

EPIDERMAL CHARACTERS OF THE CELASTRACEAE SENSU LATO

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SUMMARY

The leaf epidermal characters of 89 species belonging to 42 genera of the Celastraceae sensu lato (including Hippocrateaceae) are described in detail. The range and pattern of variation in stomatal type and presence and type of crystalliferous epidermal cells can be used to support the broad family concept of Celastraceae.

The stomata may be anisocytic, complex anisocytic, anomocytic, cyclocytic, bi- and/or tricyclic, complex cyclocytic, laterocytic, complex laterocytic, paracytic, parallelocytic, helicocytic, or of an intermediate type. The laterocytic stomata are most common, and are here recognized for the first time as a distinct stomatal type characterized by the lateral position of the subsidiary cells (3 or more) but yet different from the paracytic and cyclocytic type.

The general implications of the epidermal diversity for the grouping of genera in a natural classification are discussed. Special attention is devoted to the taxonomic position and/or delimitation of the following genera: *Kokoona* and *Lophopetalum*; *Sarawakodendron*; *Perrottetia*; *Salacia* and the related genera *Cheiloclinium*, *Peritassa* and *Tontelea*; *Hippocratea* and the putatively related genera *Aniodon*, *Apodostigma*, *Cuervea*, *Elachyptera*, *Helictonema*, *Hemiangium*, *Hylenea*, *Loeseneriella*, *Prionostemma*, *Pristimera*, *Reissantia* and *Simirestis*; *Cassine* sensu lato (including *Elaeodendron*, *Crocoxylon* and *Mystroxylon*); *Denhamia* and *Maytenus*; *Euonymus*; *Goupia*; *Siphonodon* and *Pottingeria*. Finally a tentative discussion of the wider affinities of Celastraceae is given and the scope for future studies is indicated.

1. INTRODUCTION

The family of the Celastraceae comprises about 90 genera and over 1000 species if, in accordance with the opinion of some taxonomists the previously recognized Hippocrateaceae are included. The taxonomic delimitation of the family is rather complex and has been reviewed or discussed by for example SMITH (1940), HALLÉ (1962) and HOU (1962, 1964 and 1969). The reduction of Hippocrateaceae to Celastraceae goes back to HOOKER (1862) but has been disputed by several botanists.

A world-wide treatment of Celastraceae and Hippocrateaceae still maintained as separate families was given by LOESENER (1942). On the basis of macromorphological characters of genera such as *Brassiantha* described by SMITH & BAILEY (1941), *Kokoona* and *Campylostemon* (cf. HOU 1964), *Lophopetalum* and the *Elaeodendron-Crocoxylon* group (cf. ROBSON 1965 – here treated under *Cassine*), and of *Sarawakodendron* (HOU 1967) the renewed combination of Celastraceae and Hippocrateaceae was advocated because these genera appeared intermediate in some characters between these taxa. A wood anatomical contribution to the discussion of the links between Hippocrateaceae and Celastraceae was given by

MENNEGA (1972). Pollen morphological studies with an emphasis on taxonomic problems in Celastraceae and related families were carried out by LOBREAU-CALLEN (1975 a and b).

A previous study on *Lophopetalum* and *Kokoona* (JANSEN & BAAS 1973) has shown the taxonomic value of leaf anatomy in this group. Limited data in the literature as surveyed by SOLEREDER (1899 and 1908) and METCALFE & CHALK (1950) have been added to by SHADAN & SHELLARD (1962), PANT & KIDWAI (1966), VAN COTTHEM (1971), SHAW et al. (1973), HALL & LOCK (1975), JAIN & SINGH (1975), and PEREIRO DOS SANTOS & GRISI (1976). The available information warranted a sufficient diversity in leaf epidermal characters of taxonomic interest. This study is not aimed at a complete inventory of epidermal anatomy of all species but is intended to evaluate the significance for classification above the genus level. Thus it was hoped to contribute to our understanding of affinities and delimitation of the genera, and to find additional arguments in favour of or against the broad family concept of Celastraceae. In addition the position of some genera of disputed affinity such as *Goupia*, *Pottingeria* and *Siphonodon* will be reconsidered in the light of the new leaf anatomical data.

2. MATERIAL AND METHODS

Herbarium material from the Institute of Systematic Botany at Utrecht (U) and from the Rijksherbarium at Leiden (L), identified by Dr. A. M. W. Mennega and Dr. Ding Hou respectively was used for this study. Of mature leaves, after boiling in water, a portion from the middle including midrib and leaf margin was sampled and used for obtaining paradermal free hand sections as well as cuticular macerations. Macerations were obtained using Franklin's method (equal volumes of 20% hydrogen peroxide and concentrated glacial acetic acid at 60° overnight) and mounted in glycerin-jelly after staining in Sudan IV in alcohol 70%. The free-hand sections, indispensable for observing the often submersed subsidiary cells, were stained in a safranin-haematoxylin mixture and mounted in euparal.

The material studied represented 89 species and about 42 genera (depending on the generic delimitation). Of only few species more than one specimen was studied. Information on variation below the species level was given for a number of species of *Kokoona* and *Lophopetalum* by JANSEN & BAAS (1973). The genera and species were chosen in such a way that a good representation of both representatives of the Hippocrateaceae (15 genera) and of Celastraceae sensu stricto (27) was achieved.

3. SURVEY OF THE LEAF EPIDERMAL CHARACTERS

3.1. Indumentum (fig. 2, plate II)

Hairs are usually absent from Celastraceae sensu lato. If present they are unicellular or uniseriate multicellular. The genus *Prionostemma* has very characteristic low, cone-shaped, unicellular hairs (fig. 2, plate II, 1 & 2). More usual types were found in *Goupia* (plate II, 3) and *Helictonema*, where the hairs are uniseriate and

rather thick-walled with pointed ends. In *Perrottetia* (plate II, 4) the hairs are unicellular or uniseriate but have delicate walls and rather blunt ends. Besides, in the literature hairs have also been recorded for *Celastrus articulatus* (= *C. orbiculatus*) and *Fraunhoferia multiflora* (SOLEREDER 1899), for some species of *Euonymus*, *Mystroxyton* (cf. *Cassine*), *Myginda*, *Tripterygium* and *Wimmeria* (METCALFE & CHALK 1950), and for *Celastrus hirsutus* (HOU 1955). Tall epidermal papillae occur in *Fraunhoferia* and *Wimmeria* according to METCALFE & CHALK (1950), in some species of *Lophopetalum* (JANSEN & BAAS 1973) and in *Salacia laterita* (HALL & LOCK 1975).

3.2. Domatia

In accordance with the literature, domatia were found in the genus *Perrottetia* only. According to HOU (1962) they are of variable occurrence in *Perrottetia alpestris*. They are also present in *P. ovata* and conform to the lebetiform or bowl-shaped type sensu STACE (1965).

3.3. Stomatal complex (fig. 1, 3–38, plate I)

In Celastraceae the stomata are usually restricted to the abaxial surface, but occasionally they also occur on the adaxial surface, either infrequent and than mainly restricted to the midrib region or more frequent and scattered over the whole upper leaf surface. Species or specimens of the following genera show adaxial stomata: *Anthodon*, *Apodostigma*, *Bhesa*, *Campylostemon*, *Denhamia*, *Hippocratea*, *Kokoona*, *Lophopetalum*, *Maytenus*, *Plenckia*, *Pristimera*, and *Siphonodon*. This list could probably be expanded if more species would have been studied.

In general the terminology adopted by VAN COTTHEM (1970, 1971) and STACE (1965) for stomatal types was used. The terms "complex anisocytic" (see fig. 38) and "complex cyclocytic" were used following JANSEN & BAAS (1973) for types, where subdivisions of one or more subsidiary cells are present. For stomata encircled by more than one ring of subsidiary cells the terms bicyclic or tricyclic (see fig. 25) were used, and these are treated as subtypes of cyclocytic stomata.

For a great number of Celastraceae Stace's or van Cotthem's terminology, in combination with the other types mentioned above or distinguished in the literature, is, however, not satisfactory because these Celastraceae show a deviating type of subsidiary cell arrangement (fig. 11–17, plate I, 1 & 2). For this type we introduce the term *laterocytic*. This type can be defined as follows: stomata flanked by three or more subsidiary cells all bordering on the lateral sides of the guard cell pair; anticlinal walls separating adjacent subsidiary cells radiating from the guard cell pair (not to be confused with paracytic stomata with subdivided subsidiary cells, which are distinct from laterocytic stomata by anticlinal walls of subsidiary cells of unequal thickness; also not to be confused with parallelocytic stomata sensu PAYNE 1970, where each guard cell is only in touch with one subsidiary cell, and the outer subsidiary cells do not border on the guard cells). The term complex laterocytic stomata was used for laterocytic stomata with subdivided subsidiary cells (easily confused with paracytic stomata with subdivided

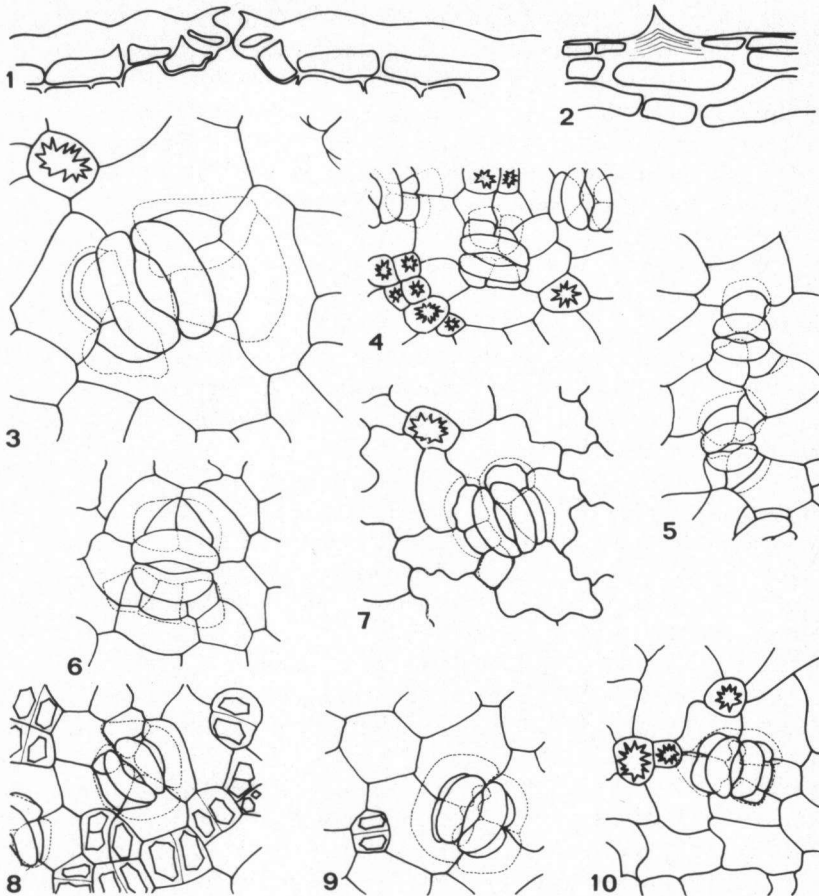


Fig. 1. *Cheilocladium jenmanii*: transverse section of abaxial epidermis showing submersion of subsidiary cells (compare fig. 22); 2. *Prionostemma aspera*: transverse section through adaxial epidermis showing cone-shaped hair (compare plate II, 1, 2); 3–10. Abaxial epidermis with laterocytic stomata in *Hippocratea* and related genera; 3. *H. obtusifolia*; 4. *H. angustifolia*; 5. *H. volubilis*; 6. *H. myriantha*; 7. *H. andamanica*; 8. *Simirestis goetzii*; 9. *Loeseneriella pauciflora*; 10. *Helictonema velutina*. All $\times 470$. Dotted lines give submersed boundaries of subsidiary cells.

subsidiary cells or with other types of complex stomata. In VAN COTTEM's terminology (1970, 1971) our laterocytic type would be included in his cyclocytic type (cf. fig. 7D, 8A and 13C in VAN COTTEM 1971), but in our opinion this would do injustice to the characteristic arrangement in many Celastraceae. The distinction from truly cyclocytic stomata is quite easy because the poles of the guard cells touch upon unspecialized neighbouring cells instead of subsidiary cells. The distinction from paracytic stomata with subdivided subsidiary cells is facilitated by the fact that, even in mature stages it is evident that each of a pair or group of adjacent subsidiary cells originated from different surrounding cells (cf. PANT &

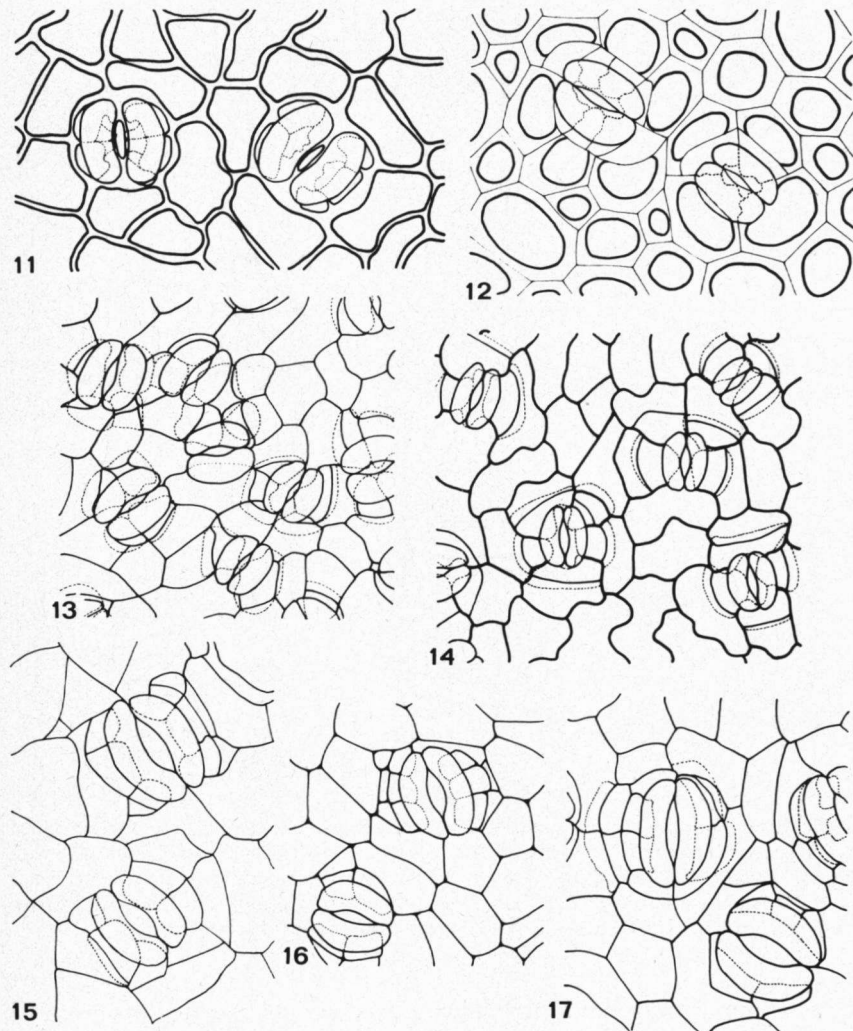


Fig. 11-17. Laterocytic stomata in various taxa; 11. *Tontelea ovalifolia*; 12. *Maytenus ilicifolia*, note thick anticlinal walls of unspecialized cells; 13. *Cuerveva integrifolia*; 14. *Reissantia cassinooides*, note irregularly cyclocytic stomata completely or incompletely encircling the guard cells in addition to the laterocytic ones; 15. *Siphonodon membranaceum*; 16. *Siphonodon pendulum*; 17. *Plenckia populnea*. Complex laterocytic stomata illustrated in fig. 15-17. All $\times 470$. Dotted lines give submersed boundaries of subsidiary cells.

