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COMPARATIVE LEAF ANATOMY OF KOKOONA AND LOPHOPETALUM (CELASTRACEAE)

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CONTENTS

SUMMARY

The leaf anatomy of *Kokoona* and *Lophopetalum* is described in detail. Separation of the two genera as effectuated by Hou (1963) is supported by differences in vascular anatomy of the distal end of the petiole, which is invariably more complex in *Lophopetalum* than in *Kokoona*. Other differential characters (p. 000) only apply to part of the species of *Lophopetalum*. As based on leaf anatomy it is impossible to define groups of closely related species within the genera because of a lack of mutual correlation between the different leaf anatomical characters. *Lophopetalum* in particular shows some striking anatomical features such as a very variable and complex arrangement of vascular tissue in petiole and midrib, complex types of cyclocytic and anisocytic stomata, crystarque cells, and epidermal papillae. Most of these characters occur in part of the genus only. The variability below the species level of characters such as epidermal wall thickness, number of subsidiary cells per stoma, dimension of guard cell pairs, presence or absence of stomata in upper epidermis etc. is reported for some species. Because of the great range of anatomical variation it is impossible to identify species, using leaf anatomical characters only.

INTRODUCTION

In his revision of the family *Celastraceae* for the Flora Malesiana Hou considered the genera *Kokoona* Thwaites and *Lophopetalum* Wight *ex* Arn. as distinct, on the grounds of differences in floral and seed characters (1963: 264). Herewith he refuted Kurz's suggestion (1870: 73) to reduce *Kokoona* to *Lophopetalum*. A natural classification of the wood of

*) This paper reports on the results of a post graduate study carried out by the first author under the supervision of the second author.

Kokoona and *Lophopetalum* coincides with Hou's botanical classification (Balan Menon 1964: 20). A study of pollen morphology by Hou (1969) resulted in the discovery of another character supporting the generic status for both *Kokoona* and *Lophopetalum*.

This study of leaf anatomy was undertaken in order to have a more complete survey of the characters of these genera and to find out whether there is leaf anatomical support for their separation. Furthermore, the results of such a study might be helpful in the identification of sterile material which is very difficult for these genera (Hou 1963: 260 and 264). A further contribution to the knowledge of the leaf anatomy in *Celastraceae* was regarded as another justification of this detailed study.

Some data on the leaf anatomy of some species of *Kokoona* and *Lophopetalum* can be found in publications by Stenzel (1893: 50, 70), Metz (1903: 27—28), Loesener (1892: 192—193), Solereder (1908: 87—96), and Metcalfe and Chalk (1950: 389—391). In the present paper descriptions and tables of characters of all species of *Kokoona* and *Lophopetalum*, known at present (Hou, 1962, and Byrnes, 1971), will be given.

In order to gain some impression of leaf anatomical variation within a species (be it either ecologically or genetically controlled) 11 specimens of *Kokoona littoralis* and *Lophopetalum javanicum* were selected for study. These species are known to show much leaf morphological variation (Hou, 1963). Of *K. sessilis* 6 specimens were studied. Of all remaining species at least 1, mostly 2 specimens were studied.

MATERIALS AND METHODS

All material was taken from dried specimens present in the Rijksherbarium, Leiden, except for a specimen of *Kokoona coriacea*, which was kindly provided by Mr. J. P. M. Brenan, Keeper of the Herbarium, Royal Botanic Gardens, Kew. Because of the possibility of misidentification of non-flowering material the leaves were always taken from specimens with flowers. They were taken from a branchlet just below the basis of a flowering shoot in order to be certain that fully developed leaves were studied.

Permanent preparations, 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 sections of the leaf surface. Transverse sections were stained with a safranin-haematoxylin mixture. Hand sections were stained with safranin only. This procedure was followed for one specimen of each species. Semi-permanent slides, mounted in glycerine jelly, were made of all other specimens of which transverse sections were made. 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 glycerine jelly.

Measurements 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 in all cuticular preparations. Lamina and cuticle thickness were measured in glycerine jelly preparations. In most specimens no sharp distinction was present between uncutinised cell wall, cuticular layer, and cuticle (cf. Stace, 1965). Therefore the total outer periclinal wall thickness of the epidermal cells half way in between the anticlinal walls was measured instead of the thickness of the cuticle. Stomatal indices were calculated according to the formula:

$$\text{S.I.} = \frac{\text{number of stomata}}{\text{number of epidermal cells} + \text{stomata} + \text{subsidiary cells}} \times 100$$

This formula deviates from the one given by Salisbury (1927) in the presence of the number of subsidiary cells in the fraction's denominator. I have not found whether the

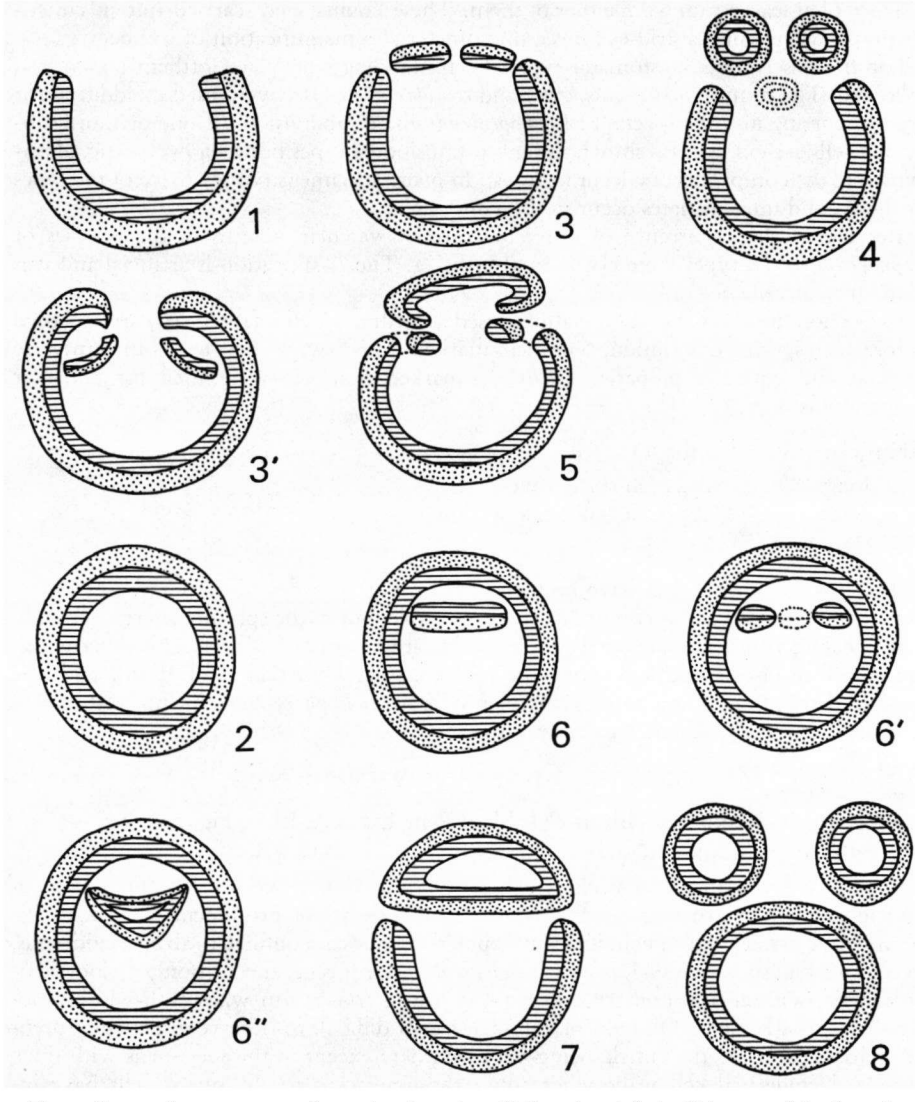


Fig. 1. Types of arrangement of vascular tissue in midrib and petiole in *Kokoona* and *Lophopetalum*. Types 1 and 3 are simple, the other types are complex. Type 1 and 3—5 are 'open', types 2 and 6—8 are 'closed'.

subsidiary cells should be counted apart or taken together with the stomata in any publication in which the stomatal index is used. It seems logical to include the number of subsidiary cells in the sum total of cell types used in the fraction's denominator. Probably Salisbury worked with plants with anomocytic stomata which would account for the omission of subsidiary cells.

Average values of stomatal sizes are based on 25 measurements. Stomatal indices are based on 10 counts in the part of the lamina between midrib and leaf margin at a

distance of at least 3 mm from either of them. These counts were carried out in cuticular preparations using a grid eye piece micrometer at a magnification of × 1000.

For the description of stomatal types the terminology of Van Cotthem (1970) was followed. The terms *complex* anisocytic and *complex* cyclocytic were used in addition for types occurring in some species of *Lophopetalum* where subdivisions of one or more subsidiary cells are evident. As shown in fig. 24, transitional types between cyclocytic, anisocytic, and the complex types occur (arrows). In many specimens two or more of the types of fig. 24 and intermediates occur in the same leaf.

Because of the occurrence of different complex vascular systems in the petioles of *Lophopetalum*, the types were classified as in fig. 1. The classification is artificial and was made for convenience only.

Collection numbers and abbreviations, used according to Hou (1969: 103) are recorded before each specific description. Numbers marked with * were used for both transverse sections and cuticular preparations. All unmarked numbers were used for cuticular preparations only.

Abbreviations used in the text:

l = long	S.V. = in surface view
w = wide	T.S. = in transverse section

RESULTS

The leaf anatomical data have been recorded using both descriptions and tables. The generic descriptions are as comprehensive as possible, but in the specific descriptions only those characters not suitable for listing in a table are mentioned. The specific descriptions are therefore unbalanced and should be used together with table I or II and with the generic description. The complex vascular systems in *Lophopetalum* are not elaborately described, but only reference to figures is made.

