VEGETATIVE ANATOMY AND THE AFFINITIES OF AQUIFOLIACEAE, SPHENOSTEMON, PHELLINE, AND ONCOTHECA

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CONTENTS

SUMMARY

The anatomy of leaf, node, twig, and bark of *Ilex*, *Nemopanthus*, *Oncotheca*, *Phelline*, and *Sphenostemon* is described, together with the wood anatomy of the 4 latter genera. Several characters are recorded for the first time.

The systematic value of some anatomical characters for judging the wider affinities of the genera involved is discussed. Considering these characters together with macromorphological and palynological data, it is concluded that *Phelline* and *Sphenostemon* each merit family status, and have affinities with *Aquifoliaceae* and *Icacinaceae* of the *Celastrales*. *Oncotheca* shows no affinities with the families of *Celastrales*, and may possibly have its closest relatives in *Theales*, but this problem has not been studied in great detail.

The leaf anatomy of 95 *Ilex* species is described, and the great leaf anatomical diversity of *Ilex* is discussed with reference to Loesener's infrageneric classification. In general, leaf anatomy cannot be used to support his elaborate subdivision of the genus. Infraspecific leaf anatomical variability is reported and discussed for 15 species of *Ilex*. Attention is paid to some geographical, ecological, and functional aspects of the leaf anatomical range of variation in *Ilex*. This range has a general significance for systematic leaf anatomy, because it shows the restricted value of several characters for the discussion of affinities above the genus level.

INTRODUCTION

Aims of this study

The affinities of *Sphenostemon* from New Guinea, New Caledonia, and Queensland, and of *Oncotheca* from New Caledonia have been discussed and disputed over the last decades in many publications. The inclusion of *Phelline* from New Caledonia in the *Aquifoliaceae* has also been challenged by several authors. The three genera have in common that they have been mentioned repeatedly in connection with the *Aquifoliaceae*. For the development of further views the collecting of more anatomical data on the two undisputed members of the *Aquifoliaceae*: *Ilex* and *Nemopanthus*, therefore seemed essential. With this aim in mind a detailed and elaborate survey of the wood anatomical range in *Ilex* has been published (Baas, 1973); in the present paper the leaf anatomy of *Ilex* will be treated in a similar way. Besides, the leaf and wood anatomy of *Nemopanthus*, *Oncotheca*, *Phelline*, and *Sphenostemon* will be comprehensively described, together with observations on nodal, twig, and bark anatomy. It is considered that these data should provide a sounder basis for anatomical comparison than the rather haphazard choice of miscellaneous species which in the past contributed to such diverse conclusions by several authors. Comparisons with other putative relatives will be based mainly on data from the literature, and will consequently suffer more from incompleteness than the comparisons with *Aquifoliaceae* *sensu stricto*.

The leaf anatomical survey of *Ilex* should also be considered as an aim in itself. Although it will be attempted to find correlations with the infrageneric classification proposed by Loesener (1901, 1908, and 1942), this survey is mainly aimed at determining the leaf anatomical range in a large and widely distributed genus, and at indicating possibly useful characters for a future taxonomic revision which is badly needed for this genus.

Historical

As a starting point for a historical survey of views on the affinities of *Ilex*, *Nemopanthus*, and *Phelline*, Loesener's treatments (1901, 1908 and 1942) of the *Aquifoliaceae* can be conveniently used; older literature is comprehensively listed by him.

The close affinities of *Ilex* and *Nemopanthus* are beyond doubt; the only differences in

external morphology are in the reduced calyx and in the free petals of *Nemopanthus* as contrasted by the well-developed calyx and the at their base almost always more or less fused, imbricate petals of *Ilex*.

Loesener treated *Phelline* in a separate tribe, characterized by valvate apiculate petals. Recently some doubts have been expressed about the inclusion of *Phelline* in *Aquifoliaceae*. On the grounds of pollen morphology Erdtman (1952) stated that arguments might be advanced in favour of the assumption that *Phelline* has not yet been given its correct place in the system. Airy Shaw (1966, in Willis) doubtfully referred *Phelline* to '*Araliaceae* (~ *Aquifoliaceae*)', without giving further arguments. Takhtajan (1966) erected the family *Phellineaceae* 'related to *Aquifoliaceae*, from which it differs, however, by having valvate petals, by the character of the inflorescence, the hemitropous or weakly campylotropous ovules, the wood anatomy, the quite different sporoderm morphology, and the leaf venation' (quoted from Takhtajan, 1969). His suggestion was followed by Airy Shaw in the latest edition of Willis' Dictionary (1973); the family name was corrected by the latter into *Phellinaceae*.

When Baillon (1891) first described the genus *Oncotheca*, he indicated links with *Phelline* and *Sphenostemon* from the 'Ilicinées' and at the same time he suggested a relationship with *Ebenaceae*. Later (1892) he formally included the genus in *Ilicaceae*, in his concept also including *Cyrilla* and *Cliftonia*, which are now in *Cyrillaceae*. Kronfeld (1892) included *Oncotheca* in his treatment of the *Aquifoliaceae*, but Loesener (1897, 1901, and 1942) never accepted the genus in this family and assigned it to *Ebenaceae* (1897, 1942) and also suggested affinities with *Sapotaceae* (1901). Guillaumin (1938) most strongly advocated the Ebenaceous nature of *Oncotheca* and formally erected the tribe *Oncotheceae* within *Ebenaceae* on the basis of both macromorphological and anatomical characters. More recently Airy Shaw (1965) erected the family *Oncothecaceae*, following unpublished suggestions by Kobuski. An Ebenaceous affinity was suggested to be erroneous, and affinities with *Theaceae* were considered to be rather close. The pollen of *Oncotheca* has not yet been properly described; Erdtman (1952) could only dispose of an inadequate slide of mixed ilicoid and smooth grains. Both types would, in any case, not be suggestive of Ebenaceous affinities.

The exceedingly chaotic taxonomic history of the genus *Sphenostemon* (including *Idenburgia* and *Nouhuysia*) has been very comprehensively reviewed by Bernardi (1964). With reference to his paper a survey of the views held before 1964 can be very brief. The reduction of *Idenburgia* Gibbs and *Nouhuysia* Lauterb. to *Sphenostemon* Baillon (Van Steenis, 1952, 1955) implies presumed affinities with *Aquifoliaceae* (Baillon, 1875; Van Steenis, 1955), with *Trimeniaceae* (Gibbs, 1917; Gilg & Schlechter, 1923), and with *Guttiferae* (Lauterbach, 1912; Van Steenis, 1952). Older views on the affinities of *Sphenostemon sensu stricto* had also differed: Loesener (1901, 1942) expelled the genus from *Aquifoliaceae* and suggested a Theaceous or Ochnaceous affinity, leaving possibilities open for a separate family. Anatomical and palynological contributions have so far only added to the confusion: Money *c.s.* (1950), Bailey & Swamy (1953), and Bailey (1956) excluded *Sphenostemon* (*Idenburgia* and *Nouhuysia*) from *Monimiaceae*, *Trimeniaceae*, and *Guttiferae*, and Bailey (1956) was also reluctant to accept an Aquifoliaceous affinity. Previously Money *c.s.* (1950) had excluded *Idenburgia* from *Monimiaceae* on morphological grounds. Metcalfe's anatomical contribution (1956) to the problem also led him to conclude that it is evident that none of the genera (*Sphenostemon, Idenburgia, Nouhuysia*) is closely related to either the *Monimiaceae, Aquifoliaceae*, or *Guttiferae*. The occurrence of styloid crystals prompted him to mention a resemblance in this respect with *Escalloniaceae*, without, however, implying and Escalloniaceous affinity for *Sphenostemon s.l.* Ingle & Dadswell

(1961) in comparing the wood of *Nouhuysia* (New Guinean and Australian *Sphenostemon*) with that of *Ilex*, *Platea* (*Icacinaceae*), and *Polyosma* (*Escalloniaceae*) concluded that of these genera *Ilex* bears least resemblance to *Nouhuysia*, and that *Icacinaceae* have at least as big a claim for affinity as the *Escalloniaceae*. Erdtman (1952, 1954) drew attention to the 'strange ± unique' pollen grains of *Sphenostemon sensu lato*, stressing their lack of resemblance with pollen of *Aquifoliaceae*. Lobreau (1969) in studying the pollen of *Sphenostemon*, found it similar to that of *Dichapetalaceae* rather than to other putative relatives. Hutchinson (1959, 1964, 1969, and 1974) meanwhile maintained *Sphenostemon* in *Trimeniaceae*, and Airy Shaw, when formally publishing a family diagnosis for *Sphenostemonaceae* in 1972 also advocated a Trimeniaceous affinity, although the anatomy and pollen morphology 'forbid' its inclusion in that family. Airy Shaw moreover repeated objections against inclusion in *Aquifoliaceae*, *Guttiferae*, *Monimiaceae*, and *Escalloniaceae*. Bernardi (1964) extending the numerous observations scattered in the literature with an original observation on the unitegmic nature of the ovules, concluded from many sources of evidence that *Sphenostemon* should after all be included in *Aquifoliaceae* as suggested by Baillon who first described the genus.

The extensive amount of publications, listed above, seems to make further attempts to find a proper taxonomic position of the three enigmatic genera *Oncotheca*, *Phelline*, and *Sphenostemon* rather useless or without prospect. However, most previous anatomical publications have in common that they do not take the entire anatomical range of *Aquifoliaceae sensu stricto* into account and that the comparisons with this and other families are too superficial. By adding to our knowledge of the anatomical range in *Aquifoliaceae sensu stricto* and by considering the anatomical and macro-morphological characters in other putative relatives, it is hoped that this study can at least finally settle the argument with respect to possible affinities between *Aquifoliaceae* and these genera.

A considerable amount of descriptive data has accumulated on the vegetative anatomy of the 5 genera studied. Older literature has been comprehensively summarized by Solereder (1899, 1908), and Metcalfe & Chalk (1950), though special mention should be made of Thévenard's (1906) anatomical study of *Sphenostemon*, *Phelline*, *Ilex*, and *Nemopanthus*. However, his accurate descriptions appear to leave out many features now considered as important diagnostic or taxonomic characters. Anatomical data on *Ilex* are furthermore provided by Senglet (1928), Zahur (1955), Ashworth (1963), Copeland (1963), Gasanov (1969), Fretz & Dunham (1972), Korn & Frederick (1973), and by Baas (1973), who also listed the more recent wood anatomical literature.

The anatomy of *Sphenostemon* has received attention in papers by Thévenard (1906), Bailey & Swamy (1953), Metcalfe (1956), Jutte (1958), and Ingle & Dadswell (1961). Pennington (1953) also gave an account of the wood of *Sphenostemon*, but a comparison with the vouched material I could study leaves no doubt that the wood specimen she studied does not belong to *Sphenostemon*.

Phelline is included in Thévenard's survey of *Aquifoliaceae* anatomy, and Takhtajan (1966) included anatomical data when he raised the genus to family rank. He recorded anomocytic stomata, narrow vessels with many-barred scalariform perforation plates, scalariform to alternate vessel wall pitting, scanty paratracheal parenchyma, mixed homogeneous rays with short tails, and fibres with distinctly bordered pits. Pennington's (1953) account of the wood of *Phelline* again suggests mislabelled or misnamed material.

Oncotheca has received comparatively little anatomical attention, with scanty and very superficial observations by Guillaumin (1938) and unpublished studies by Kobuski (see Airy Shaw, 1965). Recently Miss C. S. Bissett (Chapel Hill, North Carolina, U.S.A.) independently embarked on an anatomical study of *Oncotheca*, and her conclusions

emphasizing floral morphological features will be the subject of a separate publication.

More or less simultaneous with this study Madame Danielle Lobreau-Callen has carried out a pollen morphological survey of all genera involved. She has shared her results prior to publication, so that I could include arguments from pollen morphology in my discussion of the affinities and status of the enigmatic genera. The results were published in a thesis when these investigations had been completed (Lobreau-Callen, 1975). Her conclusions on *Phelline* and *Sphenostemon* are in general agreement with those presented here. *Oncotheca* is said to have affinities with *Salvadoraceae* because of more or less identical pollen.

SYNOPSIS OF MORPHOLOGICAL CHARACTERS

The descriptions below are mainly taken from the literature (Airy Shaw in Willis, 1973; Loesener, 1942). For *Sphenostemon*, *Phelline*, and *Oncotheca* most characters have been checked in the material present in the Rijksherbarium.

ILEX L.

Flowers unisexual, in axillary cymes or racemes, or fasciculate, rarely solitary, 4(5—9)-merous, isomerous, rarely heteromerous, often with pleiomerous ovary. *Sepals* connate at base, lobes imbricate. *Petals* mostly connate at the base, rarely free, lobes rounded, imbricate. *Stamens* alternipetalous, adnate to the base of the corolla, rarely free; filaments thin, anthers basidorsifixed, introrse, connective not prolonged. Pollen tricolporate, ectoapertures long, endoapertures developed as constrictions of the ectoapertures, tectate-clavate. *Ovary* superior, with sessile capitate or discoid stigma, (2—)4—9(—22)-locular, with 1 (rarely 2) axile, pendulous, anatropous, unitegmic ovule(s) per locule. Funicle frequently thickened ('obturator' or site of repressed second ovule, *cf.* Herr, 1959). *Fruit* a 2—22-pyrened drupe. Seeds with copious endosperm.

Trees or shrubs, rarely climbers, evergreen or deciduous, with alternate, rarely opposite or whorled, stipulate leaves.

About 400 species; cosmopolitan.

NEMOPANTHUS Raf.

Calyx reduced to a narrow seam with 0—5 small tips. *Petals* free. In other characters as *Ilex*, subgenus *Prinus*.

Two species in N. America.

ONCOTHECA Baill.

Flowers bisexual, in ± narrow thyrses with angular rhachis, 5-merous, isomerous, *Sepals* connate, lobes orbiculate, strongly imbricate, persistent. *Petals* connate, lobes rounded, imbricate. *Stamens* alternipetalous, inserted on the corolla; filaments thin, very short, anthers basifixed, extrorse, with thick connective, produced into a subulate, sharply inflexed, appendage. Pollen tricolporate, ectoapertures long, endoapertures subcircular, tectate-finely perforate. *Ovary* superior, with 5 free recurved styles, 5-locular, with 1 (rarely 2) pendulous, anatropous, unitegmic ovule(s) per locule. Funicle without obturator. *Fruit* a 5-locular, ± woody drupe. Seed unknown.

Evergreen shrubs with alternate, exstipulate leaves.

One species in New Caledonia.

PHELLINE Labill.

Flowers unisexual, in spicate or paniculate inflorescences, 4—6-merous, with a 2—5-merous ovary. *Sepals* connate at base, small. *Petals* free, valvate, with a small inflexed apiculus. *Stamens* alternipetalous, free; filaments thin, anthers basidorsifixed, introrse, connective not prolonged. Pollen tricolporate, ectoapertures long, endoapertures developed as constrictions of the ectoapertures, tectate-echinate or tectate-smooth. *Ovary* superior, with sessile lobed stigma, and 1 axile, pendulous, hemitropous or slightly campylotropous, unitegmic ovule per locule. Funicle without obturator. *Fruit* a drupe with 2—5 stones. Seeds with copious endosperm.

Evergreen shrubs with alternate, exstipulate leaves.

About 10 species in New Caledonia.

SPHENOSTEMON Baill.

Flowers unisexual or bisexual, in subterminal racemes, heteromerous. *Sepals* 4, free, decussate, early caducous. *Petals* 4, free, decussate, or rudimentary, or absent, ± fleshy, early caducous. *Stamens* 4—12, 1-seriate, free; with thick, very short or obsolete filaments, thecae laterally on thick connective, or ventrally on thick petaloid stamen. Pollen tri- or tetraporate, rarely inaperturate, tectate-reticulate or finely verrucate. *Ovary* superior, with sessile capitate stigma, 2-locular with 1 (rarely 2*) pendulous, anatropous, unitegmic ovule per locule. Funicle with obturator. *Fruit* a drupe with 1 or 2 bony pyrenes. Seeds with copious endosperm, ruminate or not.

Evergreen trees or shrubs with alternate (sometimes subopposite or pseudoverticillate) exstipulate leaves.

Seven species, in New Caledonia (series *Sphenostemon*), and New Guinea and Queensland (series *Apetala*).

TECHNIQUES AND MATERIALS

Microtechnical procedures have been largely the same as reported elsewhere (Baas, 1970, 1972b, 1973). For leaf anatomy additional observations were made using cuticular macerations (cf. Van Staveren & Baas, 1973), because these provide characters which are not or hardly visible in sections. Stomata were measured in euparal mounts of free hand paradermal sections; average values are based on 10 measurements.

Almost all material studied is from the Rijksherbarium, but special mention should be made of leaf material of some South American species from the Utrecht Herbarium (U), and some material of *Oncotheca, Sphenostemon*, and *Phelline* especially collected for this study by Dr. H. S. McKee in New Caledonia. Part of the wood samples of *Sphenostemon, Nemopanthus*, and *Phelline* were furthermore received from Madison (MADw & SJRw), and Sydney (SFCw) (abbreviations according to Stern, 1967).

Although virtually all of the studied leaf material of *Ilex* was taken from flowering specimens, the possibility of misidentification cannot be excluded, so that in this respect this study bears the same limitations as the wood anatomical survey (Baas, 1973). This is mainly due to the lack of an up to date world revision of the genus.

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*) Smith (1957) recorded the sporadic occurrence of 2 ovules per locule in *S. lobosporus*.

DESCRIPTIVE PART

Leaf anatomy

ILEX

(see Plate I—V; fig. 1—8, 17, 18)

In s u r f a c e   v i e w: Glabrous or with indumentum of varying density. *Hairs* usually short, thick-walled, and unicellular, often confined to petiole and adaxial side of midrib, sometimes also present on abaxial side of midrib, and rarely present over abaxial surface of the whole lamina. Other hair types confined to a small number of species and including slender 2-cellular hairs with a warty cuticle (fig. 5); similar hairs with a thick basal sept and a smooth cuticle (fig. 4); long hairs with a varying number of thin septs, and short thick-walled hairs with a very broad base subdivided by numerous closely spaced septs (fig. 8; Plate I, 6). Hairs straight or with recurved tips and with fairly narrow or broad bases. *Cuticle* of adaxial and/or abaxial surface smooth, coarsely to finely granular and/or faintly to strongly striated. *Epidermal cells* of abaxial and/or adaxial surface polygonal with straight to undulated anticlinal walls; undulations often confined to outer part; adaxial epidermal cells in some species with thin, secondary, anticlinal division walls. Anticlinal cuticular flanges and cell walls pitted or not. Cells overlying midrib flattened to elongated abaxially, isodiametric (not modified) or flattened to elongated adaxially. Primary, secondary, and tertiary *veins* prominent or not. *Stomata* confined to abaxial epidermis, randomly orientated, mainly cyclocytic, sometimes with 2 rings of subsidiary cells (bicyclic), but anomocytic, anisocytic, and complex cyclocytic in a fair number of species (Plate II; fig. 17); many species with a combination of 2 or more of these different stomatal types or with intermediate stomatal types. Peristomal rim usually present; outer stomatal ledges well developed; inner stomatal ledges absent or very inconspicuous; polar T-pieces well-developed to absent, guard cell pairs on average 18—42 μm long, 16—34 μm wide. Giant stomata usually present, but varying in frequency. *Cork warts* frequent and of regular, circular or angular outline (Plate IV, 3 & 4), or infrequent and of irregular outline (probably traumatic) to absent.

In t r a n s v e r s e   s e c t i o n: *Lamina* dorsiventral, 90—700 μm thick. Adaxial *cuticle* 1—28 μm thick, abaxial cuticle 1—16 μm thick. Unspecialized *epidermal cells* erect to flattened; adaxial cells much bigger than to slightly smaller than abaxial cells. Adaxial epidermis, and rarely also abaxial epidermis, containing a varying number of bulging, usually tall, mucilage cells, often with periclinal division walls, sometimes resulting in a complete 2—3-layered multiple epidermis (Plate IV, 2, 5, 6; fig. 10—15). Unspecialized abaxial epidermal cells with lignified pitted thickenings to the inner periclinal walls and the inner part of the anticlinal walls in some species (Plate III, 1—3; IV, 1). Adaxial *hypodermis* of 1 cell layer present or absent, composed of unlignified parenchymatous to collenchymatous cells or of lignified cells; rarely of more than one cell layer, and than mostly composed of bulging mucilagenous cells. *Mesophyll* composed of 1—3(—4) layers of short to tall palisade cells and loose to compact spongy tissue which may be partly (abaxially) or wholly lignified in a number of species. *Midrib* with a grooved, flattened, or raised adaxial surface and prominently raised abaxial surface, supplied with a simple to complex vascular system partly or wholly sheathed by varying amounts of sclerenchyma fibres. Ground tissue of midrib collenchymatous to parenchymatous. *Veins* mostly embedded, with a lignified or unlignified parenchymatous, rarely sclerenchymatous, bundle sheath; bundle sheath enclosing various amounts of sclerenchyma (Plate V, 5 & 6);
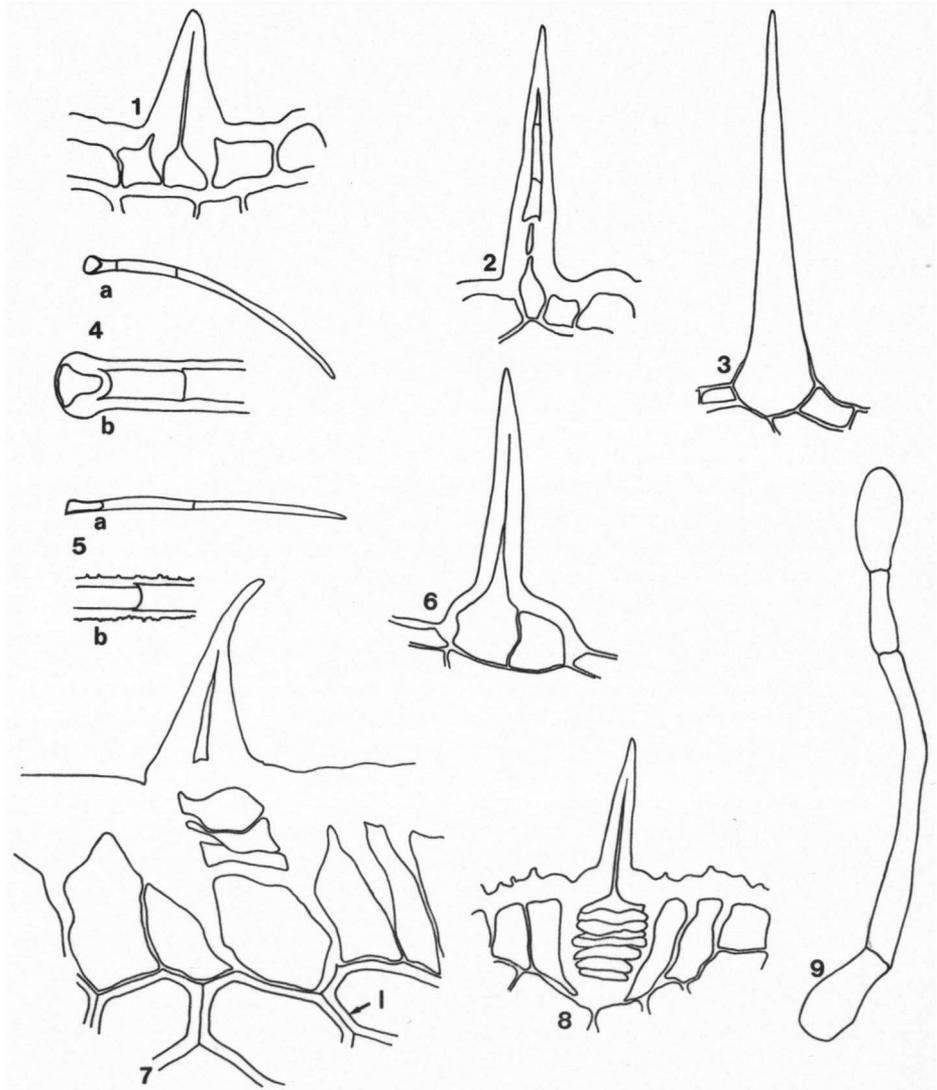
Fig. 1—9. Camera lucida drawings of hair types. — 1. *Ilex pernyi (Boom 27299)*. — 2. *Ilex micrococca.* — 3. *Ilex serrata (Boom 6165)*. — 4. *Ilex brasiliensis.* — 5. *Ilex amelanchier.* — 6. *Ilex cissoidea.* — 7. *Ilex zygophylla* (l = lignified hypodermis). — 8. *Ilex hypoglauca (Hallier B 2875)*. — 9. *Phelline lucida (Schlechter 15340)*. — One may construct the following morphological series: 1—2—5—4, 1—3—6, and 1—7—8. Fig. 4a and 5a × 110; other figs. × 470.

veins occasionally vertically transcurrent through collenchymatous to parenchymatous or sclerenchymatous bundle sheath extensions. *Leaf margin* with hardly modified ± compact chlorenchyma or with a solid strand of sclerenchyma fibres (Plate V, 4). *Petiole* with a ± similar vascular pattern as midrib or more complex (Fig. 18). *Crystals* almost exclusively represented by small to large druses throughout lamina, rarely crystals minute and solitary (prismatic to needle-shaped) in adaxial epidermis, or crystals solitary, prismatic and accompanying major vascular bundles; very rarely absent. Idioblastic *sclereids* of various shapes, but mostly irregularly fusiform, in the mesophyll of a restricted number of species (Plate V, 1—3); rarely of regular elongated shape and confined to ground tissue of midrib and petiole.