KIDWAI 1966, on the perigenous ontogeny and resulting stomatal patterns in some Celastraceae). In some genera the distinction between paracytic and laterocytic stomata becomes arbitrary because in one and the same leaf truly paracytic stomata with one subsidiary cell bordering on each side of the guard cell pair and not reaching the guard cell poles, occur together with laterocytic stomata. If in

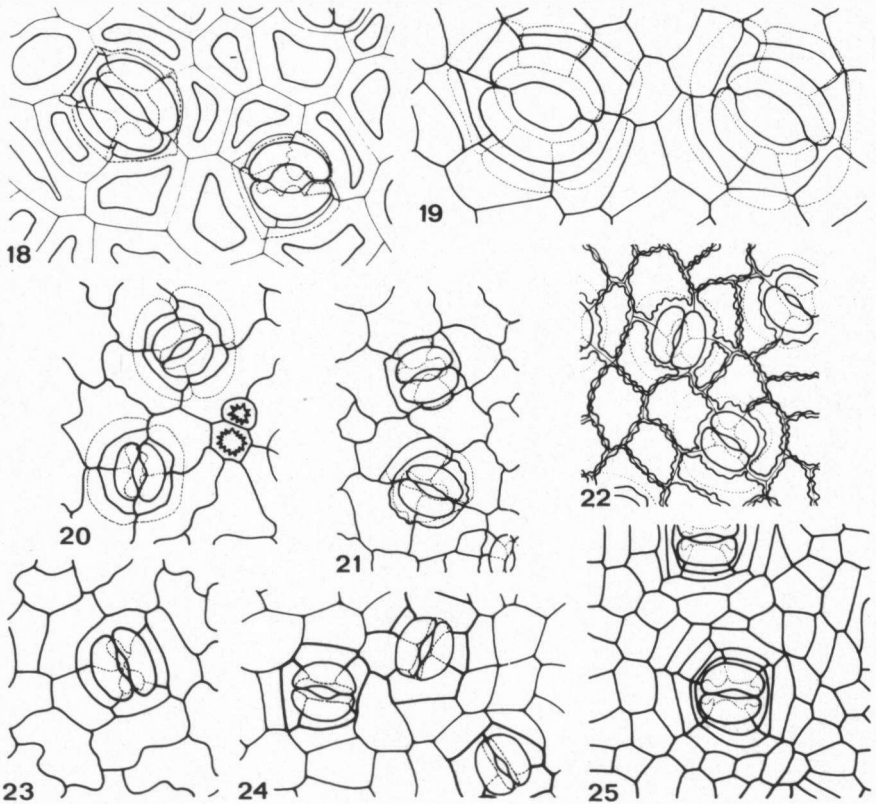


Fig. 18–25. Cyclocytic stomata in various taxa; 18–21. *Salacia*; 18. *S. miqueliana*, note thick anticlinal walls of unspecialized cells; 19. *S. martiana*; 20. *S. opacifolia*, also showing crystalliferous cells with druses; 21. *S. debilis*; 22. *Cheiloclinium cognatum*, subsidiary cells completely submersed under guard cells and surrounding cells; 23. *Peritassa granulata*; 24. *Pleurostyliya opposita*; 25. *Denhamia obscura*, tricyclic stomata. All $\times 470$. Dotted lines give submersed boundaries of subsidiary cells.

such cases laterocytic stomata predominate, the description in this paper records laterocytic with 2–e.g. 5 subsidiary cells; if the paracytic stomata are strongly in evidence (e.g. in *Wimmeria*) the descriptions record paracytic to laterocytic stomata. Intermediates between laterocytic and cyclocytic stomata also occur due to e.g. the presence of subsidiary cells on only one pole of the guard cell pair in addition to the lateral subsidiary cells (such stomata can also be termed incompletely cyclocytic, cf. some stomata in fig. 14). Rarely one can also speak of intermediates between laterocytic and complex anisocytic stomata. This is the case in *Goupia* and *Hartogia* (fig. 35, plate 1, 3) where the laterocytic stomatal complex is often encircled by three surrounding cells in an anisocytic pattern; in some *Cassine* species (those previously treated as *Elaeodendron*) the subdivisions of the subsidiary cells of the complex anisocytic stomatal complex are sometimes so arranged as to result in a laterocytic pattern within the anisocytic framework

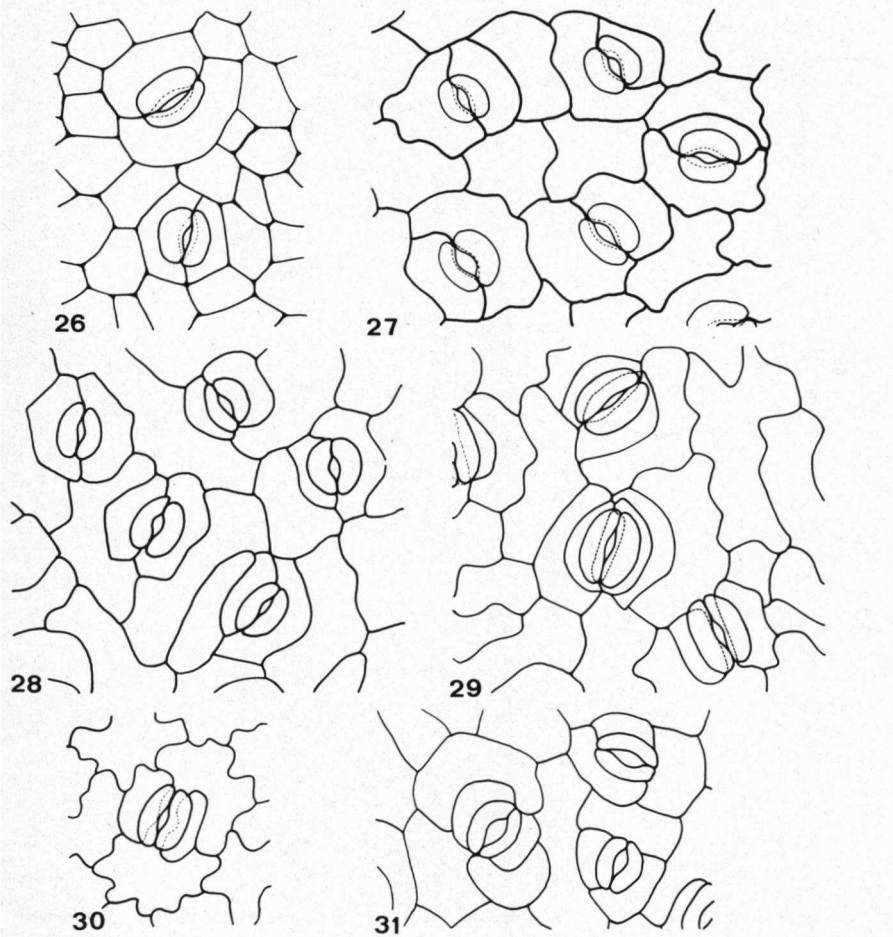


Fig. 26-31. Paracytic stomata in various taxa; 26. *Bhesa paniculata*; 27. *Bhesa robusta*; 28. *Hedraianthera porphyropetala*; 29. *Euonymus globularis*, stomata paracytic and parallelocytic; 30. *Xylonymus versteeghii*; 31. *Brassiantha pentamera*, two of the three stomata illustrated are anisocytic rather than paracytic. All $\times 470$. Dotted lines give submerged boundaries of subsidiary cells.

(fig. 32). In both cases the situation is basically similar, and it is only the most striking "habit" of the stomatal complex which induces to make an arbitrary choice between the two alternative ways to describe these stomatal types.

Dr. H. P. Wilkinson (Jodrell Laboratory, Kew) kindly drew our attention to the unfortunate combination of Greek and Latin terminology in the term "laterocytic". We have, however, maintained this rather clumsy term because a purely Greek alternative like "amphicyclic" would be ambiguous. Whether laterocytic stomata deserve full recognition as a distinctive stomatal type also depends on whether they will be found more often outside the Celastraceae. It is our belief that this will be the case, for instance stomata in some species of Buxaceae described by

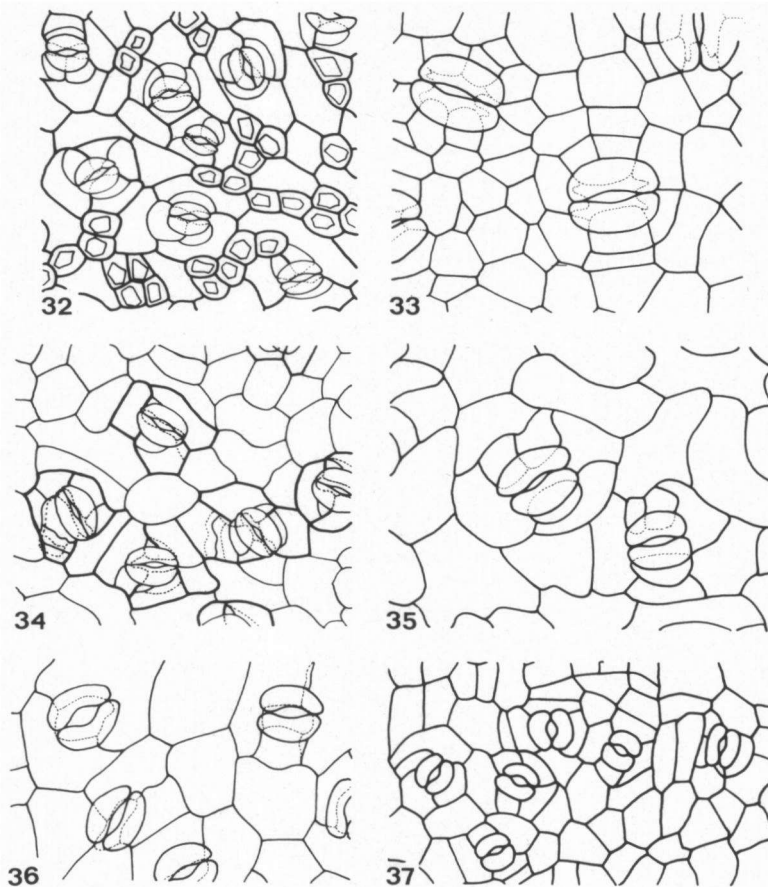


Fig. 32–37. Various stomatal types; 32. *Cassine vitensis*, complex anisocytic stomata and numerous crystalliferous cells with rhomboidal crystals; 33. *Cassine maritima*, stomata cyclocytic; 34. *Catha edulis*, stomata complex anisocytic; 35. *Goupia tomentosa*, stomata laterocytic and embedded in anisocytic pattern – see text; 36. *Perrottetia alpestris*, stomata anomocytic and anomocytic to anisocytic; 37. *Sarawakodendron filamentosum*, stomata intermediate between cyclocytic and anomocytic. Fig. 32 and 37, $\times 300$; Fig. 33–36, $\times 470$. Dotted lines give submersed boundaries of subsidiary/neighbouring cells.

VAN COTTHEM (1971) as cyclocytic but easily recognizable as laterocytic in his illustrations, and “intermediates” between cyclocytic and paracytic stomata described by one of us for Icacinaceae (BAAS 1974).

Laterocytic stomata are the most common type found in Celastraceae s. l. (see table 6). Cyclocytic (including bicyclic, tricyclic and complex cyclocytic) and paracytic stomata also occur in a fair number of genera. Anisocytic and anomocytic types are restricted to a small number of genera or species only. Helicocytic and parallelocytic stomata are of rare occurrence and are here treated as subtypes of anisocytic and paracytic stomata respectively.

The subsidiary cells may vary in number for the cyclocytic and laterocytic types, and their position varies from complete submersion under guard cells and unspecialized neighbouring cells (see also REHFUS 1914) to a normal position in level with guard cells and unspecialized epidermal cells. Partial to complete submersion is a feature of many Celastraceae with laterocytic or cyclocytic stomata. If submersion is complete or almost complete, the laterocytic and cyclocytic stomata can easily be mistaken for anomocytic stomata, especially in cuticular macerations (cf. *fig. 1, 22, plate I, 5*).

All Celastraceae studied are provided with fairly well-developed to pronounced outer cuticular ledges. The inner cuticular ledges vary from inconspicuous to well-developed, with or without adhering cuticular flaps in cuticular macerations as remnants of the cuticular lining of the back cavities (cf. STACE 1965). In some species the cuticle shows a T-shaped thickening or T-piece at the stomatal poles. Because of the dubious diagnostic value and the arbitrary distinction of poorly- or well-developed stomatal ledges or T-pieces, these features have been omitted from the descriptions. In only few genera or species there is a well-developed, cuticular peristomal rim. In some species the stomatal pores appeared occluded with granular, unidentified material.

