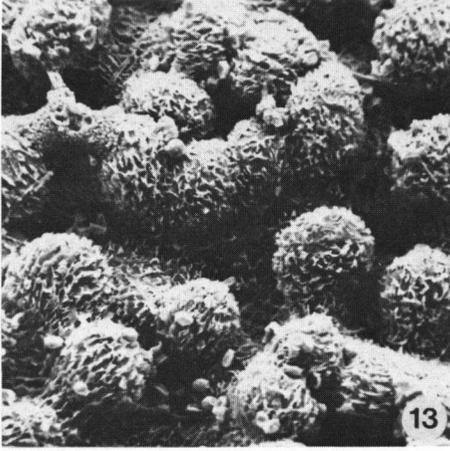
Photos 1–6. Scanning electron micrographs of hair types in *Knema*. — 1. *K. laurina*, hair type 1,  $\times 170$ . — 2. *K. percoriacea*, hair type 3, note tall stalk cells of free lying hairs,  $\times 85$ . — 3. *K. lunduensis*, hair type 5,  $\times 170$ . — 4. *K. plumulosa*, hair type 6, note tall bodies of hair cells,  $\times 80$ . — 5. *K. globularia*, hair type 7, note also alveolar material on abaxial cuticle,  $\times 820$ . — 6. *K. oblongata*, hair type 8a, note dome-shaped unspecialized epidermal cells with alveolar material,  $\times 170$ .

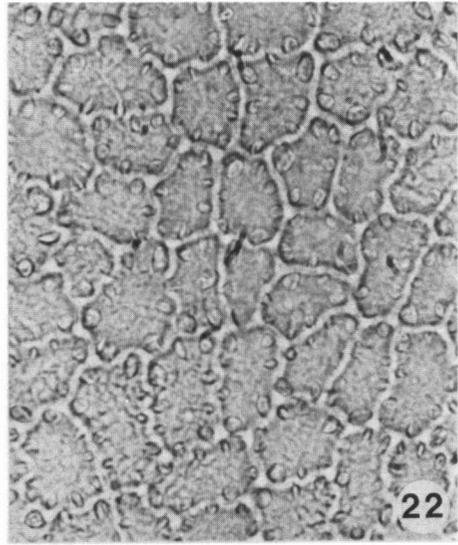
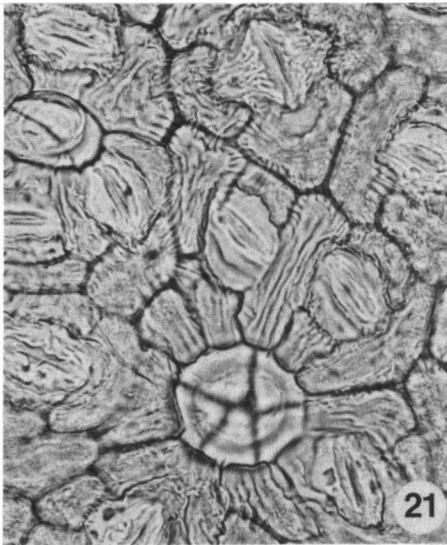
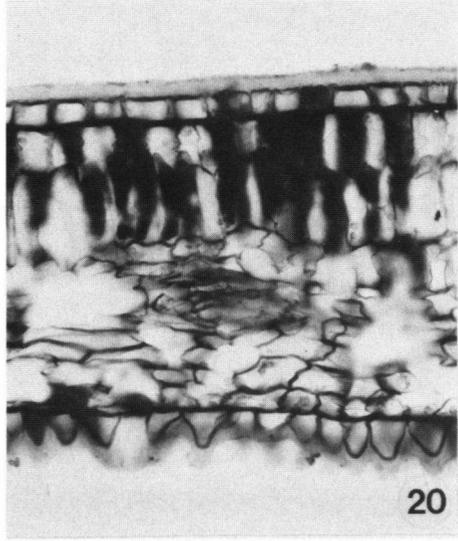
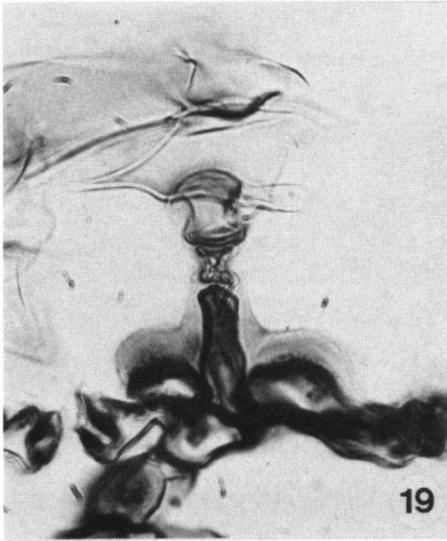
Photos 7–12. Scanning electron micrographs of hair types and alveolar material. — 7. *Knema retusa*, hair types 8b,  $\times 140$ . — 8. *Knema mandarahan*, hair type 8c,  $\times 90$ . — 9. *Myristica cinnamomea*, thin-walled hairs,  $\times 350$ . — 10. *Myristica villosa*, thick-walled, tall hairs,  $\times 150$ . — 11. *Knema oblongata*, alveolar material as a reticulum of erect, lobed plates covering the entire abaxial surface (except margin, midrib and major veins),  $\times 1730$ . — 12. *Knema intermedia*, alveolar material ( $\pm$  as in photo 11) restricted to cells overlying stomatal complex,  $\times 410$ .