N o t e: The leaf anatomy of the individual species and its implications for systematics in *Ilex* will be treated in a separate section (see p. 359).

NEMOPANTHUS
(see Plate VI, 3)

In s u r f a c e v i e w: Glabrous. *Cuticle* of abaxial epidermis with conspicuous, rather widely spaced ridges (Plate VI, 3), adaxial cuticle faintly to conspicuously striated. *Epidermal cells* of adaxial surface polygonal with curved walls; walls of abaxial surface curved to undulated. Cuticular flanges weakly developed, not pitted. Cells overlying midrib elongate; cells over primary, secondary, and also many tertiary *veins* also modified (usually elongate) in both adaxial and abaxial epidermis. *Stomata* confined to abaxial epidermis, randomly orientated, irregularly cyclocytic (tending to complex anisocytic or anomocytic) with 4—6 subsidiary cells; peristomal rims present; outer stomatal ledges not very conspicuous, polar T-pieces absent; guard cell pairs on average 21—23 μm long, 18—21 μm wide. Giant stomata rather frequent. *Cork warts* absent or very infrequent and of irregular shape.

In t r a n s v e r s e s e c t i o n: *Lamina* dorsiventral, 90—150 μm thick. Adaxial and abaxial *cuticle* 1 μm thick or thinner. *Epidermal cells* square to flattened; those of adaxial epidermis often with convex inner walls and periclinal subdivision walls, possibly containing mucilage; proportion of subdivided cells variable with the specimen. Abaxial epidermal cells smaller than adaxial cells. *Hypodermis* absent. *Mesophyll* composed of 1 layer of palisade cells and unlignified spongy tissue. *Midrib* with flat to grooved adaxial surface and raised abaxial surface, supplied with crescentiform main vascular strand and two small dorsal bundles, accompanied by little or no sclerenchyma. Ground tissue of midrib collenchymatous. *Veins* with parenchymatous unlignified bundle sheaths, extending to lower and upper epidermis in most cases; only smallest veins embedded in mesophyll. Bundle sheath enclosing small adaxial and abaxial fibre strands in major veins. *Petiole* with a similar system as midrib. *Crystals* infrequent to frequent as druses in mesophyll, but mainly in vicinity of veins.

Material studied. *Nemopanthus mucronata* (L.) Trel. (*N. fascicularis* Raf.); CANADA, Ontario: *Kirk 308*, Quebec: *Rolland Germain 1444.* — U.S.A., Pennsylvania: *Herb. J. R. Lowrie s—8* (1852). — BELGIUM, cult. Calmpthout: *Boom 27763.*

ONCOTHECA
(see Plate VI, 4 & 5; fig. 19—21)

In s u r f a c e v i e w: Glabrous. *Cuticle* smooth. *Epidermal cells* of both adaxial and abaxial surface with straight to slightly curved anticlinal walls; anticlinal cuticular flanges well-developed, not pitted. Cells overlying midrib hardly modified adaxially, square to elongate abaxially; cells over *veins* not modified. *Stomata* confined to abaxial epidermis,
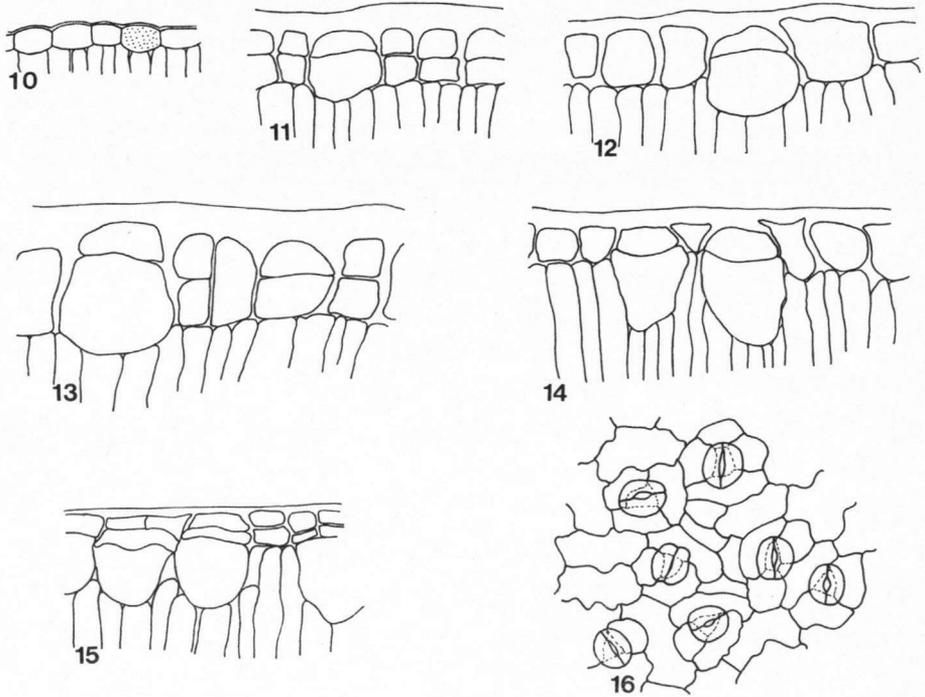
Fig. 10—15. Camera lucida drawings of adaxial epidermis in transverse section, × 300. — 10. *Ilex amelanchier.* idioblastic mucilage cell dotted. — 11. *Ilex theezans (Reitz & Klein 3222)*, frequent periclinal subdivisions and infrequent bulging mucilage cells. — 12. *Ilex theezans (Dusén 10608)*, infrequent bulging mucilage cells with periclinal subdivisions. — 13. *Ilex archboldiana*, frequent anticlinal and periclinal subdivisions. — 14. *Ilex umbellata*, strongly bulging mucilage cells deeply penetrating into palisade tissue. — 15. *Ilex argentina*, ibid., with frequent subdivisions.

Fig. 16. Abaxial epidermis of *Ilex guianensis (Broadway 4052)*, mixture of anisocytic and cyclocytic stomata, × 300.

randomly orientated, of unusual type: possibly to be interpreted as paracytic and anisocytic with subdivided subsidiary cells (Plate VI, 5), peristomal rims absent, outer stomatal ledges well-developed, inner ledges small, polar T-pieces absent, guard cell pairs on average 29—32 μm long, 20—22 μm wide. Giant stomata occasionally present. *Cork warts* absent, but necrotic patches of epidermal tissue rather frequent.

In transverse section: *Lamina* dorsiventral 470—510 μm thick. Adaxial *cuticle* 2—5 μm, abaxial cuticle 1—2 μm thick. *Epidermal cells* square to flattened, adaxially larger than abaxially. Adaxial *hypodermis* well-developed, composed of (1—2) 3 layers of thick-walled ± square parenchyma cells, continuous over midrib. *Mesophyll* composed of 2—3 layers of tall to short palisade cells and rather compact unlignified spongy tissue which is more or less differentiated into a thin-walled adaxial portion and a more thick-walled abaxial portion. *Midrib* with slightly raised adaxial and prominently raised abaxial surface, supplied with vascular system as in fig. 21. Ground tissue of midrib parenchyma-

tous to collenchymatous, but on adaxial side composed of 1 layer of short palisade cells and 3-layered hypodermis. *Veins* embedded, with parenchymatous unlignified bundle sheaths, enclosing well-developed adaxial sclerenchyma caps; abaxial sclerenchyma caps only present in major veins. *Petiole* with complex open vascular system (fig. 19 & 20), devoid of accompanying sclerenchyma. *Crystals* present as ordinary druses in ground tissue of lamina, and as minute star- or needle-shaped crystals in unspecialized abaxial and adaxial epidermal cells. Thick-walled *brachysclereids* infrequent in ground tissue of midrib and petiole.

Material studied. *Oncotheca balansae* Baill.; NEW CALEDONIA: *McKee 3439, 3597, 4849.*

PHELLINE

(see Plate VIII & IX; fig. 9 & 30)

In s u r f a c e v i e w: Glabrous. *Cuticle* of adaxial epidermis mostly smooth, sometimes finely granular or faintly striated; abaxial cuticle more frequently striated or granular (if striated, striae sometimes confined to neighbouring cells around stomata). Adaxial *epidermal cells* polygonal with straight to curved anticlinal walls; abaxial unspecialized cells with straight to undulated walls, not pitted or with granular appearance due to closely spaced irregular pits in anticlinal cuticular flanges. Cells overlying midrib usually square to elongate, rarely flattened abaxially. *Veins* mostly not prominent, sometimes only primary or even more rarely also secondary veins prominent. *Stomata* confined to abaxial epidermis, randomly orientated, anomocytic, with 4—7 (mostly 4—5) neighbouring cells, with well-developed peristomal rims, very conspicuous inner and outer stomatal ledges, without polar T-pieces; guard cell pairs 45—88 μm long, 44—77 μm wide. Giant stomata present in varying frequencies, occasionally necrotic and surrounded by some suberized cells (minute 'cork warts'). Irregular cork patches, probably of traumatic origin absent to fairly frequent.   ·

In t r a n s v e r s e s e c t i o n: *Lamina* dorsiventral, 240—480 μm thick. Adaxial *cuticle* 1—26 μm thick, abaxial cuticle 1—14 μm thick. *Epidermal cells* erect to flattened, abaxial cells slightly or much smaller and more strongly flattened than adaxial cells. *Hypodermis* absent. *Mesophyll* not distinctly differentiated into palisade and spongy tissue but composed of *c.* 2 adaxial layers of very short cylindrical to almost isodiametric cells and fairly loose unlignified spongy tissue. *Midrib* with prominently raised adaxial and abaxial surface, containing a varying number of centric (amphicribral) vascular bundles (4—12) and a varying number of collateral 'split-off' vascular bundles (0—6), the whole system fused and not clearly built up of centric bundles in one specimen of *P. lucida* (*McKee 5337*), bundles with or without thin sclerenchyma sheaths, segments of centric bundles separated by sclerenchymatous or parenchymatous 'rays' (Plate VIII, 4). Ground tissue of midrib parenchymatous to collenchymatous. *Veins* embedded in mesophyll, with unlignified parenchymatous bundle sheaths enclosing no or little (mainly abaxial) sclerenchyma. *Petiole* with a similar or slightly more simple arrangement of vascular bundles as midrib (Plate IX), with 4—15 bundles in distal end of petiole. *Crystals* absent or infrequent as minute druses in petiole, more rarely also in midrib and lamina. *Sclereids* absent, but some sclerified mesophyll cells present in *P. dumbeënsis* and some sclerified ground tissue cells in midrib and petiole of *P. comosa* and *P. dumbeënsis.*

Material studied. See table I, which also gives the species-to-species variation of some leaf anatomical features. On the whole the leaf anatomy of *Phelline* is very constant.
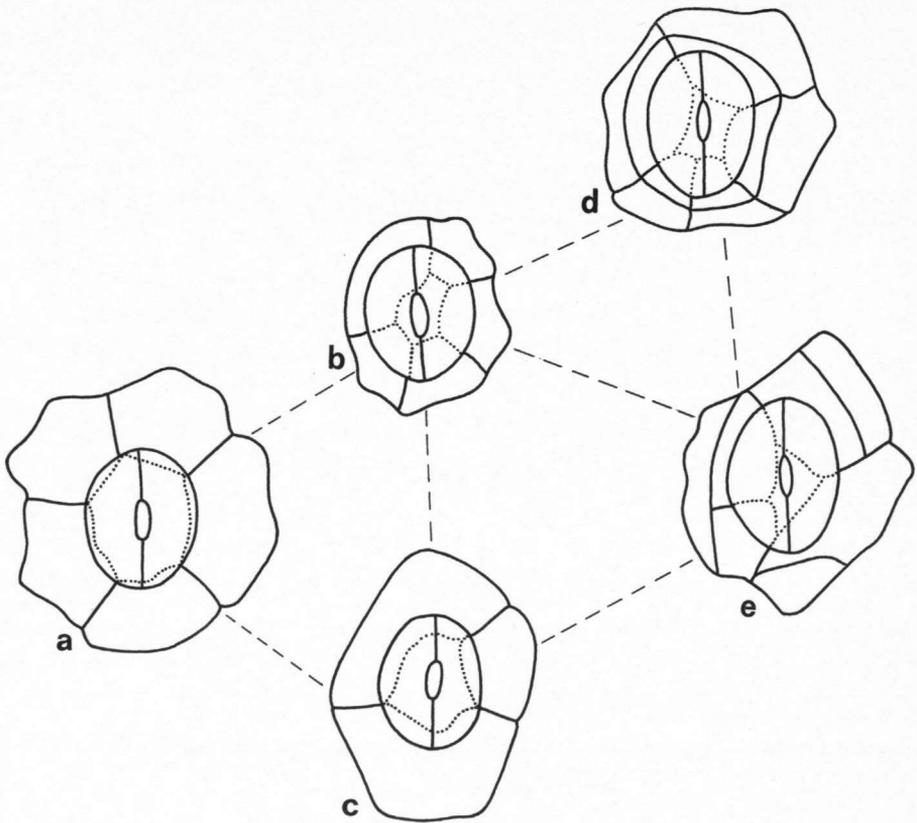
Fig. 17. Stomatal types in *Ilex*. — a=anomocytic; b=cyclocytic; c=anisocytic; d=bicyclic; e=complex. Broken lines indicate presumed possibilities for phylogenetic derivation.

SPHENOSTEMON
(see Plate XI; fig. 22—24)

In s u r f a c e v i e w: Usually glabrous, but unicellular adpressed *hairs* infrequent on abaxial surface of *S. arfakensis*; larger unicellular hairs with a narrow base and a much thicker undulating body infrequent in 1 specimen of *S. papuanum* (*BW 12160*) and abundant in *S. pauciflorum*. Adaxial *cuticle* smooth to coarsely granular; abaxial cuticle smooth, faintly striated or granular. Adaxial *epidermal cells* with straight to slightly undulated anticlinal walls, unspecialized abaxial cells with straight to strongly undulating ('zig-zag') walls. Cuticular flanges well-developed, rarely pitted. Cells overlying midrib usually elongate, cells over primary and secondary *veins* (rarely also over tertiary veins) usually modified in abaxial epidermis, rarely modified in adaxial epidermis. *Stomata* confined to abaxial epidermis, randomly orientated or with pores tending to be parallel with primary veins, anomocytic with 4—6 neighbouring cells; peristomal rims absent or poorly developed, outer and inner stomatal ledges well-developed, polar T-pieces absent or only partly distinct (only cross-piece), guard cell pairs on average 30—35 μm long, 25—33 μm wide. Giant stomata rarely present. *Cork warts* usually absent but present and of irregular outline on adaxial surface of 1 specimen of *S. papuanum (NGF 19932)*.

Table I — Phelline. Distribution of some leaf anatomical features over different species and specimens.

Material studied (all from New Caledonia)	cuticle striated	cuticle granular	abaxial epidermal cell walls undulated	cuticular flanges pitted	stomatal size	lamina thickness	thickness of adaxial cuticle	sclerified cells in mesophyll (m) or petiole and midrib (p)	number of (centric) bundles in distal end of petiole
P. billardieri Panch.									
Franc s.n. (=Herb. Bonati 439)	-	±	±	-	58 x 52	360	4—6	-	15
P. brachyphylla Baill.									
McKee 10020	-	-	+	-	45 x 44	300	1—2	-	8
P. comosa Labill.									
McKee 4552 a	±	-	-	-	66 x 59	400	3—4	p	6
McKee 4552 b*	+	-	-	-		300	6—8	p	9
P. confertifolia Baill.									
Schlechter 15215	-	+	-	+	72 x 69	320	10—12	-	4
P. dumbeënsis Guill.									
McKee 4540	±	+	-	-	74 x 69	480	8—10	m+p	13
P. erubescens Baill.									
McKee 5367	-	-	-	-	49 x 46	360	3—4	-	4
P. lucida Vieill.									
McKee 4856	-	+	-	±	80 x 72	390	18—22	-	7
McKee 5337	-	±	-	+	88 x 77	460	24—26	-	5
Franc s.n.	-	±	-	+	72 x 67	350	12—14	-	7
Schlechter 15340	-	+	-	+	64 x 57	240	4—5	-	5
P. macrophylla Baill.									
Franc 2489	±	-	±	-	58 x 55	370	7—8	-	17
McKee 2686	-	-	+	-	68 x 62	400	9—11	-	7
Balansa 583	-	-	+	-	47 x 46	240	2—4	-	15

* of McKee 4552 two leaves were studied of the same herbarium sheet; stomata were not measured in b.

In transverse section: *Lamina* dorsiventral, 250—670 µm thick. Adaxial *cuticle* 1—6 µm thick, abaxial cuticle 1—3 µm thick. *Epidermal cells* (erect) square to flattened, adaxially much bigger than abaxially. *Hypodermis* absent or 2—3-layered of ± collenchymatous translucent cells on adaxial side of lamina, continuous but less regular over midrib. *Mesophyll* composed of 2—5 layers of short to tall palisade cells and a variable amount of lignified or unlignified spongy tissue. *Midrib* with slightly raised to grooved adaxial surface and prominently raised abaxial surface, supplied with open ± V- to arch-shaped vascular system with strongly incurved margins or with a closed ± triangular system (fig. 22—24), in both cases sheathed by varying amounts of sclerenchyma fibres.

Ground tissue of midrib collenchymatous to parenchymatous; lignified in 'pith'. *Veins* embedded in mesophyll, with lignified or unlignified parenchymatous bundle sheaths enclosing varying amounts of abaxial sclerenchyma. *Petiole* through distal part with open or closed system as in midrib, with additional latero–dorsal wing bundles, which may be collateral or centric (amphicribral). *Crystals* present as medium-sized to very large styloids (up to $350 \times 30 \mu m$) in mesophyll and phloem of major vascular bundles.

Material studied. See table II.

N o t e . Within *Sphenostemon* there are two distinct leaf anatomical groups: the New Caledonian species, which are characterized by a multilayered epidermis and a closed vascular system in petiole and midrib, and the remaining species. This coincides with the infrageneric classification proposed by Van Steenis (1955).

Table II — Sphenostemon. Distribution of some leaf anatomical features over different species and specimens.

Material studied	slender adpressed hairs	undulating hairs	cuticle striated	cuticle granular	abaxial anticlinal epidermal walls undulating	stomatal size	lamina thickness	vascular system of midrib and petiole closed	hypodermis present	spongy tissue lignified	bundle sheaths lignified
NEW CALEDONIAN SPECIES											
S. balansae Baill.											
Balansa 1330*	-	-	-				360	+	+	-	±
S. comptonii Baker											
Compton 1693*	-	-					670	+	+	-	-
Bernardi 10164	-	-	-	+	-	31 x 28	570	+	+	-	+
S. pachycladum Baill.											
McKee 23070	-	-	-	+	-	31 x 25	580	+	+	-	-
McKee 5428	-	-	-	+	-	30 x 27	480	+	+	-	-
Franc s.n.	-	-	-	+	-	31 x 27	610	+	+	-	-
NEW GUINEAN SPECIES											
S. arfakensis (Gibbs) Steen.											
Kostermans 2217	+	-	±	+	+	35 x 32	380	-	-	+	+
S. papuanum (Lauterb.) Steen.											
NGF 19932	-	-	-	+	-	31 x 29	370	-	-	-	+
BW 12160 (transverse sections only)	-	+	-	+			250	-	-	-	±
S. pauciflorum (Smith) Steen.											
Brass 30858	-	++	-	±	±	31 x 30	290	-	-	±	+
QUEENSLAND SPECIES											
S. lobosporus (F.Muell.) Smith											
Rodd 269	-	-	-	+	+	32 x 30	400	-	-	±	+
Clemens (1947)	-	-	±	+	+	34 x 33	310	-	-	+	+

* specimens of which only slides were available borrowed from the Jodrell Laboratory, and which could not be used for certain characters.

Nodal anatomy

ILEX

(see fig. 25—28)

The range in nodal anatomy of *Ilex* is illustrated in fig. 25—28. The nodes may be unilacunar with a single trace (*I. asprella, I. longipes,* and *I. serrata*) or trilacunar with three traces (the other species studied), the median one of which may be composed of 3—7 more or less separate units.

The unilacunar node corresponds with a single vascular strand throughout the petiole in the species studied (fig. 25). The rudimentary stipules are devoid of vascular supply in this case.

The trilacunar nodes may be subdivided into several types:

1. Lateral traces very small and running from stipules to the stele without taking part in vascular supply of the petiole (fig. 26; *I. goshiensis* and *I. verticillata*).
2. Lateral traces giving off side branches to the stipules, of varying size, sometimes centric, and assuming the position of latero–dorsal wing bundles in the petiole (fig. 27; *I. anomala, I. aquifolium, I. clemensiae, I. coriacea, I. grandifolia, I. hypoglauca, I. oppositifolia p.p., I. pedunculosa, I. spicata, I. stapfiana, I. theezans,* and *I. zygophylla*).
3. Lateral traces as above, but fusing with the median vascular strand in the petiole (*I. opaca, I. oppositifolia p.p.,* and *I. versteeghii*). Latero–dorsal bundles then split off at a higher level in the petiole (fig. 28).

The median vascular strand always enters the stele at the level of leaf insertion on the stem, but the laterals may sometimes enter the stele at a much lower level, even below the next lower leaf insertion (*I. clemensiae* and *I. pedunculosa p.p.*).

Unusual deviations from the above variants have been encountered in some specimens of *I. oppositifolia,* and in *I. hypoglauca.* In *I. oppositifolia* (*Clemens 31375*) one side of the opposite-leaved node conforms to the normal trilacunar condition, but the opposite side has 4 gaps with 2 lateral traces on one side of the median trace and 1 on the other side. The median traces are each composed of three units. In *Clemens 31895* the node is trilacunar on both sides, but one median trace is composed of three units, and the other of seven. The latter trace is in the vicinity of wound tissue (probably insect attack) and the splitting up of the median trace may have a traumatic cause. In *Clemens 32557* the situation is again different with single median strands and lateral traces which are fused with the median trace over some distance. In *I. hypoglauca* the median traces are composed of 3 more or less distinct units, probably corresponding with three independent traces at the primary growth stage. The different nodal conditions may be linked with a diversity of vascular tissue arrangement in the distal end of the petiole, but besides the few correlations mentioned above, it should be noted that in *Ilex* complex vascular bundle arrangements are always associated with trilacunar nodes.