Giant stomata occur in some representatives. The average size of the normal guard cell pairs varies from 16–41 μm in length and 13–35 μm in width. Very small stomata occur in *Perrottetia* and *Reissantia* whilst some species of *Loeseneriella* and *Salacia* have the biggest stomata. At the genus level the stomatal size is highly variable: in *Salacia* for instance the range of stomatal sizes covers most of the total range in Celastraceae sensu lato.

3.4. Crystals (*fig. 3–10, 20, 32, plate I, 1, 2*)

In a number of Celastraceae (see *table 6*) solitary, rhomboidal crystals or druses occur in small, often subdivided epidermal cells. These cells may be solitary, arranged in pairs, rows or clusters, scattered over the whole lamina or sometimes restricted to areas overlying the veins. In almost all genera crystals occur in the mesophyll, sometimes especially in layers adjacent to the epidermis and easily mistaken for epidermal crystals. These crystals from deeper layers are not recorded in the generic descriptions.

3.5. Unspecialized cells

The anticlinal walls of the unspecialized cells may be straight, or curved to sinuous. In some species the cells have sinuous walls with thin periclinal areas of cuticle in the loops. The cuticle overlying the anticlinal and periclinal walls has a smooth or finely to coarsely granular appearance due to the nature of the cuticular layer. In a number of genera some of the species show conspicuously thickened, unligified anticlinal walls (cf. *fig. 12, 18*). Only in *Bhesa robusta* the abaxial epidermal cell walls are lignified. *Perrottetia alpestris* is the only species with mucilage cells, scattered between the normal “unspecialized cells” (*plate I, 6*).

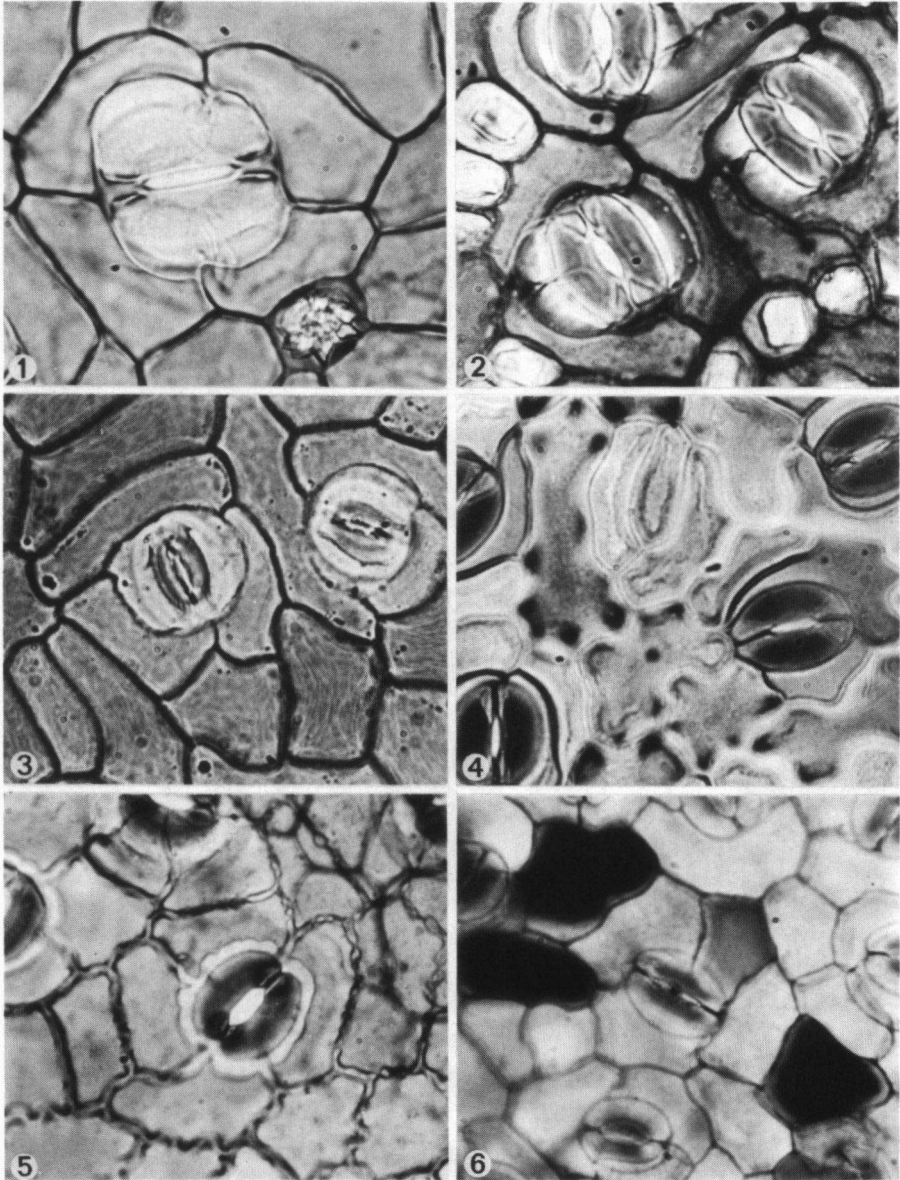


Plate I. Abaxial epidermis showing different stomatal types and unspecialized cells, all $\times 600$. 1. *Hippocratea obtusifolia*, laterocytic stoma and crystalliferous cell with druse; 2. *Cassine australe*, laterocytic stomata and crystalliferous cells containing rhomboidal crystals; 3. *Hartogia capensis*, laterocytic stomata embedded in anisocytic pattern of surrounding cells – true subsidiary cells hardly visible in maceration; 4. *Euonymus globularis*, paracytic stomata and arrested stage of stomatal development (centre) suggestive of mesogenous ontogeny of stomatal complex; 5. *Cheiloclinium cognatum*, cyclocytic stomata with strongly submersed subsidiary cells resulting in anomocytic appearance at high focus; 6. *Perrottetia alpestris* ssp. *alpestris*, anomocytic and anomocytic to anisocytic stomata, and mucilage cells intermingled with normal epidermal cells. Photograph 3 taken from cuticular maceration; remainder from free hand sections.

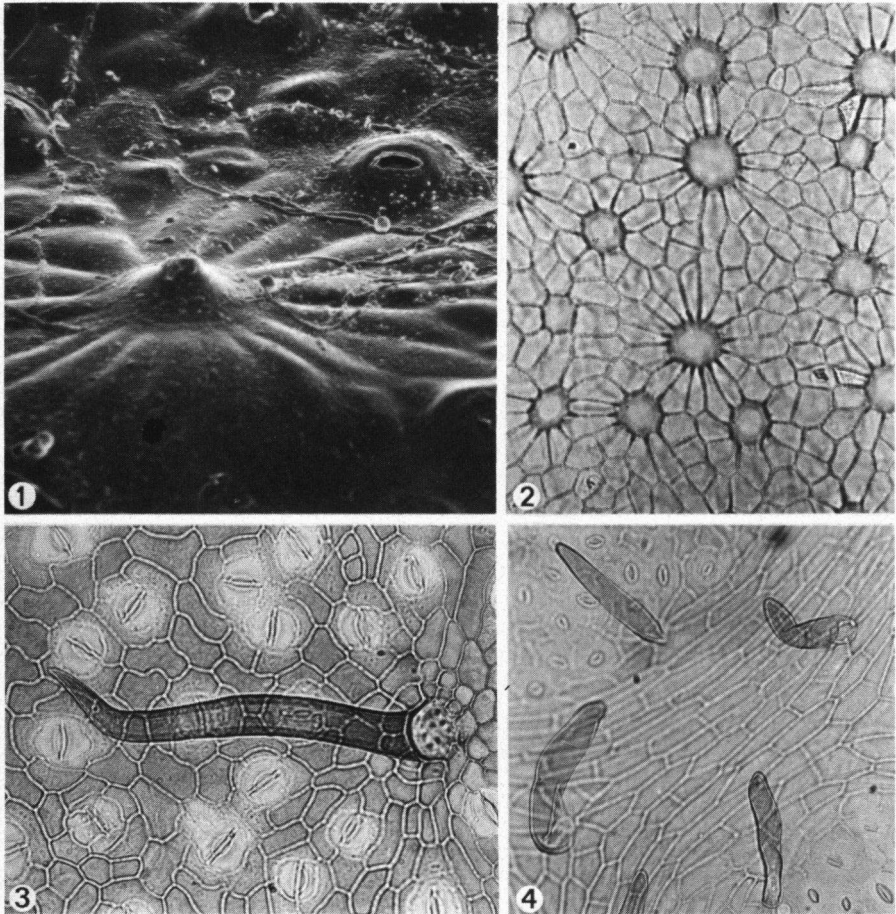


Plate II. Hairs. 1 & 2. *Prionostemma aspera*, 1. scanning electron micrograph of abaxial surface showing large conical hair and stomata, $\times 700$, 2. light micrograph of adaxial surface showing radiating pattern of unspecialized cells round conical hairs, $\times 220$; 3. *Goupia tomentosa*, uniseriate hair with thick-walled, pitted base, $\times 220$; 4. *Perrottetia lanceolata*, thin-walled hairs, $\times 220$. Photograph 2-4 from cuticular macerations.

3.6. Veins

The prominence of veins as expressed in a deviating epidermal cell pattern over the veins varies considerably within Celastraceae. In a number of representatives only the midrib shows an arrangement of epidermal cells in rows, whilst in others the complete network of minor veins is visible in the epidermal cell pattern.

3.7. Cork warts

Cork warts of varying size and frequency are of rare occurrence in the Celastraceae used for this study and probably always of traumatic origin. Unlike the regularly

shaped and distributed cork warts in some *Ilex* species (BAAS 1975) they do not constitute a feature of diagnostic or systematic interest and are therefore omitted from the descriptions. DING HOU (1963) reported black dots on the abaxial leaf surface of *Euonymus castaneifolius*; since this species was not included in this study it remains uncertain whether these dots represent regular cork warts of diagnostic value.

4. GENERIC DESCRIPTIONS

Explanatory note

In the generic descriptions absence of special anatomical features has not been recorded. For characters like degree of submersion of subsidiary cells under guard cells and/or neighbouring cells only extreme cases have been included in the descriptions. Several characters have been omitted for reasons explained in the previous part of this paper. For stomatal size the average values or range of average values are given between extremes. In those cases where averages of only two species or specimens are known the values are not connected by a hyphen but by &.

The numbers behind the generic names give the (estimated) total number of species and the number of species studied respectively. Under material studied the source of the herbarium material is indicated by (L) or (U), i.e. Leiden or Utrecht.

Anthodon Ruiz et Pav. 2/2

Stomata confined to abaxial surface or (in *A. decussatum*) also present on adaxial surface over midrib; laterocytic with 2–6 subsidiary cells in *A. decussatum*; paracytic to laterocytic with 2–4 subsidiary cells in *A. panamense*; guard cell pairs 15–20–28 μm long and 15–18 & 19–28 μm wide. Abaxial epidermis with some very small crystalliferous cells in groups or pairs, containing druses. Unspecialized cells with straight to slightly curved anticlinal walls. Anticlinal cuticular flanges of *A. panamense* strongly granular. Cuticle smooth (*A. decussatum*) or finely granular (*A. panamense*). Vein reticulum prominent, except in adaxial epidermis of *A. panamense*, where the primary veins and midrib are prominent only.

Material studied: *A. panamense* A.C. Sm., Panama, Dodge 16755 (U); *A. decussatum* Ruiz et Pav., Venezuela, Breteler 4683 (U).

Apodostigma R. Wilczek 1/1

Stomata on abaxial epidermis and on adaxial surface over midrib, laterocytic, occasionally cyclocytic, with 4–6 subsidiary cells; guard cell pairs 20–24–25 μm long, 17–19–22 μm wide. Unspecialized cells of adaxial epidermis with curved to undulated anticlinal walls with thin areas of cuticle in loops of undulations, of abaxial epidermis with straight to curved anticlinal walls. Adaxial cuticle smooth, abaxial cuticle slightly granular. Primary, secondary and tertiary veins prominent in abaxial epidermis only.

Material studied: *A. pallens* (Planch. ex Oliv.) R. Wilczek, Ivory Coast, Leeuwenberg 3282 (L).

Bhesa Ham. ex Arn. 5/4 (Fig. 26)

Stomata confined to abaxial surface or (in *B. robusta*) also present on adaxial surface over midrib; paracytic with subsidiary cells extending beyond the poles of the guard cells and usually of different size, very rarely anisocytic through subdivision of one of the subsidiary cells; guard cell pairs (19–)22–25(–27) μm long, (16–)17–25(–26) μm wide (most slender in *B. ceylanica*). Unspecialized cells of adaxial epidermis with undulated anticlinal walls (with thin areas of cuticle in loops of undulations in *B. robusta*), of abaxial epidermis with straight or curved to undulated anticlinal walls. Epidermal cells

occasionally with secondary division walls, especially in abaxial epidermis. Abaxial unspecialized cells and some subsidiary cells with lignified anticlinal and periclinal walls in *B. robusta*. Cuticle smooth to finely granular. Anticlinal cuticular flanges granular in *B. paniculata* and pitted in *B. robusta*. Primary veins prominent in both adaxial and abaxial epidermis; secondary veins prominent in abaxial epidermis only or not prominent.

Material studied: *B. archboldiana* Ding Hou, West New Guinea, BW 435 (L); *B. ceylanica* (Arn. ex Thwaites) Ding Hou, Sri Lanka, Hallier s.n. (L); *B. paniculata* Arn., Malaya, Millard 1938 (L); *B. robusta* (Roxb.) Ding Hou, Vietnam, Pierre 214 (L).

Note: In all species numerous rhomboidal crystals are present in the mesophyll layer adjacent to the abaxial epidermis. In *B. paniculata* and less markedly so in *B. ceylanica* the crystalliferous cells have unilaterally thickened, lignified walls and can be termed "cristarque cells" (cf. JANSEN & BAAS 1973 for similar cells in *Kokoona*).