GENERIC AND SPECIFIC DESCRIPTIONS

Kokoona Thwaites (Table I; Plate I, 2 & 3, III, 2; Fig. 24)

S.V.: *Cuticle* smooth to granular. Unspecialized *epidermal cells* polygonal, with straight to slightly curved anticlinal walls which range from thin to very thick. Thin areas of cuticle or pit-like structures absent. Minor *veins* mostly not prominent in adaxial epidermis, not to fairly prominent in abaxial epidermis. *Stomata* confined to abaxial epidermis, except for one specimen of *Kokoona ovatolanceolata* (see specific description), cyclocytic or anisocytic, with 2—9 subsidiary cells, 13—38 μm l., 10—34 μm w., length-width ratios 0.9—1.5, mostly *ca.* 1. Outlines of subsidiary cells difficult to observe in cuticular preparations because of the cuticle being very thin here except in the specimens with thick anticlinal epidermal cell walls where only those adjacent to the guard cells have inconspicuous cuticular flanges. Outer and inner stomatal ledges not conspicuous. Polar T-pieces absent. Granular material sometimes present in the stomatal pore. Subsidiary cells partly or almost completely underlying the guard cells. Stomatal index 6.2—12.4. *Cork warts* present in varying amounts.

T.S.: *Lamina* dorsiventral or tending to isobilateral, 140—470 μm thick. Unspecialized *epidermal cells* rectangular, tall to flattened, those of abaxial epidermis usually lower than those of adaxial epidermis. Anticlinal walls often tapering towards the mesophyll, in some species bulging in the middle (Plate I, 1). Outer periclinal walls 4—12 μm thick. *Hypodermis* consisting of 1, rarely 2 adaxial or abaxial layer(s) of square to flattened, sometimes pentagonal, translucent cells which are mostly somewhat bigger than adjacent epidermal

cells. *Mesophyll* composed of 1—4 adaxial layer(s) of palisade parenchyma cells (up to 5 times as long as wide) and spongy tissue of varying compactness and thickness. Part of mesophyll cells sometimes with thickened, lignified, pitted walls. *Midrib* adaxially shallowly grooved, flattened, or raised, abaxially always prominently raised, supplied with a simple open or closed vascular system (type 1 or 2, fig. 1), whether or not accompanied by single or grouped sclerenchyma fibres. Cells with lignified pitted walls often present in ground tissue. Vascular bundles of minor *veins* embedded in mesophyll, supplied with sclerenchyma caps or few sclerenchyma fibres, often partly or completely sheathed by a layer of translucent parenchyma cells. *Petiole* supplied with a vascular system similar to that of midrib and with grouped or solitary sclerenchyma fibres, rarely without sclerenchyma. Cells with lignified pitted walls often present in medullary tissue. *Brachysclereids* present or absent in ground tissue of petiole and midrib in clusters and/or solitary. *Crystals* solitary or both solitary and clustered, scarce to abundant, most frequent in petiole, midrib, and near minor veins, absent to scanty in mesophyll. *Crystarque cells* absent.

1. **Kokoona coriacea** King

Material: Malaya, *King's collector 4226**.

S.V.: *Stomata* anisocytic-cyclocytic, with 3(4) subsidiary cells. T.S.: Anticlinal walls of adaxial *epidermal cells* tapering to narrow towards the mesophyll. *Hypodermal cells* somewhat bigger than adjacent epidermal cells. *Brachysclereids* solitary and in conspicuous clusters.

2. **Kokoona filiformis** (Laws.) Fischer

Material: Thailand, *Kerr 12450**.

S.V.: *Stomata* anisocytic and/or cyclocytic, with 3, rarely 2 or 4—6 subsidiary cells. T.S.: *Lamina* tending to isobilateral. *Hypodermal cells* somewhat bigger than adaxial epidermal cells. *Brachysclereids* absent.

3. **Kokoona littoralis** Laws. (Plate I, 3)

Material: Malaya, *KEP. 94398*, S.F. 30177**; Sarawak, *S. 17893*, S. 23654*, S. 23693, S. 9537, Smythies 15242**; Sumatra, *Endert 349*, Endert 34E.1P.639, Soepadmo 168, Buwalda 7113*.

S.V.: *Stomata* anisocytic-cyclocytic, with (2)3—5(6) subsidiary cells. Granular material sometimes present in stomatal pore. T.S.: Anticlinal walls of unspecialized *epidermal cells* ranging from thin to very thick. Anticlinal walls tapering to narrow towards mesophyll in thick-walled specimens. *Hypodermis* consisting of 1 or 2 layer(s) of cells that are slightly bigger than adjacent epidermal cells in thick-walled specimens only. Spongy *mesophyll* cells in some specimens with thickened, lignified, densely pitted walls. *Brachysclereids* solitary or in conspicuous clusters.

N o t e: It is remarkable that the strikingly thick-walled epidermis of *K. littoralis* (similar to situation in *K. sessilis* as illustrated in Plate I, 2) appears to be a variable character. The whole range from fairly thin-walled to extremely thick-walled is present in the material investigated. Plate I, 3 represents an intermediate form. The possibility that we deal with different stages in extremely slow leaf development was ruled out by the finding of extremely thick-walled epidermal cells in some rather young leaves.

Table I: KOKOONA

Legend: sizes in μm
stomatal indices in %
lamina thickness $\pm 20\ \mu$m
stomatal sizes: averages between extremes
vascular systems: types according to fig. 1
+ = abundant; ± = scarce; — = absent
F = flattened; G = grooved; SR = slightly raised; R = raised
er = erect; sq = square; fl = flattened

character / specimen	thickness of lamina	stomatal index	width of stomata	length of stomata	thickness of ad. periclinal cell walls	thickness of ab. periclinal cell walls	shapes of adaxial epidermal cells in T.S.	shape of midrib ad.	vasc. system midrib	vasc. system petiole	brachysclereids	solitary crystals	clustered crystals
1. *K. coriacea*	280	12.0	15—18—20	15—18—20	7—9	6—8	sq-fl	R	2	2	+	—	+
2. *K. filiformis*	140	12.0	12—14—16	14—16—18	4—6	4—6	sq-fl	F	1	1	—	—	+
3. *K. littoralis*													
KEP 94893	330		16—17—19	15—18—20	9—11	6—8	sq-fl	G	1	1	+	±	±
S.F. 30177	280	10.4	13—16—17	14—16—18	6—8	4—6	sq-fl	G	1	1	+	—	±
S. 17893	300	11.5	21—23—25	22—24—28	6—8	4—6	er-sq	G	1	1	+	—	±
S. 23654	400	12.4	14—16—19	14—16—21	8—10	7—11	sq-fl	G	1	1	+	±	±
Sm. 15242	470	11.1	13—15—18	13—16—18	11—13	9—11	er	G	1	1	+	—	±
End. 349	250		13—16—19	14—17—22	3—5	3—5	sq-fl	G	1	1	±	±	+
S. 23693			13—15—17	13—16—18									
S. 9537			19—21—23	22—24—26									
Soepadmo 168		8.9	16—18—20	17—19—21									
End. 34E. 1P. 639		10.3	16—17—20	17—19—22									
Buw. 7113			15—17—20	16—18—22									
4. *K. ochracea*													
SAN. 47614	250	11.1	15—17—20	14—16—19	4—5	4—5	sq-fl	F	1	1	±	+	+
Kost. 9159	320		14—17—19	16—17—19	5—7	4—6	sq-fl	SR	1	1	±	+	+
5. *K. ovatolanceolata*													
And. 7910	280	7.6	22—25—34	20—25—31	6—8	7—9	sq-fl	F	1	1	—	±	+
bb. 32394	320	7.8	19—22—25	21—24—29	7—9	9—11	er-fl	F	1	1,2	±	±	+
6. *K. reflexa*													
End. 34E. 1P. 634	230	9.1	10—12—14	16—18—20	5—8	5—6	sq-fl	R	1	1	—	±	±
bb. 34E. 1P. 635	200		13—14—16	16—18—20	4—6	3—5	er-fl	R	1	1	±	±	±
Sutr. 92		10.5	12—13—15	16—18—20									
Kost. 12045			12—14—15	14—16—19									
bb. E. 3P. 1158			12—13—15	16—18—20									
bb. E. 736			10—12—13	14—16—18									
7. *K. sessilis*													
S.F. 36296	250	6.2	23—26—28	22—29—33	9—12	10—12	er-sq	R	2	2	+	—	+
FRI. 5375	220	8.0	24—27—29	24—27—29	11—13	10—12	er-sq	R	1	1,2	+	—	+
8. *K. zeylanica*	370	6.2	24—27—32	30—32—38	8—11	11—13	er-sq	R	1	1	+	+	+

4. **Kokoona ochracea** (Elm.) Merr.

Material: Indonesian Borneo, *Kostermans 9159**; Sabah, *SAN. 47614**.

S.V.: *Stomata* anisocytic-cyclocytic with 3 or 4 subsidiary cells, often giving the impression of paracytic, but with one big lateral cell and 2 smaller cells on the other side of the guard cell pair. T.S.: *Hypodermal cells* bigger than adjacent epidermal cells. *Brachysclereids* solitary.

5. **Kokoona ovatolanceolata** Ridley

Material: Indonesian Borneo, *bb. 32394**; Brunei, *Brun. 0822**, *Brun. 5524**; Sarawak, *Anderson 7910**, *S. 9224*; 2-years old seedling from the greenhouse of the Hortus Botanicus, Leiden*.

S.V.: *Cuticle* granular. *Stomata* cyclocytic, frequent in adaxial epidermis of *bb. 32394*, with 3—6 subsidiary cells. Granular material sometimes present in the stomatal pore. T.S.: *Hypodermis* absent in cultivated seedling, composed of flattened cells which may be slightly bigger or smaller than epidermal cells in other specimens. Clustered *crystals* abundant in hypodermis of *Anderson 7910* and in adaxial epidermis of *bb. 32394*.

N o t e: Abundance of stomata in the adaxial epidermis of *bb. 32394* and absence in *Anderson 7910* led to the checking of more specimens for this feature. No other material than the former was found to have stomata in the adaxial epidermis.

6. **Kokoona reflexa** (Laws.) Ding Hou

Material: Indonesian Borneo, *Sutrisno 92*; Sumatra, *bb. E. 736*, *bb. E. 3P. 1158*, *bb. 34E. 1P. 635**, *Endert 34E. 1P. 634**, *Kostermans 12045*.

S.V.: *Stomata* anisocytic-cyclocytic with 3 or 4 subsidiary cells, resembling paracytic stomata as in *K. ochracea*. T.S.: *Hypodermis* poorly differentiated from mesophyll.