Material studied (for localities see material cited under leaf anatomical descriptions, unless stated otherwise).
I. anomala, Heller 2735; I. aquifolium, De Wilde & Dorgelo 2528; I. asprella, PNH 21584; I. clemensiae, Clemens 50259; I. goshiensis, Beyrick 926, Moran 5131 (Japan); *I. grandifolia, De Voogd 1134; I. hypoglauca, Anderson 8536, Hallier 2875; I. longipes, Biltmore Herb. 4063; I. opaca, Lawrence & Dress 246; I. oppositifolia, Clemens 31375, 31895, 32557; I. pedunculosa, Wilson s.n., Moran 5329* (Japan); *I. serrata, Boom 6165; I. spicata, Van Ooststroom 13113; I. stapfiana, Haviland 3357, Jacobs 5057, Hallier 650; I. theezans, Dusén 10608; I. versteeghii, Brass 11772; I. verticillata, Rolland-Germain 6216; I. zygophylla, SAN 39419.*
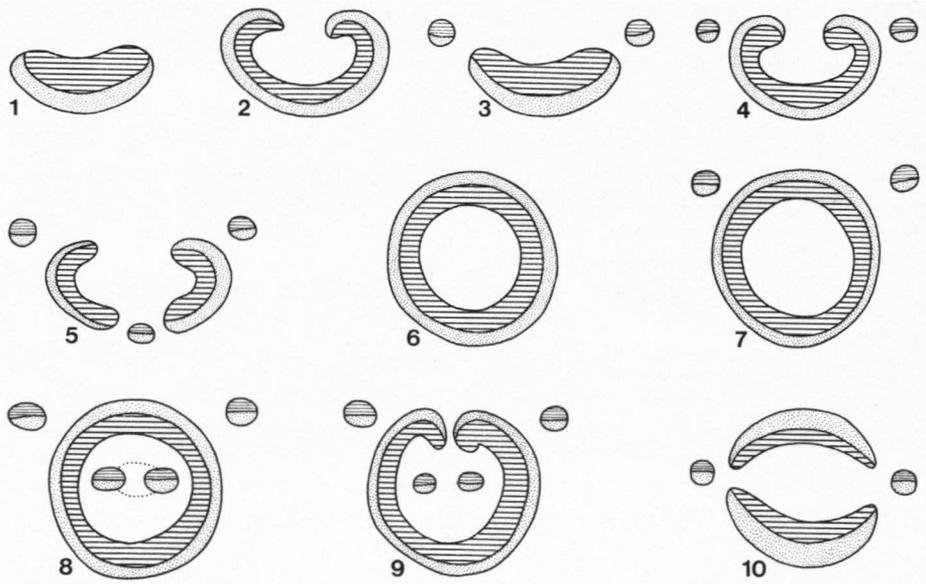
Fig. 18. Vascular bundle arrangements in the distal end of the petiole in *Ilex*. — Types 1—4: simple open; type 5: abaxially open; types 6 & 7: simple closed; type 8: complex closed; type 9: complex open; type 10: 'double'. — Xylem hatched, phloem dotted.

NEMOPANTHUS

Node unilacunar with a single trace.

Material studied. *N. mucronata, Rolland-Germain 1444.*

ONCOTHECA

(see fig. 29)

Node pentalacunar with 5 traces, the median one somewhat larger than the laterals. The individual bundles become strongly incurved to centric in the basal part of the petiole and show some fusion and splitting up higher up in the petiole.

Material studied. *O. balansae, McKee 3439, 4859.*

PHELLINE

(see fig. 30)

Nodes trilacunar with three traces, all of which are ± centric in the cortex and the petiole, through incurving of the collateral stelar traces. Three types may be distinguished:

1. Lateral traces attached to the stele at the same level as the leaf and median trace. Splitting of bundles occurs from the basal part of the petiole upwards (*P. brachyphylla* and *P. lucida*).
2. Lateral traces attached to the stele several nodes below the innervated leaf, giving the impression of cortical bundles throughout the stem. Splitting of bundles as in 1. (*P. erubescens*).
3. As above, but splitting of both median and lateral traces occurs in cortex prior to entering the petiole so that 6(—7) traces enter the base of the petiole (*P. billardieri*).

The final number of vascular bundles in the distal end of the petiole results from varying numbers of splits or 'branching' of median and lateral traces in the petiole. In the simplest cases only the median bundle splits into an adaxial and abaxial bundle so that the final number of bundles is 4 (see table I).

Material studied. *P. billardieri, Herb. Bonati 439; P. brachyphylla, McKee 7944; P. erubescens, McKee 5367; P. lucida, Schlechter 15345.*

SPHENOSTEMON

Nodes trilacunar with three traces. The lateral traces fuse with the median trace in the base of the petiole, and always are connected with the stele at the same level as the median trace (as in fig. 28). *S. pachycladum, McKee 5428,* presents the only exceptional case with a unilacunar node with a trace composed of three units; large amounts of necrotic tissue in the pith of this specimen are suggestive of traumatic causes underlying this aberrant nodal anatomy.

Material studied. *S. arfakensis, Kostermans 2217; S. cf. comptonii, Bernardi 10164; S. pachycladum, McKee 5428, Franc s.n.; S. papuanum, NGF 19932; S. lobosporus, Rodd 269.*

Twig anatomy

Based on limited observations.

ILEX

Hairs absent or present, as on leaves but often more frequent. *Cork* arising in subepidermis, mostly composed of flattened cells, in some species containing cells with unilateral adaxial lignified wall thickenings, in *I. zygophylla* of palisade-like cells which are mostly heavily sclerified. *Cortex* homogeneous and parenchymatous to collenchymatous, or with scattered brachysclereids. *Perivascular sclerenchyma* in a more or less continuous cylinder, composed of fibres interspersed with brachysclereids, absent from young twig of *I. coriacea. Pith* parenchymatous, lignified or not, with very large air spaces in nodal region of *I. coriacea* (aerenchyma; the intercellular spaces are much smaller in the internodes of this species). *Crystals* mainly as clusters in cortex and pith, but also as solitary prismatic ones in some species (this type mainly confined to the pith), rarely as styloid-like crystals (maximum size $30 \times 8 \mu m$) mixed with clustered ones in nodal region (*I. zygophylla* and *I. hypoglauca*). Crystals always more abundant in nodal region than in internodes.

Material studied. See under Nodal anatomy.

NEMOPANTHUS

Glabrous. *Cork* arising in subepidermis, composed of flattened cells. *Cortex* parenchymatous to collenchymatous. *Perivascular sclerenchyma* ring as in *Ilex. Pith* not lignified or lignified in peripheral part only. *Crystals* present as clusters in cortex and less frequently in pith.

Material studied. See under Nodal anatomy; a very young and a 3 year old twig were studied.

ONCOTHECA

Glabrous. *Cork* arising in subepidermis, composed of flattened cells. *Cortex* parenchymatous, containing idioblastic branched sclereids. *Perivascular sclerenchyma* composed of individual fibre groups linked to each other by sclerified parenchyma tissue. *Pith* lignified

with clusters of thick-walled brachysclereids. *Crystals* as irregular clusters in cortex and pith parenchyma.

Material studied. See under Nodal anatomy.

PHELLINE

(see fig. 9)

Hairs confined to leaf axils, thin-walled uniseriate with subglobular top-cells (see fig. 9; glandular?). *Cork* arising in subepidermis, composed of square to flattened cells, containing
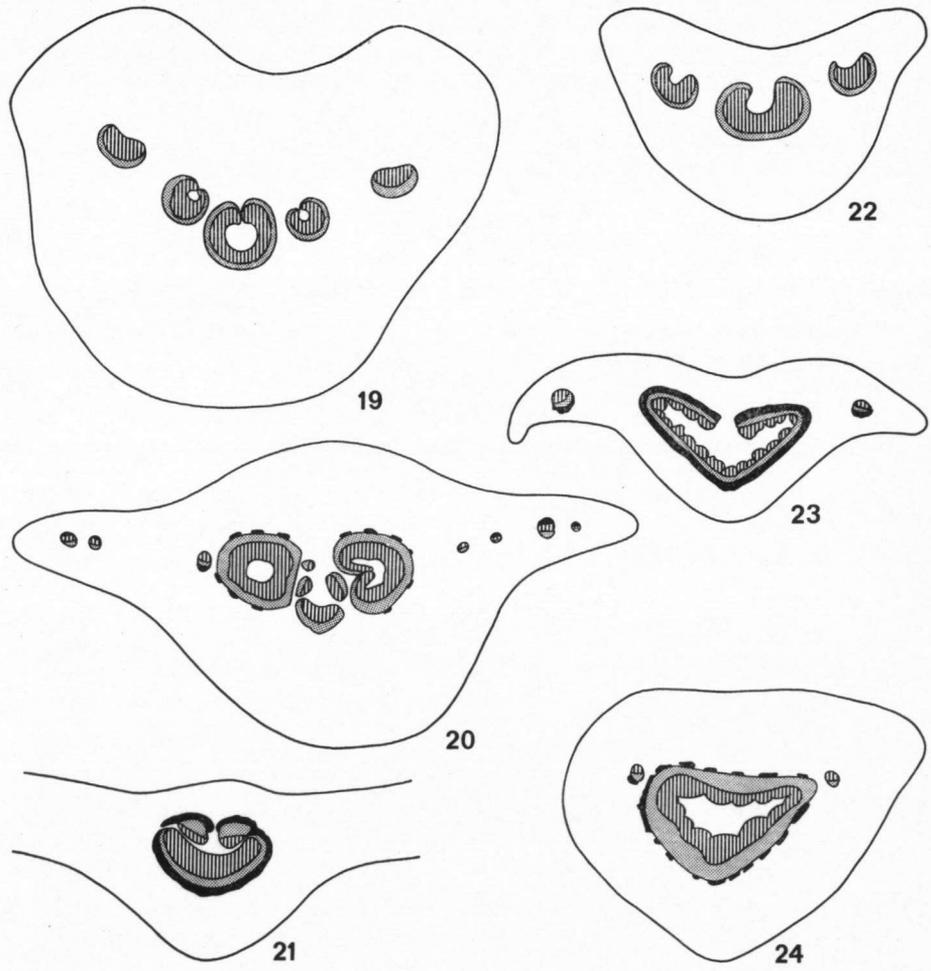
Fig. 19—24. Camera lucida drawings of midrib and petiole in transverse section, ×17. — 19—21. *Oncotheca balansae* (*McKee 4849*), basal and distal part of petiole, and midrib respectively. — 22 & 23. *Sphenostemon lobosporus* (*Rodd 269*), basal and distal end of petiole. — 24. *Sphenostemon pachycladum* (*Franc s.n.*), distal end of petiole. — Xylem hatched, phloem dotted, sclerenchyma black.

a varying number of cells with unilateral adaxial U-shaped lignified wall thickenings. *Cortex* parenchymatous to collenchymatous, in some species containing brachysclereids. *Perivascular sclerenchyma* absent or composed of individual fibre groups only. *Pith* parenchymatous, lignified or not. *Crystals* present as very rare to frequent minute druses in cortex and pith.

Material studied. See under Leaf anatomy (table I).

SPHENOSTEMON

Indumentum usually absent, in hairy species early caducous because of cork formation (*S. arfakensis*). *Cork* arising in subepidermis, composed of flattened cells, containing some cells with unilateral adaxial lignified wall thickenings. *Cortex* parenchymatous, containing a variable amount (usually very high) of lignified to sclerotised cells. *Perivascular sclerenchyma* composed of small fibre groups linked by lignified to sclerified parenchyma. *Pith* mostly entirely lignified, rarely of mixed lignified and unlignified cells (*S. pachycladum*). *Crystals* as styloids of varying size (140×8—$200 \times 14 \mu$m) mainly in cortex, but also in pith.

Material studied. See under Leaf anatomy (table II).

Bark anatomy
Based on limited observations.

ILEX

Tissue outside secondary phloem usually split off during microtechnical procedures and not studied (cf. Twig anatomy). Preserved in slides of *I. marquesii* and composed of broad homogeneous *cork* zone of flattened cells, *cortical tissue* containing sclerified cells and groups of cells, and a mixed perivascular sclerenchyma ring.

Ground tissue of secondary *phloem* with homogeneous appearance in transverse sections, composed of sieve tubes, companion cells and phloem parenchyma; at some distance from the cambium with infrequent and irregularly distributed large groups of thick-walled brachysclereids, which are often crystalliferous. *Fibres* absent. Rays broad and narrow, the former triangular in transverse section due to dilatation, mostly unlignified, but parts adjacent to sclereid-groups in ground tissue sometimes sclerified; entirely lignified in *I. sp.* (*Jacobs 7928*, a climbing species). *Crystals* solitary prismatic and confined to sclereids.

Material studied. Miscellaneous specimens of the following species studied for wood anatomy with adhering bark fragments (for collection numbers see Baas, 1973): *I. anomala, I. aquifolium, I. caroliniana, I. cassine, I. curranii, I. decidua, I. fargesii, I. glabra, I. montana, I. sideroxyloides, I. subrugosa, I. theezans*, and *I. sp.* (*Jacobs 7928*, climber from the Philippines).

NEMOPANTHUS

Similar to *Ilex* bark in all characters. Broad rays not lignified.

Material studied. *N. mucronata*, see under Wood anatomy.

ONCOTHECA

Cork layers also deep-seated in secondary *phloem*, composed of layers of thin-walled flattened cells, some of the cell-layers being crystalliferous.

Ground tissue of sieve tubes, companion cells, and parenchyma alternating with $\pm$ layered patches of axially elongate sclereids, many of which are crystalliferous. *Fibres*
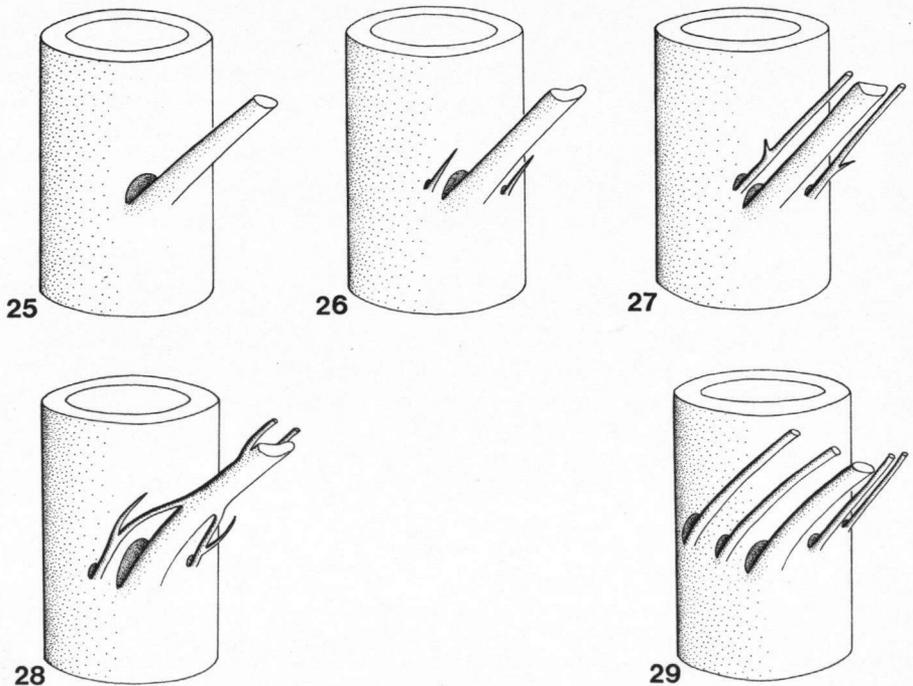
Fig. 25—28. Reconstructions of nodal types in *Ilex*. — 25. Unilacunar with 1 trace. — 26. Trilacunar; lateral traces supply stipules only. — 27. Trilacunar; lateral traces continuous as wing bundles throughout petiole; stipules supplied by side-branches of lateral traces. — 28. Trilacunar; lateral traces fuse with median trace. — 29. Node of *Oncotheca*; pentalacunar.

absent. Rays broad and narrow, the former with very little dilatation and usually sclerified. *Crystals* of irregular shapes but mostly solitary in special cork layers; solitary prismatic in phloem sclereids.

Material studied. *O. balansae, McKee 22947.*

PHELLINE

Material of mature bark not available. Secondary *phloem* of sieve tubes, companion cells and phloem parenchyma traversed by narrow and broad unlignified rays in twigs. *Crystals* absent. See also under Twig anatomy.

SPHENOSTEMON

Cork superficial, of thin-walled flattened cells. *Cortical tissue* almost entirely sclerified. Perivascular sclerenchyma mainly of brachysclereids, interspersed with small fibre groups. Secondary *phloem* of sieve tubes, companion cells, and partly sclerified phloem parenchyma interspersed with secondary phloem *fibres*. The latter more or less tangentially banded or diffuse in aggregates. Rays broad and narrow, the former triangular and mostly sclerified. *Crystals* abundant as styloids, mostly accompanied by small irregular 'satellite' crystals in phloem parenchyma cells.

Material studied. Bark fragments adhering to specimens used for wood anatomical studies of the following species: *S. lobosporus, S. pachycladum,* and *S. papuanum.*

Wood anatomy

ILEX

See Baas, 1973.

NEMOPANTHUS

(see Plate VI, 1 & 2)

G e n e r a l   f e a t u r e s: Wood light and fairly soft. Colour white. Growth rings distinct. Texture fine. Heartwood not differentiated.

M i c r o s c o p i c   f e a t u r e s: Wood semi-ring porous. *Growth rings* distinct. *Vessels* 98—156/mm², solitary and in radial multiples of 2—4(—7), 41—46% solitary, angular to oval in T.S., tangential diameter 21—34—35—50 μm, vessel member length 380—570—610—780 μm. Inter-vessel pits opposite, rarely tending to alternate; pits rounded rectangular 4—6 μm, with oval to slit-like apertures enclosed within the pit borders. Vessel—ray and vessel—parenchyma pits similar but half-bordered. Perforations scalariform in oblique end walls with 13—18—20—27 bars. Helical thickenings and vessel contents absent. Thin-walled *tyloses* in *MADw 19208* only occurring in first-formed secondary xylem. Ground tissue composed of thin-walled *fibre-tracheids* with bordered pits mainly confined to the radial walls; pits *c.* 4 μm with slit-like apertures extending beyond the pit borders; fibre-tracheid length 580—750—850—980 μm. Helical thickenings absent. *Parenchyma* scanty diffuse, strands of mostly 4, occasionally up to 6 cells. *Rays* heterogeneous II, uniseriate rays 9—11/mm, multiseriate rays up to 5 cells wide, 3—4/mm, tallest rays up to 1.3 mm high, infrequent sheath cells present. *Crystals, silica,* and *pith flecks* absent.

Material studied. U.S.A. *N. mucronata: MADw 783, MADw 19208, SJRw 40591* (material of stems *c.* 3—4 cm diam.; low altitude).

ONCOTHECA

(see Plate VII)

G e n e r a l   f e a t u r e s: Wood heavy and hard. Colour brown. Growth rings absent. Texture rather fine. Heartwood not differentiated.

M i c r o s c o p i c   f e a t u r e s: Wood diffuse porous. *Growth rings* absent. *Vessels* 29 & 46/mm², 88 & 96% solitary, rarely in radial pairs, round to oval in T.S., tangential diameter 34—55—84 μm, vessel member length 460—990 & 1030—1580 μm. Inter-vessel pits alternate to diffuse, round to oval, 4—5 μm, with slightly oblique slit-like apertures confined within the pit borders. Vessel—ray and vessel—parenchyma pits ± similar but half-bordered and sometimes elongate and transitional. Perforations scalariform in oblique end walls with 8—15—24 bars, sometimes almost reticulate. Helical thickenings and *tyloses* absent. Dark solid *contents* present in vessels outside sapwood region. Ground tissue composed of very thick-walled *fibre-tracheids* with very numerous bordered pits on both radial and tangential walls, pits 4—5 μm with slit-like apertures confined within the pit-borders; fibre-tracheid length 820—1150 & 1550—2370 μm. Helical thickenings absent. *Parenchyma* mainly very scanty paratracheal, rarely as scattered diffuse cells, strands of 3—7, mostly of 4—5 cells. *Rays* heterogeneous II, uniseriate rays 11/mm, multiseriate rays 2—3(—5) cells wide, 3/mm, tallest rays up to 1.2 mm high; infrequent sheath cells present. Central cells of broad rays square to erect. Solitary rhomboidal *crystals* frequent in ray cells. *Silica* and *pith flecks* absent.
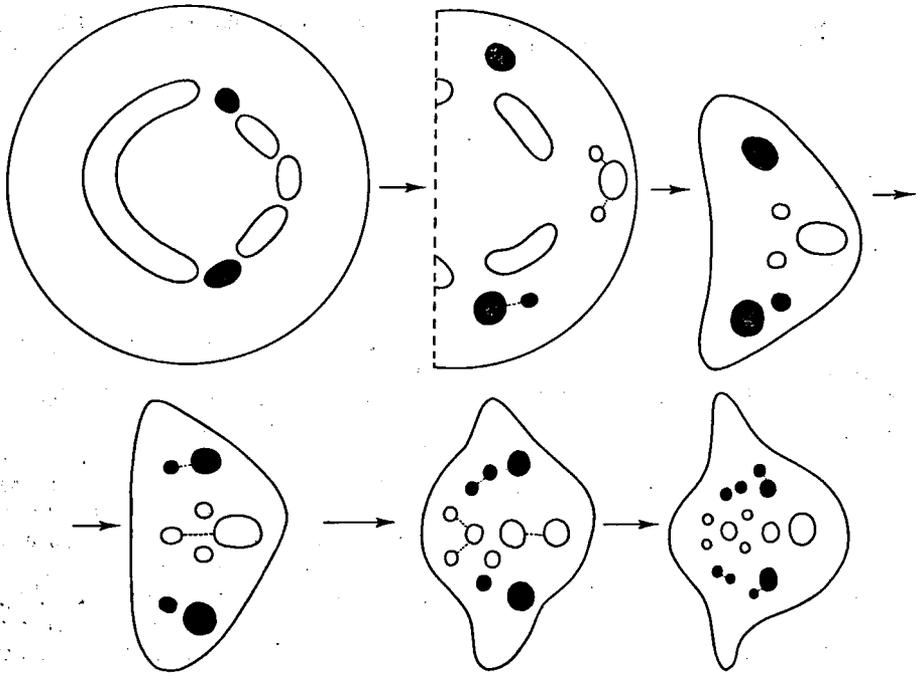
Fig. 30. Diagrams of vascular bundle arrangement from node to distal end of petiole in *Phelline billardieri*. — Lateral traces and their derivatives black. Broken lines indicate derival from the same bundle.

Material studied. NEW CALEDONIA. *O. balansae: McKee 22947, Schmid s.n.* (material of stems 3—4 cm diam.; altitude 600—1200 m).

PHELLINE

(see Plate X)

G e n e r a l   f e a t u r e s : Wood fairly light and soft. Colour yellowish. Growth rings indistinct. Texture coarse through very conspicuous broad rays. Heartwood not differentiated.