Brassiantha A.C. Sm. 1/1 (fig. 31)

Stomata confined to abaxial epidermis, mainly paracytic, or (unilaterally) parallelcytic, with subsidiary cells of different or equal size extending beyond one of the guard cell poles, occasionally anisocytic or even helicocytic (see fig. 31); guard cell pairs 20–25–32 μm long, 15–17–20 μm wide. Some adaxial epidermal cells or groups of cells with irregular crystalline bodies (different from solitary crystals or clusters or druses). Unspecialized cells with straight to slightly curved anticlinal walls. Cuticle smooth. Primary veins prominent in abaxial epidermis, very faint in adaxial epidermis.

Material studied: *B. pentamera* A.C. Sm., New Guinea, Brass 8889 (L).

Campylostemon Welw. 12/3

Stomata most frequent on abaxial surface, but also on adaxial side over midrib and in *C. warneckeanum* also over primary veins, in *C. laurentii* infrequent over whole adaxial surface, laterocytic, rarely cyclocytic, with 3–6 partly to strongly submersed subsidiary cells; guard cell pairs 20–22–31–34 μm long, 17–19–25–28 μm wide (in *C. laurentii* appreciably bigger than in other two species). Unspecialized cells with straight to slightly curved anticlinal walls, with pitted anticlinal cuticular flanges in abaxial epidermis of *C. mitophorum*. Cuticle smooth in *C. warneckeanum*, finely granular in *C. mitophorum* and coarsely granular in *C. laurentii*. Primary veins prominent, secondary veins and some tertiary veins prominent in abaxial epidermis only.

Material studied: *C. laurentii* De Wild., Zaire, Louis 4313 (L); *C. mitophorum* Loes., Cameroon, Zenker 3234 (L); *C. warneckeanum* Loes., West Africa, Warnecke 302 (L).

Cassine L. (including *Elaeodendron*, *Crocoxylon* and *Mystroxyton*) ca. 60/7 (See also table 1; fig. 32, 33; plate 1, 2)

Stomata confined to abaxial epidermis, laterocytic, (complex) anisocytic or cyclocytic with 3–8 partly to strongly submersed subsidiary cells, with faint peristomal rim in *C. vitiensis*. Part of the species (see table 1) with numerous small, crystalliferous cells on both surfaces containing solitary crystals; crystalliferous cells solitary, in pairs, rows or clusters. Unspecialized cells with straight to curved or undulated anticlinal walls. Anticlinal walls in *C. maritima* very thick. Cuticle finely or coarsely granular. Veins prominent to various extent or not prominent in epidermal cell pattern.

Material studied: *C. australe* (Vent.) O. Kuntze (*Elaeodendron australe* Vent.), Australia, Constable 46227 (L); *C. barbara* L., South Africa, Cape Peninsula, Lotsy & Goddijn 1560 (L); *C. crocea* (Thunb.) O. Kuntze (*Crocoxylon croceum* (Thunb.) N. Robson), South Africa, Laughton s.n., 1938 (U); *C. glauca* (Rottb.) O. Kuntze var. *cochinchinensis* Pierre, Java, Neth. Ind. For. Serv. Ja 1898 (L); *C. maritima* Bolus (*Mystroxyton maritimum* (Bolus) Loes.), South Africa, Kapp 66 (L); *C. peragua* L., Cult. hort. bot. Göttingen, Hallier s.n., 1892 (L); *C. vitiensis* (A. C. Sm.) A. C. Sm. (*Elaeodendron vitiense* A. C. Sm.), Fiji, A. C. Smith 6259 (L).

Note: In *C. maritima* the stomatal pores are often occluded with granular material and the cuticle overlying the guard cells is strongly thickened.

For a discussion of the taxonomic implication of the epidermal range in *Cassine* sensu lato see 5.2.2.

Table 1. Variation of some leaf anatomical characters in *Cassine sensu lato*.

	stomatal type	number of subsidiary cells	length of guard cell pairs (μm)	width of guard cell pairs (μm)	solitary crystals in epidermis	texture of cuticle	prominence of veins, adaxial	prominence of veins, abaxial	undulations of adaxial antichlinal walls	undulations of abaxial antichlinal walls
<i>C. australe</i>	c.ani-lat	3-4	28-30-33	22-25-27	+	f. gr -	1	1	+	+
<i>C. barbara</i>	lat	3-5	20-21-22	15-18-20	-	f. gr. 1	4	-	-	-
<i>C. crocea</i>	c.ani	3-4	24-26-29	20-21-25	+	f. gr 1	3	-	-	-
<i>C. glauca</i> var.										
<i>cochinchinense</i>	c.ani	3-5	24-26-28	17-19-20	+	f. gr -	1	-	+	+
<i>C. maritima</i>	cyclo	5-8	34-37-38	27-30-32	-	c. gr -	-	-	-	-
<i>C. peragua</i>	lat	3-5	18-21-22	15-18-20	-	f. gr 1	V.R.	-	±	±
<i>C. vitiensis</i>	c.ani	3-4	25-27-30	22-23-25	+	f. gr -	1	-	-	-

Legend to tables 1-5: + = character present or well developed; ± character weakly developed; (-) = infrequent; +/- = present or absent; c.ani = complex anisocytic to anisocytic; cyclo = cyclocytic; bic = bicyclic; lat = laterocytic; c.cyclo or c.lat = complex cyclocytic or laterocytic; f.gr = finely granular; c.gr = coarsely granular; s = smooth; str = striated; 1, 2, 3 and 4 = primary, secondary, tertiary and quaternary veins prominent respectively; V.R. = venule reticulum prominent.

Catha Forsk. ex Scop. 1/1 (fig. 34)

Stomata confined to abaxial epidermis, sometimes in pairs, complex anisocytic, occasionally complex cyclocytic with 3–6 subsidiary cells; inner subsidiary cells submersed under guard cells as well as surrounding cells or outer subsidiary cells; guard cell pairs 17–20–21 μm long, 12–15–17 μm wide. Unspecialized cells of adaxial epidermis with straight to slightly undulated anticlinal walls, of abaxial epidermis with curved to undulated anticlinal walls. Cuticle smooth. Venule reticulum prominent on both surfaces.

Material studied: *C. edulis* (Vahl) Forsk. ex Endl., Rhodesia, Goldsmith s.n., 1967 (L).

Celastrus L. 30/1

Stomata confined to abaxial epidermis, laterocytic to complex laterocytic and cyclocytic to complex cyclocytic with 4–6(–8) subsidiary cells; guard cell pairs 26–28–30 μm long, 23–25–28 μm wide. Unspecialized cells of both surfaces with curved to undulated anticlinal walls. Cuticle finely granular, anticlinal flanges more coarsely granular. Lateral veins prominent in abaxial epidermis only.

Material studied: *C. monospermoides* Loes., N. Sumatra, Van Steenis 9651 (L).

Cheiloclinium Miers 23/4 (fig. 1, 22; plate I, 5)

Stomata confined to abaxial epidermis, mostly cyclocytic with 3–5 subsidiary cells, often seemingly anomocytic due to complete submersion of subsidiary cells under guard cells and surrounding cells; laterocytic or rarely incompletely cyclocytic in *C. hippocratioides*; guard cell pairs 21–23–25 μm long and 21–23–25 μm wide in *C. cognatum* and of about the same size in *C. jenmanii* and *C. serratum*, much bigger and 30–32–35 μm long and 30–33–35 μm wide in *C. hippocrateoides*. Unspecialized cells with strongly undulated anticlinal walls with thin areas of cuticle in loops of undulations except in *C. hippocrateoides* in which the adaxial epidermal cells have straight anticlinal walls and the abaxial cells straight to curved anticlinal walls. Cuticle smooth. Primary veins prominent on both surfaces, secondary veins prominent in abaxial epidermis only.

Material studied: *C. cognatum* (Miers) A.C. Sm., Tobago, Broadway 4699 (L); *C. hippocrateoides* (Peyr) A.C. Sm., Bolivia, Krukoff 10832 (U); *C. jenmanii* A.C. Sm., Venezuela, Steyermark & Rabe 96108 (L); *C. serratum* (Camb.) A.C. Sm., Brasil, Santa Catarina, Reitz & Klein 6353 (L); and Parana, Dusén 17462 (L).

Note: *C. hippocrateoides* stands out from the other species on account of its laterocytic, large stomata and straight anticlinal epidermal cell walls. The other three species are very similar to each other. *C. hippocrateoides* is furthermore provided with irregularly distributed, but regularly shaped cork warts, while the other species only show some irregularly shaped cork warts. A further inventory of the leaf anatomical diversity within *Cheiloclinium*, including all species groups recognized by SMITH (1940) may prove rewarding. Slender foliar sclereids were noted in the mesophyll of the two specimens studied of *C. serratum*.

Crocoxylon – see *Cassine*.*Cuervea* (Benth. & Hook.) Triana 3/3 (fig. 13)

Stomata confined to abaxial epidermis, sometimes in pairs, laterocytic, rarely paracytic, with 2–5 subsidiary cells strongly to completely submersed under guard cells and surrounding cells; guard cell pairs (14–)16–22(–25) μm long, (14–)15–20(–23) μm wide. Abaxial epidermis with numerous small crystalliferous cells, solitary, in pairs or in rows, containing rhomboidal crystals, especially abundant over veins; adaxial epidermis with less frequent solitary crystalliferous cells; crystalliferous cells on the whole less frequent in *C. macrophylla*. Unspecialized epidermal cells with straight to slightly curved anticlinal walls. Cuticle coarsely granular. Venule reticulum more or less prominent in abaxial epidermis, less so in adaxial epidermis.

Material studied: *C. integrifolia* (Rich.) A.C. Sm., Cuba, Webster 4663 A (U); *C. kappleriana* (Miq.) A.C. Sm., Brasil, Irwin, Pires & Westra 47864 (U); *C. macrophylla* (Vahl) R. Wilczek, Zaire, Evrard 4061 (L).

Denhamia Meissn. 4/4 (fig. 25)

Stomata confined to abaxial epidermis or also abundant on adaxial surface (in *D. oleaster*), typically

bicyclic to tricyclic but cyclocytic to complex cyclocytic in *D. pittosporoides*, with (3–)4–6 subsidiary cells per ring; inner ring of subsidiary cells hardly to strongly submersed under guard cells and thin-walled, outer ring composed of cells with about the same wall thickness as unspecialized epidermal cells; guard cell pairs (20–)22–28(–30) μm long, (20–)22–27(–28) μm wide. Unspecialized cells with straight to slightly curved, thick to very thick anticlinal walls. Cuticle smooth. In *D. obscura* venule reticulum prominent in abaxial epidermis and primary veins in adaxial epidermis; in *D. oleaster* only primary veins prominent abaxially; in *D. parvifolia* primary veins prominent abaxially, and primary and secondary veins prominent adaxially; in *D. pittosporoides* only primary and secondary veins prominent abaxially.

Material studied: *D. obscura* Meissn., Australia, Speck 188 (L); *D. oleaster* F.V.M., Australia, Mitchell 1846, 423 (L); *D. parvifolia* L.S. Smith, Australia, Lam 7678 (L); *D. pittosporoides* F.v.M., Australia, Constable 23748 (L).

Elachyptera A.C. Sm. 3/1

Stomata confined to abaxial epidermis, laterocytic to complex laterocytic or incompletely to completely cyclocytic with 2–4(–6) subsidiary cells; guard cell pairs 22–23–25 μm long, 19–21–22 μm wide. Small crystalliferous cells, with rhomboidal crystals scattered in abaxial and adaxial epidermis. Unspecialized cells of both surfaces with straight to slightly curved and pitted anticlinal walls. Cuticle granular. Primary veins prominent on both surfaces, secondary veins prominent in abaxial epidermis only.

Material studied: *E. floribunda* (Benth. & Hook.) A.C. Sm., Brasil, Prance, Pena & Ramos 3234 (U).

Elaeodendron – see *Cassine*.

Euonymus L. 180/4 (fig. 29; plate 1, 4)

Stomata confined to abaxial epidermis, laterocytic to complex laterocytic, or paracytic to parallelocytic (in *E. globularis*), with 2–7 subsidiary cells; guard cell pairs 22–25–28 μm long and 19–20–21 μm wide in *E. globularis*, but bigger in other species: (29–)32–33(–37) μm long and (22–)24–28(–32) μm wide. Unspecialized cells with straight to curved anticlinal walls (with pitted cuticular flanges in *E. europaeus*), but anticlinal walls strongly undulating and with thin areas of cuticle in loops of undulations in *E. globularis*. Cuticle finely granular in *E. europaeus* and *E. javanicus*, smooth in *E. grandiflorus* and *E. globularis*. Venule reticulum prominent in abaxial epidermis except in *E. javanicus* where only primary veins are prominent. Veins in adaxial epidermis prominent to various but lesser extents.

Material studied: *E. europaeus* L., Sweden, Samuelson 1142 (L); *E. globularis* Ding Hou, Australia, Brass 20019 (L); *E. grandiflorus* Wall., China, Fan & Li 185 (L); *E. javanicus* Bl., Java, Van Steenis 12621 (L).

Note: *E. globularis* stands out because of its aberrant stomatal type and conspicuously undulating anticlinal walls. See also notes under taxonomic discussions.

Glyptopetalum Thwaites 27/1

Stomata confined to abaxial epidermis, laterocytic with 4–5 strongly submersed subsidiary cells; guard cell pairs 30–31–34 μm long, 25–26–28 μm wide. Unspecialized cells with straight to slightly curved anticlinal walls. Cuticle smooth. Primary veins prominent.

Material studied: *G. loheri* Merr., Celebes, Kjellberg 499 (L).

Note: The stomatal pores frequently appear occluded with granular material. Cork warts of varying shape and size are fairly common in the abaxial epidermis, less so in the adaxial epidermis.

Goupia Aubl. 3/2 (fig. 35; plate II, 3)

Uniseriate hairs abundant on midrib and veins of abaxial surface of *G. tomentosa*, infrequent on adaxial surface; in *G. glabra* more or less confined to midrib and veins of abaxial surface. Hairs with thick-walled, pitted base which is broader in *G. tomentosa* than in *G. glabra*; with 4–10 septa in *G. tomentosa* and 1–3 septa in *G. glabra*. Stomata confined to abaxial epidermis, laterocytic, rarely anisocytic, but laterocytic stomatal complexes often surrounded by "neighbouring cells" in anisocytic arrangement, with 3–5 subsidiary cells; guard cell pairs 22–24 & 26–31 μm long and 18–22–25 μm wide.