Photos 13–18. Scanning electron micrographs of miscellaneous features. — 13. *Myristica maingayi*, papillose abaxial epidermis covered with alveolar material of erect plates. Note ring of cells surrounding opening above stomatal complex,  $\times 820$ . — 14. *Myristica globosa*, alveolar material as a reticulum of warty rods (heavily infested with fungal hyphae),  $\times 1660$ . — 15. *Myristica villosa*, alveolar material restricted to a warty layer. Note basal part of hair (arrow) and ring of cells overlying and surrounding stomatal complex (s),  $\times 800$ . — 16. *Horsfieldia iryaghedhi*, abaxial, papillate epidermis with porous ('spongy') alveolar material,  $\times 270$ . — 17. *Myristica maingayi*, adaxial surface with grooves in cuticle corresponding with anticlinal walls; note basal part of hair in centre;  $\times 400$ . — 18. *Knema rufa*, adaxial surface with convex sculpturings of cuticle which are much smaller than individual cells,  $\times 1470$ .



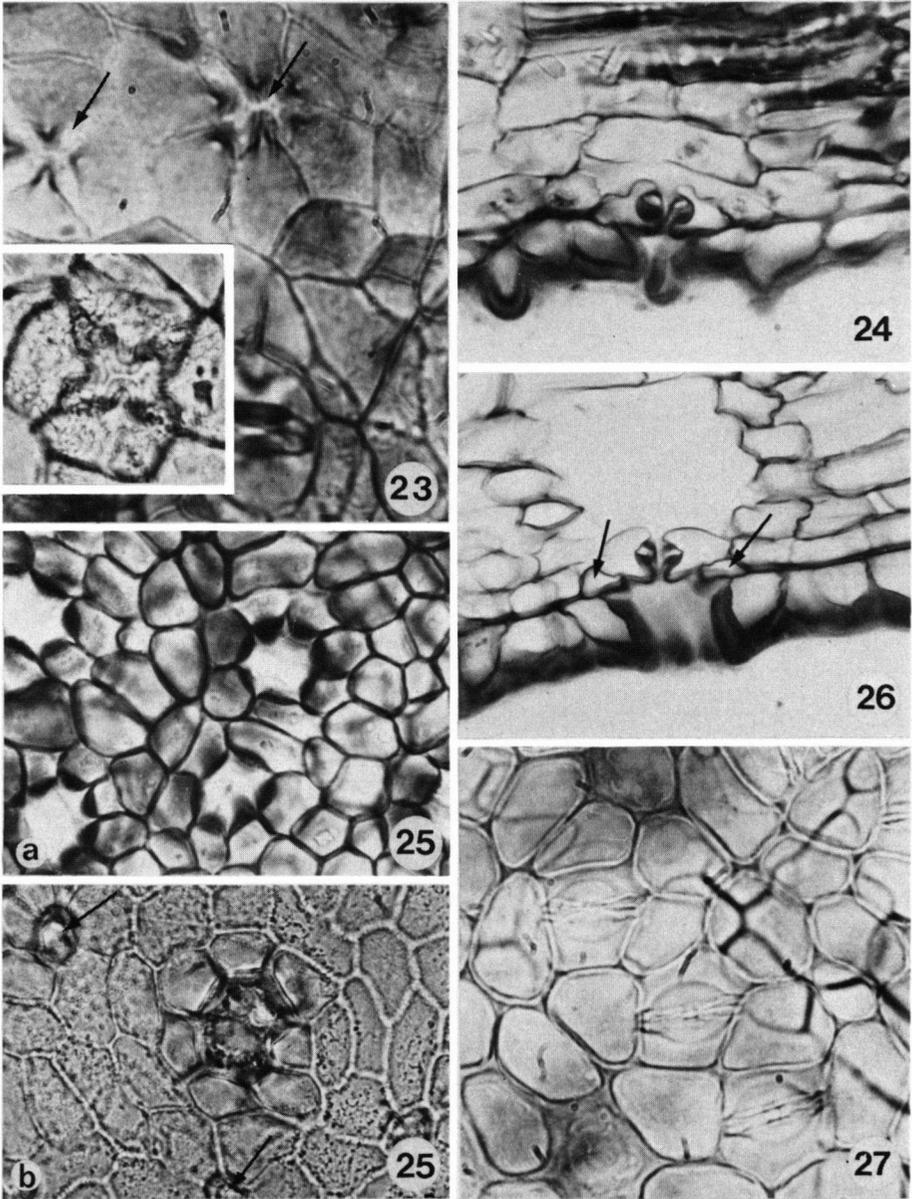




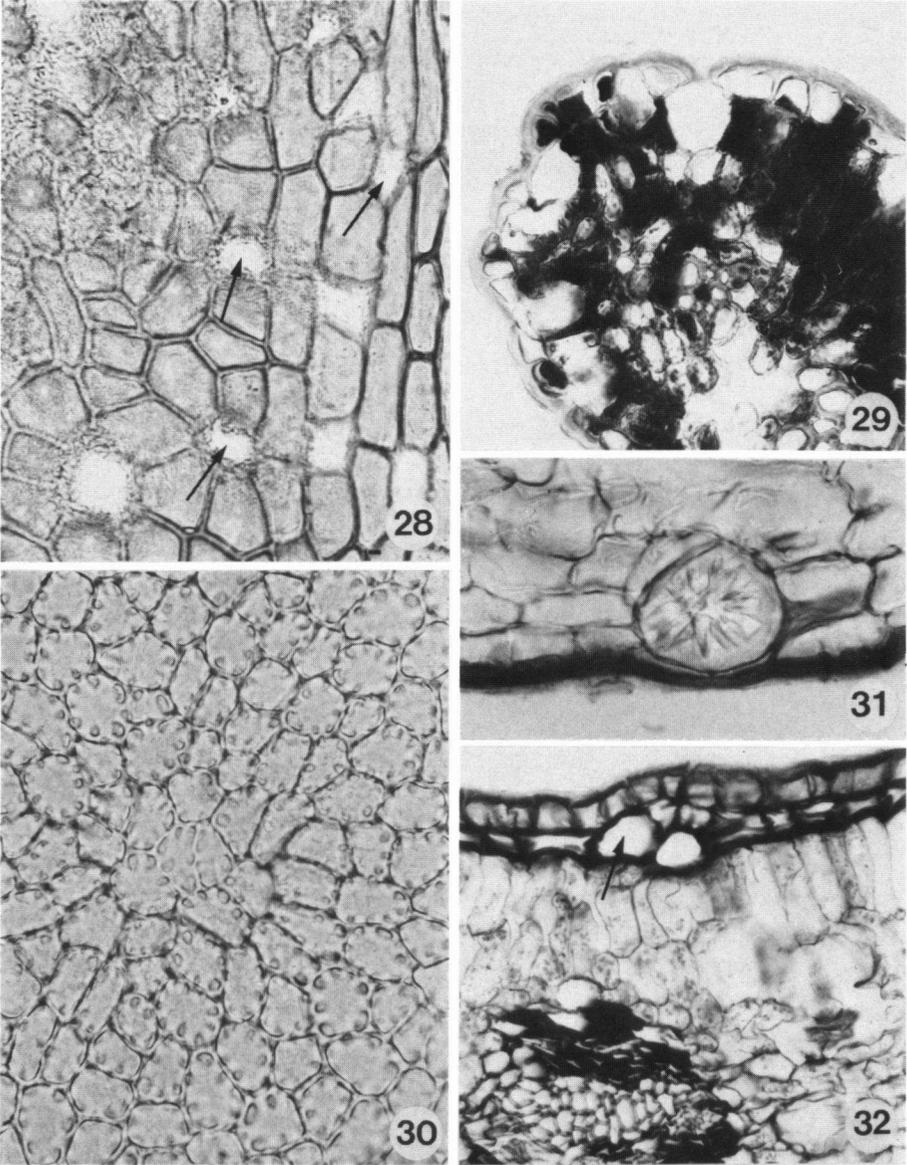


Photos 19–22. Light micrographs of various epidermal features. — 19. *Myristica guatteriifolia*, hair with tall basal cell,  $\times 600$ . — 20. *Myristica maingayi*, transverse section with papillate epidermis. Note thick cuticle on tips of papillae;  $\times 240$ . — 21. *Horsfieldia crassifolia*, abaxial cuticular maceration with prominent striations, and basal part of hair with five cells,  $\times 