M i c r o s c o p i c   f e a t u r e s : • Wood diffuse porous. *Growth rings* very faint to absent. *Vessels* 51/mm², mainly solitary (*c.* 90%), occasionally in radial pairs, angular to rounded in T.S., tangential diameter 29—43—63 μm, vessel member length 1530—2130— 2900 μm. Perforations scalariform in almost vertical end-walls, resulting in strong overlap of adjacent vessel-members, with 91—134—204 bars. Inter-vessel pits in a single vertical row, oval and variously flattened, 7—10 μm wide. Vessel—parenchyma pits similar but half-bordered. Vessel—ray pits transitional to scalariform, half-bordered, occasionally unilaterally compound. *Tyloses, vessel contents,* and helical thickenings absent. Ground tissue composed of fairly thick-walled *fibre-tracheids* with numerous bordered pits on the radial and tangential walls; pits 6—7 μm with slit-like apertures extending to the pit border margins; fibre-tracheid length 1760—2420—3030 μm. Helical thickenings absent. *Parenchyma* diffuse, often touching on the vessels and easily to be mistaken for vessels in T.S., because of ± similar cell diameter; strands 4—7 cells long. *Rays* heterogeneous II, uniseriate rays 4/mm, broad rays extremely large, occupying about 40% vol. of the

wood, up to 14 cells wide, often over 2 cm high, composed of large cells, and with frequent sheath cells, 1.3/mm. *Crystals, silica* and *pith flecks* absent.

Material studied. *Phelline lucida* Vieillard; NEW CALEDONIA: *SJRw 14399* (altitude 600—1200 m).

SPHENOSTEMON

(see Plate XII)

G e n e r a l   f e a t u r e s: Wood of medium density and hardness. Colour light brown to reddish brown. Growth rings absent or very faint. Texture rather fine, but broad rays usually visible to the naked eye, especially in *S. lobosporus*. Heartwood not differentiated.

M i c r o s c o p i c   f e a t u r e s: Wood diffuse porous. *Growth rings* absent or extremely faint. *Vessels* 12—24/mm², 37—84% solitary, remainder in radial multiples of 2—4, oval to slightly angular, tangential vessel diameter 45—71—90—143 μm, vessel member length 950—1690—2730—3500 μm. Inter-vessel pits typically scalariform, covering the whole tangential wall with a single row of pits, infrequently transitional to opposite. Vessel—parenchyma and vessel—ray pits mostly opposite to transitional, also diffuse to alternate in *S. papuanum*, and sometimes tending to scalariform in *S. lobosporus*, half-bordered, 6 μm or wider, rarely unilaterally compound. Perforations scalariform in very oblique end-walls, with 32—67—118—185 bars. Bars of several perforation plates repeatedly forked to form a honey-comb-like pattern (Plate XII, 5) in part of the perforations. *Tyloses, vessel contents,* and helical thickenings absent.

Ground tissue composed of *fibre-tracheids* with bordered pits on both radial and tangential walls; those on the tangential walls only where in contact with parenchyma; pits *c.* 5 μm with slit-like oblique apertures extending beyond the pit borders; fibre-tracheid length 920—1840—3100—3920 μm. Helical thickenings absent. *Parenchyma* diffuse in aggregates (mainly in short tangential lines), rather frequently touching on the vessels, strands of 3—8 cells. *Rays* heterogeneous II, uniseriate rays 5—8/mm, broad rays usually 2—4(—6) cells wide; in *S. lobosporus* up to 10 cells wide, 1—3/mm, up to 3 mm high (in *S. pachycladum* only up to 1.2 mm), with fairly frequent sheath cells. *Silica* and *pith flecks* absent. Large styloid *crystals* accompanied by smaller irregular crystals in axial parenchyma of *S. pachycladum* only.

Material studied. QUEENSLAND. *S. lobosporus: Rodd 269, CSIRO 13692, 14216, 33125* (alt. *c.* 1200 m). — NEW CALEDONIA. *S. pachycladum: McKee 23070* (alt. *c.* 1000 m). — NEW GUINEA. *S. papuanum: Pulle 266, Pullen 5422, Schodde 1528, Vink 17086, 17492* (alt. 1200—3000 m).

N o t e s   o n   i n d i v i d u a l   s p e c i e s. The differences in wood anatomy between the 3 species studied are very small and have mostly been recorded in the generic description. *S. papuanum* covers the whole range in vessel frequency, percentage of solitary vessels, and number of bars per perforation of the genus. Vessel members are shortest in *S. pachycladum* and longest in *S. papuanum*, but the range is ±continuous. The only clear qualitative distinctive species character is the presence of styloid crystals in *S. pachycladum*. Judging from the twig anatomy studied of the other *Sphenostemon* species, the presence of styloids in the secondary xylem parenchyma characterizes the New Caledonian group of species only.

DISCUSSION OF SOME ANATOMICAL CHARACTERS

Indumentum

Hair types found on the leaves of the genera studied play only a minor part in the taxonomic discussions, because in most species the indumentum is absent or of an 'unspecialized' nature, that is of a type which is widely distributed in the dicots as a whole.

The hair types of *Ilex* are arranged in morphological series in fig. 1—8. One may well imagine that these series reflect phylogenetic trends. However, no evidence can be produced as to the directions such developments might have had. The — to my knowledge unique — hair type of *I. hypoglauca* is probably specialized and can be derived from the common unicellular type through an intermediate stage as present in *I. zygophylla*, which species is in other respects also close to *I. hypoglauca*.

The unspecialized cells of the leaf epidermis

There is a considerable variational range in outline of the unspecialized cells, due to varying degrees of anticlinal wall undulation in both *Ilex*, *Phelline*, and *Sphenostemon*. As discussed on p. 400, this feature is not even diagnostic at the species level within *Ilex*. An exception should probably be made for the strongly zig-zagging walls of *I. verticillata*, also present (but to a lesser extent) in *I. longipes* and *I. serrata*, which produce highly characteristic cell patterns. Presence or absence of pitting of the anticlinal cuticular flanges and of granular structures in the cuticular layers are variable features in *Ilex*, even at the species level (see p. 400). These characters have also been tested in *Icacinaceae* (Van Staveren & Baas, 1973), and *Winteraceae* (Bongers, 1973), and were found to vary in their diagnostic value in the different families and genera.

The lignification of (part of) the abaxial epidermal cells in several species of *Ilex* is noteworthy. Though not absolutely constant at the species level (cf. *I. canariensis*, *I. crenata*, *I. triflora*), the distribution of this character over the different sections recognized by Loesener indicates some taxonomic importance. The variability at the species level may be due to age of the persistent leaves involved (cf. Napp-Zinn, 1973 & 1974). There are three variants to the feature 'abaxial epidermis lignified': (1) unspecialized cells lignified only (*I. argentina*, *I. boliviana*, *I. canariensis p.p.*, *I. cassine*; Plate III, 1, *I. crenata p.p.*, *I. dumosa*, and *I. ovalifolia*; Plate III, 3; (2) unspecialized cells and guard cells lignified (*I. opaca*, *I. retusa*, and *I. triflora*); (3) all cells, including subsidiary cells, lignified (*I. amara*; Plate IV, 1, *I. martiniana*; cf. similar situation in aberrant stoma of *I. cassine*: Plate III, 2). Cador (1900) reported sclerified abaxial epidermal cells in *I. affinis*, *I. amara*, *I. cassine p.p.*, *I. chamaedrifolia*, *I. glazioviana*, *I. symplociformis*, *I. vitis-idaea*. Thévenard (1906) and several other authors mentioned thick-walled pitted abaxial epidermal cells in some species, now known to possess lignified cells (*I. cassine*, and *I. opaca*). For *I. triflora*, however, Thévenard did not give any details about the abaxial epidermis. He did, however, report sclerified epidermal cells for *I. chamaedrifolia*. Lignified abaxial epidermal cells occur in the — according to Loesener — closely related sections *Polyphyllae*, *Brachythyrsae*, *Thyrsiflorae*, and *Symplociformes* (Cador, 1900) as well as in several sections (*Crassifoliae*, *Dasyneurae*, and *Cassinoides*) which Loesener (1908) all thought to be derived from a common stock. The occurrence of this character in *I. triflora* and *I. argentina* as isolated species of section *Microdontae* may indicate erroneous placement in the system by Loesener himself.

The range of epidermal organization as seen in transverse section and with reference to the occurrence of anticlinal and periclinal subdivisions is given in fig. 10—15 (see also Plate IV, 5 & 6). Below the species level there is a very strong variability in the extent to

which the adaxial epidermis has thin periclinal or anticlinal division walls, or in the number of cells differentiated into bulging mucilage cells. The absolute presence or absence of these features is, however, of rather good diagnostic value. The character complex of the unspecialized epidermal cells in all genera studied is not as such that it can be used in discussions of the wider affinities of the taxa concerned.

The stomatal complex

The range in stomatal type in the genus *Ilex* is quite considerable. Comprehensive studies in other genera have also provided examples which are heterogeneous with regard to stomatal type, e.g. Webster (1956) for *Phyllanthus*; Jansen & Baas (1973) for *Lophopetalum*; Baas (1974) for *Citronella*. This should induce great care in using the stomatal type in discussions of wider affinities of enigmatic taxa. Within *Ilex* the occurrence of several stomatal types or intermediate types in one leaf of certain species even limits the diagnostic value at the species level.

The range of stomatal types in *Ilex* is illustrated in fig. 17. It seems most plausable from a morphological point of view, to regard the anomocytic type as the least specialized, and the anisocytic, cyclocytic, and bicyclic types as derived in *Ilex*. There is, however, no evidence to prove this hypothesis, and it seems even likely that anomocytic stomata may have arisen from other types in certain groups of *Ilex*, because the species of subgenus *Prinus* — generally regarded as specialized *Ilex* representatives — are often characterized by anomocytic stomata.

Anomocytic stomata as occur in some *Ilex* species, are also present in *Phelline* and *Sphenostemon*, so that the anatomical evidence is neutral with respect to presence or absence of mutual affinities. The stomatal size range in *Phelline*, considerable as it is, however, is beyond the — equally considerable — range in *Ilex*, *Nemopanthus*, *Oncotheca*, and *Sphenostemon*. In fact, the stomata of *Phelline* belong to the largest in the Dicotyledons as a whole (cf. Napp-Zinn, 1973 & 1974). This quantitative difference may be used as a weak additional argument in favour of the isolated position of *Phelline* with respect to the other genera. The stomatal complex of *Oncotheca* is difficult to assign to any of the types proposed in the past (cf. Fryns-Claessens & Van Cotthem, 1973; see Plate VI, 5). It is different from any type occurring in the other genera and can be used to argue in favour of an isolated position of *Oncotheca*.

Cork warts

Cork warts of regular shape and regular frequency on the lower leaf surface, are of good diagnostic value in those *Ilex* species which are characterized by them. Within *Ilex* they are widely distributed over most sections recognized by Loesener, but in combination with other characters they may be profitably used in discussions of infrageneric affinities. Controversial opinions about their diagnostic value are probably due to the fact that taxonomists, probably including Loesener, have not always been able to distinguish at low magnifications the regular cork warts from irregular traumatic cork patches, which are of very variable frequency in several *Ilex* species studied by me.

Leaf hypodermis

The term hypodermis is here applied to (an) adaxial subepidermal layer(s) deviating from the chlorenchyma tissue, and in mature leaves not obviously derived from the epidermis.

Hypodermal development in *Ilex* is restricted to some species only (see p. 389); yet these few species show a considerable structural diversity in hypodermal anatomy. The 2—3-layered mucilaginous hypodermis of *I. anomala*, and the lignified hypodermis of *I. zygophylla* constitute examples of features, which are rare in Dicotyledons as a whole (Napp-Zinn, 1973 & 1974). Within *Sphenostemon* the presence of a multi-layered hypodermis characterizes one series only, so that the character here coincides with taxonomic subdivision. The great variability in presence or absence and/or type of hypodermis in *Ilex* and *Sphenostemon* renders this character useless for discussing the wider affinities of the genera studied.

Crystals, sclereids, and marginal sclerenchyma

Thévenard (1906) already attached great diagnostic value to the various crystal types of *Ilex*, *Nemopanthus*, *Phelline*, and *Sphenostemon*. Considering the entire crystal complement from stem and leaf, *Ilex* shows a wide range with solitary prismatic, clustered, minute rod-like, and styloid-like crystals. The latter types are of rare occurrence and restricted to upper leaf epidermis and nodal region respectively of few species only.

The conspicuous and frequent styloids of *Sphenostemon* have always played an important part in the discussions of possible affinities of *Sphenostemon*. Bernardi (1964) has rightly criticized the overweighting of this feature. In most families for which styloids have been reported in the literature (cf. Metcalfe & Chalk, 1950) they are restricted to a few representatives only. The present observations of styloid-like crystals in the nodes of two *Ilex* species (p. 327), might even be used as supporting evidence for mutual affinities of *Ilex* and *Sphenostemon*. This would, however, be equally unjustified as using styloids too strongly for negative evidence, since the crystals of *Ilex* are much smaller and have a distribution pattern different from those in *Sphenostemon*. Incidentally I recently found styloids of exactly the same type as in *Sphenostemon* in the enigmatic genus *Paracryphia*, also from New Caledonia. This genus has many of its twig, leaf, and nodal anatomical features in common with *Sphenostemon*, but its floral morphology (cf. Baker, 1921) is entirely different from that of *Sphenostemon*. With more detailed studies of the overall vegetative anatomy of the Dicotyledons, probably much more groups with styloid crystals would be found than reported thus far in the literature. The situation may well be comparable to that for the so-called rare cristarque cells (cf. Baas, 1972, a, b; Jansen & Baas, 1973). Yet, the presence of styloids in *Sphenostemon* remains a distinctive feature, to be taken into account in the overall comparisons with other groups.

The foliar sclereids of some *Ilex* species, mainly belonging to subsection *Repandae* of section *Microdontae* are — to my knowledge — reported here for the first time. Their distribution over very similar species make them useful indicators of infrageneric affinities within *Ilex*. They are probably derived from the sclerenchyma tissue supporting the vascular bundles. This is most clear in species like *I. confertiflora* and *I. cornuta*, where only few sclereids are present which are always, over some length, part of the vascular bundle caps. These 2 species moreover constitute the leaf anatomical links to *Ilex* species with marginal sclerenchyma strands of section *Aquifolioides* (see p. 367). In other species the more or less fusiform sclereids constitute an irregular network throughout the mesophyll (Plate V, 1—3) of which only a part is directly in contact with the mechanical tissue of the veins.

The marginal sclerenchyma strands, briefly mentioned above, are also restricted to a small number of closely related *Ilex* species. In some species (*I. confertiflora*, *I. insignis*, *I. integra*, and *I. latifolia*) a more or less intermediate condition is present, with a rudimentary

marginal vascular bundle, mostly associated with massive abaxial to lateral sclerenchyma caps; locally these caps — or rather strands — are detached from the vascular bundle and then form true marginal sclerenchyma strands. It is therefore probable that the marginal sclerenchyma strands in *Ilex* are derived from marginal vascular bundles, and should be regarded as specialized structures. This would be in agreement with the generally specialized floral structure, inflorescence morphology, and stomatal type (frequently bicyclic) of the species exhibiting this feature. Likewise the occurrence of foliar sclereids may be regarded as a specialization.

The above discussed sclerenchymatous structures in some *Ilex* species are absent from the other genera, and cannot be used in the discussion of the wider affinities of these taxa.

Nodal anatomy and petiole vascularization

From the time of Sinnott's classical paper on nodal anatomy (1914), *Ilex* has been quoted as an example of a genus with both trilacunar and unilacunar nodes, whilst species with very small lateral traces were regarded as intermediate in this respect. The present study confirms this view, but also extends the known range in *Ilex* with the type as in *I. goshiensis* and *I. verticillata*, where the lateral traces supply the stipules only (a condition similar to that in some *Euphorbiaceae*, Singh, 1972), or with lateral traces entering the stele at much lower levels than the median trace, and finally cases where several traces depart from the median gap. Probably the unilacunar node constitutes the derived condition in *Ilex*. This is in agreement with the distribution of unilacunar nodes over species with a specialized inflorescence morphology and gynoecium (Loesener, 1908).

The vascularization of the petiole, particularly as seen in the distal part, covers an even wider range in *Ilex* than its nodal anatomy (fig. 18, 25—28). This range also considerably limits the use of this character complex in the discussion of the wider affinities of the taxa involved. Even within *Ilex* its taxonomic value may be disputed because the different types (simple and complex) may occur within a single species (notably *I. hypoglauca*, where the peculiar hairs virtually exclude the possibility of misidentification of the material studied). Ranges of a similar magnitude as in *Ilex* have been reported in for instance the genus *Commiphora* (*Burseraceae*, Van der Walt, 1971) and for the tribe *Tilieae* of the *Tiliaceae* (Herlemont, 1951). In *Ilex* the complex type of vascular arrangement is mainly confined to species belonging to the subgenera *Rybonia* and *Byronia*, with the exception of two species of section *Indico-Malaicae*, which Loesener (1908) supposed to be derived from the same ancestral stock as subgenus *Byronia*. These subgeneric taxa have retained several primitive characters (Loesener), and one may advance this in favour of regarding the complex vascularization patterns as the primitive, and the simple pattern as the derived condition in *Ilex*.

The nodes and petiole anatomy of *Nemopanthus* and *Sphenostemon* are more or less within the range of *Ilex*, but *Phelline* and *Oncotheca* appear to be isolated in this respect. The pentalacunar node and the associated petiolar vascular pattern in *Oncotheca*, and the centric bundles throughout the petiole in *Phelline* in particular, constitute unusual conditions for the Dicotyledons as a whole (Sinnott, 1914; Metcalfe & Chalk, 1950; Napp-Zinn, 1973 & 1974).

Petioles most similar to those of *Phelline* occur as far as I know, in some members of *Winteraceae*; species of *Exospermum* and *Zygogynum* also having a high proportion of centric bundles (Bailey & Nast, 1944). These species also have some collateral bundles in addition, however, and the whole vegetative anatomy and floral morphology of the *Winteraceae* is a far cry from that of *Phelline*. Many Dicotyledons, including some species

of *Ilex, Icacinaceae*, etc., have centric or more or less centric latero–dorsal wing bundles. It is not known whether these are comparable to the centric bundles occurring throughout the petiole in *Phelline*. Ontogenetic studies would be needed to check this.

Twig and bark anatomy

The histology of young twigs has not yielded much useful information for taxonomic discussion. It is difficult to evaluate the taxonomic significance of the absence of brachy-sclereids in the perivascular region of *Phelline*, because it is not impossible that these are formed in older material. The pith and cortex of *Oncotheca* and *Phelline* are very broad if compared with those of the other three genera; this character has not been recorded in the descriptions, because it is impossible to give useful quantitative values which are independent of the developmental stage.

Bark anatomical studies have not been carried out on a sufficiently wide scale in Dicots as a whole to evaluate the significance of the diversity reported here (Esau, 1969). For the moment the differential bark characters can only be listed and used in addition to other distinguishing characters and similarities in the systematic discussion.

Within *Ilex*, it is of interest to note that complete sclerification of the broad rays is confined to the only climber used for this study. Although such rays are known to occur in erect trees as well (e.g. *Fagus* and *Platanus*), it is tempting to me to give a functional interpretation for *Ilex*: the sclerified rays together with the perivascular sclerenchyma provide a mechanical protection of the phloem, which may be of more functional significance in climbers than in erect trees or shrubs.

Wood anatomy

The wood of all 5 genera is of an unspecialized type with its scalariform vessel perforations, fibre-tracheids, and heterogeneous rays. This complex of characters occurs in a fairly large number of miscellaneous dicot families (cf. Metcalfe & Chalk, 1950) without necessarily indicating mutual affinities of the groups concerned. Apparently primitive wood structure has been retained in most major groups of the Dicotyledons.

The wide wood anatomical range in *Ilex* has been elaborately discussed in a previous paper (Baas, 1973), and most of the latitudinal and altitudinal trends found in *Ilex* have since been established as general trends in a wider sample of genera (Van der Graaff & Baas, 1974). Because the 'ecological' or 'geographical' trends are very significant for wood anatomical features which are generally regarded as of phylogenetic importance, we must take the distribution of the 4 other genera into account in comparing their woods with that of *Ilex*.

Nemopanthus conforms in its wood anatomy to *Ilex* species of high latitudes, and witnesses close affinities with species of subgenus *Prinus* through some special features (cf. Baas, 1973).

Sphenostemon shows some overlap in vessel member length with *Ilex*, but its number of bars per perforation exceeds the highest values in *Ilex*. The quantitative differences gain in importance if one considers the altitudinal distribution of *Sphenostemon* (1000—3000 m; cf. Baas, 1973). Pronounced scalariform inter-vessel pits as in *Sphenostemon* do not occur in *Ilex*, although some species, notably *I. anomala*, show tendencies in this direction. As will be discussed elsewhere closer similarities with the wood of *Sphenostemon* are found in some *Icacinaceae* (*Platea*). Yet there is a great overall wood anatomical similarity between some tropical *Ilex* species and *Sphenostemon*. The wood anatomy is thus inconclusive with regard to affinities and taxonomic status of *Sphenostemon*.

The wood of *Phelline* differs strongly from that of *Ilex* in general and from species from the same latitudes and altitudes in particular in vessel diameter, vessel member length, number of bars per perforation, uniseriate short inter-vessel pits, very large rays, and to a lesser extent in percentage of solitary vessels. Particularly its vessels are of a more primitive type with its numerous closely spaced bars which only differ from the elaborate scalariform pit areas in the tracheids of some vesselless dicotyledons as e.g. *Trochodendron*, by the absence of pit membranes. Amongst the dicotyledons with vessels, the wood anatomy of *Phelline* belongs to the most primitive.

The wood of *Oncotheca* also differs rather strongly from that of *Ilex* and the other three genera, but here the differences are, apart from some quantitative ones, mainly in qualitative features. Vessel member length and number of bars per perforation are low in comparison to *Ilex* species of the same altitude and latitude. The type of fibre-tracheid: very thick-walled with very numerous large bordered pits on the radial and tangential walls, is not encountered in any of the other genera. The type is in fact rather common in several families of the *Theales* and several other groups. The mainly paratracheal parenchyma is also different from that in the other genera.

Wood anatomy may thus be used to argue in support of the isolated position of *Phelline*, *Oncotheca*, and to a much lesser extent also of *Sphenostemon*. However, much larger wood anatomical ranges in presumably natural families as *Icacinaceae*, *Myrtaceae*, etc., make the wood anatomical evidence inconclusive with respect to a decision about the status and affinities of those genera. One might equally well use the unspecialized wood anatomical characters, shared by all genera, to support mutual affinities. This, however, would imply that one also should support relationships between *Symplocaceae*, *Aquifoliaceae*, *Cornaceae*, *Theaceae*, *Eucryphiaceae*, *Styracaceae*, *Ericaceae*, etc. etc., on the basis of similar low specialization levels in their woods.

AFFINITIES AND TAXONOMIC RANK

Introduction

In my paper on the affinities of *Hua* and *Afrostyrax* (1972b) I have summarized the results of most of my comparisons with families from widely different plant orders. I refrain from this practice here, because it would mean summing up differential characters from external morphology, vegetative anatomy, palynology, etc., etc., for numerous families. Such information is readily available in the literature to those who would like to explore all possibilities not recorded in the following pages. The discussion of the affinities and status of the different genera has been largely limited to positive conclusions only, whilst the negating of affinities with certain families is restricted to those families seriously considered as putative relatives. The actual comparative work has been carried out along the same lines as in my *Hua* and *Afrostyrax* study, and embraced all families of *Celastrales* and *Theales*, taken in the widest possible sense, together with numerous other families scattered throughout the system, which invited more detailed comparisons for one reason or another. The anatomical characters used for the comparisons are summarized in table III.