7. **Kokoona sessilis** Ding Hou (Plate I, 2)

Material: Malaya, *S.F. 36296**, *KEP FRI. 5375**.

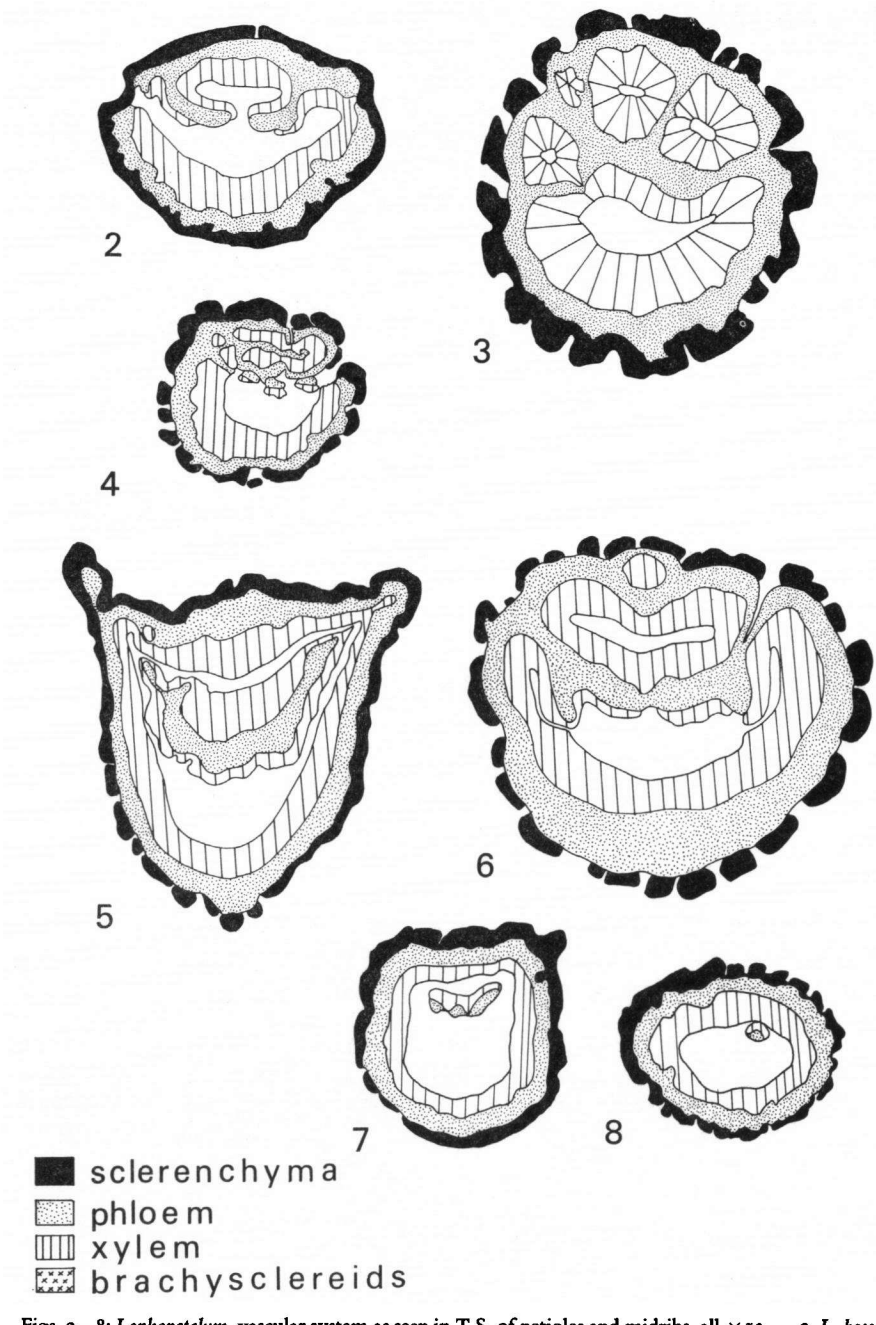
S.V.: Anticlinal walls of *epidermal cells* very thick. *Stomata* cyclocytic with 4—7 thin-walled subsidiary cells. Granular material present in stomatal pore. T.S.: *Lamina* tending to isobilateral. Anticlinal walls of unspecialized *epidermal cells* bulging (cf. Plate I, 1). *Hypodermal cells ca.* 1/3 in height of epidermal cells. *Brachysclereids* solitary or in conspicuous clusters.

N o t e: The outstanding thickness of the anticlinal walls of the unspecialized epidermal cells was also found in some specimens of *K. littoralis* and in the adaxial epidermis of *Lophopetalum pachyphyllum* (Plate I, 2).

8. **Kokoona zeylanica** Thwaites (Plate III, 2)

Material: Ceylon, *Thwaites C.P. 2584**.

S.V.: Abaxial *cuticle* with reticulate thickenings on inner side. *Stomata* cyclocytic with 6—9 subsidiary cells. T.S.: *Hypodermis* consisting of an abaxial layer of cells which are considerably bigger than adjacent epidermal cells, interrupted by stomatal air cavities.



Figs. 2—8: *Lophopetalum*, vascular system as seen in T.S. of petioles and midribs, all × 13. — 2. *L. beccarianum* (*SAN. 52957*), midrib. — 3. ibid., basal end of petiole. — 4. *L. glabrum* (*C.F. 34564*), distal end of petiole. — 5—8. *L. javanicum*. — 5. *bb. Cel/V—145*, distal end of petiole. — 6. ibid., basal end of petiole. — 7. *SAN. 25059*, distal end of petiole. — 8. ibid., basal end of petiole.

Part of palisade parenchyma cells with thin periclinal division walls, part of spongy mesophyll cells with slightly thickened walls. Vascular system of basal end of *petiole* composed of 6 free vascular bundles.

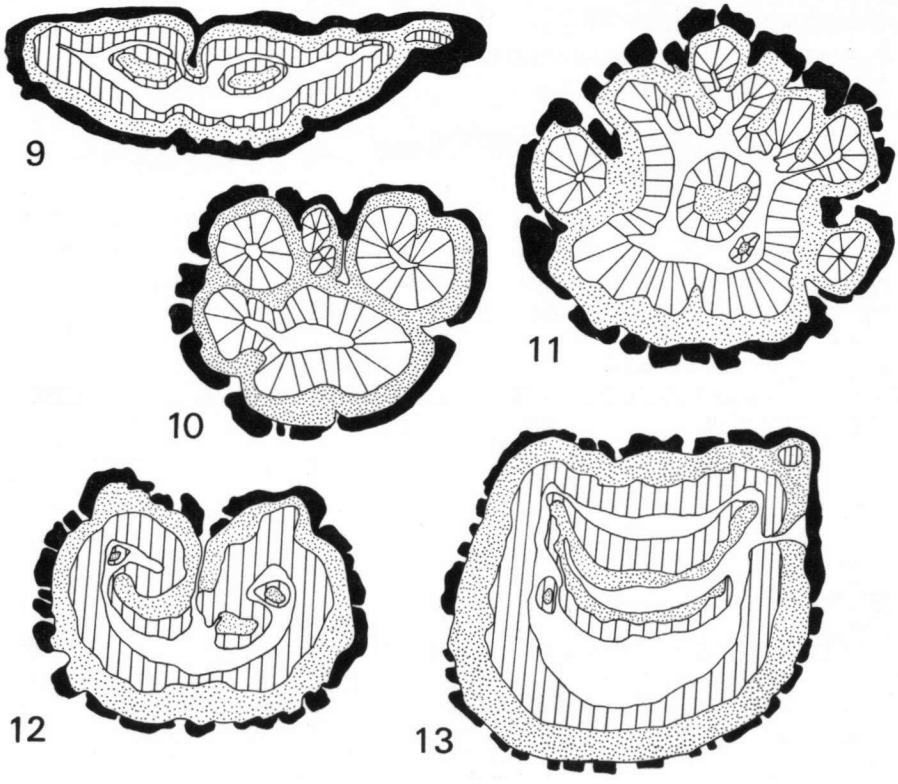
N o t e: The presence of a hypodermis on the lower instead of the upper side of the lamina is noteworthy in this specimen.

Lophopetalum Wight *ex* Arn.

(Table II; Plate I, 1, 4, 5, and 6; II, 1—6; III, 1 and 3—6; Figs. 2—22).

S.V.: *Cuticle* smooth to coarsely granular and/or slightly striated. Unspecialized *epidermal cells* polygonal, with straight to undulated anticlinal walls. Thin areas of cuticle in loops of undulations and/or cell corners or pit-like structures in cell corners sometimes present. Anticlinal walls fairly thin except in adaxial epidermis of *L. pachyphyllum*, cuticular flanges rarely pitted. Minor *veins* mostly not prominent in adaxial epidermis, fairly prominent in abaxial epidermis of most species. *Stomata* present on both surfaces or confined to abaxial epidermis, anisocytic, helicocytic, cyclocytic, or complex aniso- or cyclocytic, often present as different types in one specimen, with 3—5(11) subsidiary cells, 11—38 μm l., 7—29 μm w., length-width ratios 1.0—1.3—1.7. Outlines of subsidiary cells sometimes difficult to observe because of the cuticle being thin here. Outer and inner stomatal ledges inconspicuous to fairly conspicuous, small polar T-pieces rarely present. Granular material absent from stomatal pores or very inconspicuous. Subsidiary cells partly underlying guard-cells. Stomatal index 3.7—11.3%. *Cork warts* present in varying amounts.