Unspecialized cells with pitted anticlinal walls, which are curved to slightly undulated in adaxial epidermis and straight to curved in abaxial epidermis. Adaxial cells with thin anticlinal division walls. Cuticle granular. Primary veins prominent adaxially, minor veins prominent abaxially.

Material studied: *G. glabra* Aubl., Surinam, Samuels 270 (L); *G. tomentosa* Aubl., French Guyana, Martin s.n., 1918 (L.).

Hartogia L. f. 3/1 (plate I, 3)

Stomata confined to abaxial epidermis, laterocytic with 3–4 subsidiary cells; stomatal complex often embedded in anisocytically arranged “neighbouring cells”; guard cell pairs 22–25–28 μm long, 21–24–26 μm wide. Unspecialized cells with straight to curved anticlinal walls. Cuticle smooth. Primary veins prominent only, abaxially and adaxially.

Material studied: *H. schinooides* A.C. Sm., South Africa, Burkell 7225 (L).

Hedraianthera F.v.M. 1/1 (fig. 28)

Stomata confined to abaxial epidermis, paracytic with subsidiary cells usually extending beyond the poles of the guard cells and of different size, occasionally resulting in an anisocytic appearance; guard cell pairs 17–19–22 μm long, 14–16–17 μm wide. Unspecialized cells of the adaxial epidermis with straight to curved anticlinal walls, of the abaxial epidermis with undulated anticlinal walls. Cuticle finely granular. Primary veins prominent in abaxial epidermis only.

Material studied: *H. porphyropetala* F.v.M., Australia, Brass 20018 (L).

Helictonema Pierre 1/1 (fig. 10)

Uniseriate, 4–8-cellular, slender hairs abundant on both surfaces. Stomata confined to abaxial epidermis, laterocytic with 3–6 strongly submersed subsidiary cells which are also submersed under surrounding epidermal cells; guard cell pairs 20–22–25 μm long, 17–18–20 μm wide. Crystalliferous cells containing druses solitary, in pairs or small groups. Unspecialized cells with straight to slightly curved anticlinal walls. Cuticle smooth. Primary veins of abaxial epidermis prominent only.

Material studied: *H. velutina* (Afz.) R. Wilczek ex N. Hallé, Cameroon, Zenker 351 (U).

Hemiangium A.C. Sm. 1/1

Stomata confined to abaxial epidermis, laterocytic, with 2–5 subsidiary cells; guard cell pairs 25–29–30 μm long, 19–20–22 μm wide. Small, crystalliferous cells containing rhomboidal crystals present in groups or rows. Unspecialized cells with straight to curved, pitted anticlinal walls. Cuticle finely granular. Veins not prominent.

Material studied: *H. excelsum* (H.B.K.) A.C. Sm., Paraguay, Woolston 1161 (U).

Hippocratea L. ca. 5/5 (see also table 2; fig. 3–7; plate I, 1)

Stomata confined to abaxial epidermis, or also present on adaxial surface over midrib and major veins, laterocytic, or laterocytic and irregularly cyclocytic, with 2–7 subsidiary cells which are also partly submersed under surrounding cells. Crystalliferous cells containing druses very infrequent (absent in some specimens of *H. volubilis*) to abundant, solitary, paired or in groups. Unspecialized cells with straight to slightly curved anticlinal walls, but in *H. andamanica* with slightly to strongly undulated anticlinal walls. Cuticle smooth to granular. Veins prominent to various extent.

Material studied: *H. andamanica* King, India, King's collector s.n. (L); *H. angustipetala* H. Perr., Madagascar, Lam & Meeuse S 524 (L); *H. myriantha* Oliv., Zaire, Louis 13110 (L); *H. vignei* Hoyle, Ivory Coast, Versteegh & Den Outer 345 (U); *H. volubilis* L., Tobago, Eggers 5595 (L); Brasil, Ule 7284 and Maguire, Pires, Maguire & Silva 56005 (U).

Note: The generic concept of *Hippocratea* has varied considerably from taxonomist to taxonomist. See discussion of anatomical evidence in taxonomic part and also descriptions of *Anthodon*, *Cuervea*, *Elachyptera*, *Helictonema*, *Hemiangium*, *Hylenaea*, *Loeseneriella*, *Prionostemma*, *Pristimera*, *Reisantia* and *Simirestis*. *H. andamanica* and *H. angustipetala* are from regions for which no modern taxonomic treatment of the *Hippocratea* group exists, and we are therefore uncertain whether these species should in fact be treated under *Hippocratea* or under another allied genus.

Table 2. Variation of some leaf anatomical characters in *Hippocratea*.

	stomata in adaxial epidermis	stomatal type	number of subsidiary cells	length of guard cell pairs (μm)	width of guard cell pairs (μm)	druses in epidermal cells	texture of cuticle	prominence of veins, adaxial	prominence of veins, abaxial
H. andamancia	-	lat	3-5	23-25-27	16-18-20	+	c.gr	2	3
H. angustipetala	(+)	lat + cyclo	3-6	17-21-25	14-15-18	+	s	V.R.	V.R.
H. myriantha	(+)	lat + cyclo	4-7	26-29-30	20-22-24	+	f.gr	1	5
H. vignei	(+)	lat + cyclo	2-6	17-20-22	14-16-19	(+)	f.gr	2	3
H. volubilis	(+)	lat	2-4	18-20-22	16-17-18	+/-	f.gr	1	3

Legend: see table 1.

Hylenaea Miers 2/2

Stomata confined to abaxial epidermis, laterocytic to cyclocytic or complex cyclocytic, with 2-5 subsidiary cells; guard cell pairs 17-19-20 μm long, 14-16-19 μm wide. Small, crystalliferous cells containing druses infrequent in abaxial epidermis of *H. praecelsa*; extremely rare in *H. comosa*. Unspecialized cells adaxially with straight, abaxially with straight to curved anticlinal walls. Cuticle smooth to faintly granular. Minor veins prominent.

Material studied: *H. comosa* (Sw.) Miers, British Guyana, Fanshawe 4730 (U); *H. praecelsa* (Miers) A.C. Sm., Panama, Duke 10299 (U).

Kokoona and *Lophopetalum* - see JANSEN & BAAS 1973

Loeseneriella A.C. Sm., ca. 20/3 (fig. 9)

Stomata confined to abaxial epidermis, sometimes in pairs, laterocytic in *L. obtusifolia* and *L. pauciflora*, also occasionally complex laterocytic or complex cyclocytic in *L. cumingii*, with 3-6 strongly submersed subsidiary cells; also submersed under surrounding cells; guard cell pairs in *L. cumingii* 30-32-34 μm long, 25-27-30 μm wide; in *L. obtusifolia* 37-38-40 μm long, 30-32-34 μm wide; in *L. pauciflora* 27-28-30 μm long, 21-22-25 μm wide. Crystalliferous cells containing druses numerous in *L. obtusifolia* (small and solitary or in pairs); containing rhomboidal crystals and solitary, paired, or in rows or large groups in *L. pauciflora* and *L. cumingii*. Unspecialized cells with straight to slightly curved anticlinal walls; in *L. cumingii* anticlinal walls of adaxial epidermis straight and rather thick. Cuticle finely granular in *L. cumingii* and *L. pauciflora*, smooth in *L. obtusifolia*. Primary veins prominent in *L. cumingii* only.

Material studied: *L. cumingii* (Laws.) Ding Hou, Malaya, Sinclair 40054 (L.); *L. obtusifolia* (Roxb.) A.C. Sm., South Africa, Herb. Transvaal Museum 28849 (L.); *L. pauciflora* (DC.) A.C. Sm., Sumatra, Achmad 1792 (L).

Maytenus Molina ca. 225/5 (see also table 3; fig. 12)

Stomata confined to abaxial epidermis, or also abundant on adaxial surface in *M. texana*, laterocytic to complex laterocytic, rarely with some anisocytic ones, or cyclocytic to bicyclic (in *M. texana*), with 3-10 strongly to weakly submersed subsidiary cells. Unspecialized cells with straight to curved anticlinal walls which are thick and strongly cutinized in *M. ilicifolia*. Cuticle smooth, finely granular, or striated. Veins prominent to various extents.

Material studied: *M. acuminatus* (L. f.) Loes., South Africa, Schlechter 2454 (L.); *M. boaria* Molina, Argentina, De Barba 1669 (L.); *M. emarginata* (Willd.) Ding Hou, New Guinea, Brass 6229 (L.); *M. ilicifolia* Mart. ex Reissek, Uruguay, Marchesi 1310 (L.); *M. texana* Lundell, Texas, Lundell 10708 (L).

Note: In this group of species *M. texana* stands out markedly on account of its bicyclic stomata occurring on both leaf surfaces. *M. ilicifolia* has its stomatal pores occluded by granular material. This species is also remarkable for its thick anticlinal epidermal walls.

Table 3. Variation of some leaf anatomical characters in *Maytenus*.

	Stomata in adaxial epidermis	stomatatal type	number of subsidiary cells	length of guard cell pairs (μm)	width of guard cell pairs (μm)	texture or sculpturing of cuticle	prominence of veins, adaxial	prominence of veins, abaxial
<i>M. acuminatus</i>	-	lat-c. lat	3-5	19-23-26	18-20-24	s	-	1
<i>M. boaria</i>	-	lat-c. lat	2-6	30-35-37	27-30-32	f.gr	-	1
<i>M. emarginata</i>	-	lat	4-5	22-24-27	20-22-23	s	2	3
<i>M. ilicifolia</i>	-	lat-c. lat	4-7	28-30-32	20-23-24	s	-	1
<i>M. texana</i>	+	cyclo-bic	4-10	30-32-34	24-27-29	str	-	-

Legend: see table 1.

Microtropis Wall. ex Meissn. ca. 70/1

Stomata confined to abaxial epidermis, sometimes in pairs, cyclocytic to anisocytic or complex anisocytic, with 3-5 partly submersed subsidiary cells; guard cell pairs 21-23-24 μm long, 20-22-25 μm wide. Unspecialized cells with straight to curved anticlinal walls. Cuticle smooth. Primary veins of abaxial epidermis prominent only.

Material studied: *M. platyphylla* Merr., Borneo, Chew & Corner 4425 (L).

Mystroxyton - see *Cassine*.

Peritassa Miers 14/2 (fig. 23)

Stomata confined to abaxial epidermis, cyclocytic with 4-6 subsidiary cells, which are partly submersed under guard cells as well as under surrounding epidermal cells; guard cell pairs 20-21 & 24-25 μm long, 19-20 & 22-24 μm wide. Unspecialized cells with straight to undulated anticlinal walls and with thin areas of cuticle in loops of undulations. Cuticle smooth. Primary veins of adaxial epidermis prominent; in abaxial epidermis minor veins also prominent.

Material studied: *P. laevigata* (Hoffman) A.C. Sm., Brasil, Prance & Silva 59433 (U); *P. granulata* (Urb.) A.C. Sm., Surinam, BW 735 (U).

Perrottetia H.B.K. 20/7 (fig. 36; plate I, 6 & II, 4)

Unicellular to uniseriate (1-5 cellular), thin-walled hairs present in various densities in most specimens studied. Stomata confined to abaxial epidermis, predominantly anomocytic, also partly anisocytic, especially in *P. alpestris* and *P. ovata*; guard cell pairs 11-16-23-25 μm long, 10-13-20-22 μm wide. Abaxial epidermis of all *P. alpestris* specimens containing mucilage cells. Unspecialized cells with straight to curved anticlinal walls. Cuticle very delicate. Venule reticulum prominent on both surfaces, except in *P. alpestris* ssp. *moluccana* where veins are only partly prominent in abaxial epidermal cell pattern. Bowl-shaped domatia observed in primary vein axils of *P. lanceolata* and *P. ovata*.

Material studied: *P. alpestris* (Bl.) Loes. ssp. *alpestris*. Sumatra, Bunnemeijer 4371 and Rahmat si Boeca 10917 (L); *P. alpestris* (Bl.) Loes. ssp. *moluccana* (Bl.) Ding Hou. New Guinea, Hoogland 9381 (L); *P. alpestris* (Bl.) Loes. ssp. *philippensis* (Vidal) Ding Hou, Borneo, Chew, Corner & Stainton 2548 (L); *P. lanceolata* Karst, Guatemala, Türckheim 1622 (L); *P. ovata* Hemsly, Mexico, Pringle 8088 (L); *P. sandwicensis* A. Gray, Hawaii, Stauffer & Gillet 5859 (L).

Note: The Malesian species *P. alpestris* differs from the Hawaiian and South American species by the occurrence of mucilage cells in the abaxial epidermis.

Plenckia Reiss. 4/1 (fig. 17)

Stomata present on both surfaces, but of varying frequency on adaxial surface, laterocytic to complex laterocytic, rarely also cyclocytic to complex cyclocytic, with 4–7 subsidiary cells; guard cell pairs 33–36–40 μm long, 25–26–28 μm wide. Unspecialized cells of both surfaces with straight to curved anticlinal walls. Cuticle smooth. Venule reticulum fairly prominent on both surfaces.

Material studied: *P. populnea* Reiss., Brasil, Irwin, Anderson, Stiebers & Lee 34425.

Note: A study of macerations of 5 other *P. populnea* specimens showed that the frequency of adaxial stomata varies considerably within this species; one specimen (of var. *microcarpa* (Lundell) Reiss.) even completely lacked them. In *P. bahiensis* Loes. infrequent adaxial stomata were also observed.

Pleurostylia W. & A. 4/1 (fig. 24)

Stomata confined to abaxial epidermis, cyclocytic, rarely anisocytic, with 3–4(–5) subsidiary cells; guard cell pairs 20–21–22 μm long, 17–18–20 μm wide. Unspecialized cells of both surfaces with straight to curved anticlinal walls. Cuticle smooth. Primary and secondary veins of adaxial epidermis prominent, in abaxial epidermis minor veins prominent as well.

Material studied: *P. opposita* (Wall.) Alston, New Guinea, BW 4095 (L).

Note: The stomatal pores were often found to be occluded by granular material.