SPHENOSTEMON

In comparing the anatomy of *Sphenostemon* with that of *Aquifoliaceae sensu stricto* (*Ilex* and *Nemopanthus*), it appears that only few differentiating characters are present: crystal complement, bark histology, and some vessel characters. One may contrast this with a

Table III — Survey of some important microscopical characters.
Data for Icacinaceae are from Bailey & Howard (1941), Van Staveren & Baas (1973), together with original observations.
Data on pollen kindly provided by Madame Callen-Lobreau.
For macromorphological data see Synopsis of morphological characters, and Sleumer (1942) for Icacinaceae.

	ILEX	NEMOPANTHUS	ONCOTHECA	PHELLINE	SPHENOSTEMON	ICACINACEAE
Stomatal type	anomocytic anisocytic cyclocytic bicyclic	± cyclocytic	unusual type	anomocytic	anomocytic	polymorphous
Range of guard cell length in /um	18—42	21—23	29—32	45—88	30—35	18—50
Nodes (number of gaps and traces)	1—3	1	5	3	3	1—3
Petiole vascularization	simple—complex	simple	± complex	of centric bundles	simple	simple—complex
Secondary phloem	not stratified without fibres	not stratified without fibres	stratified with elongated stone cells	?	stratified with phloem fibres	stratified with phloem fibres (+ other types ??)
Vessel member length	600—1920	600	1030	2130	1600—2400	c. 300—2200
Number of bars	13—58	18	15	134	67—118	0 to c. 60
Inter-vessel pits	alternate to opposite, rarely ± scalariform	alternate to opposite	alternate	uniseriate	scalariform	alternate to scalariform
Crystal complement	druses or clusters and solitary prismatic very rarely styloid-like	druses and solitary prismatic	druses and solitary prismatic	minute druses	styloids	druses or clusters solitary prismatic styloids
Pollen	colporate clavate	colporate clavate	colporate finely perforate	colporate echinate-smooth	porate reticulate-verrucate	polymorphous

good overall similarity in wood anatomy, and to a lesser extent also in leaf anatomy. Considering differential characters from the floral region: arrangement and morphology of the perianth, morphology of stamens, pollen, and fruit (Bailey & Swamy, 1953; Bailey, 1956; Lobreau, 1969), there are, however, enough reasons to look for relatives of *Sphenostemon* outside *Aquifoliaceae*.

Recently Airy Shaw (1972) again advocated affinities of *Sphenostemon* with *Trimeniaceae*, and although he was aware of the anatomical differences 'forbidding' inclusion in *Trimeniaceae* it seems useful to repeat once more the anatomical differences between the 2 taxa: stomatal type, oil and mucilage cells, crystal complement, nodal anatomy, and septate fibres in the wood of *Trimeniaceae* provide a whole complex of differences, although in other wood anatomical features *Sphenostemon* and *Trimeniaceae* are much alike. From the reproductive sphere one could add several more important differences (floral whorl, merousness of the ovary, absence of an obturator in *Trimeniaceae*, morphology of the style). All these differences make a close mutual affinity very unlikely. *Monimiaceae*, in some interpretations also embracing *Trimeniaceae*, offer an equal or even larger number of differences in anatomy and external morphology (Money *c.s.*, 1950).

Escalloniaceae, Dichapetalaceae, Guttiferae, Ochnaceae, Theaceae, and *Icacinaceae* are the remaining families mentioned in the literature (see p. 313), because of resemblances in one or more characters. Of these the *Escalloniaceae, Dichapetalaceae, Guttiferae,* and *Ochnaceae* need not to be discussed because of obvious dissimilarities, most of which have been extensively discussed in the literature. For anatomical differences the reader may be referred to Metcalfe & Chalk (1950).

Theaceae, suggested by Loesener as possible relatives, share a number of primitive wood characters with *Sphenostemon* (for their systematic value see p. 338); however, nodal anatomy, number of integuments, pollen morphology, and many other characters (see Keng, 1962) exclude the family as a close relative.

Icacinaceae, like *Aquifoliaceae* a member of the *Celastrales*, first entered the discussion when Ingle & Dadswell (1961) compared the wood of *Platea* with that of *Sphenostemon*, and concluded that the genera were very similar in this respect. The wood anatomical resemblance is very striking indeed, particularly because of the shared scalariform intervessel pits. The leaf anatomy of *Platea* is, however, quite different (Van Staveren & Baas, 1973). If one extends the comparisons beyond *Platea* there are, however, many points of similarity between *Sphenostemon* and *Icacinaceae*. This is mainly due to the enormous anatomical diversity of this family (Bailey & Howard, 1941; Heintzelmann & Howard, 1948; Van Staveren & Baas, 1973; Baas, 1974), but some similarities with genera of group I (*Icacinaceae* with scalariform vessel perforations and trilacunar nodes, cf. Bailey & Howard, 1941) are so striking that they may be used to advocate natural affinity. Both leaf- and wood anatomy of e.g. *Apodytes* are rather similar to that of *Sphenostemon*, and the same holds for the other genera with anomocytic or anomocytic to cyclocytic stomata of group I. Elaborate forking of bars of the perforation plates as in *Sphenostemon* also occurs in some *Icacinaceae* (Metcalfe & Chalk, 1950). The few bark samples of *Icacinaceae* studied by me contain phloem fibres in more or less regular bands, also including some sclerified short cells, as in *Sphenostemon*. The presence of styloids in the bark of *Gonocaryum calleryanum* (belonging to Bailey & Howard's group II) reported by Ingle & Dadswell (1961) I could confirm. On the whole *Sphenostemon* would fit into *Icacinaceae* quite well on the basis of vegetative anatomy. The differences in other characters are of about the same order as those with *Ilex*: perianth, stamens, and ovary differing in several respects. However, the pendulous unitegmic anatropous ovules with a thickened funicle are shared by *Ilex, Sphenostemon,* and *Icacinaceae*. The unusual stamens of *Sphenostemon* would not

be very much out of place in *Icacinaceae*, since this family shows a very wide range in stamen morphology (Sleumer, 1942, 1971). The wide pollen morphological range of *Icacinaceae* (Lobreau, 1969, 1973) could also accomodate the so-called unusual type of *Sphenostemon*.

The complete evidence from vegetative anatomy and external morphology therefore leaves possibilities open for either Aquifoliaceous or Icacinaceous affinities. To settle this question one should realize that choosing between the two alternatives is a rather futile exercise, because *Icacinaceae* and *Aquifoliaceae* are both anatomically and also macromorphologically (see also Valeton, 1886; Sleumer, 1942) very close. If we compare the differential macromorphological and anatomical features for *Ilex*, *Icacinaceae*, and *Sphenostemon* (table III, synopsis, and Sleumer, 1942), *Sphenostemon* appears to be more similar to *Icacinaceae* than to *Aquifoliaceae*; in passing it should be remarked that the differences between *Aquifoliaceae* and *Icacinaceae* are very few. Bernardi's strong plea for maintaining *Sphenostemon* in *Aquifoliaceae* must therefore be declined. Accepting his solution would imply that one should also merge the *Aquifoliaceae* with *Icacinaceae*, and although the affinities between the two families are close, such a solution would be unpractical, and would not reflect the (admittedly few) constant differential characters separating the two taxa. Including *Sphenostemon* in the *Icacinaceae* would meet similar, though less strong objections, and I therefore prefer to support the family status for *Sphenostemon* as also done by Erdtman (1954) and Airy Shaw (1972). This status clearly recognizes the unusual floral morphology, supported by only one anatomical oddment (styloids) and avoids problems of upsetting the system of *Celastrales* by lumping well-established families. I disagree with Erdtman's and Airy Shaw's opinions on the natural affinity of *Sphenostemonaceae*. This monogeneric family is according to the whole character complex of macromorphology and anatomy related to both *Icacinaceae* and *Aquifoliaceae*, and should accordingly be treated as a member of the *Celastrales*.

Bailey (1956) and Metcalfe (1956) have left the question unanswered whether *Nouhuysia* sensu Van Steenis and *Sphenostemon* Baillon should be regarded as one genus. The anatomical differences reported in the descriptive part and table II are so much outweighed by anatomical similarities that I fully support Van Steenis' decision (1955) to merge *Nouhuysia* with *Sphenostemon*.