T.S.: *Lamina* dorsiventral, 150—450 μm thick. Unspecialized *epidermal cells* rectangular, tall to flattened, those of abaxial epidermis mostly lower than those of adaxial epidermis. Anticlinal walls sometimes tapering towards the mesophyll, those of adaxial epidermis of *L. pachyphyllum* tapering and bulging like in *Kokoona sessilis* (cf. Plate I, 1). Outer periclinal walls of both epidermides sometimes with thin places or pitlike structures next to cell corners, corresponding to thin areas of cuticle as seen in surface view. Abaxial epidermis in some species with low or high *papillae*. Thickness of outer periclinal walls 1—12 μm. *Hypodermis* present in some species only. *Mesophyll* composed of 1—5 adaxial layers of square to very tall palisade parenchyma cells and spongy tissue of varying compactness and thickness. Part of mesophyll cells with thickened, lignified, pitted walls in many species. *Midrib* adaxially shallowly grooved to prominently raised,abaxially always prominently raised, with a simple open to complex closed vascular system without or with 1—3 medullary bundles; the whole system surrounded by an interrupted to closed ring of sclerenchyma fibres. Cells with thickened, lignified, densely pitted walls present in the medullary tissue except in *L. subobovatum* and *L. sessilifolium*. Vascular bundles of minor *veins* embedded in mesophyll except for the species with prominent veins in surface view where dorsiventral bundle sheath extensions to the epidermis are present, provided with sclerenchyma caps, whether or not sheathed by a layer of translucent parenchyma cells. *Petiole* supplied with a vascular system ranging from complex open to closed in basal end, whether or not with one or more medullary bundles, in distal end always with at least 1 medullary bundle, latero-dorsal wing bundles and/or wing fibre strands present in distal end. Sclerenchyma fibres mostly present like in midrib. Cells with thickened, lignified, densely pitted walls often present in medullary tissue. *Brachysclereids* only noted in *L. pachyphyllum* and one specimen of *L. javanicum*. *Crystals* mostly solitary, sometimes clustered or both clustered and solitary. *Crystarque cells* present in some species.



Figs. 9—13: *Lophopetalum multinervium*, vascular systems as seen in T.S. of petioles and midribs, all × 13. — 9. *bb. 8953*, midrib. — 10. ibid. basal end of petiole. — 11. *Kostermans 10375*, basal end of petiole. — 12. *bb. 8953*, distal end of petiole. — 13. *Kostermans 10375*, distal end of petiole.

1. **Lophopetalum arnhemicum** Byrnes

Material: Australia, *Byrnes 1180**.

S.V.: *Stomata* complex cyclocytic. Minor *veins* prominent in adaxial epidermis. T.S.: Features as listed in table II.

2. **Lophopetalum beccarianum** Pierre (Plate III, 5 & 6; figs. 2 & 3)

Material: Sabah, *Ping Sam A. 1896**; Sabah, *SAN. 37508*, *SAN. 52957**; Sarawak, *S. 23829*.

S.V.: Outer periclinal walls of *epidermal cells* with thin areas of cuticle in loops of undulations and/or cell corners. *Stomata* anisocytic-complex anisocytic. Polar T-pieces faint to fairly conspicuous. T.S.: *Mesophyll* with numerous thickened, lignified, pitted walls. *Midrib*: vascular system very complex in *SAN. 52957* (fig. 2). *Petiole*: vascular system in basal end of *SAN. 52957* as in fig. 3.

3. **Lophopetalum duperreaneum** Pierre

Material: South Vietnam (Cochinchina), *Pierre 4082**.

S.V.: *Stomata* anisocytic-complex anisocytic-complex cyclocytic. Incomplete stomata with one guard cell infrequently present. T.S.: *Hypodermis* present at adaxial side, clearly differentiated near veins, faintly differentiated in other areas.

4. **Lophopetalum floribundum** Wight

Material: Malaya, *KEP. 99907**, *FRI. 4800**.

S.V.: Outer periclinal walls of *epidermal cells* without or with rather inconspicuous thin areas of cuticle in loops of undulations and/or cell corners. *Stomata* complex anisocytic in *FRI. 4800*, complex cyclocytic in *KEP. 99907*. T.S.: Part of spongy mesophyll cells in *FRI. 4800* with lignified, densely pitted walls.

N o t e: The two specimens show rather striking differences, e.g. in abaxial epidermal cell pattern, stomatal sizes and types, presence of crystarque cells and lignified mesophyll cells (Table II).

5. **Lophopetalum glabrum** Ding Hou (Plate III, 1, 2, 4; fig. 4)

Material: Brunei, *CF. 34564**; Sarawak, *S. 20987*.

S.V.: Outer periclinal walls of *epidermal cells* with thin areas of cuticle in loops of undulations and cell corners, particularly conspicuous in adaxial epidermis. *Stomata* sometimes anisocytic, mostly complex anisocytic or helicocytic. T.S.: Part of spongy *mesophyll* with lignified walls. *Petiole*: vascular system as in fig. 4 in distal end of *CF. 34564*, slightly different in basal end and in *S. 20987* (Table II).

6. **Lophopetalum javanicum** (Zoll.) Turcz. (Plate I, 5; III, 3; figs. 5—8)

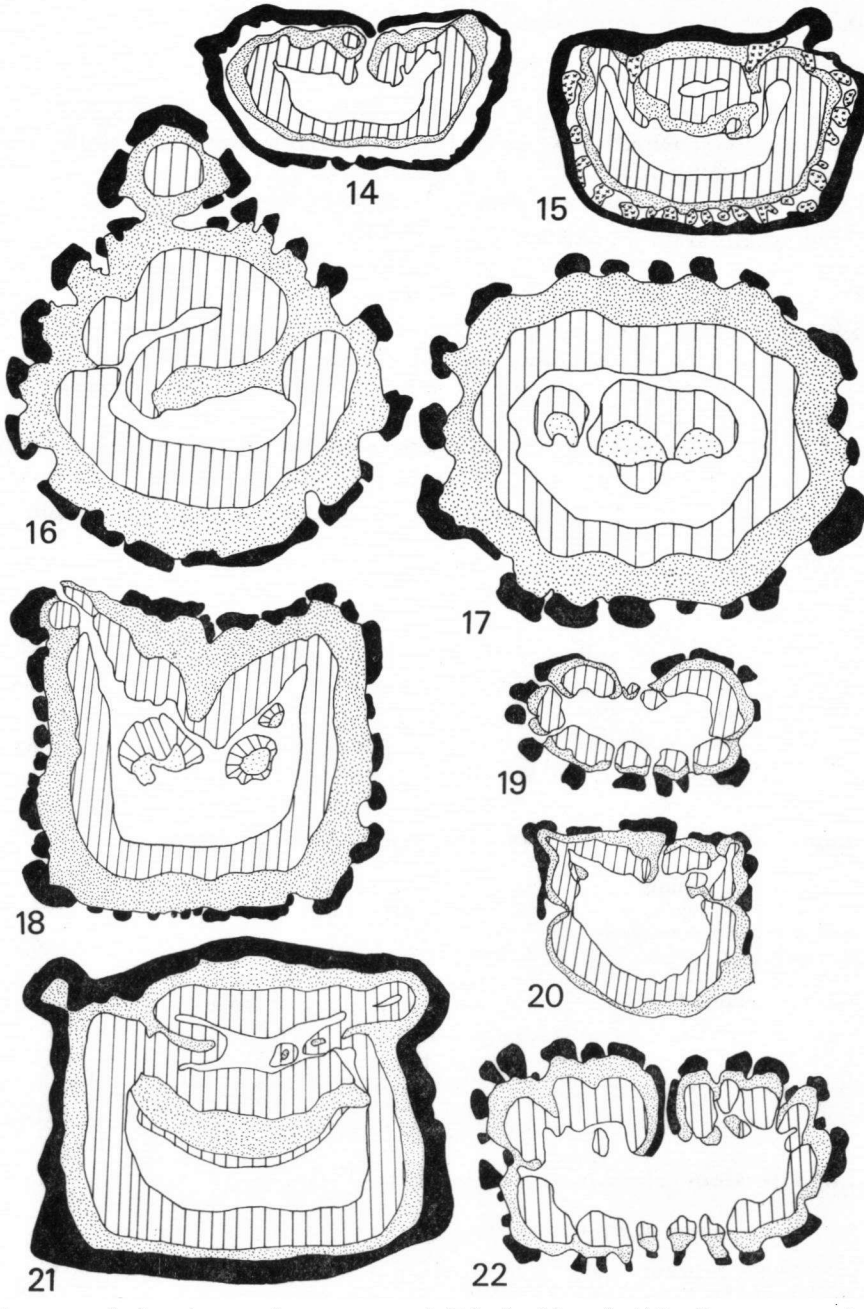
Material: Indon. Borneo, *Endert 5150**, *Kostermans 6602 & 9580*; Sabah, *SAN. 25059**; Celebes, *bb. Cel/V—145**; New Guinea, *bb. 30540*; Moluccas, *bb. 29957*; Philippines, *Sulit 12360*; Sumatra, *bb. 6426**, *Endert 48E. 1P. 538**, *Forbes 3151**.

S.V.: *Stomata* often complex, anisocytic-cyclocytic-helicocytic. Polar T-pieces faintly present. T.S.: *Hypodermis* present in *bb. Cel/V—145* and probably in *bb. 29957* (2 cutinized cell layers: epidermis + hypodermis noted in cuticular preparations), at adaxial side. Part of *mesophyll* cells with thickened, lignified, pitted walls in some specimens. *Petiole*: vascular system very complex in *bb. Cel/V—145* (figs. 5 & 6), as in figs. 7 & 8 in *SAN. 25059*.

7. **Lophopetalum ledermannii** (Loes.) Ding Hou

Material: New Guinea, *bb. 30969**, *Aet & Idjan 388**.

S.V.: Outer periclinal walls of *epidermal cells* with thin areas of cuticle in loops of undulations and cell corners in *Aet & Idjan 388*, inconspicuously so in *bb. 30969*. *Stomata* mostly complex, anisocytic-cyclocytic. Minute polar T-pieces usually present. T.S.: *Hypodermis* present in *Aet & Idjan 388* only, poorly differentiated. Part of *mesophyll* cells with thickened, lignified, pitted walls.



Figs. 14—22: *Lophopetalum*, vascular systems as seen in T.S. of petioles and midribs, all ×13. — 14—18. *L. pachyphyllum*. — 14. *S. 16212*, midrib. — 15. *FRI. 0632*, midrib. — 16. ibid., basal end of petiole. — 17. *S. 16212*, basal end of petiole. — 18. ibid., distal end of petiole. — 19. *L. pallidum* (*K.L. 1566*), basal end of petiole. — 20. ibid., distal end of petiole. — 21. *L. torricellense* (*BW. 5683*), distal end of petiole. — 22. *L. wightianum* (*Endert 59E. 1P. 567*), basal end of petiole.

8. Lophopetalum macranthum (Loes.) Ding Hou

Material: New Guinea, *Gjellerup 701*, NGF. 37402**.