Pottingeria – see SHAW et al. 1973

Prionostemma Miers 1/1 (fig. 2; plate II, 1 & 2)

Low, thick-walled, broad-based, conical hairs (fig. 2) abundant on adaxial surface, less frequent on abaxial epidermis (here most frequent over veins); diameter of hair bases ranging from 20 to 65 μm ; some hairs subdivided by thin anticlinal walls. Stomata confined to abaxial epidermis, laterocytic, occasionally irregularly cyclocytic, with 4–6 strongly submersed subsidiary cells; guard cell pairs 18–20–22 μm long, 19–20–22 μm wide. Crystalliferous cells containing rhomboidal crystals infrequent. Unspecialized cells of the adaxial epidermis mostly elongate and radiating from the hair bases, with straight and pitted anticlinal walls; of the abaxial epidermis with straight to curved, pitted anticlinal walls. Cuticle smooth. Primary, secondary and tertiary veins prominent in abaxial epidermis only.

Material studied: *P. aspera* (Lam.) Miers, Colombia, Smith 893 (L).

Note: The frequent conical hairs of *Prionostemma* make this genus stand out from all other Celastraceae studied.

Pristimera Miers 14/2

Stomata on both surfaces scattered over lamina, but more frequent abaxially than adaxially, laterocytic in *P. nervosa*, laterocytic as well as irregularly cyclocytic due to subdivision of polar “neighbouring” cells in *P. andina*; guard cell pairs 17–18 & 20–22 μm long, 15–17 & 18–20 μm wide. Crystalliferous cells containing rhomboidal crystals frequent and solitary, paired or in groups; “individual” crystalliferous cells mostly subdivided, each daughter cell containing one crystal. Unspecialized cells with straight anticlinal walls. Cuticle granular. Primary veins prominent on both surfaces; secondary veins prominent in abaxial epidermis of *P. andina* only.

Material studied: *P. andina* Miers, Brasil, Inez Mexia 5235 (U); *P. nervosa* (Miers) A.C. Sm., Brasil, France, Rodriguez, Ramos & Farias 8490 (U).

Note: In *P. nervosa* the stomatal pores are sometimes occluded by granular material.

Reissantia Hallé 7/1 (fig. 14)

Stomata confined to abaxial epidermis, laterocytic to complex laterocytic, or sometimes irregularly cyclocytic with 2–5 subsidiary cells, slightly submersed under the guard cells as well as under the surrounding cells; guard cell pairs 16–19–33 μm long, 15–16–17 μm wide. Unspecialized cells of adaxial epidermis with straight to curved anticlinal walls, of abaxial epidermis with straight to undulated anticlinal walls. Cuticle smooth. Primary veins prominent adaxially, abaxially secondary

and tertiary veins prominent in epidermal cell pattern as well.

Material studied: *R. cassinoides* (DC.) Ding Hou, Sumatra, De Voogd 295 (L).

Salacia L. 200/6 (see also table 4; fig. 18–21)

Stomata confined to abaxial epidermis, cyclocytic with 4–7 subsidiary cells, often submersed under the guard cells as well as the surrounding cells. Peristomal cuticular rims well developed in *S. martiana* and *S. miqueliana*. Crystalliferous cells containing druses solitary, paired or in groups in abaxial epidermis of *S. opacifolia*; in *S. korthalsiana* infrequent in cells overlying veins. Unspecialized cells with curved to undulated anticlinal walls; undulations with short wavelength and with thin areas of cuticle in loops; or anticlinal walls straight to slightly curved in *S. martiana* and *S. miqueliana*, in the latter species very thick. Cuticle smooth or finely granular. Mostly primary veins prominent only, sometimes also secondary and tertiary veins prominent.

Material studied: *S. debilis* (G. Don) Walp., Zaire, Louis 14653 (L); *S. korthalsiana* Miq., Java, Kostermans 16A (L); *S. macrophylla* Bl., Java, Djoemadi 122 (L); *S. martiana* Peyr., Brasil, Ule 5642 (L); *S. miqueliana* Loes., Brasil, Pires, Rodriguez & Irvin 5072 (U); *S. opacifolia* (Macbr.) A.C. Sm., Brasil, Krukoff 4762 (U).

Note: In *S. miqueliana* the stomatal pores are often occluded with granular material and similar material is also present along the peristomal rims.

Table 4. Variation of some leaf anatomical characters in *Salacia*

	number of subsidiary cells	length of guard cell pairs (µm)	width of guard cell pairs (µm)	peristomal rims	druses in epidermis	texture of cuticle	prominence of veins, adaxial	prominence of veins, abaxial	undulations of adaxial anticlinal walls	undulations of abaxial anticlinal walls
<i>S. debilis</i>	4–6	18–20–21	17–18–21	–	–	f.gr	1	1	++	+
<i>S. korthalsiana</i>	4–6	19–21–23	16–18–19	–	+	s	3	3	+	+
<i>S. macrophylla</i>	5–6	20–21–23	19–21–24	–	–	s	1	1	++	+
<i>S. martiana</i>	4–7	36–41–46	34–35–36	+	–	s	1	1	–	–
<i>S. miqueliana</i>	4–5	24–27–30	15–20–24	+	–	f.gr	1	2	–	–
<i>S. opacifolia</i>	4–5	18–19–22	17–18–19	–	+	s	1	1	+	+

Legend: see table 1.

Sarawakodendron Ding Hou 1/1 (fig. 37)

Stomata confined to abaxial epidermis, irregularly cyclocytic, or tending to anomocytic, sometimes paracytic or aniso- to complex anisocytic, with 2–4–5 subsidiary cells; guard cell pairs 20–23–25 µm long, 18–19–20 µm wide. Unspecialized cells with straight to slightly curved anticlinal walls. Cuticle smooth to finely granular. Veins not prominent.

Material studied: *S. filamentosum* Ding Hou, Borneo, S 24506 (L).

Note: It is difficult to classify the stomata of *Sarawakodendron* due to the fact that the subsidiary cells are only slightly different from the unspecialized cells, the majority of stomata in *Sarawakodendron* could therefore be called intermediate between cyclocytic and anomocytic.

Simirestis Hallé (fig. 8)

Stomata confined to abaxial epidermis, laterocytic, with 3–6 subsidiary cells submersed under guard cells as well as under surrounding cells; guard cell pairs 18–22–25 µm long, 15–16–17 µm wide. Crystalliferous cells containing rhomboidal crystals, solitary, in pairs or groups of, often subdivided, epidermal cells, abaxially more frequent than adaxially. Unspecialized cells with straight to slightly curved anticlinal walls. Cuticle smooth to finely granular. Primary, secondary and tertiary veins

prominent in both adaxial and abaxial epidermis.

Material studied: *S. goetzei* (Loes.) N. Hallé ex R. Wilczek, Nyassa Highlands, Stolz s.n. (U).

Siphonodon Griff. 6/5 (see also table 5; fig. 15 & 16)

Stomata confined to abaxial epidermis, but in *S. pendulum* also fairly abundant on adaxial surface, laterocytic, sometimes complex laterocytic or cyclocytic to complex cyclocytic, with 4–6(–7) subsidiary cells. Infrequent crystalliferous cells containing druses noted in *S. annamensis*. Unspecialized cells with straight to curved, in *S. annamensis* thick, anticlinal walls. Cuticle finely granular. Mostly only primary veins prominent; sometimes secondary and tertiary veins prominent as well, or veins not prominent at all.

Material studied: *S. annamensis* (H. Lec.) Merr., Laos, Poilane 11400 (L); *S. celastrineus* Griff., Java, Nengah Wirawan 388 (L); *S. membranaceum* Bailey, Australia, Queensland, Kajewski 1271 (L); *S. peltatus* Ding Hou, New Guinea, Jacobs 9177 (L); *S. pendulum* Bailey, Australia, Queensland, Brass 18365 (L).

Table 5. Variation of some leaf anatomical characters in *Siphonodon*.

	stomatal type	length of guard cell pairs (μm)	width of guard cell pairs (μm)	druses in epidermis	prominence of veins, adaxial	prominence of veins, abaxial
<i>S. annamensis</i>	lat + c.lat + c.cyclo	25–28–30	23–26–30	+	1	3
<i>S. celastrineus</i>	lat	22–27–30	18–22–24	–	–	1
<i>S. membranaceum</i>	lat + c.lat	26–28–30	25–27–30	–	–	2
<i>S. pendulum</i>	lat (+ c.lat)	32–35–38	26–28–31	–	–	1
<i>S. peltatus</i>	lat + c.lat + c.cyclo	28–30–32	23–26–28	–	1	2

Legend: see table 1.

Tontelea Aubl. 30/2 (fig. 11)

Stomata confined to abaxial epidermis, laterocytic with 3–6 strongly or totally submersed subsidiary cells; guard cell pairs 25–28 & 30–32 μm long, 24–28–32 μm wide. Unspecialized cells with straight to curved anticlinal walls; in *T. ovalifolia* abaxial epidermal cells with straight to slightly undulated, pitted anticlinal walls. Cuticle smooth. Primary veins prominent only.

Material studied: *T. brachypoda* Miers, Brasil, Philcox, Ramos & Sansa 3079 (U); *T. ovalifolia* (Miers) A.C. Sm., Brasil, Ule 8416 (U).

Note: According to some authors *Tontelea* should be reduced *Salacia*. See also taxonomic discussions.

Wimmeria Schlechtend. 14/1

Stomata confined to abaxial epidermis, paracytic to laterocytic with 2–5 subsidiary cells; guard cell pairs 15–21–25 μm long, 13–15–18 μm wide. Unspecialized cells of adaxial epidermis with straight, of abaxial epidermis with straight to curved anticlinal walls. Cuticle smooth. Venule reticulum prominent.

Material studied: *W. persicifolia* Radlk., Mexico, Pringle 10392 (L).

Xylonymus Kalkman 1/1 (fig. 30)

Stomata confined to abaxial epidermis, paracytic; guard cell pairs 23–25–27 μm long, 15–17–20 μm wide. Unspecialized cells with undulated anticlinal walls, abaxially more strongly so than adaxially. Cuticle finely granular. Primary veins prominent adaxially, secondary and tertiary veins also pro-

minent in abaxial epidermis.

Material studied: *X. versteeghii* Kalkman, New Guinea, BW 4686 (L).

5. DISCUSSIONS

5.1. Variability and taxonomic value of the epidermal characters

The characters recorded in the descriptions are not all of the same diagnostic or taxonomic value. VAN STAVEREN & BAAS (1973), JANSEN & BAAS (1973) and others have already stressed the restricted value of characters such as undulations of anticlinal walls, granulation of the cuticle, and pitting of anticlinal flanges, because these characters are often found to vary below the species level. For this reason, characters such as distinctness of outer and inner stomatal ledges and adhering cuticular flaps, and of polar cuticular T-pieces have been left out of the descriptions altogether; also because of the difficulties in defining these gradually varying characters unambiguously. The only leaf epidermal characters considered to be of taxonomic value in discussing affinity or taxonomic boundaries within Celastraceae s.l. are stomatal type, crystalliferous cells, and to a much lesser extent the indumentum. The other characters recorded such as stomatal size and distribution, number and degree of submersion of subsidiary cells, outline of epidermal cells, texture of the cuticle and prominence of veins are all of variable and mostly limited taxonomic and diagnostic value below the genus level.

In spite of the greater taxonomic value postulated for stomatal type, occurrence of crystalliferous cells, and indumentum, these characters may still vary considerably within genera, within species or even in a single leaf. This variability limits the absolute diagnostic value of these characters, but does not necessarily restrict their taxonomic value: it rather enables an insight into the relationships which may exist between the different character states, especially of the stomatal complex (see below).

The stomatal type of a single leaf was often found to vary; mostly this concerned the occurrence of a few stomata of another type than the predominating one. More rarely two or more different types occurred in abundance on the same leaf. Leaves with predominantly paracytic stomata, sometimes also showed anisocytic, helicocytic or parallelocytic ones. Laterocytic stomata were often found in leaves which also showed a portion of paracytic and/or cyclocytic stomata. Assuming a perigenous development for these three types of stomata in Celastraceae (cf. PANT & KIDWAY 1966) this is not surprising, because they would then represent a series of increasing divisions of the epidermal cells initially surrounding the stoma mother cell. Cyclocytic stomata are quite often the exclusive stomatal type, but in a number of species they occur together with anomocytic and anisocytic stomata and are then linked through intermediates; similarly they may be found together with laterocytic stomata. The truly anomocytic stomata of *Perrottetia* occur together with sporadic anisocytic ones. Finally the predominantly anisocytic stomata of *Catha* occur together with sporadic cyclocytic ones. It remains a matter of taste whether one should call the laterocytic stomata of *Goupia* and *Hartogia*, which are embedded in an anisocytic pattern of surrounding

cells, "complex anisocytic". In that case laterocytic and complex anisocytic stomata occur in one and the same leaf (see also survey of characters, 3.3).

Some variability of stomatal type at the species level was reported for certain *Kokoona* and *Lophopetalum* species (JANSEN & BAAS 1973). Our material was not sufficient to evaluate this variation in more detail. Extra variation, exceeding the variability within single leaves must, however, be anticipated. At the generic level only 16 out of the 37 genera studied were represented by more than one species. In 12 genera the main stomatal type appeared to be constant while in *Cassine*, *Cheilochlinium*, *Euonymus* and *Maytenus* different main types occurred in different species. At least in *Cassine* this diversity seems related to infrageneric subdivision or can be used to reinstate separate genera recognized by some authors. In *Euonymus* it may also imply erroneous placement of one species. In *Cheilochlinium* and *Maytenus* the diversity in stomatal type concerns mutually related laterocytic and cyclocytic types; and the taxonomic position of the aberrant *Maytenus texana* with its bicyclic stomata certainly merits reconsideration. On the whole the taxonomic value of the stomatal type on the genus level remains therefore considerable in the material used for this study. However, the exhaustively studied *Kokoona* and *Lophopetalum* (JANSEN & BAAS 1973) show a substantial variation in main stomatal type, which again limits the application of this character on the genus level in the other Celastraceae of which only a very limited number of species was studied.

Fig. 38 gives a schematic representation of possible "relationships" of the different stomatal types in Celastraceae. This scheme is based on morphological similarities between the adult stomatal types and also on the occurrence of different types and their intermediates in a single leaf.