PHELLINE

The fact that Loesener always has accepted *Phelline* as a member of the *Aquifoliaceae* probably accounts for it that only in recent years its taxonomic position has been questioned. Yet if we consider the anatomical and morphological differences with *Ilex*, these are at least of the same order as those between *Sphenostemon* and *Ilex*. The very unusual petiole anatomy with concentric vascular bundles, the extremely large guard cell pairs, the very primitive narrow vessels and huge rays, together with valvate petals, hemitropous to weakly campylotropous ovules, and different pollen ectexine make the genus rather outstanding from *Aquifoliaceae sensu stricto* as well as from *Icacinaceae* and from *Sphenostemonaceae*. In the comparison with *Ilex*, one may contrast these differences by similarities in fruit anatomy (Thévenard, 1906), floral plan, and an unspecialized wood anatomy. Comparisons with *Icacinaceae* yield more or less the same overall similarities and the wood of *Phelline* is more compatible with the huge range in that family than with the wood of *Ilex*; rays similar to those in *Phelline* occur for instance in *Citronella*. Within or outside the *Celastrales* I have not been able to find genera or plant families with a bigger claim for affinity than *Aquifoliaceae* or *Icacinaceae*. *Araliaceae*, vaguely suggested by Airy Shaw in
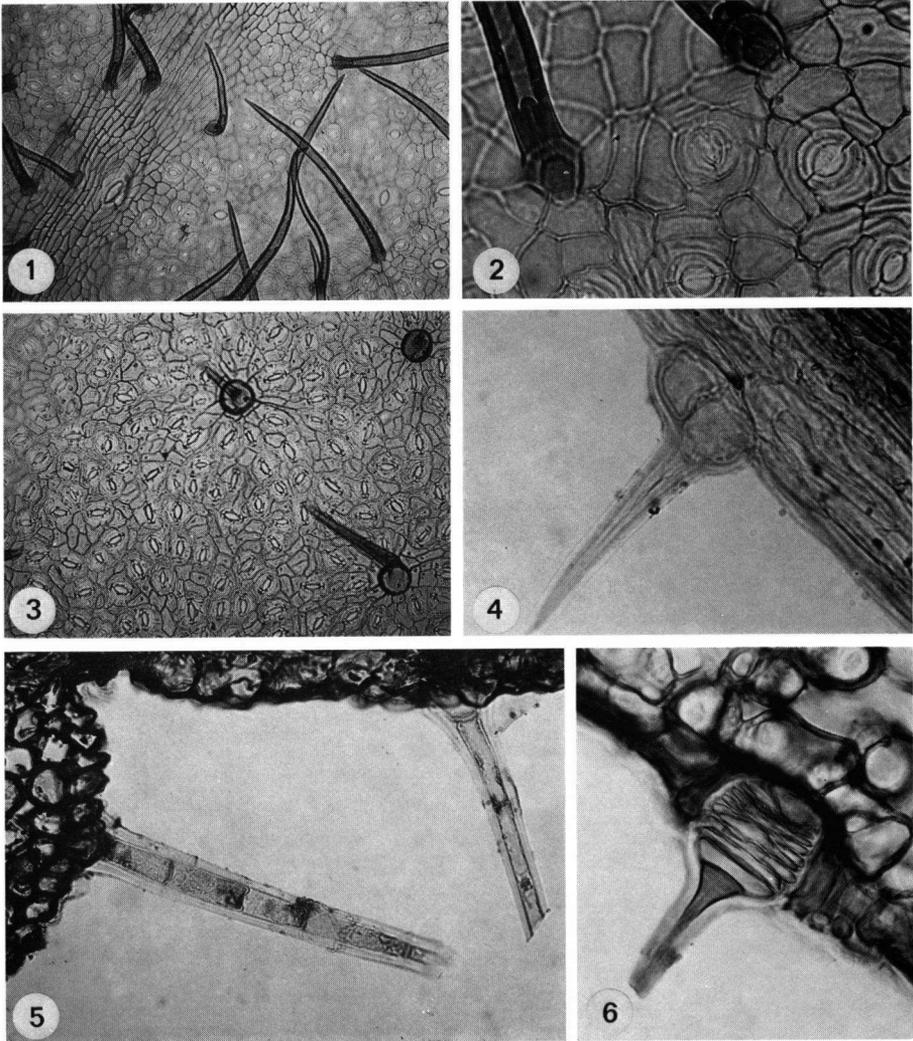
Plate I. *Ilex.* Hairs. — 1. *I. brasiliensis*, ×90. — 2. ibid., showing thick basal septs, ×360. — 3. *I. cissoidea*, ×90. — 4. ibid., showing broad base and anticlinal division wall, ×360. — 5. *I. pubescens*, long septate hairs, tips broken off. — 6. *I. hypoglauca* (*Hallier B 2875*), broad base with numerous septs, tip broken off, ×360.
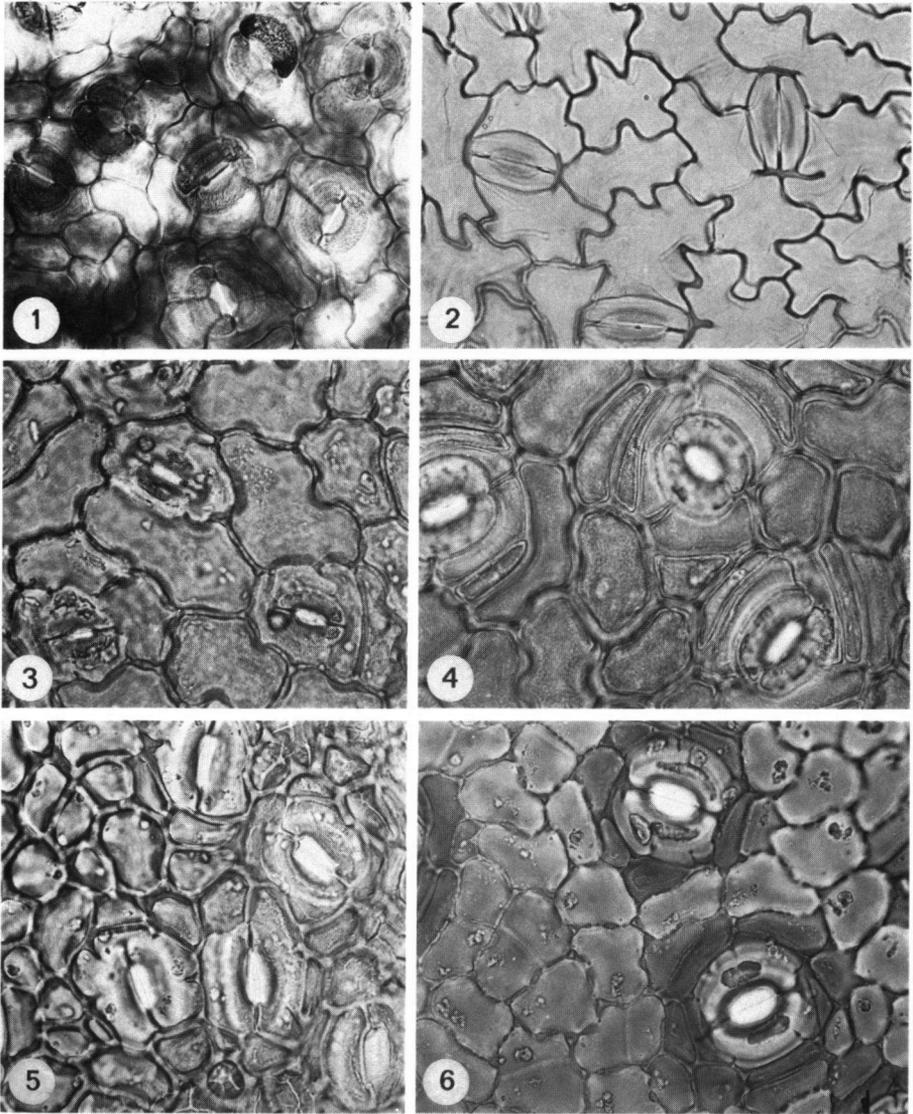
Plate II. *Ilex*. Stomata, all × 360. — 1. *I. amara*, stomata anomocytic. — 2. *I. verticillata*, stomata anomocytic. — 3. *I. integerrima*, stomata anisocytic. — 4. *I. clemensiae*, stomata 'complex'. — 5. *I. pulogensis*, stomata cyclocytic. — 6. *I. altaclarensis*, stomata bicyclic. — 1 & 2: paradermal sections; 3—6: cuticular macerations.
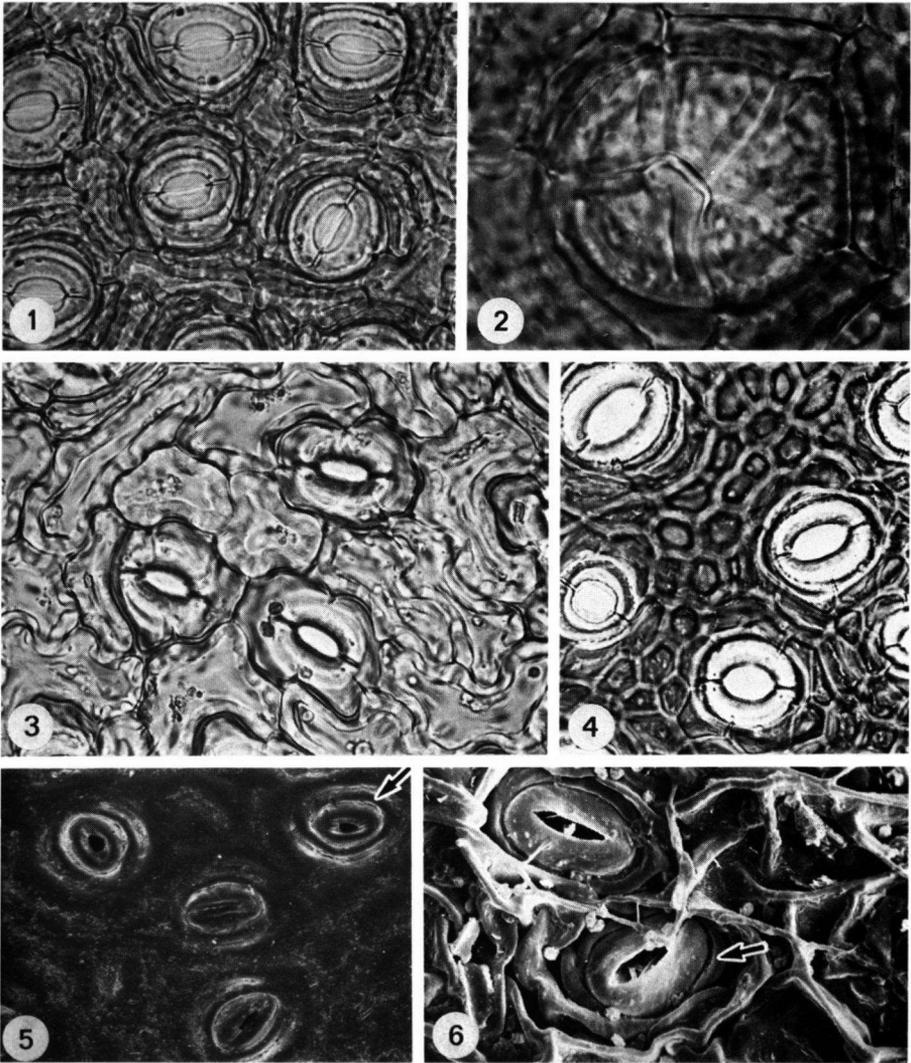
Plate III. *Ilex.* Abaxial epidermis. — 1. *I. cassine* (*Boom 38139*), unspecialized cells lignified, stomata cyclocytic with thin-walled subsidiary cells, ×360. — 2. ibid., aberrant stomatal complex with lignified subsidiary cells at low focus, ×800. — 3. *I. ovalifolia*, unspecialized cells lignified, stomata anisocytic with thin-walled subsidiary cells, ×360. — 4. *I. paraguariensis*, unspecialized cells thick-walled (not lignified), stomata cyclocytic with thin-walled subsidiary cells, ×360. — 5. *I. aquifolium* var. *heterophylla*, cuticle smooth, peristomal rims (arrow), SEM, ×350. — 6. *I. hypoglauca* (*Hallier B 2875*), cuticle with conspicuous striations, peristomal rims (arrow), SEM, ×730.
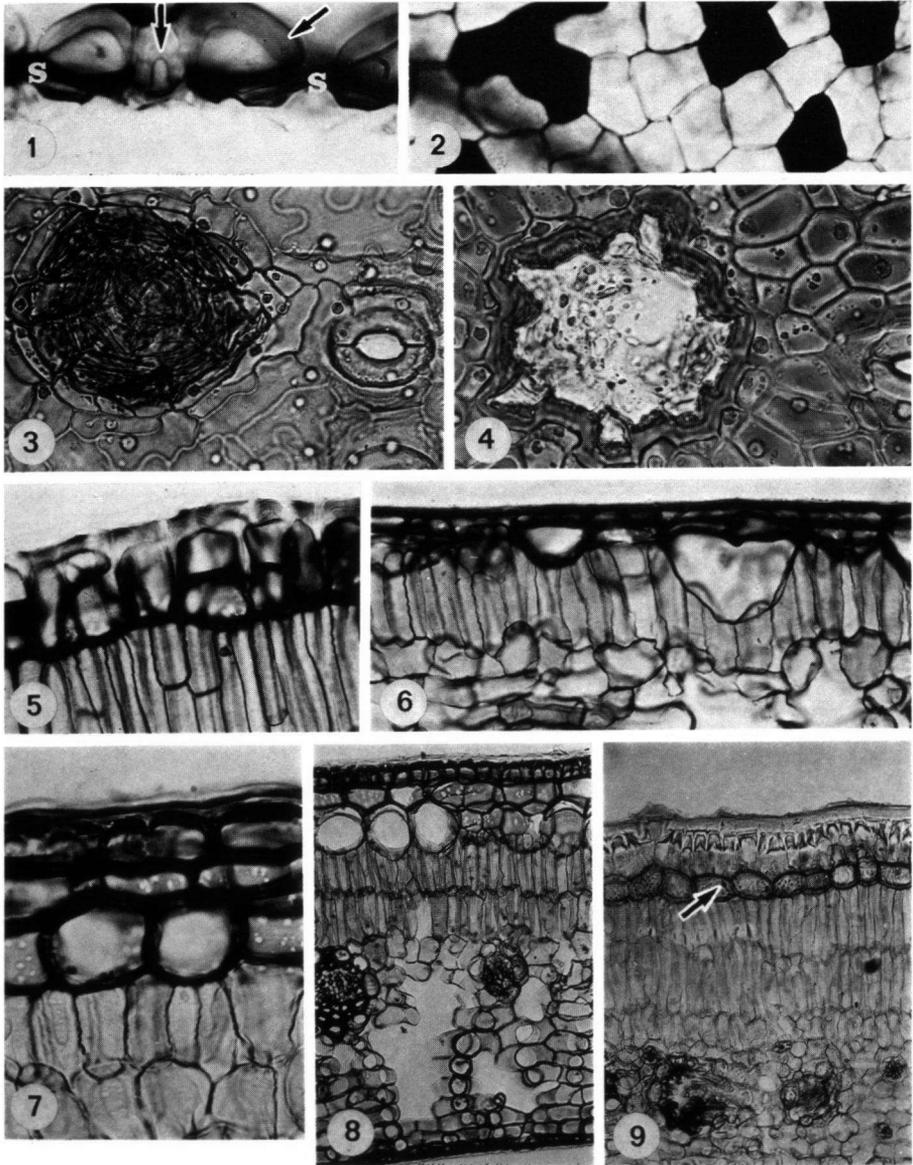
Plate IV. *Ilex.* — 1. *I. amara*, transverse section of abaxial epidermis showing thickened adaxial lignified cell walls (arrows) and stomata (s), ×800. — 2. *I. amelanchier*, paradermal section of adaxial epidermis with scattered mucilage cells, ×360. — 3. *I. amplifolia*, regular cork wart, maceration, ×360. — 4. *I. coriacea*, regular cork wart of peculiar outline, maceration, ×360. — 5. *I. archboldiana*, adaxial epidermis with anticlinal and periclinal division walls, ×220. — 6. *I. argentina*, bulging mucilage cells and division walls of adaxial epidermis, ×220. — 7. *I. perado (Lems 2722)*, locally 2-layered adaxial hypodermis + epidermis, ×220. — 8. *I. anomala (Van Balgooy 1689)*, 2-layered hypodermis of bulging mucilage cells, ×90. — 9. *I. zygophylla*, lignified adaxial hypodermis (arrow), note very tall epidermis cells, ×90.
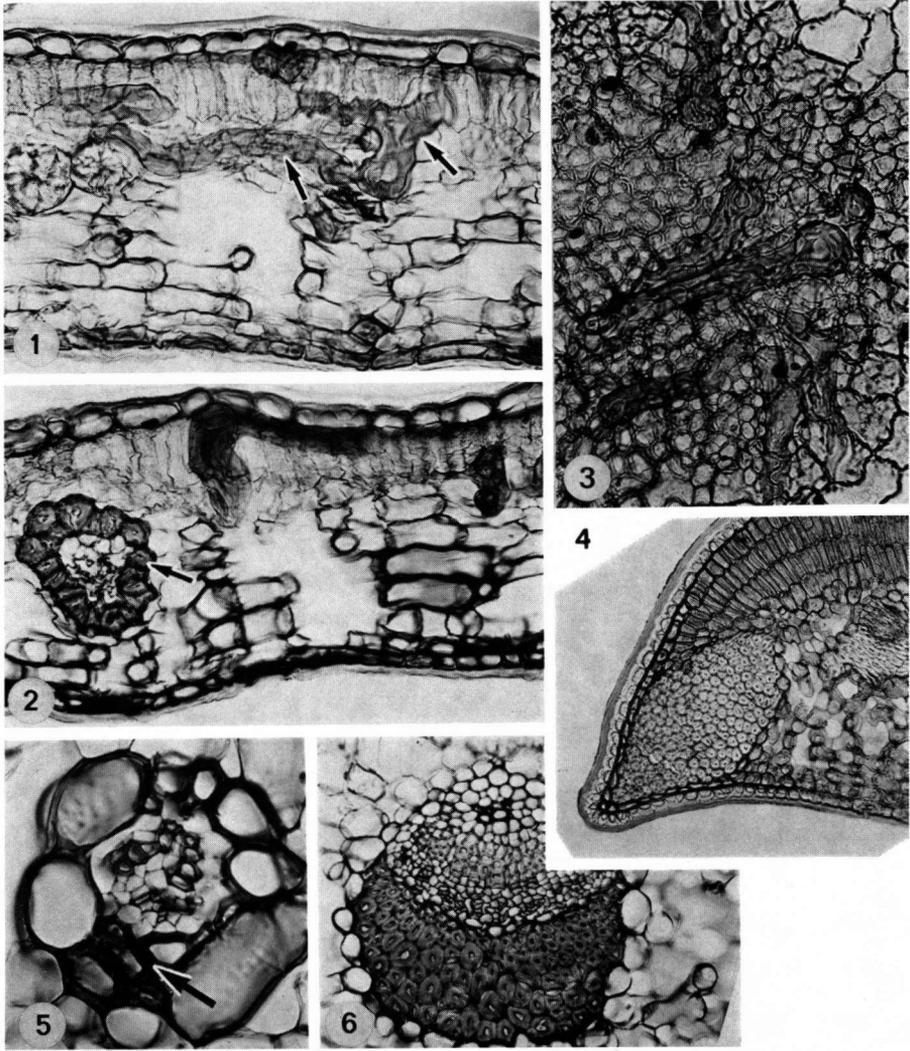
Plate V. *Ilex.* Sclerenchyma. — 1—3. *I. buergeri*, foliar sclereids, ×220; 1. transverse section showing elongated branched sclereids (arrow) mainly in palisade tissue; 2. ibid., note also fibrous bundle sheath (arrow); 3. paradermal section showing sclereids in between palisade cells. — 4. *I. pernyi* (cult. hort. Leiden), transverse section with marginal sclerenchyma strand, ×90. — 5. *I. anomala (Van Balgooy 1689)*, lignified bundle sheath enclosing very little abaxial sclerenchyma (arrow), ×360. — 6. *I. bioritsensis* (cult. hort. Leiden), bundle sheath unlignified, enclosing massive abaxial sclerenchyma cap, ×220.
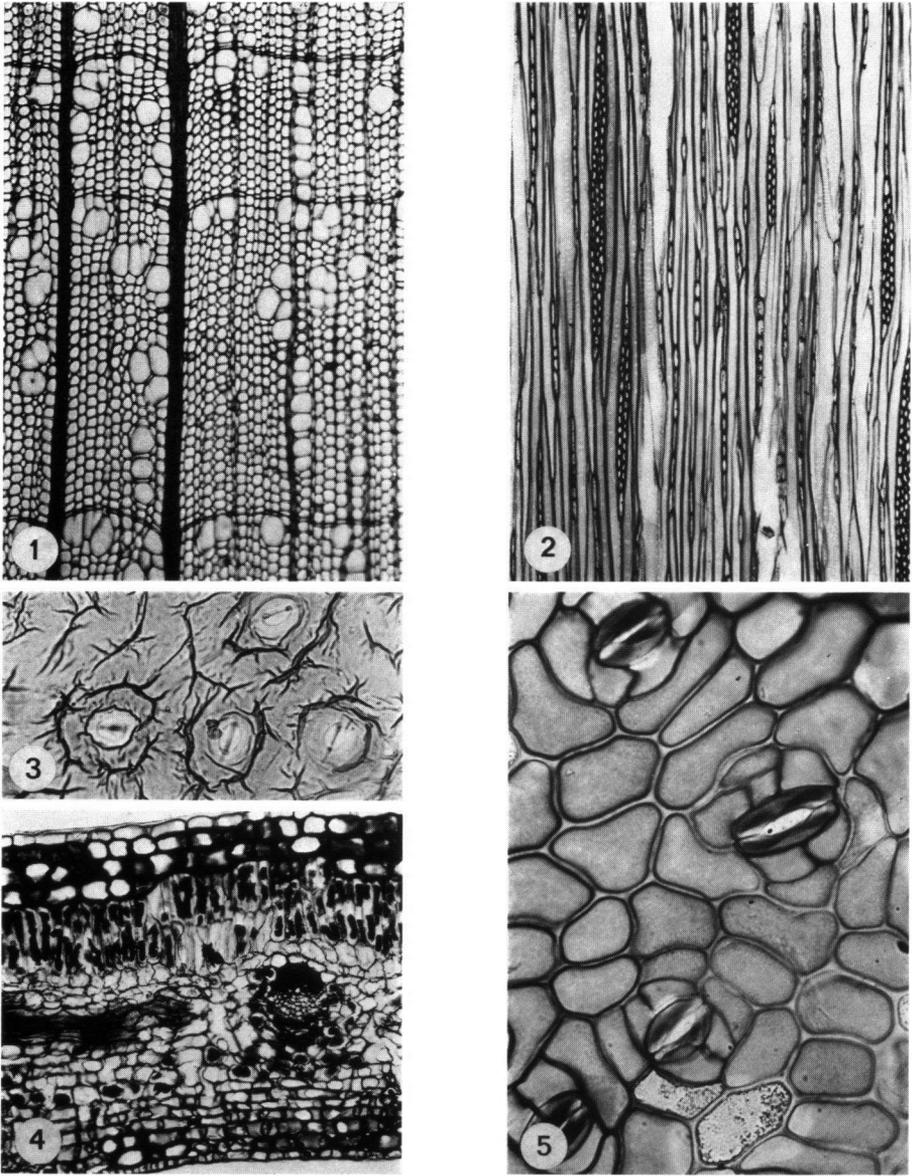
Plate VI. 1—3. *Nemopanthus mucronata*. 1. *MADw 19208*, transverse section of wood, ×90; 2. ibid., tangential section of wood, ×90; 3. *Kirk 308*, abaxial epidermis, maceration showing characteristic cuticular ridges and peristomal rims, ×360. — 4 & 5. *Oncotheca balansae* (*McKee 3439*). 4. transverse section of lamina, with 2—3-layered hypodermis, ×90; 5. abaxial epidermis, paradermal section with characteristic arrangement of subsidiary cells, ×360.
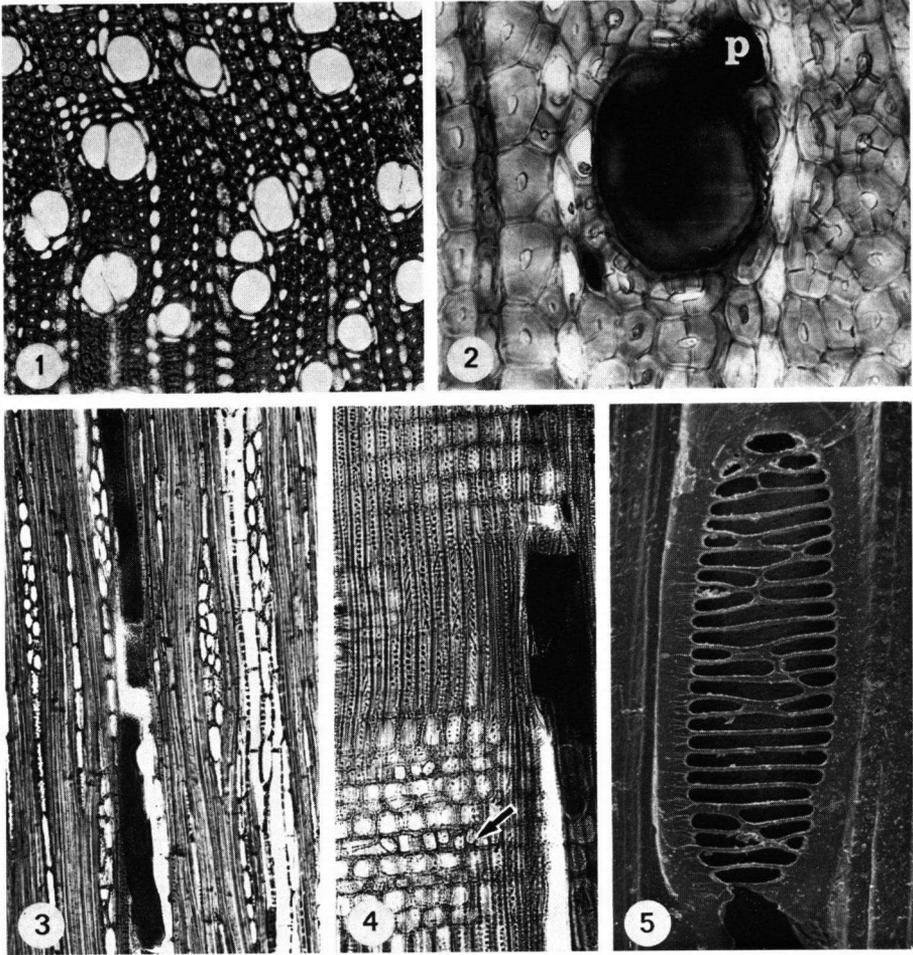
Plate VII. *Oncotheca balansae.* Wood structure (*McKee 22947*). — 1. transverse section, bleached, ×90. — 2. ibid., unbleached (p = parenchyma cell), ×360. — 3. tangential section, bleached, ×90. — 4. radial section, note crystals (arrow), bleached, ×90. — 5. radially split surface, perforation plate, SEM, ×350.
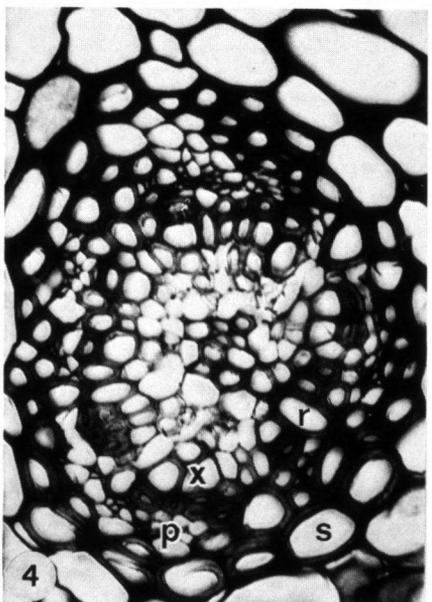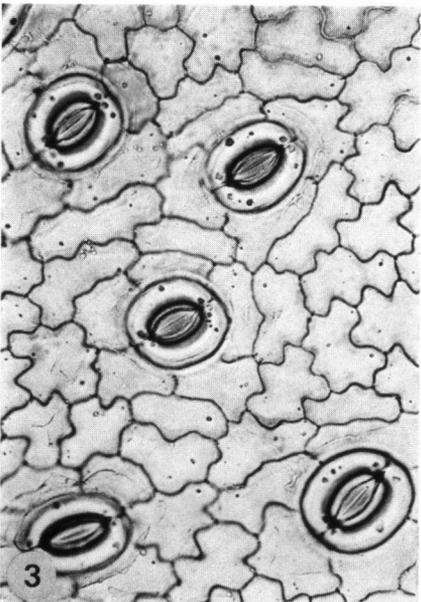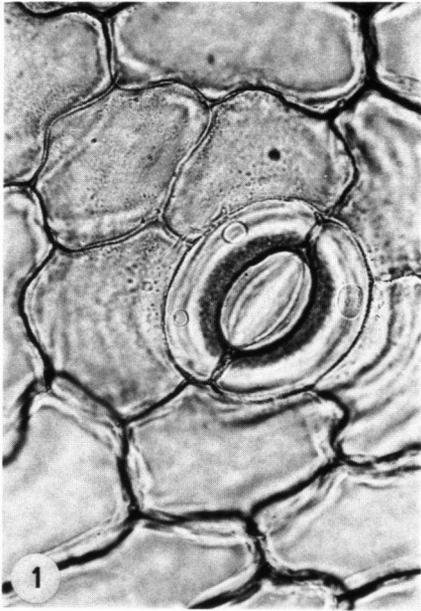
Plate VIII. *Phelline.* Leaf anatomy. 1—3: macerations. — 1. *P. comosa*, anomocytic stomatal complex, anticlinal flanges not granular, ×360. — 2. *P. confertifolia*, ibid., anticlinal flanges granular, ×360. — 3. *P. macrophylla* (*Balansa 583*), anticlinal flanges undulated, ×220. — 4. *P. lucida* (*McKee 4856*), transverse section of concentric midrib bundle; p: phloem, x: xylem, s: sclerenchyma, r: 'ray'.
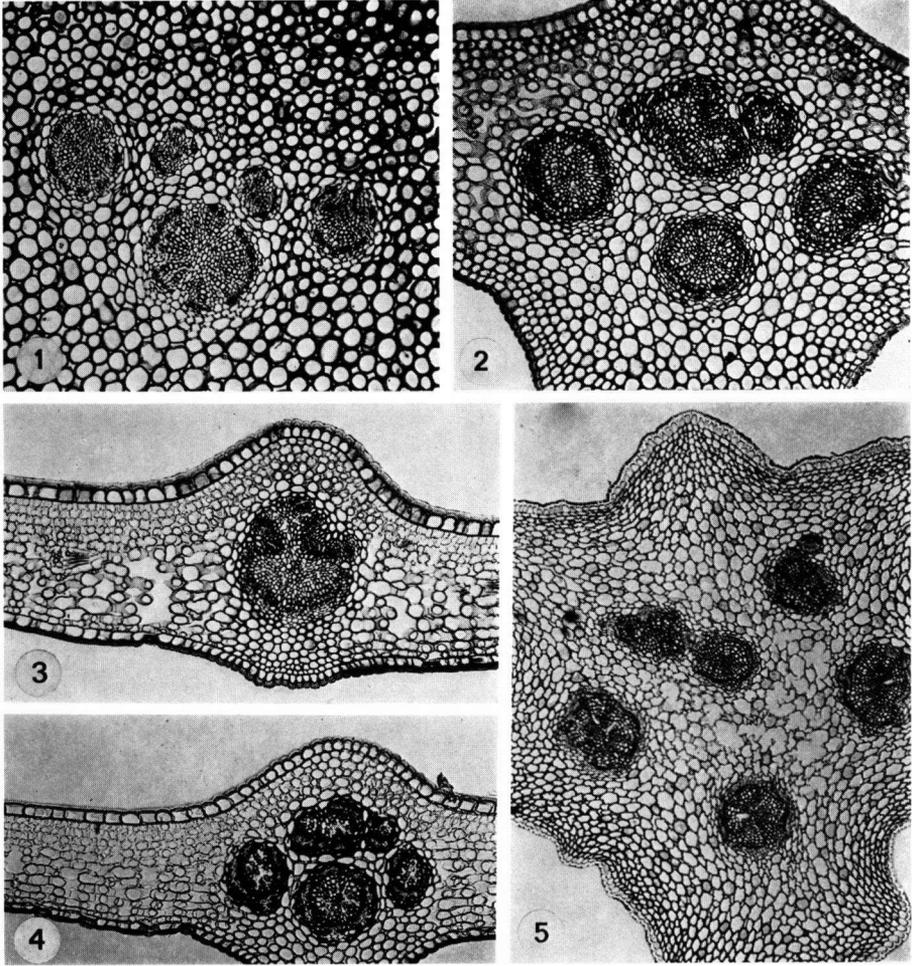
Plate IX. *Phelline.* Leaf anatomy. — 1—3. *P. lucida* (*McKee 5337*), ×36; 1. basal part of petiole; 2. distal part of petiole; 3. midrib. — 4. *P. confertifolia*, midrib, ×36. — 5. *P. macrophylla* (*McKee 2686*), distal part of petiole, ×22.
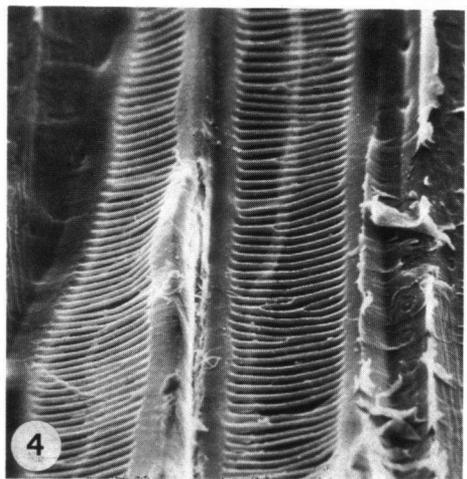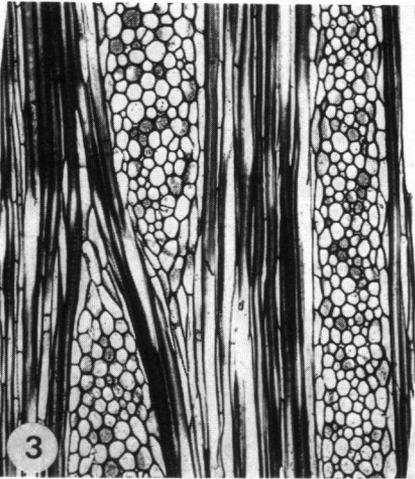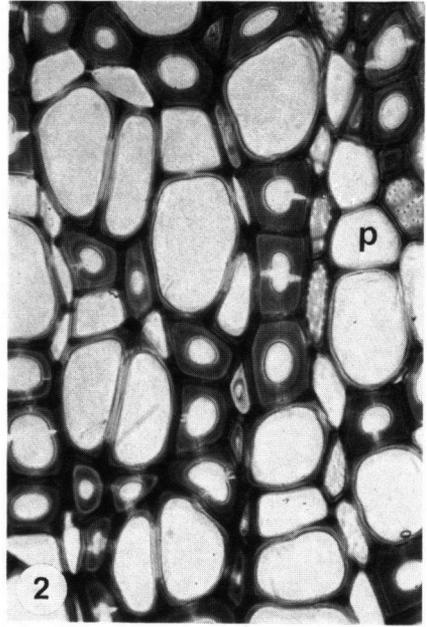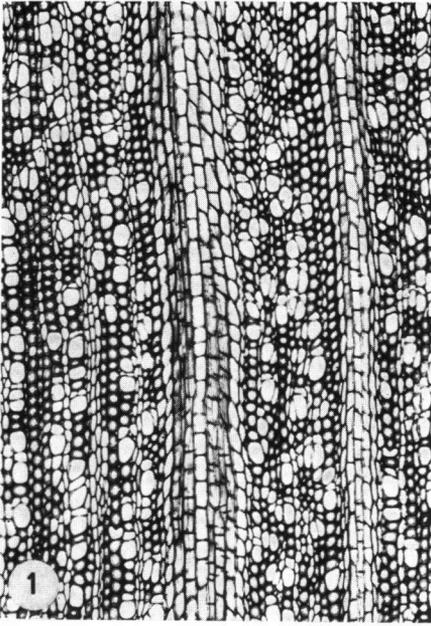
Plate X. *Phelline lucida*. Wood structure. — 1. transverse section, ×36. — 2. ibid. (p=parenchyma cell), ×220. — 3. tangential section, ×36. — 4. radially split surface, scalariform perforation plates, SEM, ×370.
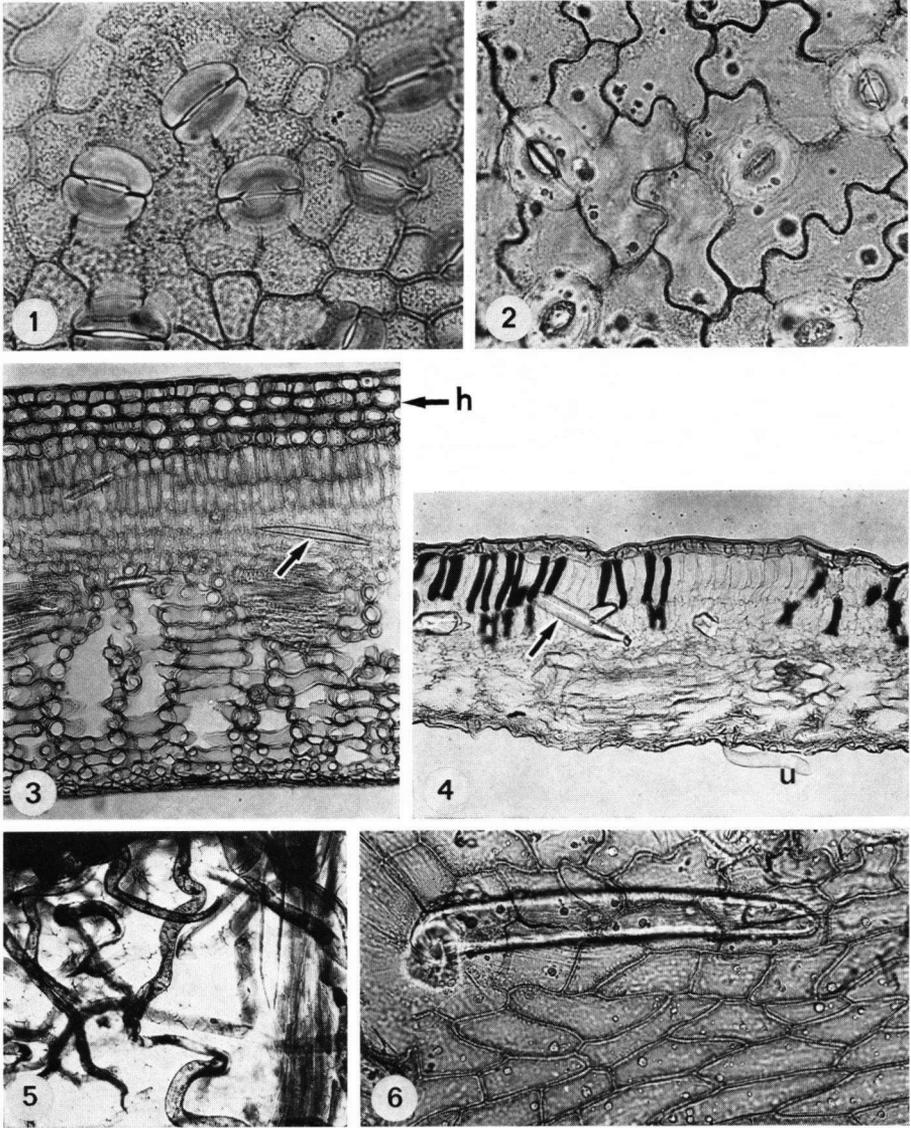
Plate XI. *Sphenostemon.* Leaf anatomy. — 1. *S. pachycladum (McKee 23070)*, cuticular maceration, ano-mocytic stomata, ×360. — 2. *S. arfakensis*, ibid., ×360. — 3. *S. pachycladum (McKee 23070)*, transverse section of lamina with styloids (arrow) and hypodermis (h), ×90. — 4. *S. pauciflorum*, transverse section of lamina with styloids (arrow) and part of undulating hair (u), ×90. — 5. ibid., paradermal section of abaxial epidermis showing indumentum of undulating hairs, ×90. — 6. *S. arfakensis*, maceration of abaxial surface with adpressed hair, ×220.
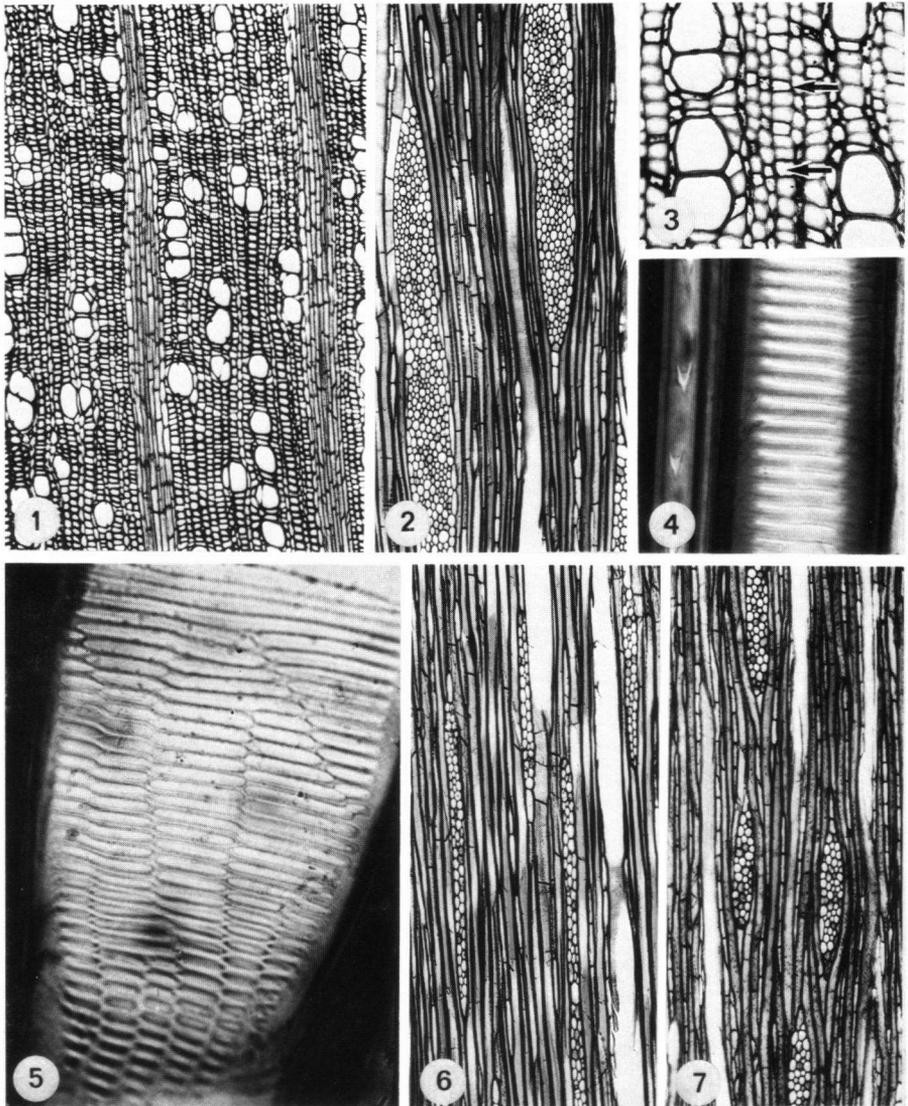
Plate XII. *Sphenostemon*. Wood structure. — 1—4. *S. lobosporus (CSIRO 14216)*. 1. transverse section, bleached, ×36; 2. tangential section, bleached, ×36; 3. transverse section, unbleached, showing parenchyma distribution (arrow), ×90; 4. tangential section showing scalariform inter-vessel pits, ×360. — 5. *S. papuanum (Van Royen 3692)*, radial section, detail of branching in scalariform perforation plate, ×360. — 6. ibid. *(Pullen 266)*, tangential section, bleached, ×36. — 7. *S. pachycladum (McKee 23070)*, ibid., ×36.