S.V.: Outer periclinal walls of *epidermal cells* with rather thin areas of cuticle in cell corners at adaxial side. *Stomata* frequently complex, anisocytic-cyclocytic. T.S.: Features as listed in table II.

9. Lophopetalum micranthum Loes. (Plate I, 6)

Material: New Guinea, *Versteeg 1773**.

S.V.: Abaxial *cuticle* coarsely granular except over the stomatal complex. *Stomata* complex cyclocytic. T.S.: Part of *mesophyll* cells with thickened, pitted, lignified walls. *Midrib*: vascular system composed of a number of more or less free vascular bundles.

10. Lophopetalum multinervium Ridley (figs. 9—13)

Material: Indon. Borneo, *Kostermans 10375**; Sumatra, *bb. 8953**.

S.V.: *Stomata* complex cyclocytic. Small polar T-pieces mostly present. T.S.: *Hypodermis* of one or two adaxial cell layers present, poorly differentiated in some places. Part of *mesophyll* with thickened, lignified, pitted walls. *Midrib* flattened and broad, vascular system as in fig. 9. *Petiole*: vascular system very complex, particularly in basal end (figs. 10 & 11). Vascular system in distal end as in figs. 12 & 13.

11. Lophopetalum pachyphyllum King (Plate I, 1; II, 1 & 2; figs. 14—18)

Material: Sarawak, *S. 16212**; Malaya, *FRI. 0632**.

S.V.: Anticlinal walls of *epidermal cells* very thick in adaxial epidermis; adaxial periclinal walls with pit-like structures in cell corners; abaxial cells with well-developed *papillae*. *Stomata* cyclocytic, difficult to observe because of overarching papillae of subsidiary cells (Plate II, 2). Papillae on veins arranged in rows (Plate II, 1). T.S.: Anticlinal walls of adaxial *epidermal cells* as ik *Kokoona sessilis* (Plate I, 1). Lumina of epidermal cells narrow in thick-walled, acute to obtuse papillae. *Papillae ca.* 30—60 μm tall. *Midrib*: vascular system as in fig. 14 (*S. 16212*) or in fig. 15 (*FRI. 0632*). *Petiole*: vascular system very complex in basal end (figs. 16, 17), in distal end as in fig. 18. *Asterosclereids* present throughout mesophyll.

12. Lophopetalum pallidum Laws. (Plate I, 4; figs. 19 and 20)

Material: Indon. Borneo, *bb. 18997**; Malaya, *KL 1566**.

S.V.: *Cuticle* coarsely granular in *KL. 1566*, striated in *bb. 18997*. Anticlinal walls of *epidermal cells* conspicuously pitted. *Stomata* anisocytic or cyclocytic, rarely complex anisocytic. T.S.: Outer periclinal walls of abaxial *epidermal cells* dome-shaped (very lowly papillate). *Stomata* sunken below lamina surface. *Petiole*: vascular system of *KL 1566* as in fig. 19 (basal end) and fig. 20 (distal end).

N o t e: This species, together with *L. wightianum*, shows a very simple arrangement of vascular tissue in petiole and midrib. Particularly the basal part of the petiole of *L. pallidum* recalls the situation in *Kokoona*. Yet, medullary bundles are present in the distal end of the petiole in this species.

Table II: LOPHOPETALUM

Legend: ab. = abaxial(ly); ad. = adaxial(ly); ep. = epidermis; pericl. = periclinal; st. = stomata; v.c. = very complex; vasc. syst. = vascular system (see fig. 1); und. ad. walls = undulations of anticlinal cell walls of adaxial epidermis; + = sinuous; ± = slightly sinuous to curved; — = straight to slightly curved. See also legend to Table I.

character / specimen	thickness of lamina	stomatal index	width of stomata	length of stomata	st. in ad. ep.	und. ad. walls	und. ab. walls	thickness adaxial pericl. walls	thickness abaxial pericl. walls	shape adaxial epidermal cells in T.S.	vasc. syst. midrib	vasc. syst. petiole	shape midrib, ad.	crystarque cells	solitary cryst.	clustered cryst.	brachysclereids.
1. *L. arnhemicum*	200	7.8	16—19—22	20—23—26	±	+	—	3—5	3—5	sq-fl	2	1—6	SR	—	±	—	±
2. *L. beccarianum*																	
Ping Sam A. 1896	250	11.3	11—13—15	12—14—17	+	±	—	8—10	6—8	sq-fl	6	6″	SR	+	+	—	+
SAN. 52957	240		15—17—20	15—16—19	+	+	±	8—10	6—8	sq-fl	5	8—6″	SR	+	+	—	+
SAN. 37508			13—15—18	14—15—17	+	+	+										
S. 23829			13—16—18	14—16—17	+	±	+										
3. *L. duperreaneum*	200		19—21—25	19—21—23	±	—	—	3—5	2—3	sq-fl	6′	6′—6″	F	—	+	—	—
4. *L. floribundum*																	
KEP. 99907	370	7.1	15—18—20	19—22—24	—	—	—	6—8	6—8	er-fl	6	6′—6″	R	—	+	±	±
FRI. 4800	150		10—12—15	13—14—17	—	+	+	4—6	1—2	er-fl	6	6″	R	+	+	±	±
5. *L. glabrum*																	
C.F. 34564	170	7.0	7— 8— 9	11—13—14	+	+	+	3—5	3—4	sq-fl	4	4—6	R	+	+	—	—
S. 20987	200		9—10—12	13—15—19	+	+	+	5—7	3—5	sq-fl	6	4—6′	R	+	+	—	±
6. *L. javanicum*																	
End. 5150	200	8.2	9—11—14	12—13—15	+	—	—			er-fl	6″	6″	R	±	+	—	+
bb. Cel/V—145	320	9.1	13—14—15	14—17—21	+	—	—	1—2	1—2	er-fl	6″	6″	R	±	+	—	±
bb. 6426	300	7.0	11—13—16	13—16—20	—	—	—	1—2	1—2	er-fl	6″	6″	R	—	+	—	±
End. 48E. 1P. 538	180		16—19—22	23—25—31	—	—	—	1—2	1—2	er-fl	6″	8—6″	R	±	+	—	+
Forbes 3151	190	7.1	12—14—15	14—16—22	+	—	—	1—2	1—2	er-fl	6″	6″	R	+	+	—	±
Kost. 6602		6.0	11—12—14	13—15—18	+	—	±										
Kost. 9580		5.6	11—13—15	15—17—19	+	—	—										
SAN. 25059	210	6.0	10—12—14	14—16—17	+	±	—	1—2	1—2	er-fl	3		G	±	+	—	±
[illegible]																	

Sulit 12360		4.6	14—15—17	18—19—21	+	—	—										
bb. 29957		8.1	12—13—15	13—17—19	±	—	±										
7. L. ledermannii																	
bb. 30969	240		17—18—20	17—20—22	±	—	—	5—7	5—7	er-sq	6	3′—6′	R	—	+	±	+
Aet & Idjan 388	170	6.9	10—11—13	12—14—17	—	±	±	2—4	1—2	fl	6′	6′	R	+	+	—	+
8. L. macranthum																	
Gjellerup 701	250	8.7	*ca.* 16	14—17—21	+	—	±	4—5	2—5	er-fl	6′	3′—6/6′	SR	—	±	—	±
NGF. 37402	250		15—16—18	17—18—20	±	—	—	4—6	3—5	er-fl	2	6/6′	SR	—	+	—	±
9. L. micranthum	350	3.7	14—17—21	19—22—27	+	—	—	8—10	7—8	sq-fl	2	6′	R	—	+	—	—
10. L. multinervium																	
Kost. 10375	340		16—19—21	16—20—23	+	—	—	1—3	1—3	er-sq	3′	v.c.—6″	G	—	+	—	±
bb. 8953	270	7.2	15—17—19	16—18—21	+	—	—	2—4	2—3	er-fl	6′	v.c.—6″	G	—	+	—	±
11. L. pachyphyllum																	
S. 16212	400		?	?	—	—	—	11—12		er-sq	3	6′	F	+	+	—	±
FRI. 0632	280		?	?	—	—	—	11—12		er-sq	7	6	F	+	+	—	+
12. L. pallidum																	
bb. 18997	220		27—28—29	33—35—38	—	—	—	6—8	7—9	sq-fl	2	1—6′	R	+	±	—	—
K.L. 1566	170	9.3	21—23—27	23—26—35	—	±	—	3—5	4—6	sq-fl	6′	2—6′	R	+	±	—	—
13. L. rigidum																	
Haviland 2236	450	6.2	14—16—19	16—18—19	±	±	±	5—7	6—9	er-sq	6′	6″	F	+	+	—	±
SAN. 16814	210		11—13—14	13—16—18	±	+	±	4—5	2—4	er-sq	2	3′—6″	SR	+	+	—	±
14. L. sessilifolium																	
S. 13737	240		17—18—20	16—20—22	±	±	+	2—4	1—3	er-fl	7	?	R	±	+	—	±
Native coll. 543	310	6.9	16—19—22	17—21—24	±	+	+	2—3	1—2	er-fl	6′	?	R	±	+	—	—
15. L. subobovatum																	
SAN. 17833	450	6.2	17—18—20	19—21—23	±	—	—	9—10	3—5	er	6	6″	R	+	+	—	±
KEP. 71523	280		12—14—16	14—17—18	±	—	—	2—4	1—3	er	6	6″	R	+	+	—	±
16. L. torricellense																	
Brass 12326	310	4.2	14—18—21	19—24—31	—	—	—	6—9	4—6	er-fl	4—6′	4	R	+	+	—	+
B.W. 5683	320		15—18—24	21—24—28	±	—	—	8—10	4—6	er-fl	6—8	6″	R	+	+	—	+
T.G.H. 12400			16—18—20	18—21—25	±	—	—										
17. L. wallichii																	
Garrett 1053	320		19—22—26	22—24—27	±	—	—	6—8	4—6	sq-fl	6	3′—6″	R	+	+	+	—
Native coll. 3219	260	8.2	20—22—25	21—24—29	±	—	—	7—9	5—7	sq-fl	2	6″	R	+	+	+	±
18. L. wightianum																	
Gallatly 811	150		17—18—20	20—22—26	—	—	—	3—5	2—4	er-fl	5	2—6′	SR	—	+	—	—
End. 59E. 1P. 567	250	4.1	13—15—18	19—25—30	±	—	—	3—6	3—4	er-fl	4	1—2—6′	SR	—	+	—	—

13. **Lophopetalum rigidum** Ridley

Material: Sabah, *SAN. 16814**; Sarawak, *Haviland 2236**.