380$ . — 22. *Gymnacranthera forbesii*, adaxial cuticle with undulating anticlinal flanges at high focus and thin areas of cuticle in loops of undulations,  $\times 600$ .

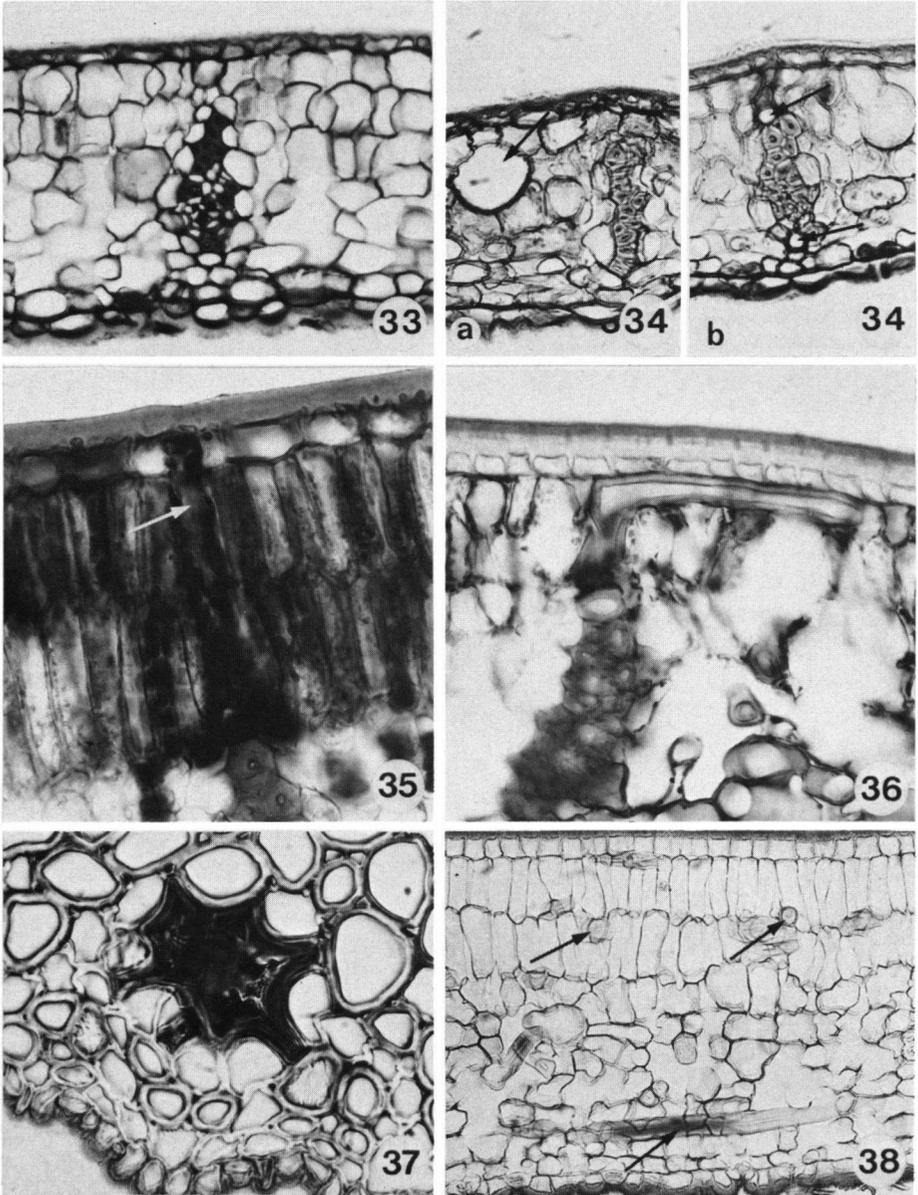
Photos 23–27. Light micrographs of stomatal complexes. — 23. *Knema laurina*, paradermal section of abaxial epidermis showing star-shaped opening (arrows) overlying stomatal complex; at bottom stomatal complex in focus; inset: star-shaped structure as seen in cuticular maceration,  $\times 600$ . — 24. *Knema laurina*, transverse section showing  $\pm$  horizontally directed papillae overarching the stomatal complex and leaving a star-shaped opening as shown in photo 23,  $\times 600$ . — 25. *Myristica*. — a. *M.*