Variability of the occurrence of crystalliferous cells with either druses or rhomboidal crystals also exists at different taxonomic levels. JANSEN & BAAS (1973) for instance reported the occurrence of solitary crystals in epidermal cells to be variable in some *Lophopetalum* species. In this study we found several genera to be constant for the occurrence of a given type of crystals, but variable with respect to the frequency of crystalliferous cells. In our opinion the presence of crystalliferous cells can be used as a positive character to indicate affinity, while the absence of crystals is not necessarily indicative of a lack of affinity. Similar views have been forwarded and substantiated for crystalliferous cells in other plant parts, notably in the secondary xylem.

The occurrence of hairs is so much limited to a few Celastraceous taxa that they cannot be used for interpreting affinities. However, type and presence can help to recognize the generic identity of for instance *Prionostemma* and *Perrottetia*. Within some of the larger genera, for instance *Celastrus*, *Euonymus* and *Hippocratea* the indumentum is only of (limited) diagnostic value at the species level (Ding Hou, personal communication).

5.2. Systematic implications

5.2.1. General remarks

The distribution of the most important leaf epidermal characters over the genera

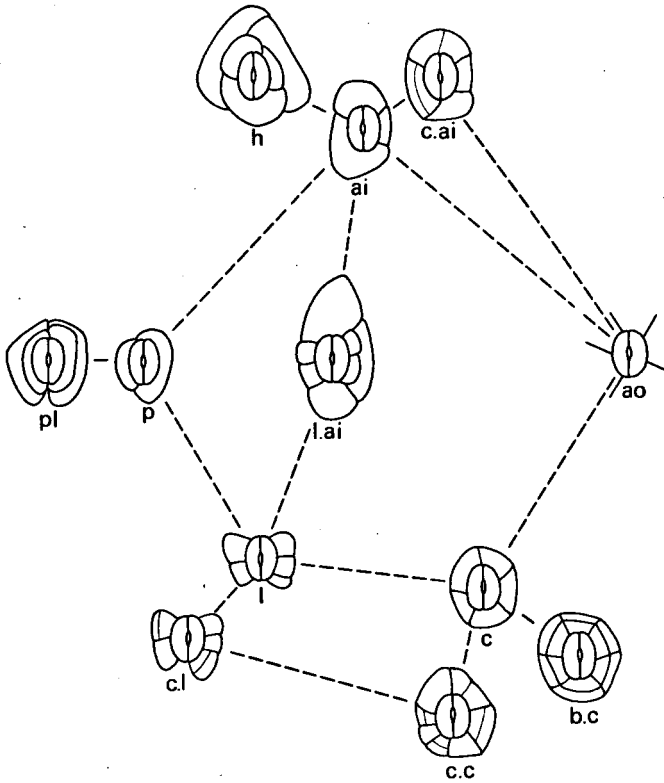


Fig. 38. Stomatal types and subtypes in Celastraceae sensu lato and their possible relationships. ai = anisocytic; c.ai = complex anisocytic; h = helicocytic; l.ai = laterocytic embedded in anisocytic pattern of surrounding cells; l = laterocytic; cl = complex laterocytic; c = cyclocytic; c.c = complex cyclocytic; b.c = bicyclic (tricyclic stomata have an extra ring of subsidiary cells); ao = anomocytic; p = paracytic; pl = parallelocytic.

studied is given in *table 6*. Besides stomatal type and occurrence of crystalliferous epidermal cells, other characters such as merousness of the androecium, occurrence of scalariform perforation plates in the secondary xylem are also recorded in the table (the wood anatomical data were kindly provided by Dr. Alberta M. W. Mennega; see also METCALFE & CHALK 1950). From the table it becomes immediately apparent that the leaf epidermal range of variation of Celastraceae sensu stricto (= Celastroideae) completely overlaps that of the "Hippocrateaceae" (= Hippocrateoideae). Both groups show laterocytic stomata as the predominating type; additionally Hippocrateoideae have cyclocytic and cyclocytic to anomocytic stomata. The Celastroideae are somewhat more diverse and also have representatives with chiefly anisocytic or paracytic stomata. There is a tendency for crystalliferous cells to be more in evidence in Hippocrateoideae than in Celastroideae, but both subfamilies have representatives with either rhomboidal crystals or druses in epidermal cells. On the whole, the major leaf epidermal

Table 6. Distribution of the main stomatal types over the genera of Celastraceae s.l.

Anomocytic	Cyclocytic	Laterocytic	Anisocytic	Paracytic
		Cuervea ◊ Elachyptera ◊ Hemiangium ◊ Loesneriella ◊/* Pronostemma ◊ Pristimera ◊ Simirestis ◊ Anthodon * Helictonema * Hippocratea * Hylenaea * Apodostigma Reissantia Tontelea		
Stamens 3 (2) ("Hippocrateaceae")	Peritassa Salacia (*) Sarakakodendron			
<i>Perrottetia</i>	Cassine maritima Cheiloclinium p.p. Denhamia Kokoona p.p. Lophopetalum p.p. Maytenus texana Microtropis Pleurostyliia	Cassine p.p. Cheiloclinium hippocratioides Euonymus p.p. Kokoona p.p. <i>Maytenus</i> p.p. Campylostemon Celastrus Glyptopetalum <i>Goupia</i> Hartogia Plenckia Siphonodon* Wimmeria	<i>Cassine</i> p.p. ◊ Catha Kokoona p.p. Lophopetalum p.p. (◊)	<i>Bhesa</i> Brassiantha Euonymus globularis Hedraianthera Xylonymus
Stamens 5 (4) (Celastraceae s.s.)				

Legend to table 6: ◊ = with solitary, rhomboidal crystals in part of epidermal cells; * = with druses in part of epidermal cells. The *italicized* taxa have scalariform vessel perforations in their wood (Mennega, personal communication).

characters lend support to a broad family concept of the Celastraceae, including the previously recognized "Hippocrateaceae". The common occurrence of laterocytic stomata, and to a lesser extent the shared occurrence of crystalliferous epidermal cells even raises the question whether the recognition of subfamily "boundaries" between Hippocrateoideae and Celastroideae is natural.

Table 6 cannot depict a complete interpretation of mutual affinities based on leaf epidermal data. From the possible relationships between the different main stomatal types (see fig. 38) it is obvious that there are many alternative possibilities to group genera based on different stomatal types. Such groupings would, however, be the result of a rather academic exercise because more characters should be considered, and preferably one should have an insight in the derived or primitive condition of each character state. For the epidermal characters used this is impossible at this stage of our knowledge.

Comparison of table 6 with LOESENER's system for Celastraceae sensu stricto (1942) and with LOBREAU-CALLEN's grouping of Celastraceae sensu lato as based on pollen types (1975b) shows that most of their groups (in Loesener's case formally given subfamily or tribal status) are heterogeneous for stomatal types as well as the occurrence of crystalliferous epidermal cells. This lack of correlation of anatomical diversity with macromorphological or pollen morphological grouping can be interpreted in two ways: 1) it may lead to the suggestion that previous classifications are inadequate and partly unnatural, or 2) it can be taken as an indication of parallel and/or convergent development in the evolution of stomatal types in the Celastraceae s.l. Both possibilities probably reflect part of the truth.

For instance, the apparently specialized bicyclic stomata of *Maytenus texana* and *Denhamia* have probably originated independently from similar stomata in *Cassine maritima* and are therefore not indicative of close mutual affinity; on the other hand the shared paracytic stomata of *Bhesa*, *Hedraianthera*, *Brassiantha*, *Xylonymus* and *Euonymus globularis* all from Malesia or Queensland are probably indicative of true affinity despite the fact that LOESENER (1942) treated *Bhesa* (as *Kurrimia*) and *Hedraianthera* in different tribes and LOBREAU-CALLEN (1975b) grouped *Xylonymus* somewhat apart from *Hedraianthera*, *Brassiantha* and *Bhesa* on ectexine characters.

In some instances there is a good agreement with the grouping by LOBREAU-CALLEN (1975b) especially where the "satellite genera" of the *Hippocratea* group (see below) are concerned, which all share the same pollen type.

Although it is not possible to use the newly acquired leaf epidermal data for discussions of a comprehensive picture of relationships within Celastraceae as a whole, specific issues on which taxonomists have expressed different opinions in the past can be reconsidered in the light of our new evidence. This will be done for certain genera and/or groups of genera below.

5.2.2. Notes on individual genera or groups of genera

Kokoona and *Lophopetalum*

JANSEN & BAAS (1973) recorded anisocytic and cyclocytic stomata for *Kokoona*; for *Lophopetalum* moreover they found complex anisocytic and cyclocytic sto-

mata and helicocytic ones. After having recognized laterocytic stomata as a distinct type, it was considered appropriate to reinterpret the results of the above-mentioned study. It appeared that the laterocytic type occurs quite frequently in *Kokoona* but is absent from *Lophopetalum*. The layterocytic type was included in the cyclocytic type in JANSEN & BAAS' paper. For easy reference the full ranges of stomatal type for all species of *Kokoona* are given here: *K. coriacea*, anisocytic, sometimes laterocytic; *K. filiformes*, anisocytic, laterocytic and cyclocytic; *K. littoralis*, anisocytic and laterocytic, sometimes cyclocytic; *K. ochracea*, anisocytic, laterocytic and cyclocytic; *K. ovatolanceolata*, laterocytic, occasionally cyclocytic; *K. reflexa*, laterocytic, rarely anisocytic; *K. sessilis*, cyclocytic; *K. zøylanica*, cyclocytic-laterocytic.

In their general conclusion Jansen & Baas listed six differential characters for the separation of *Kokoona* and *Lophopetalum*, which, although applicable for part of the species only provided an argument in favour of keeping the two genera apart. We now can add another differential character, albeit not an absolute one: Stomata in *Kokoona* almost always partly laterocytic—Stomata in *Lophopetalum* never laterocytic. The view expressed by HOU (1964) that *Kokoona* provides a link between taxa from Celastraceae s.s. and genera formerly treated as Hippocrateaceae cannot be supported or rejected on leaf anatomical grounds. The fairly frequent occurrence of anisocytic stomata—a type absent from Hippocrateoideae—seems to plead for a stronger affinity of *Kokoona* with the Celastroideae. *Lophopetalum*, regarded as a link by ROBSON (1965) figures as a less suitable candidate because it lacks laterocytic stomata typical for the major part of both (sub)families.

Sarawakodendron

DING HOU (1967) when describing *Sarawakodendron* for the first time drew the attention to its intermediate nature between "Hippocrateaceae" and "Celastraceae". Macromorphologically it shares characters with *Kokoona* and *Lophopetalum* (Cel.) and *Salacia* (Hipp.) and also resembles *Polycardia* (Cel.). A study of the pollen of *Sarawakodendron* showed similarities with *Xylonymus* and *Kokoona* (DING HOU 1969). In its leaf-epidermis *Sarawakodendron* stands out from all other material studied by us in showing a predominant stomatal type somewhat intermediate between anomocytic and cyclocytic, which is accompanied by less frequent paracytic and anisocytic stomata. The tendency towards anomocytic stomata might induce a comparison with *Perrottetia* with its truly anomocytic stomata, but this genus differs in both indumentum and wood anatomical characters significantly from *Sarawakodendron*. On balance the epidermal characters of *Sarawakodendron* indicate an isolated rather than an intermediate position of the genus.

Perrottetia

METCALFE & CHALK (1950) and others, for example CORNER (1976), have pointed out the aberrant position of this genus within Celastraceae. Leaf anatomically the isolated position of the genus is confirmed by the indumentum, stomatal type and

tendency to form domatia in the vein axils. In all three characters *Perrottetia* is unique amongst the material used for this study. Wood anatomically *Perrottetia* is moreover one of the few Celastraceous genera with scalariform perforations in its xylem (Mennega, personal communication).

Salacia, Cheilochlinium, Peritassa and Tontelea

In the last few decades LOESENER (1942), METCALFE & CHALK (1950), MACBRIDE (1951), MENNEGA (1972) and LOBREAU-CALLEN (1975b) have stressed the similarities between all or part of the genera *Salacia*, *Cheilochlinium*, *Peritassa* and *Tontelea*. Anatomically *Peritassa*, *Sarawakodendron* and *Cheilochlinium* p.p. (three of the four species studied) all share cyclocytic stomata. *Tontelea* and *Cheilochlinium hippocrateoides* show laterocytic stomata. In view of the occurrence of both cyclocytic and laterocytic stomata within *Cheilochlinium* and of the morphological "relationships" between the laterocytic and cyclocytic stomatal type, the close affinities of the four genera can be supported by leaf anatomy.

Hippocratea and related genera

The generic delimitation of *Hippocratea* has been subject of different opinions. A. C. SMITH (1940) recognized only one, variable species, *H. volubilis* in the New World and considered the Old World "Hippocrateas" to represent other genera. WILCZEK (1960) however, maintained *Hippocratea* in his treatment for the Flore du Congo. ROBSON (1965) also recognized *Hippocratea* on the African continent and even reduced *Anthodon*, *Apodostigma*, *Cuervea*, *Elachyptera*, *Helictonema*, *Hemiangium*, *Hylenea*, *Loeseneriella*, *Prionostemma*, *Pristimera*, *Reissantia* and *Simirestis* to *Hippocratea*. The shared laterocytic stomatal type of all these "genera" may be taken as an argument in favour of Robson's treatment. Other epidermal characters such as presence and type of crystals in the epidermal cells and presence of hairs show some diversity. *Prionostemma* for instance merits a separate status on account of its highly unusual indumentum. The diversity of different types of crystals is more difficult to interpret in taxonomic terms, especially in view of the fact that within the limited material studied of *Loeseneriella* the Asiatic species appeared to show a different crystal type than the African *L. obtusifolia*.

Cassine, Elaeodendron, Crocoxylon and Mystroxylon

The taxonomic history of the genus *Cassine* and putative relatives is complex and still there is little agreement on the generic delimitation in this group. LOESENER (1942) distinguished three genera: *Elaeodendron* (including *Crocoxylon*), *Cassine* and *Mystroxylon*. ROBSON (1965) recognized five genera: *Cassine*, *Crocoxylon*, *Elaeodendron*, *Mystroxylon* and *Allocassine*. DING HOU (1964) treated *Elaeodendron* as a synonym of *Cassine*. PALMER & PITMAN (1972) finally only recognized *Cassine* (including *Elaeodendron*, *Mystroxylon* and *Crocoxylon*) and *Allocassine* for Southern Africa. LOBREAU-CALLEN (1975a) found some pollen morphological diversity within this group of taxa but found the evidence insufficient to keep the genera apart.