S.V.: Outer periclinal walls of *epidermal cells* with thin areas of cuticle in loops of undulations and cell corners. *Stomata* anisocytic in *SAN. 16814*, anisocytic to complex anisocytic in *Haviland 2236*. T.S.: Part of *mesophyll cells* with thickened, lignified walls.

14. **Lophopetalum sessilifolium** Ridley

Material: Sarawak, *S. 13737**, *Native collector 543**.

S.V.: Outer periclinal walls of *epidermal cells* with thin areas of cuticle in loops of undulations and cell corners. *Stomata* anisocytic, complex anisocytic, or helicocytic. T.S.: Features as listed in Table II.

15. **Lophopetalum subobovatum** King

Material: Malaya, *KEP. 71523**; Sabah, *SAN. 37833**.

S.V.: *Stomata* anisocytic or complex anisocytic-complex cyclocytic. Small polar T-pieces usually present. T.S.: *Hypodermis* poorly differentiated, present at adaxial side. Palisade parenchyma cells extremely tall.

16. **Lophopetalum torricellense** Loes. (fig. 21)

Material: New Guinea, *Brass 12326**, *BW. 5683**, *Hartley 12400*.

S.V.: *Stomata* complex, anisocytic-cyclocytic. Small polar T-pieces present in *BW. 5683*. T.S.: *Petiole*: vascular system very complex in distal end of *BW. 5683* (fig. 21). Solitary *crystals* abundant in epidermis of *BW. 5683*.

17. **Lophopetalum wallichii** Kurz (Plate II, 3 and 6)

Material: Thailand, *Garrett 1053**, *Native collector 3219**.

S.V.: *Stomata* anisocytic-cyclocytic, occasionally complex. T.S.: Outer periclinal walls of abaxial *epidermal cells* low dome-shaped (sometimes lowly papillate) (Plate II, 3). Minute *crystals* present in epidermal cells.

18. **Lophopetalum wightianum** Arn. (Plate II, 4 and 5; fig. 22)

Material: Burma (Tenasserim), *Gallatly 811**; Sumatra, *Endert 59E. 1P. 567**; and nail varnish replicas of 3 more specimens to check for presence of papillae.

S.V.: *Stomata* mostly anisocytic, sometimes cyclocytic or complex anisocytic. Many irregular *cork* formations and necrotic cells in lower epidermis of *Gallatly 811*. T.S.: Abaxial *epidermal cells* lowly papillate in *Gallatly 811*. *Guard cells* sunken. *Petiole*: vascular system as in fig. 22 in basal end. Solitary *crystals* abundant in epidermis of *Gallatly 811*; in subepidermal layer of *Endert 59E. 1P. 567*.

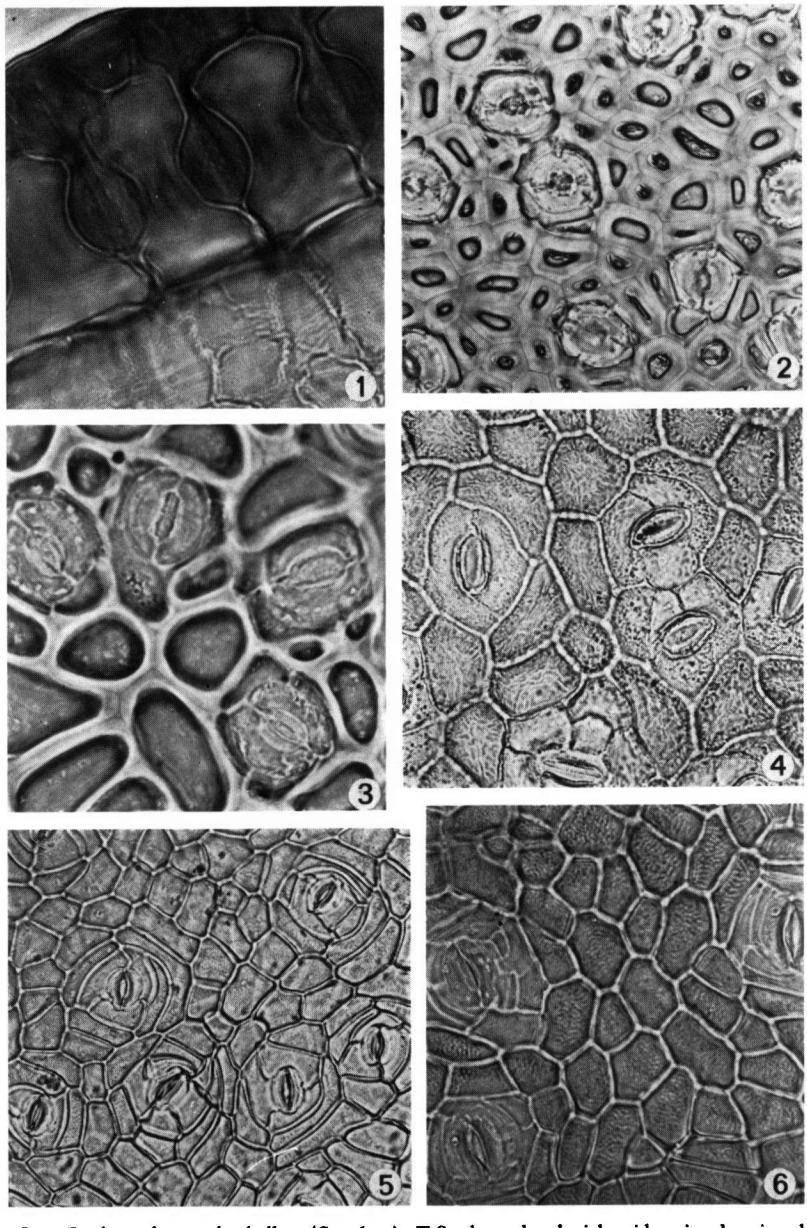


Plate I. 1. *Lophopetalum pachyphyllum* (*S. 16212*), T.S. through adaxial epidermis, showing bulging anticlinal walls and pit-like structures in outer cell corners, ×825. — 2. *Kokoona sessilis* (*FRI. 5375*), cuticular preparation of thick-walled epidermis, ×330. — 3. *Kokoona littoralis* (*S. 17893*), cuticular preparation of abaxial epidermis with intermediate cell wall thickness, ×530. — 4. *Lophopetalum pallidum* (*bb. 18997*), cuticular preparation of abaxial epidermis with anisocytic stomata, ×330. — 5. *Lophopetalum javanicum* (*Sulit 12360*), cuticular preparation of abaxial epidermis with complex anisocytic stomata, ×530. — 6. *Lophopetalum micranthum* (*Versteeg 1773*), cuticular preparation of abaxial epidermis with complex cyclocytic stomata and granular cuticle, ×530.

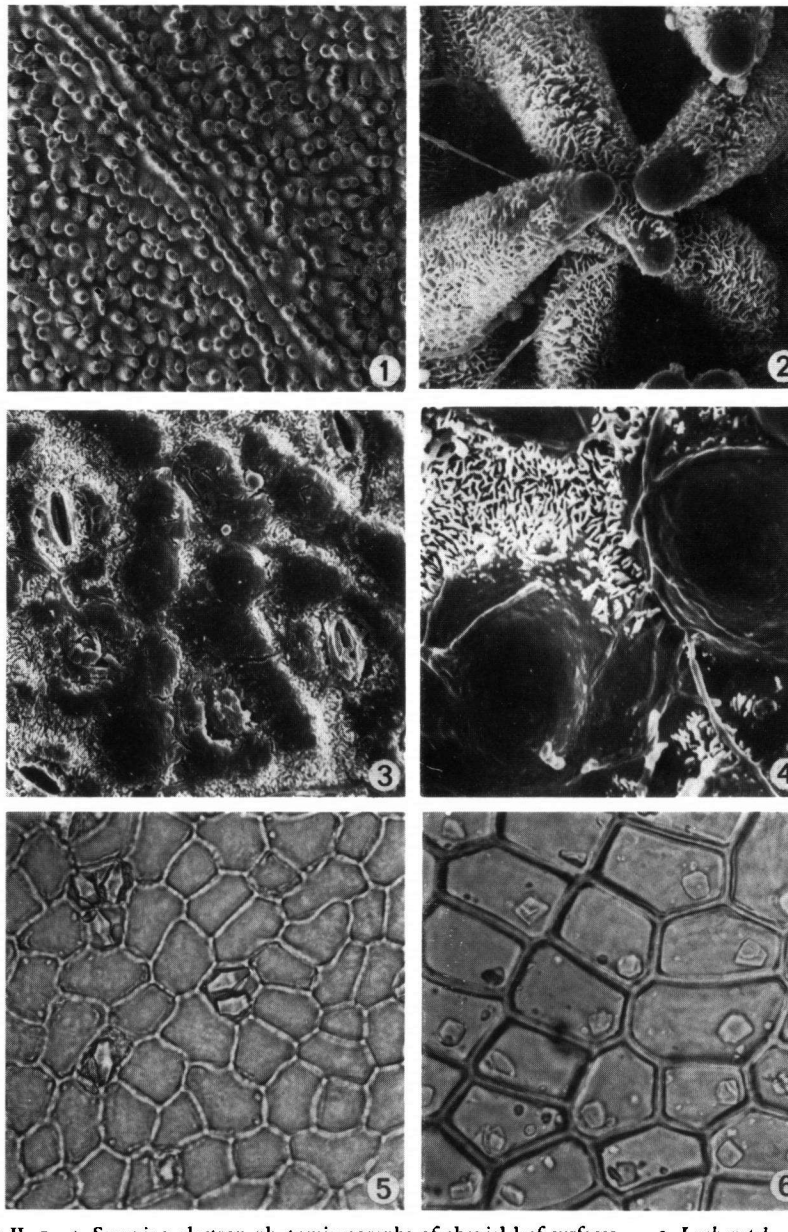


Plate II. 1—4. Scanning electron photomicrographs of abaxial leaf surfaces. — 1. *Lophopetalum pachyphyllum* (*S. 16212*), papillae, note arrangement in rows over vein, ×800. — 2. ibid., group of papillae overarching a stoma and covered with waxy particles, ×2000. — 3. *Lophopetalum wallichii* (*Garret 1053*), low papillae and stomata, waxy particles confined to areas in between papillae, ×2000. — 4. *Lophopetalum wightianum* (*Gallatly 811*), low papillae and waxy material, ×4000, fungal hyphe present on all leaf surfaces. — 5. ibid., upper epidermis with prismatic solitary crystals, × 330. — 6. *Lophopetalum wallichii* (*Native coll. 3219*), upper epidermis with minute cubical crystals, ×530.