*chrysophylla*, paradermal section showing rings of cells overlying and bordering the stomatal complex. — b. *M. cinnamomea*, *ibid.* in cuticular maceration. Note also small basal parts of hairs (arrows), both  $\times 380$ . — 26. *Myristica chrysophylla*, transverse section of stomatal complex overarched by  $\pm$  papillate cells, forming ring as shown in photo 25. Note also small cells (arrows) between subsidiary cells and ring cells,  $\times 600$ . — 27. *Gymnacranthera contracta*, paradermal section with paracytic stomata,  $\times 600$ .



Photos 28–32. Light micrographs of miscellaneous features. — 28. *Knema pallens*, maceration of abaxial cuticle near leaf margin. Note cells with very thin cuticle (some arrowed); alveolar material absent near leaf margin (right),  $\times 380$ . — 29. *Ibid.*, transverse section, showing globular cells in epidermis (or mesophyll cells intruding into epidermis?) with very thin cuticle as shown in photo 28;  $\times 240$ . — 30. *Gymnacranthera contracta*, maceration of adaxial cuticle, showing region with relatively thin anticlinal flanges in centre, corresponding with location of large crystal idioblast in subepidermal mesophyll,  $\times 380$ . — 31. *Ibid.*, transverse section with subepidermal druse idioblast, cf. photo 30;  $\times 380$ . — 32. *Horsfieldia sylvestris*, adaxial hypodermis with locally swollen cells (arrow),  $\times 240$ .



Photos 33–38. Light micrographs of miscellaneous features. — 33. *Knema malayana*, vein with vertically transcurrent bundle sheath,  $\times 240$ . — 34. *Knema laurina*, minor veins devoid of xylem or phloem, entirely composed of fibres; a. note oil cell in mesophyll (arrow); b. note tanniferous tubules (arrows),  $\times 240$ . — 35. *Knema pallens*, tanniferous tubule running from vein into epidermis (arrow); palisade very thick-walled,  $\times 380$ . — 36. *Knema percoriacea*, thick filiform sclereid connecting sclerenchyma cap of vein with adaxial epidermis,  $\times 240$ . — 37. *Gymnacranthera forbesii*, midrib with brachy- to astrosclereid,  $\times 380$ . — 38. *Gymnacranthera contracta*, mesophyll with numerous filiform sclereids, mostly in cross section (some arrowed),  $\times 150$ .