Leaf anatomically three groups can be distinguished in the very limited material studied by us: 1) with laterocytic stomata and without crystalliferous epidermal cells containing rhomboidal crystals ("*Crocoxylon*" and "*Elaeodendron*" as exemplified by *C. croceum* from Southern Africa, *C. australe* from Australia and *C. vitiensis* from Fiji); 3) with cyclocytic stomata and without crystalliferous epidermal cells ("*Mystroxylon*" = *C. maritima* from Southern Africa; this species is moreover outstanding in this group on account of its thick epidermal cell walls). More material of additional species should be studied to test whether the anatomical differences between these groups hold true. In view of the transitions between laterocytic and complex anisocytic stomata in *C. australe* of the "*Elaeodendron* group" further intermediates might be anticipated. The present leaf epidermal diversity together with a wood anatomical variability found by Dr. A. M. W. Mennega (personal communication) seems to plead against the whole-sale lumping of all genera kept apart by ROBSON and several other authors.

Denhamia and *Maytenus*

DING HOU (1964) expressed his suspicion that the Australian genus *Denhamia* is probably not distinct from *Maytenus*. Leaf anatomically *Denhamia* is clearly characterized by bicyclic to tricyclic stomata or cyclocytic to complex cyclocytic stomata. The limited material of *Maytenus* studied showed predominantly laterocytic stomata in Malesian, African and South American species and cyclocytic to bicyclic stomata in the North American *M. texana*. Through the latter species one could support Ding Hou's suggestion leaf anatomically, but obviously more *Maytenus* species should be studied to indicate possible close relatives of *Denhamia*. This is especially necessary in view of taxonomic disagreement on the position of *M. texana*. LUNDELL (1971) treated this species in the genus *Tricerna*, but LOBREAU-CALLEN (1975a) challenged his views on the basis of pollen morphological evidence.

Euonymus

When in 1975 DING HOU described *Euonymus globularis* from Australia he remarked that "the appropriate position of the species *E. globularis* in the rather heterogeneous genus *Euonymus* can hardly be ascertained until a comprehensive revision of it is available". This statement obviously also applies to a taxonomic interpretation of the leaf anatomical diversity of this large and macromorphologically heterogeneous genus. The aberrant stomatal type (paracytic) of *E. globularis* in the limited material of *Euonymus* studied by us (3 species with laterocytic stomata) strongly supports suggestions by DING HOU l.c. that *E. globularis* is allied to *Brassiantha* and *Hedraianthera*, but leaves the question of the position in *Euonymus* unanswered and doubtful.

Enigmatic genera: *Goupia*, *Siphonodon* and *Pottingeria*

Several authors advocate the distinction of separate families Goupiaceae and Siphonodontaceae on the basis of aberrant macro- and/or micromorphological characters of these genera.

Goupia has the strongest claim for family status since its wood and pollen differ from that of Celastraceae (Mennega, personal communication; LOBREAU-CALLEN 1975b). With its laterocytic stomata embedded in an anisocytic pattern of surrounding cells (a variation on the complex anisocytic pattern if one prefers), *Goupia* would fit in the Celastraceae on account of its leaf epidermal pattern. Its indumentum is also insufficient reason to exclude it from Celastraceae, because other doubtless members of the family show slightly similar hairs, e.g. *Helictonema*. The evidence from other plant parts seems, however, rather overwhelming to recognize the monotypic family Goupiaceae.

Siphonodon and its taxonomic affinities have been discussed at some length by DING HOU (1963 & 1964). The macromorphological evidence (HOU l.c.) together with data from wood anatomy (INGLE & DADSWELL 1961) and pollen morphology (LOBREAU-CALLEN 1975b) at least do not exclude close affinities of *Siphonodon* with Celastraceae. The leaf anatomy of *S. annamensis* with its laterocytic stomata is completely within the range of other Celastraceae and provides an additional argument to retain *Siphonodon* in Celastraceae.

Recently the Asiatic genus *Pottingeria* has been transferred from Escalloniaceae to Celastraceae (SHAW et al. 1973) in a subfamily of its own. We did not study material of this genus, but the anomocytic stomata illustrated by SHAW et al. make the genus comparable to *Perrottetia* and *Sarawakodendron* in its leaf epidermal morphology. It should, however, be stressed that truly anomocytic stomata are an unusual feature within Celastraceae sensu lato, contrary to what is suggested by the authors cited.

5.2.3. Wider affinities of Celastraceae s.l.

According to LOESNER (1942) the affinities of Celastraceae are probably with Cyrillaceae, Icacinaceae, Staphylaceae, and Aquifoliaceae. Similarities with some Euphorbiaceae and Rhamnaceae are also mentioned. Unfortunately our knowledge of the epidermal morphology of some of these families and of others treated in the order Celastrales is insufficient to use these limited characters to full advantage in a discussion of the wider affinities of Celastraceae. Such discussions should, moreover, be very careful and tentative in view of the unproved taxonomic value of epidermal characters above the family level. Icacinaceae and Aquifoliaceae have been thoroughly studied recently (VAN STAVEREN & BAAS 1973; BAAS 1974 & 1975) and it appears that these families share a number of leaf epidermal trends found in part of the Celastraceae. Anisocytic, cyclocytic, anomocytic and paracytic stomata are shared by Icacinaceae and Celastraceae; a reinterpretation of the paracytic and paracytic to cyclocytic stomata recorded for *Citronella* (BAAS 1974) make these also assignable to the laterocytic type newly introduced here.

Aquifoliaceae show such a range in stomatal types and also in other characters such as the occasional occurrence of thick epidermal walls etc. that they often recall some members of the Celastraceae; this holds particularly true for the taxa sharing bicyclic stomata. It is, however, quite plausible that the leaf epidermal similarities of a number of Icacinaceae and of some *Ilex* species with repre-

sentatives of Celastraceae are the result of parallel or convergent evolution only. This possibility must be seriously considered in view of recent opinions that the affinities of Aquifoliaceae and Icacinaceae are with Theales rather than with Celastrales (cf. THORNE 1976 & 1977 and DICKISON & BAAS 1977).

Cyrrillaceae, itself of doubtful position in Celastrales, has exclusively anomocytic stomata (METCALFE & CHALK 1950, confirmed by personal observations) and is therefore only more or less similar to a few unusual members of Celastraceae.

Staphyleaceae are recorded to have anisocytic stomata (METCALFE & CHALK 1950), also occurring in some members of the Celastraceae.

A further discussion of the wider affinities of Celastraceae must obviously include all available characters from external morphology, palynology and anatomy and is beyond the scope of this paper.

6. CONCLUDING REMARKS – SCOPE FOR FURTHER STUDY

The leaf epidermal diversity of the Celastraceae s.l. reported in this paper lends support to the inclusion of “Hippocrateaceae” in this family. In several instances the combined characters of stomatal type, occurrence of crystalliferous epidermal cells and indumentum provide useful additional data to arrive at a natural classification below and above the generic level. The aims of this study were to indicate possible taxonomic uses of leaf epidermal characters on the basis of a broad survey: in many instances comprehensive leaf epidermal studies are now indicated to solve special and/or controversial issues (e.g. *Maytenus*, *Cassine*, *Hippocratea*, *Euonymus*, etc.). Such anatomical studies should preferably be carried out simultaneously with future taxonomic revision work to guarantee the best possible use of these promising leaf epidermal characters.

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REFERENCES

- BAAS, P. (1974): Stomatal types in Icacinaceae. Additional observations on genera outside Malesia. *Acta Bot. Neerl.* **23**: 193–200.
- (1975): Vegetative anatomy and the affinities of Aquifoliaceae, Sphenostemon, Phelline, and Oncotheca. *Blumea* **22**: 311–407.
- CORNER, E. J. H. (1976): *The seeds of Dicotyledons*. Cambridge Univ. Press.
- COTTHEM, W. R. J. VAN (1970): A classification of stomatal types. *Bot. J. Linn. Soc.* **63**: 235–246.
- (1971): Vergleichende morphologische Studien über Stomata und eine neue Klassifikation ihrer Typen. *Ber. dtsh. bot. Ges.* **84**: 141–168.
- DICKISON, W. C. & P. BAAS (1977): The morphology and relationships of Paracryphia (Paracryphiaceae). *Blumea* **23**: 417–438.

- HALL, J. B. & J. M. LOCK (1975): Use of vegetative characters in the identification of species of *Salacia* (Celastraceae). *Boissiera* **24a**: 331–338.
- HALLÉ, N. (1962): Monographie des Hippocratéacées d'Afrique occidentale. *Mém. Inst. Franç. d'Afrique Noire* No. **64**.
- HOOKE, J. D. (1862): Hippocrateaceae, in Bentham & Hooker's *Genera Plantarum* **1**: 369–371.
- HOU, D. (1955): A revision of the genus *Celastrus*. *Ann. Mo. bot. Gdn.* **42**: 215–298.
- (1962): Celastraceae I, in *Flora Malesiana* **1**, **6**: 227–291.
- (1963): Florae Malesianae Precursores XXXIV. Notes on some genera of Celastraceae in Malaysia. *Blumea* **12**: 31–38.
- (1964): Celastraceae II, in *Flora Malesiana* **1**, **6**: 389–421.
- (1967): Sarawakodendron, a new genus of Celastraceae. *Blumea* **15**: 139–143.
- (1969): Pollen of Sarawakodendron and some related genera. *Blumea* **17**: 97–120.
- (1975): A new species of *Euonymus* from Australia. *Blumea* **22**: 271–274.
- INGLE, H. D. & H. E. DADSWELL (1961): *The anatomy of the secondary xylem of South West Pacific tree species as an aid to their taxonomy*. Paper of Tenth Pacific Science Congress.
- JAIN, D. K. & V. SINGH (1975): Occurrence of giant stomata in Celastraceae and Convolvulaceae. *Curr. Sci.* **44**: 170.
- JANSEN, W. T. & P. BAAS (1973): Comparative leaf anatomy of *Kokoona* and *Lophopetalum* (Celastraceae). *Blumea* **21**: 153–178.
- LOBREAU-CALLEN, D. (1975a): Deux genres de Celastraceae, *Cassine* L. et *Maytenus* Mol. revus à la lumière de la palynologie. *Adansonia* **15**: 215–223.
- (1975b): *Les pollens des Celastrales et groupes apparentés*. Thesis Montpellier, C.N.R.S. No. A.O. 8071.
- LOESENER, T. (1942): Celastraceae and Hippocrateaceae, in ENGLER & PRANTL, *Natürliche Pflanzenfamilien* ed. 2, **20b**: 87–231.
- LUNDELL, C. L. (1971): Studies of American plants III. *Wrightia* **4**: 153–172.
- MACBRIDE, J. F. (1951): Hippocrateaceae, in Flora of Peru. *Bot. Ser. Field Mus. Nat. Hist. Chicago* **13** (eA): 200–220.
- MENNEGA, A. M. W. (1972): A survey of the wood anatomy of the New World Hippocrateaceae. In: A. K. M. GHOUSE & M. YUNUS (Eds.), *Research trends in plant anatomy*: 61–72. Bombay-New Delhi, Tata McGraw-Hill.
- METCALFE, C. R. & L. CHALK (1950): *Anatomy of the Dicotyledons*. Oxford, Clarendon Press.
- PALMER, E. & N. PITMAN (1972): *Trees of Southern Africa*. Cape Town, Balkema.
- PANT, D. D. & P. F. KIDWAY (1966): Epidermal structure and stomatal ontogeny in some Celastraceae. *New Phytol.* **65**: 288–295.
- PAYNE, W. W. (1970): Helicocytic and allelocytic stomata: unrecognized patterns in Dicotyledonae. *Amer. J. Bot.* **57**: 140–147.
- PEREIRA DOS SANTOS, A. V. & B. M. GRISI (1976): Anatomia foliar ecológica de algumas plantas da Caatinga. *Rev. bras. Biol.* **36**: 773–787.
- REHFOUS, L. (1914): Les stomates des Célastracées *Bull. Soc. Bot. Genève* **II**, **6**: 13–18.
- ROBSON, N. (1965): New and little known species from the flora Zambesiaca area XVI. Taxonomic and nomenclatural notes on Celastraceae. *Bol. Soc. Broteriana* **39**: 1–55.
- SHADAN, P. & E. J. SHELLARD (1962): An anatomical study of Ethiopian Khat (leaf of *Catha edulis* Forsk.). *J. Pharm. and Pharmac.* **14**: 110–118.
- SHAW, H. K. A., D. F. CUTLER & S. NILSSON (1973): *Pottingeria*, its taxonomic position, anatomy and palynology. *Kew Bull.* **28**: 97–104.
- SMITH, A. C. (1940): The American species of Hippocrateaceae. *Brittonia* **3**: 341–555.
- & I. W. BAILEY (1941): *Brassiantha*, a new genus of the Hippocrateaceae from New Guinea. *J. Arn. Arbor.* **22**: 389–394.
- SOLEREDER, H. (1899 & 1908): *Systematische Anatomie der Dicotyledonen & Ergänzungsband*. Stuttgart, Enke.
- STACE, C. A. (1965): Cuticular studies as an aid to plant taxonomy. *Bull. Brit. Mus. (Nat. Hist.) Bot.* **4**, **1**.
- STAVAREN, M. G. C. VAN & P. BAAS (1973): Epidermal characters of the Malesian Icacinaceae. *Acta Bot. Neerl.* **22**: 329–359.

- THORNE, R. F. (1976): A phylogenetic classification of the Angiospermae. In: HECHT, STEERE & WALLACE (Eds.), *Evolutionary Biology* **9**: 35–106.
- (1977): *Realignments in the Angiospermae*. Mimeographed, 1 page.
- WILCZEK, R. (1960): Celastraceae, and Hippocrateaceae, in *Flore du Congo Belge et du Ruandi-Urundi* **9**: 113–232.