Willis (1966), certainly do not appear to be related to *Phelline* if their anatomies are compared.

I therefore support Takhtajan's proposal to raise *Phelline* to family rank, in order to do justice to its macromorphological and anatomical features which make it distinct from *Aquifoliaceae* and *Icacinaceae*. Affinities to both these families are present, but if all characters are considered these are probably less close than those of *Sphenostemon* with these two families.

ONCOTHECA

The early and often repeated suggestions of an Ebenaceous affinity for *Oncotheca* cannot be supported on anatomical grounds. This in spite of Guillaumin's (1938) support for this idea, using superficial anatomical observations and comparisons as additional arguments. The woods of the two taxa are entirely different: in type of vessel perforations, fibre pitting, and parenchyma distribution (cf. Metcalfe & Chalk, 1950).

Within *Aquifoliaceae Oncotheca* is out of place because of its pollen, pentalacunar node, peculiar stomatal type, type of fibre-tracheids, parenchyma distribution in the wood, and also its crystal complement. The floral morphological differences between *Ilex* and *Oncotheca* (insertion of stamens, stamen morphology, number of styles, etc.) provide further arguments for excluding *Oncotheca* from *Aquifoliaceae*. The rather heterogeneous *Icacinaceae* provide no further characters in common with *Oncotheca* than *Aquifoliaceae*, so that affinities with this family are also not indicated. Affinities with *Sapotaceae* (Loesener, 1901) are most unlikely if one considers the anatomical differences (Metcalfe & Chalk, 1950). Lobreau–Callen's suggestion (1975) of affinities with *Salvadoraceae* is not supported by anatomy. Wood and leaf structure of *Salvadoraceae* differ widely from *Oncotheca*. Theaceous affinities, as recently suggested by Airy Shaw (1965) and Takhtajan (1969), find support in wood anatomy. *Caryocaraceae*, also belonging to *Theales* but with a very different wood anatomy, possess pentalacunar nodes (Schofield, 1968). It seems likely that on the grounds of the combined characters of *Oncotheca*, the genus will remain out of place in any of the existing Thealean families (for a comparison with *Theaceae*, see Keng, 1962). However, since Miss Carol Bissett (U.S.A., Chapel Hill) has independently embarked on a thorough comparison of *Oncotheca* with putative — mainly Thealean — relatives, I refrain from further elaborate discussions here.

NEMOPANTHUS

The affinities of *Nemopanthus* with *Ilex* have never been challenged and recently (Clark, 1974) the question has even been raised whether *Nemopanthus* should not be merged with *Ilex*. Such a taxonomic decision would not meet any opposition from vegetative anatomists: wood, bark, and leaf anatomy are more or less identical to that of certain *Ilex* species of subgenus *Prinus*. Only the peculiar cuticular markings on the abaxial leaf surface of *Nemopanthus mucronata* make it stand out from all *Ilex* species so far studied anatomically. The overall differences between *Nemopanthus* and *Ilex* are in fact smaller than those between *Sphenostemon* series *Sphenostemon* from New Caledonia and series *Apetala* from New Guinea and Queensland.

The position of Icacinaceae, Aquifoliaceae, Phellinaceae, and Sphenostemonaceae in the Celastrales

From a survey of recent systems for Angiosperm classification it appears that no agreement exists about the delimitation of the order *Celastrales* (Thorne, 1968; Melchior in Engler's Syllabus, 1964; Hutchinson, 1974; Takhtajan, 1969; Cronquist, 1968). Of these systems that of Thorne is most untraditional in including *Aquifoliaceae* in suborder *Theineae* of his *Theales*, whilst *Icacinaceae* and *Celastraceae*, together with *Stackhousiaceae*, are in suborder *Celastrineae* of his *Santalales*. However, I cannot agree with the separation of such anatomically and morphologically similar families as *Icacinaceae* and *Aquifoliaceae* into widely different orders.

A discussion of the affinities of all families of the *Celastrales* as based on their anatomies is beyond the scope of this paper, but it is interesting to note that *Aquifoliaceae*, *Phellinaceae*, *Sphenostemonaceae*, and part of the *Icacinaceae* have the more primitive wood anatomy of the whole order, only encountered in few other representatives of which only *Cyrillaceae* and *Celastraceae* merit further attention. *Celastraceae* are often regarded as very close to *Aquifoliaceae*, but anatomically there are not many points in common. Although few members of *Celastraceae* possess scalariform perforations in their woods, these are yet very different in overall wood anatomy from *Aquifoliaceae* (Dr. A. M. W. Mennega, Utrecht, private communication). *Cyrillaceae* are anatomically rather similar to *Aquifoliaceae* (both in wood and leaf), but characters from floral and pollen morphology have induced several students of Angiosperm classification to rank them amongst the *Ericales*, with which family they also share many wood anatomical features. One may only wonder whether the similarities of *Cyrillaceae* with *Ericales* as well as with some *Celastrales* are the result of convergent evolution, or whether they are truly indicative of affinities between the two plant orders.

Within *Celastrales* the group of *Icacinaceae*, *Aquifoliaceae*, *Phellinaceae*, and *Sphenostemonaceae* probably constitutes a natural assemblage of families, which have retained many primitive wood anatomical features. Within *Icacinaceae* many lines of specialization have occurred, so that some of its genera now show a very derived type of wood anatomy. *Aquifoliaceae*, *Phellinaceae*, and *Sphenostemonaceae* may well be regarded as isolated groups derived from the same ancestors as the primitive *Icacinaceae*.

GENERAL CONSIDERATIONS AND CONCLUSIONS

The taxonomic decisions to raise *Phelline* and *Sphenostemon* to family rank, as supported here by anatomical evidence, remain open to criticism by those who want to incorporate each of these odd genera into one of the existing families. Carlquist (1959), Swamy & Bailey (1949), and Philipson (1967) have discussed the problems of treating aberrant genera, but the matter will always remain controversial, since no universal rules for family delimitation exist. Palynological and anatomical contributions usually do not alter this problem.

Maintaining *Phelline* in *Aquifoliaceae* would render the family heterogeneous for certain floral morphological, wood anatomical, and leaf anatomical features. In itself the genus *Ilex* also covers a wide floral morphological and anatomical range (Loesener, 1942; Baas, 1973, and this paper), but here the heterogeneity can be arranged in morphological series; in other words, the structural variation is more or less continuous. The characters in *Phelline* that serve to distinguish it from *Ilex* and *Nemopanthus* do not fit at all into these morphological series; this may be used to support the treatment of *Phelline* in a distinct

family. Moreover, the inclusion of *Phelline* in *Aquifoliaceae* would do injustice to the equally strong similarities this genus has with some representatives of the — structurally very diverse — *Icacinaceae*. For *Sphenostemon* and *Oncotheca* the same reasoning would apply in comparisons with either *Ilex* or any other families.

However, considering the tremendous range in macromorphology and anatomy of the *Icacinaceae*, a family generally accepted as natural, one may question the validity of the reasoning adopted above. In this family it is hard to mention any constant character except the anatropous pendulous unitegmic ovules, and the ovary structure which varies within narrow limits (Sleumer, 1942). Most of the variation — especially in vegetative anatomy and pollen morphology — can, however, be arranged in continuous morphological series, which makes it impossible to split the family into separate groups which are distinct from each other in a combination of several characters. The lack of such continuous series of character complexes in the group of taxa: *Phelline, Sphenostemon, Aquifoliaceae sensu stricto*, and *Icacinaceae* as a whole, has induced me to support the recognition of *Phellinaceae* and *Sphenostemonaceae*.

Whatever the merits of Bailey's (1956) proposal to treat genera like *Sphenostemon* as 'incertae sedis', there is no reason now to maintain this position for *Sphenostemon* and *Phelline*, since much more information has become available on the anatomy and morphology of their possible relatives. The proposal to treat them as members of the *Celastrales* is one of the major conclusions of this study.

The significance of the structural range in *Ilex*, analysed in a separate section below, cannot as yet be fully established, as far as infrageneric classification or affinities are concerned. A new revision is required first. However, the general significance for systematic anatomy of the wide wood- and leaf anatomical range in *Ilex* should not be underestimated. The great variability of several anatomical characters within a genus implies that the systematic value of these characters is very restricted in discussions of affinities above the genus level.

SPECIAL PART: THE LEAF ANATOMICAL RANGE IN ILEX

Introduction

In this section the leaf anatomy of 95 species of *Ilex* is described and discussed. Mostly only one specimen per species was studied, but of 15 species the infraspecific anatomical variation was studied in a restricted number of specimens.

According to Shaw (1973) the total number of extant *Ilex* species may be estimated at *c.* 400. The selection of species for this study was aimed at covering most infrageneric taxa recognized by Loesener, and also to include representatives from all regions of the large distribution area of *Ilex*. Of the monotypic subgenus *Yrbonia* and of a few sections I did not study any material.

Loesener's system for Ilex

Loesener's classification (1901, 1908, 1942) of *Ilex* remains the only comprehensive one. Some proposals for adjustments based on material from certain geographic areas (e.g. Hu, 1949—1950, 1967; Edwin, 1965) have been made, and although these may be indicative of shortcomings in Loesener's system, I have not followed them because this would make the comparisons of the leaf anatomical data with systematic treatment incoherent.

For easy reference a summary of Loesener's system (1942), from which infrageneric taxa of which no material was used for this study are omitted, is given below.
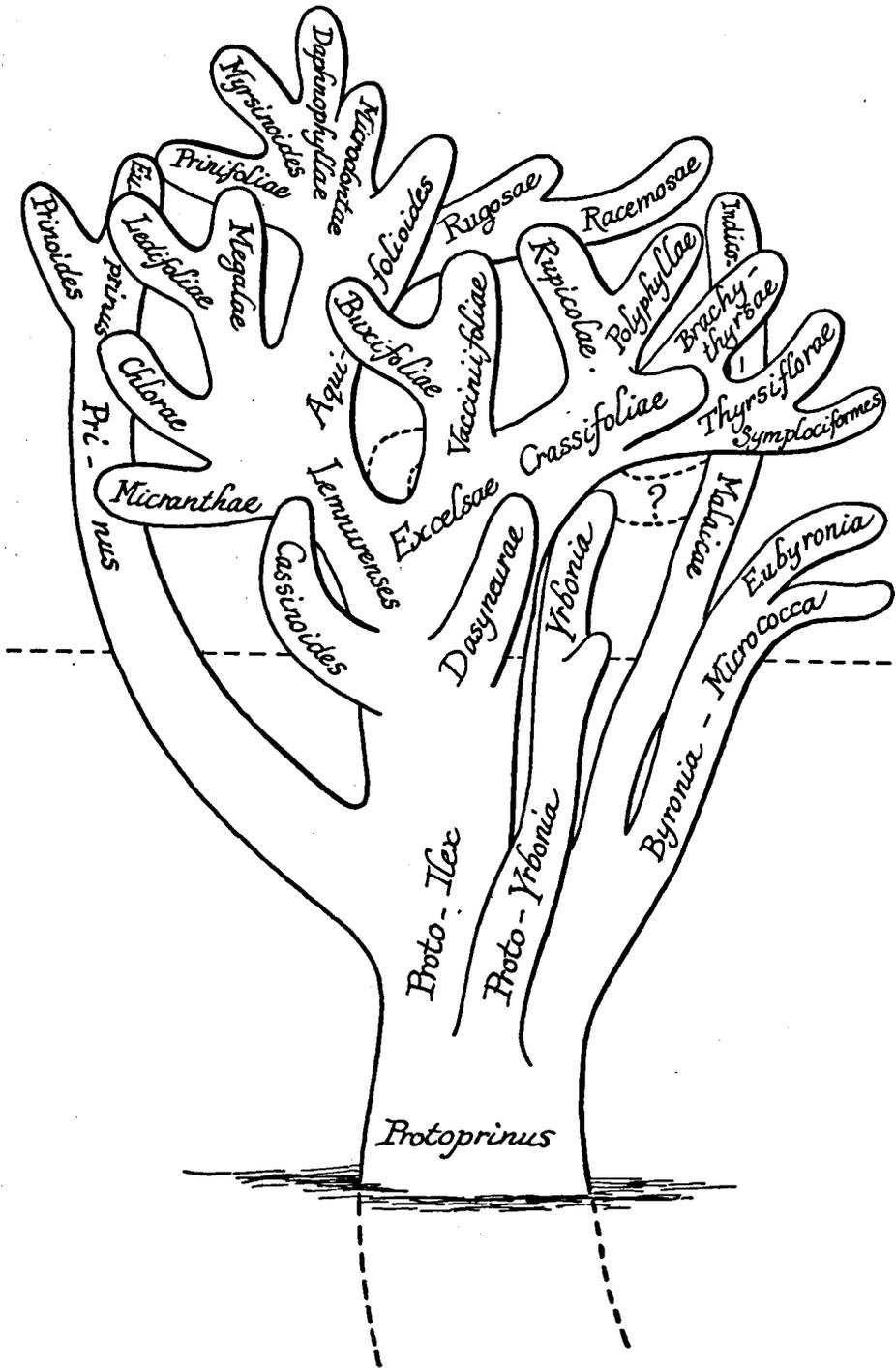
Subgenus *Rybonia*
Subgenus *Byronia*
  Series A. *Eubyronia*
  Series B. *Micrococca*
Subgenus *Euilex*
  Series A. *Lioprinus*
    Section *Excelsae*
      Subsection *Umbelliformes*
      Subsection *Laxae*
    Section *Cassinoides*
    Section *Dasyneurae*
    Section *Crassifoliae*
  Series B. *Paltoria*
    Section *Polyphyllae*
    Section *Vacciniifoliae*
  Series C. *Aquifolium*
    Section *Lemurenses*
    Section *Aquifolioides*
      Subsection *Oxyodontae*
      Subsection *Insignis*
    Section *Microdontae*
      Subsection *Eumicrodontae*
      Subsection *Repandae*
      Subsection *Vomitoriae*
      Subsection *Stigmatophorae*
      Subsection *Sideroxyloides*
    Section *Prinifoliae*
    Section *Megalae*
    Section *Micranthae*
    Section *Rugosae*
  Series D. *Thyrsoprinus*
    Section *Indico-Malaicae*
    Section *Thyrsiflorae*
    Section *Brachythyrsae*
Subgenus *Prinus*
  Series A. *Euprinus*
  Series B. *Prinoides*

For a better understanding of Loesener's ideas of infrageneric relationships and special-ization level a copy of his phylogenetic tree (1908) is given in fig. 31. At that time Loesener did not yet know the opposite-leaved species, which prompted him to erect the new subgenus *Rybonia* in 1942. It is interesting to note that Loesener's visual representation of his ideas about infrageneric classification is less rigid than his formal recognition of sub-genera, sections, and intercalated 'series'. It shows for instance that some sections from different series are in fact closer to each other than to sections from the same series in subgenus *Euilex*, and that section *Indico-Malaicae*, though treated in subgenus *Euilex* was thought to be derived from the same ancestors as subgenus *Byronia*.

Specific descriptions and taxonomic notes

Explanatory note

In the specific descriptions only positive characters have been recorded. Absence of hairs, of subdivisions in the epidermal cells, of mucilage cells, of a continuous hypodermis, of idioblastic sclereids, of marginal sclerenchyma strands, and the unlignified condition of the abaxial epidermis, the bundle sheaths and the

Fig. 31. Loesener's phylogenetic tree for *Ilex* (copied from Loesener, 1908: 94). Infrageneric taxa above the broken line correspond with extant groups. All sections derived from the 'main trunk' (*Proto-Ilex*) and section *Indico-Malaicae* belong to subgenus *Euilex*.

spongy tissue are not recorded in the descriptions. Likewise the lignification or mucilaginous nature of the hypodermis is only recorded if positively present; in case the hypodermis consists of ordinary translucent cells this is not specified in the descriptions. Only if a hypodermis is continuous over the whole adaxial side of the lamina, this character is included in the descriptions. Many species of *Ilex* show a local differentiation of hypodermis over the midrib, but this condition is not recorded. Cork warts are only recorded if they are of regular outline and of frequent occurrence. Occasional deviations from the above-mentioned adopted procedure are thought to be self-explanatory. For stomatal size average values per specimen will be given only; not the full range. The petiole types correspond with fig. 18.

Occasionally data have been recorded about the outline of the walls of unspecialized epidermal cells; this has only been done for strongly undulating walls and straight walls. In the remaining instances of curved to undulated walls the degree of undulation has been proved to have no diagnostic value in a number of species (p. 400), and therefore no data on cell wall outline as seen in surface view has been included for those species. Other characters, which appeared to be very variable below the species level in a number of cases (see p. 400) are also left out of the descriptions.

The notes on the individual species should in most cases be regarded as very tentative suggestions. I am very well aware that leaf anatomical resemblance need not be indicative of natural affinity in several instances. Yet, it is hoped that the notes will be of interest for future taxonomic work on *Ilex*. Since I have not considered macromorphological characters, I am sure that several of my suggestions will not be supported, but if only part of the suggestion leads to a better insight in the infrageneric relationships, the purpose of the taxonomic notes will have been served.

If reference is made to suggestions by Loesener, his monograph of 1901 is quoted, unless stated otherwise. Species not known to Loesener in 1908 are cited with full reference.

Ilex altaclarensis (Loud.) Dall. 'camelliaefolia' = *I. aquifolium x perado* (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Oxyodontae*) — Plate II, 6

Lamina 410 μm. Adaxial and abaxial cuticle 10 μm. Sparse unicellular hairs on midrib and petiole. Stomata bicyclic, 38 × 36 μm. Adaxial epidermal cells with frequent anticlinal subdivisions. Hypodermis of 1 cell layer. Marginal sclerenchyma strand. Petiole with simple open vascular system (type 3).

Material studied. NETHERLANDS: cult. hort. Leiden.

N o t e . This specimen is very similar to *I. aquifolium, I. bioritsensis, I. cornuta, I. dipyrena, I. integra, I. perado,* and *I. pernyii* with which it shares the marginal sclerenchyma strands and bicyclic stomata together with numerous less outstanding anatomical features.

Ilex amara (Vell.) Loes. var. **longifolia** Reiss. (subg. *Euilex,* series D, sect. *Brachythyrsae*) — Plate II, 1; IV, 1

Lamina 270 μm. Adaxial cuticle 5 μm; abaxial cuticle 3 μm. Sparse unicellular hairs on midrib and petiole. Stomata mainly anomocytic, but also tending to cyclocytic or rarely anisocytic, 26 × 21 μm. Lignified abaxial epidermis (including neighbouring/subsidiary cells and guard cells). Cork warts. Bundle sheaths and part of spongy tissue strongly birefringent. Petiole with simple open vascular system (type 4).