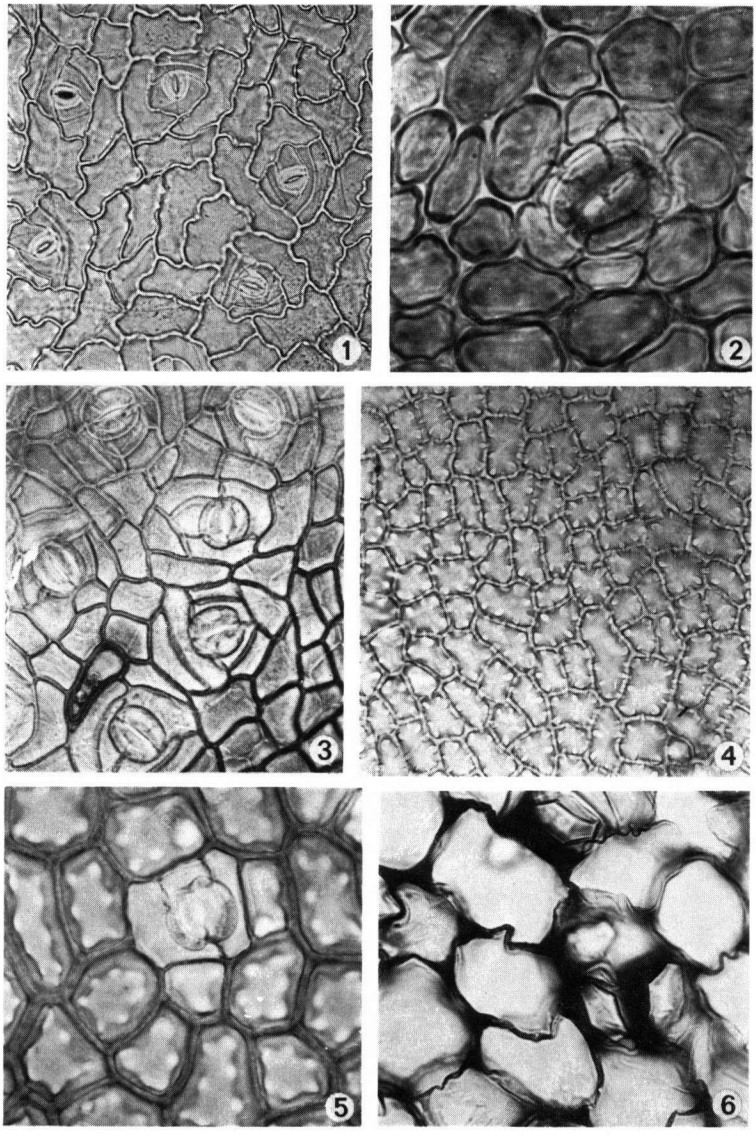


Plate III. *Lophopetalum glabrum* (*S. 20987*), cuticular preparation of abaxial epidermis with undulated anticlinal walls and complex anisocytic to helicocytic stomata, ×330. — 2. *Kokoona zeylanica* (*Thwaites C.P. 2584*), free hand section of abaxial epidermis with cyclocytic stomata. Note submersion of subsidiary cells, × 530. — 3. *Lophopetalum javanicum* (*Forbes 3151*), free hand section of abaxial epidermis with complex anisocytic stomata. Submersion of subsidiary cells only partial, × 530. — 4. *Lophopetalum glabrum* (*S. 20987*), cuticular preparation of adaxial epidermis with thin areas of cuticle showing up as light spots, × 310. — 5. *Lophopetalum beccarianum* (*Ping Sam A. 1896*), free hand section of adaxial epidermis with thin areas of cuticle in outer periclinal wall showing up as light spots, × 530. — 6. ibid. T.S. of petiole with crystarque cells in ground tissue, ×330.

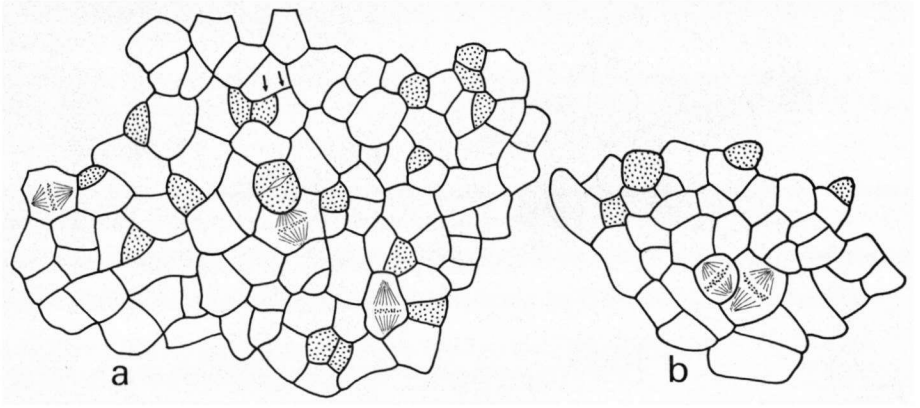


Fig. 23. Camera lucida drawings of young leaf epidermis of *Kokoona ovatolanceolata*. Densely stained cells dotted. Arrows indicate products of inequal cell division. Mitotic spindles present. Note division parallel to guard cell pair in a and perpendicular to future guard cell pair in b.

DEVELOPMENT OF THE STOMATAL COMPLEX IN *KOKOONA OVATOLANCEOLATA*

Several two years old seedlings of *K. ovatolanceolata* were present in the Hortus Botanicus, Leiden, which enabled us to study the ontogeny of the stomatal complex in this species. Free hand sections of very young leaves were stained with 2% aceto-orceine or aceto-carmine. The stomatal development as seen in surface view is as follows: Following inequal cell divisions protoderm cells give rise to a small stoma mother cell, distinguishable by its intense uptake of the stains used, and a bigger daughter cell which soon becomes indistinguishable from the other neighbouring cells.

The stoma mother cell divides equally and gives rise to the two guard cells. In mature specimens the subsidiary cells underly the guard cells partly or almost completely. Considering the different stages of development observed, this must be due to enlargement of the guard cells. The final number of subsidiary cells depends on the number of cell divisions in the neighbouring cells during the early stage of leaf development. The development of stomata in *K. ovatolanceolata* thus conforms to the mesoperigenous type (see fig. 23).

DISCUSSIONS

Stomata

The presence of different stomatal types within one genus is remarkable. *Kokoona* has both anisocytic and cyclocytic stomata. *Lophopetalum* is even more diverse in stomatal type in showing in addition complex types and a tendency for helicocytic stomata in part of the species. The fact that several types may occur on the same leaf and that often transitions between the types (see fig. 24) have been recorded, limits the taxonomic use of the type of stomata in both *Kokoona* and *Lophopetalum*. Only the restriction of complex types to part of the species of *Lophopetalum* is of some help in recognizing these species as belonging to *Lophopetalum*. Moreover, the submersion of subsidiary cells is more pronounced in *Kokoona* than in *Lophopetalum* (see Plate III, 2 and 3).

The ontogeny of stomata in *K. ovatolanceolata* is roughly similar to that reported for other genera of *Celastraceae* by Pant and Kidwai (1965). It differs slightly in showing

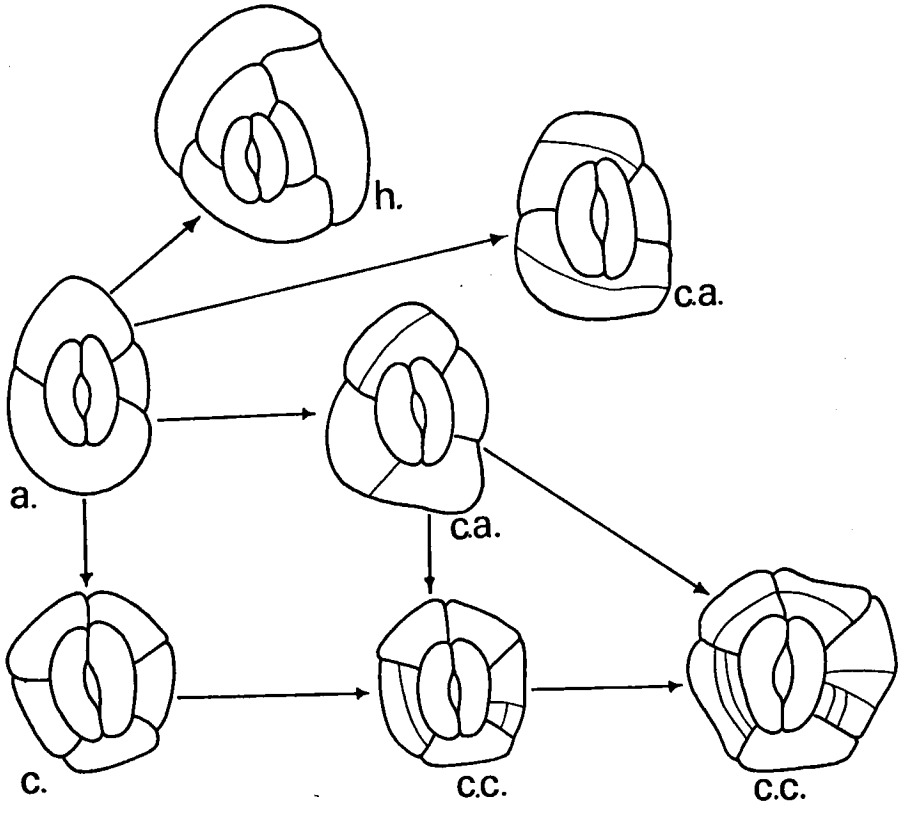


Fig. 24. Stomatal types in *Lophopetalum*. a: anisocytic; c.a. complex anisocytic; c: cyclocytic; c.c.: complex cyclocytic; h: helicocytic. Arrows indicate possibilities of relationships between different types, presumably through formation of extra division walls.

divisions more or less perpendicular to the guard cell pairs in addition to those parallel to the guard cells. Pant and Kidwai only reported the latter for the genera they studied.

An ontogenetic study of the stomatal types in *Lophopetalum* would be important for a reliable interpretation of the diversity found in the stomatal complex of that genus. The arrangement of subsidiary cells in some species gives so much the impression of having originated from a single cell (cf. Plate III, 1) that one may tentatively anticipate mesogenous stomata in those species. The complex anisocytic and cyclocytic types are presumably elaborations arising through subdivision of the subsidiary cells. Subdivision of subsidiary cells has also been recorded for other genera of *Celastraceae* by Rehfous (1914). Unfortunately, his paper was misinterpreted by Metcalfe and Chalk (1950: 390) and Pant and Kidwai (1966: 288) who suggested that Rehfous regarded the guard cells to be subdivided, though in fact he referred to subdivisions of the subsidiary cells.

The helicocytic stomata in some species of *Lophopetalum* (Plate III, 1) are never a very dominant feature. The spiral of subsidiary cells of declining size as described for this type by Payne (1970) is never elaborate and subdivisions parallel to the outer guard cell walls obscure the helicocytic pattern.

Several authors (e.g. Gupta, 1961) have regarded the stomatal index as a reliable diagnostic feature at the species level. The variation recorded in Table I and II for *K. littoralis* and *L. javanicum* clearly show that this is not valid for those species. The conclusion that the stomatal index is a very variable character in general is also supported by current studies on *Icacinaceae* and *Winteraceae* in the Rijksherbarium.

Vascular system of the petiole and midrib

In *Kokoona* the vascular system of the petiole is always of the simple type (fig. 1, types 1 and 2). The two types are represented in one petiole in some specimens (*K. sessilis* and *K. ovatolanceolata*, see Table I).

In *Lophopetalum* the interspecific and intraspecific differences are much bigger. In many specimens a great change of type from the basal end to the distal end of the petiole was found (e.g. *L. javanicum*, *L. multinervium*). This variation makes the type of vascular system of the petiole an unreliable character on the species level, although series of transverse sections might give more information.

Comparison of transverse sections of the petioles of *Kokoona* and *Lophopetalum* in the distal end results in an easy separation of the two genera. As stated before, we found no specimen of *Kokoona* with a complex vascular system in the distal part of the petiole, and no specimen of *Lophopetalum* with a simple vascular system in the distal end of the petiole was found either.

The vascular system of the midrib usually varies within one specimen. This is due to the splitting off from the midrib of the lateral veins. It often looks like the vascular system in the distal end of the petiole, but at the places of insertion of lateral veins it may be more complex.

Variability of anatomical characters in certain species

Kokoona littoralis

A study of 11 specimens of *Kokoona littoralis*, a species with leaves that show much variability in shape, texture, and size (Hou, 1963: 261), has shown that there is an overlap in anatomical characters with those of the other species and that many leaf anatomical characters are variable in this species.

Thickness of anticlinal walls of unspecialized epidermal cells: Extremely thick walls were found in *S. 9537*, just like in *Kokoona sessilis* (Plate I, 2), very thin walls in most specimens. Presence of specimens with intermediate wall thickness (*S. 17893* and to a lesser extent *Smythies 15242*) suggests a continuous variation of the character (Plate I, 3).

Number of subsidiary cells: The highest number ranges from 3—5(6) in the thick-walled specimens, the lowest from (2)3 or 4 in most of the thin-walled specimens.

Diameter of the guard cell pairs: Thin-walled specimens mostly have small stomata (less than 20 μm wide), thick-walled specimens much bigger stomata (in any case over 20 μm wide). The specimen *Smythies 15242* is an exception, with thick walls and guard cell pairs of 13—15—18 μm wide.

Kokoona reflexa

In the six specimens used for cuticular preparations much less variation was encountered than in *K. littoralis*. The two specimens used for transverse sections only showed some differences in the shape of the adaxial epidermal cells and the frequency of brachysclereids.

Kokoona ovatolanceolata

The occurrence of numerous stomata in the upper epidermis of one specimen (*bb. 32394*) is very remarkable (see also p. 159), particularly because it is the only specimen out of the whole genus with this feature. Dr. Hou kindly checked and confirmed the identity of the specimen.

Lophopetalum javanicum and other *Lophopetalum* species

Lophopetalum javanicum, a species with a high degree of variation in macro-morphological leaf characters, was chosen for a study of 11 specimens for cuticular preparations, 6 of which were also used for transverse sections. Variability of several characters will be discussed below and compared with that in some other species.

Lamina thickness: This is a highly varying character, which is not very surprising, because of the fact that lamina thickness of sun and shade leaves from the same tree can be very different. Tables I and II show that most species (cf. *Kokoona* as well) vary in lamina thickness.

Presence of stomata in upper epidermis: The whole range from virtually absent to abundant over the whole lamina occurs in Table II, for which herbarium material from different regions was checked, using nail varnish replicas, 32 specimens in total. In *ca.* 70% of the specimens stomata were found in the adaxial epidermis. The number of specimens appeared to be insufficient to see whether the presence of stomata in the adaxial epidermis exhibits a geographical pattern. The presence or absence of stomata is also variable in some other species, e.g. *L. ledermannii*, *L. torricellense*.

Sizes of stomata are rather variable in *L. beccarianum*, *L. floribundum*, *L. ledermannii*, *L. pallidum*, *L. rigidum*, *L. subobovatum*, and *L. wightianum*. In *L. javanicum* they are rather stable, but *Endert 48E. 1P. 538* differs widely from the other specimens (Table II).

Undulations of anticlinal walls of epidermal cells are rather constant for *L. javanicum* and also for the other species.

Thickness of outer periclinal walls of epidermal cells: 1—2 μm in all specimens of *L. javanicum*, but other species show great variation (*L. floribundum*, *L. subobovatum*).

Shape of adaxial part of midrib: Not constant in *L. javanicum* (*S. 25059*), but constant in most other species.

Vascular systems of petioles and midribs, see p. 175

Crystarque cells were found in some specimens of *L. javanicum* and in one specimen of *L. ledermannii* only. In other species the presence or absence of crystarque cells seems to be constant. Particularly if they are infrequent there is a fair chance of missing them in a transverse section, which may have slightly influenced our results as listed in Table II. Crystarque cells have previously not been recorded for the *Celastraceae*. These unusual cells are now known from 7 families (see Baas, 1972). The fact that they are not a constant feature in some species of *Lophopetalum* indicates a restriction of their diagnostic value in this genus.

The presence or absence of crystals, known to be a very variable feature in many plant groups, appears to be quite constant for the material of *Lophopetalum* studied. This is also true for *Kokoona*.

Diagnostic and taxonomic value of some leaf anatomical characters

From the variation of the characters discussed above it becomes apparent that these are of very doubtful or restricted diagnostic and taxonomic value in *Kokoona* and *Lophopetalum*. Very outspoken and unusual anatomical characters like extremely thick-walled

epidermal cells and crystarque cells appear to be of no diagnostic value on the species level for some species. Other characters like stomatal size, numbers of subsidiary cells, presence or absence of hypodermis, degree of complexity of the vascular system in the petiole etc. are also characters exhibiting a great range of variation below the species level.

Papillae conspicuously present in *L. pachyphyllum* and much less so in *L. wightianum* and *L. wallichii* (Plate II) have been recorded to be inconstant in species of *Cratoxylum* (*Guttiferae*) by Baas (1970). In both specimens of *L. pachyphyllum* they were present, but only one of the five *L. wightianum* specimens studied showed low papillae. Both *L. wightianum* and *L. pachyphyllum* belong to pollen group C of Hou (1969). Apparently this correlation of epidermal papillae and the presence of conspicuous subglobose verrucae on the pollen of these species is insignificant, because the presence of papillae is not constant for *L. wightianum*, and *L. wallichii* with very low papillae belongs to a different pollen group.

Thin areas of cuticle and/or pit-like structures in the corners of epidermal cells are constant features for *L. beccarianum*, *L. floribundum*, *L. glabrum*, *L. ledermannii*, *L. macranthum*, *L. pachyphyllum*, *L. rigidum*, and *L. sessilifolium*. They are absent from all other species studied. Most of the above mentioned species belong to pollen group B as classified by Hou. However, *L. pachyphyllum* and *L. sessilifolium* belong to his group C and D respectively. Moreover, some species of group B do not show thin areas of cuticle so that correlation of pollen characters with this leaf anatomical character also seems insignificant.

No other characters were found of which the distribution over the species showed a clear correlation with pollen characters.

In spite of the tremendous variation recorded here, an attempt was made to compose a synoptical key to the species based on leaf anatomical characters.

Tests of the key, however, revealed that only a very small proportion of the species could be identified satisfactorily and we therefore refrain from publishing it here.

GENERAL CONCLUSIONS

Leaf anatomy lends some support to the view that *Lophopetalum* and *Kokoona* are genera distinct from each other. Only the vascular anatomy of the distal end of the petiole provides an absolute character by which the two genera can be recognized. The other differential characters, listed below, only hold for part of the species and may be interpreted as trends of generic differentiation.

	Kokoona	**Lophopetalum**
1.	Vascular system of distal part of petiole simple.	Vascular system of distal part of petiole complex.
2.	Stomata never complex.	Stomata often complex.
3.	Hypodermis very rarely absent.	Hypodermis present in 3 species only.
4.	Anticlinal epidermal cell walls straight to slightly curved.	Anticlinal epidermal cell walls straight or sinuous or ranging from straight to sinuous.
5.	Thin areas of cuticle and/or pit-like structures in cell corners absent.	Thin areas and/or pit-like structures present in 8 species.
6.	Crystarque cells absent.	Crystarque cells present in 12 species.

It is impossible to recognize closely related groups of species (sections) within either *Lophopetalum* or *Kokoona*. Each character, as far as it is constant at the species level may be used to divide the genera into two groups, but these never coincide for the different characters employed, nor is there a correlation with groupings based on pollen morphology. Hou (1963) also refrained from subdividing the genera because of a similar lack of correlation of macromorphological characters.

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