Material studied. BRAZIL. Santa Catarina: *Reitz & Klein 3932.*

N o t e . Anatomically there are similarities with the American species *I. boliviana, I. dumosa, I. ovalifolia, I. martiniana,* and *I. retusa,* mainly through the shared lignified epidermis and regular cork warts. *I. triflora* from Malesia also resembles *I. amara* in this respect.

Ilex amelanchier Curt. (subg. *Prinus,* series B) — Plate IV, 2; fig. 5, 10

Lamina 90 μm. Adaxial and abaxial cuticle *c.* 1 μm. Indumentum of slender 2-cellular hairs with warty cuticle on lower leaf surface. Stomata anomocytic to cyclocytic, 20 × 19

μm. Adaxial epidermis with slightly bulging mucilage cells. Petiole with simple open vascular system (type 1—2).

Material studied. U.S.A.: cult. Arn. Arbor. *14740* (=herb. *Boom 40305*).

N o t e. The only outstanding character of *I. amelanchier* is the indumentum of long, uniseriate, warty hairs. The thin, anatomically rather featureless mesomorphic leaves are also characteristic for the other species of subgenus *Prinus* and some other, miscellaneous species.

Ilex amplifolia Rusby (subg. *Euilex*, series A, sect. *Excelsae*, subsect. *Laxae*) — **Plate IV, 3**
Lamina 230 μm. Adaxial cuticle *c.* 4 μm; abaxial cuticle *c.* 2 μm. Stomata cyclocytic, 34×29 μm. Epidermal cells with strongly undulating walls. Adaxial epidermis with anticlinal subdivisions and containing bulging mucilage cells. Cork warts. Petiole with simple open vascular system (type 4).

Material studied. BOLIVIA: *Krukoff 11198* (U).

N o t e. Leaf anatomy does not provide clues for affinities of this dubiously placed species (cf. Loesener, 1901: 129). The other species of sect. *Excelsae* I studied all lack regular cork warts.

Ilex anomala Hook. & Arn., incl. f. **sandwicensis** (Endl.) Loes. and f. **taitensis** (Gray) Nadaud (subg. *Byronia*, series A) — **Plate IV, 8; V, 5**
Lamina 300—500 μm. Adaxial cuticle 6—9 μm; abaxial cuticle 3—7 μm. Stomata anomocytic to cyclocytic, 29×26—41×35 μm (several intermediate sizes present!). Adaxial epidermis with anticlinal subdivisions. Hypodermis of 1—3 layers of bulging mucilaginous cells. Bundle sheaths lignified. Irregular crystalline bodies of unidentified composition in hypodermis of *OAHU 198*. Petiole with simple open vascular system (type 4). In midrib simple closed system (type 6) present in *Van Balgooy 1689* only.

Material studied. HAWAII (f. *sandwicensis*): *OAHU 198; Heller 2735.* — TAHITI (f. *taitensis*): *Van Balgooy 1689; Vesco 1847.*

N o t e. The mucilaginous hypodermis in *I. anomala* is the most striking feature of this species. A slightly similar but less well-developed hypodermis occurs in *I. brasiliensis* and *I. tuerckheimii* which, however, differ in several other respects. Stomatal size, vascularization of midrib and petiole, and outline of midrib in transverse section vary strongly within this species without, however, showing a correlation with the two geographical forms. Anatomically (also according to the wood, Baas, 1973) this species seems rather isolated.

Ilex aquifolium L., incl. f. **bacciflava** (West.) Rehder, f. **ferox** (Ait.) Schneider, and f. **heterophylla** (Ait.) Loes. (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Oxyodontae*) — **Plate III, 5**
Lamina 430—470 μm. Adaxial cuticle 5—8 μm; abaxial cuticle 7—10 μm. Sparse unicellular hairs on midrib and petiole. Stomata bicyclic, 34×33—36×36 μm. Adaxial epidermis with anticlinal subdivisions. Hypodermis of 1 cell layer. Marginal sclerenchyma strand. Petiole with simple open vascular system (type 3—4).

Material studied. MOROCCO: *De Wilde & Dorgelo 2528.* — NETHERLANDS (f. *bacciflava*, f. *ferox*, and f. *heterophylla*): cult. hort. Leiden.

N o t e . *I. aquifolium* is anatomically very close to *I. altaclarensis, I. bioritsensis, I. cornuta, I. dipyrena, I. integra, I. perado,* and *I. pernyi* (see note under *I. altaclarensis*). In spite of the great diversity of external leaf morphology, the anatomical characters are on the whole very constant.

Ilex archboldiana Merr. & Perry, J. Arn. Arb. 22 (1941) 259 (? Subg. *Euilex,* series C, sect. *Rugosae*) — **Plate IV, 5; fig. 13**

Lamina 400 μm. Adaxial cuticle 6—7 μm; abaxial cuticle 3—5 μm. Stomata cyclocytic to anomocytic, occasionally anisocytic, 32 × 27 μm. Adaxial epidermis with anticlinal and periclinal subdivisions, containing mucilage cells. Bundle sheaths and part of spongy tissue lignified. Petiole with simple open vascular system (type 3).

Material studied. New Guinea. Mt. Giluwe: *Schodde 1904.*

N o t e . This species does not show unusual anatomical features. Anatomy supports Merrill & Perry's (l.c.) statement that this species is close to *I. versteeghii,* with which it shares many characters, e.g. the xeromorphic features of thick leaves and partly lignified spongy tissue and lignified bundle sheaths.

Ilex argentina Lillo, An. Soc. Cient. Argent. 72 (1910) 171 (subg. *Euilex,* series C, sect. *Microdontae,* subsect. *Repandae*) — **Plate IV, 6; fig. 15**

Lamina 220 μm. Adaxial cuticle 3 μm; abaxial cuticle 2 μm. Stomata mainly cyclocytic, occasionally bicyclic, 28 × 27 μm. Abaxial epidermis with lignified unspecialized cells and strongly undulating anticlinal walls. Adaxial epidermis with anticlinal and periclinal subdivisions, with large bulging mucilage cells. Bundle sheaths sometimes strongly birefringent. Petiole with simple open vascular system (type 4).

Material studied. Argentina. Tucuman: *Vervoorst 6834.*

N o t e . The lignified abaxial epidermis, strongly sinuous anticlinal walls of the abaxial epidermis, and partly bicyclic stomata make this species rather outstanding. Lillo (l.c.) suggested a close affinity with *I. paraguariensis* from which it differs, however, in several leaf anatomical characters. Of the other species with a lignified epidermis, *I. canariensis* resembles *I. argentina* most closely. This may, however, be entirely due to parallel developments in rather unrelated species.

Ilex asprella (Hook. et Arn.) Champ. (subg. *Prinus,* series B)

Lamina 130 μm. Adaxial cuticle 2—3 μm; abaxial cuticle 1—2 μm. Stomata anomocytic to cyclocytic, 37 × 29 μm. Epidermal cells with strongly undulating walls. Adaxial epidermis with periclinal subdivisions, and containing bulging mucilage cells. Petiole with simple open vascular system (type 1).

Material studied. Philippines: *PNH 21584.*

N o t e . This species agrees well with other species studied in subgenus *Prinus.* Loesener's suggestion of a close affinity with *I. longipes* Chapm. from N. America is therefore also supported by leaf anatomy.

Ilex bioritsensis Hayata, J. Coll. Sc. Tokyo 30 (1911) 53 (subg. *Euilex,* series C, sect. *Aquifolioides,* subsect. *Oxyodontae*) — **Plate V, 6**

Lamina 360 μm. Adaxial cuticle 9 μm; abaxial cuticle 6 μm. Indumentum of sparse unicellular hairs confined to petiole in *cult. Leiden*, abundant on adaxial side of midrib and lateral veins in *Boom 13379*. Stomata cyclocytic to bicyclic, 27 × 27 μm. Marginal sclerenchyma strand. Petiole with simple open vascular system (type 3).

Material studied. NETHERLANDS: cult. Dedemsvaart (= Herb. *Boom 13379*) and cult. hort. Leiden.

N o t e. Hayata's remark (l.c.) that *I. bioritsensis* is very close to *I. pernyi* is fully supported by the leaf anatomical characters. See also notes under *I. aquifolium* and *I. altaclarensis*. *I. bioritsensis* is native in Formosa.

Ilex boliviana Britton (subg. *Euilex*, series A, sect. *Dasyneurae*)
Lamina 200 μm. Adaxial cuticle *c.* 25 μm; abaxial cuticle 6—7 μm. Sparse unicellular hairs on petiole and midrib. Stomata cyclocytic, 26 × 26 μm. Abaxial epidermis with lignified unspecialized cells. Adaxial epidermis with straight walls. Cork warts. Bundle sheaths lignified. Many veins vertically transcurrent. Petiole with simple open vascular system (type 4).

Material studied. BOLIVIA: *Britton & Rusby 450*.

N o t e. Leaf anatomically this species resembles *I. amara, I. martiniana, I. ovalifolia, I. retusa*, and *I. triflora* which share the frequent cork warts and lignified epidermis. *I. boliviana* stands out, however, by its extremely scleromorphic anatomy with massive sclerenchyma girders linking many of the vascular bundles with upper and lower epidermis, and by a very thick cuticle.

Ilex brasiliensis (Spreng) Loes. var. **pubiflora** (Reiss.) Loes. (subg. *Euilex*, series C, sect. *Megalae*, subsect. *Pedicellatae*) — Plate I, 1 and 2; fig. 4
Lamina 270 μm. Adaxial cuticle 4 μm; abaxial cuticle 1—2 μm. Long slender hairs with thick basal septs abundant on both leaf surfaces. Stomata cyclocytic to anomocytic, 26 × 21 μm. Adaxial epidermis with anticlinal subdivisions. Hypodermis of 1 layer of bulging, probably mucilaginous, cells. Petiole with simple open vascular system (type 4).

Material studied. BRAZIL: *Lindeman & De Haas 3367* (U).

N o t e. It is difficult to classify the subepidermal adaxial cell layer as either part of a multiple epidermis or as a 'true' hypodermis. The alignment of the bulging subepidermal cells is most suggestive of a multiple epidermis. The uniseriate hairs, with several to many septa of which the basal sept is usually much thicker than the others, constitute a distinctive feature of this species. Loesener's suggestion of an affinity with *I. theezans* agrees more or less with leaf anatomy.

Ilex brassii Merr. & Perry, J. Arn. Arb. 20 (1939) 334 (? subg. *Byronia*, series A)
Lamina 220 μm. Adaxial cuticle 3 μm; abaxial cuticle 1—2 μm. Stomata anisocytic, 27 × 20 μm. Adaxial epidermis with anticlinal and periclinal subdivisions, containing bulging mucilage cells. Bundle sheaths and part of spongy tissue lignified. Some fusiform sclereids in ground tissue of midrib. Petiole with simple open vascular system (type 4).

Material studied. NEW GUINEA: *Brass 7686*.

N o t e. Merrill and Perry's remark (l.c.) that *I. brassii* resembles *I. ledermannii* is supported by leaf anatomy, although both species do not show very outstanding distinc-

tive characters. Similar leaf histologies occur in e.g. *I. cymosa, I. laurifolia, I. macrophylla, I. sclerophylloides,* and *I. wallichii* from Malesia. There are also similarities with the New World species *I. integerrima* and *I. sideroxyloides.* All these species have predominantly anisocytic stomata and mostly lignified spongy tissue and bundle sheaths. Strongest resemblance is with *I. laurifolia* which shares with *I. brassii* the occurrence of occasional thick-walled fibres in the peripheral abaxial ground tissue of the midrib. *I. laurifolia* was, however, placed in subgenus *Euilex* by Loesener. This leaves the problem of where to place *I. brassii* unsettled.

Ilex brevicuspis Reiss. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Eumicrodontae*)

Lamina 130 μm. Adaxial cuticle 1—3 μm; abaxial cuticle 1—2 μm. Sparse irregularly curved, unicellular hairs on midrib. Stomata cyclocytic, sometimes irregular, 22 × 20 μm. Petiole with simple open vascular system (type 4).

Material studied. BRAZIL. Santa Catarina: *Smith & Klein 11440.*

N o t e . This species does not show outstanding features. Through its mesomorphic leaves it resembles species from subgenus *Prinus*, but this may be taxonomically insignificant.

Ilex brunnea Merr., Philip. J. Sc. Bot. 10 (1915) 318 (subg. *Euilex*, series D, sect. *Indico-Malaicae*)

Lamina 300 μm. Adaxial cuticle 6 μm; abaxial cuticle 9 μm. Stomata mainly anisocytic also tending to cyclocytic, 32 × 21 μm. Adaxial epidermis with periclinal subdivisions and bulging mucilage cells. Petiole with simple open vascular system (type 4).

Material studied. PHILIPPINES: *Arn. Arbor. 34404* (=*Edaño s.n.*).

N o t e . None of the leaf anatomical characters of *I. brunnea* are very outstanding. Merrill's placement (l.c.) in section *Indico-Malaicae* cannot be supported or challenged using leaf anatomy, though there is some resemblance with *I. cissoidea* and *I. stapfiana,* also from this section. However, other species from different sections or even subgenera like *I. cymosa, I. krugiana, I. laurifolia, I. macrophylla, I. rotunda, I. sebertii,* and *I. theezans* show similar or stronger resemblance in leaf anatomy with *I. brunnea.*

Ilex buergeri Miq. f. **rolfei** (Elm.) Loes. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Repandae*) — **Plate V, 1—3**

Lamina 190 μm. Adaxial cuticle 6 μm; abaxial cuticle 4—5 μm. Sparse unicellular hairs on midrib and petiole. Stomata cyclocytic, occasionally bicyclic, 28 × 28 μm. Bundle sheaths partly fibrous and lignified. Sclereids abundant throughout mesophyll. Petiole with simple open vascular system (type 2).

Material studied. PHILIPPINES: *BS 40633.*

N o t e . The abundant fusiform sclereids in the leaf mesophyll constitute the most striking feature of this species. Similarities with other species showing sclerenchyma idioblasts (*I. curranii, I. ficoidea, I. formosana, I. glomerata,* and *I. mitis*) are very striking. Of these species, Loesener included *I. ficoidea, I. formosana,* and *I. glomerata* in the same subsection. *I. mitis* is, however, from an other section. There are also similarities with some species lacking sclereids, notably *I. dipyrena, I. fargesii, I. goshiensis, I. integra,* and *I.*

tolucana. Of these *I. goshiensis* and *I. tolucana* are in the same section as *I. buergeri*, the others are from different sections but are yet all from series C. *Aquifolium* of subgenus *Euilex.*

Ilex canariensis Poir. (subg. *Euilex*, series A, sect. *Cassinoides*)

Lamina 320 μm. Adaxial cuticle 4—5 μm; abaxial cuticle 6 μm. Stomata cyclocytic, 39 × 35 μm, anticlinal walls of unspecialized epidermal cells strongly undulating. Abaxial epidermis with lignified unspecialized cells in *Bornmueller 414* only. Adaxial epidermis with periclinal subdivisions and bulging mucilage cells. Petiole with simple open vascular system (type 4).

Material studied. MADEIRA: *Bornmueller 414.* — PALMA: *Cool & Den Tex 681* (sections only). — TENERIFFE: *Pitard s.n.* (26—1—1905).

N o t e. In some parts of the lamina of *Bornmueller 414* a portion of the unspecialized epidermal cells is lignified, this is not so in *Cool & Den Tex 681* and *Pitard s.n.*, once more exemplifying the absence of absolutely diagnostic anatomical characters in the majority of *Ilex* species. In other respects the three specimens resemble each other very closely. Anatomically there is some resemblance with *I. argentina* and *I. cassine*. The species is very distinct from *I. perado* in both leaf and wood anatomy (see also Baas, 1973: 228), in spite of the same biotope they inhabit. Thévenard (1906) reported multicellular hairs and small cork warts for *I. canariensis*, but I did not find these.

Ilex caroliniana (Lam.) Loes.; *I. vomitoria* Ait. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Vomitoriae*)

Lamina 260 μm. Adaxial cuticle 3—5 μm; abaxial cuticle 1—2 μm. Unicellular hairs on lamina and petiole fairly abundant adaxially, sparse abaxially. Stomata mainly cyclocytic, occasionally anisocytic, 25 × 23 μm. Adaxial epidermis with periclinal subdivisions and bulging mucilage cells. Cork warts. Petiole with simple open vascular system (type 2).

Material studied. U.S.A. Oregon: *Suhsdorf s.n.* (4—1909).

N o t e. Except for the rather numerous small cork warts, there are no outstanding leaf anatomical characters in this species. *I. coriacea*, *I. divaricata*, *I. glabra*, and *I. pedunculosa* share many characters with *I. caroliniana*. Of these only *I. divaricata* is of the same section.

Ilex cassine L. incl. var. **angustifolia** Ait., and var. **myrtifolia** (Walt.) Chapman (subg. *Euilex*, series A, sect. *Cassinoides*) — Plate III, 1 and 2

Lamina 400 μm. Adaxial cuticle 6 μm; abaxial cuticle 3—4 μm. Fairly long, occasionally septate hairs abundant on midrib and petiole, sparse over whole abaxial surface. Stomata mainly cyclocytic, occasionally anisocytic, 31 × 26 μm. Anticlinal walls of epidermal cells strongly undulating. Abaxial epidermis with lignified unspecialized cells. Subsidiary cells rarely lignified (Plate III, 2). Adaxial epidermis with anticlinal and periclinal subdivisions, and bulging mucilage cells. Petiole with simple open vascular system (type 4).

Material studied. U.S.A. cult. Florida: *Boom 38139* (var. *angustifolia*); N. Carolina: *Schallert s.n.* (var. *myrtifolia*, maceration only).

N o t e. *I. canariensis p.p.* and *I. opaca* of the same section also have a lignified abaxial epidermis; of these two species *I. opaca* resembles *I. cassine* most closely in overall leaf

anatomy. Thévenard (1906) recorded solitary crystals for this species, but I could only find clustered ones.

Ilex celebensis Capit., Bull. Soc. Bot. France 57 (1910) 236 (subg. *Byronia*, series A)
    Lamina 180 μm. Adaxial cuticle 6—7 μm; abaxial cuticle 3 μm. Sparse unicellular hairs on midrib and petiole. Stomata mainly cyclocytic, occasionally bicyclic, 25 × 23 μm. Bundle sheaths partly fibrous and lignified. Part of spongy tissue rather strongly birefringent but probably not lignified. Minute crystals in adaxial epidermis. Petiole with simple open vascular system (type 2).
    Material studied. CELEBES: *Teysmann 14119*.

N o t e. Capitaine's suggestion (l.c.) of affinities with both *I. sandwicensis* (= *I. anomala*) and *I. cymosa* is not supported by leaf anatomy because of differences in hypodermal development and stomatal type respectively. It is, however, impossible to give alternative suggestions on the grounds of leaf anatomy.

Ilex chinensis Sims; *I. purpurea* Hassk. (subg. *Euilex*, series A, sect. *Excelsae*, subsect. *Umbelliformes*)
    Lamina 240 μm. Adaxial and abaxial cuticle 2 μm. Sparse unicellular hairs on midrib. Stomata cyclocytic, rarely bicyclic, 22 × 21 μm. Adaxial epidermis containing some bulging mucilage cells. Petiole with simple open (type 4) to almost closed vascular system. In midrib completely closed (type 6).
    Material studied. CHINA. Hunan: *Fan & Li 549*.

N o t e. Loesener's suggestion of an affinity with *I. pedunculosa* is not fully supported by leaf anatomy because of petiole anatomy and several other characters. Other affinities are hard to indicate, but affinities with *I. kwantungensis*, suggested by Hu (1950) can be supported.

Ilex cissoidea Loes. (subg. *Euilex*, series D, sect. *Indico-Malaicae*) — **Plate I, 3 and 4 fig. 6**
    Lamina 100 μm. Adaxial cuticle 3 μm; abaxial cuticle 2 μm. Broad-based hairs abundant on both surfaces; hairs frequently with anticlinal division wall in basal part (fig. 6). Stomata anisocytic to cyclocytic, 26 × 21 μm. Adaxial epidermis with anticlinal subdivisions. Bundle sheaths and mesophyll rather strongly birefringent. Petiole with simple open vascular system (type 4).
    Material studied. BORNEO: *Endert 1732*.

N o t e. The indumentum of broad-based hairs is the only outstanding feature in the leaf anatomy of this species. Similar hairs occur in *I. oppositifolia* and *I. revoluta*, also from Borneo. These species differ, however, in a considerable number of other leaf anatomical features from *I. cissoidea*. The other species of section *Indico-Malaicae* studied (*I. spicata*, *I. clemensiae*, and *I. stapfiana*) are also quite different from *I. cissoidea*. *I. brunnea* treated in this section by Merrill shares, however, quite a number of characters, but on the whole the leaf anatomical evidence is inconclusive with regard to relationships with other species.

Ilex clemensiae Heine, Mitt. Bot. Staatssaml. München I, 6 (1953) 208 (subg. *Euilex*, series D, sect. *Indico-Malaicae*) — **Plate II, 4**

Lamina 220 μm. Adaxial and abaxial cuticle 9—12 μm. Sparse unicellular hairs on midrib and petiole. Stomata anisocytic to cyclocytic, frequently tending to complex, 38 × 29 μm. Adaxial epidermis with infrequent periclinal subdivisions and mucilage cells. Cork warts. Bundle sheaths lignified. Petiole with interrupted open vascular system (type 5).

Material studied. N. BORNEO. Mt. Kinabalu: *Clemens 50259.*

N o t e. Frequent cork warts and an abaxially open vascular system in petiole and midrib are the more striking characters of this species which was put in section *Indico-Malaicae* by Heine (l.c.). However, within this section no species with a great leaf anatomical resemblance to *I. clemensiae* was encountered, nor can other candidates for close affinity be indicated on the basis of leaf anatomical characters.

Ilex confertiflora Merr., Lingnan Sc. J. 13 (1934) 35 (subg. *Euilex*, series C, sect. *Micro-dontae*, subsect. *Repandae*)
    Lamina 300 μm. Adaxial and abaxial cuticle 5—6 μm. Stomata anisocytic to cyclocytic, occasionally complex, 23 × 23 μm. Spongy tissue partly strongly birefringent. Few irregular sclereids associated with but tending to be detached from sclerenchyma caps of veins. Very small marginal sclerenchyma strand, occasionally associated with vascular elements. Petiole with simple open vascular system (type 3).

Material studied. CHINA. Kwantung: *Tsang 20347.*

N o t e. Merrill's suggestion (l.c.) of affinities with *I. ficoidea*, as supported by Hu (1950), are in agreement with the leaf anatomical evidence because of the presence of foliar sclereids. *I. confertiflora* at the same time provides a leaf anatomical link with subsection *Oxyodontae* of section *Aquifolioides* through the presence of marginal sclerenchyma.

Ilex coriacea (Pursh) Chapm. (subg. *Euilex*, series A, sect. *Cassinoides*) — **Plate IV, 4**
    Lamina 260 μm. Adaxial cuticle 16 μm; abaxial cuticle 12 μm. Sparse unicellular hairs on midrib and petiole. Stomata cyclocytic to anomocytic, 27 × 26 μm. Adaxial epidermis with anticlinal and periclinal subdivisions, containing idioblastic bulging mucilage cells. Cork warts of characteristic shape. Petiole with 'double' vascular system (type 10).

Material studied. U.S.A. Georgia: *Beyrick 926.*

N o t e. Affinities with *I. canariensis*, *I. cassine*, and *I. glabra* as suggested by Loesener are supported by leaf anatomy only for *I. glabra*, which shares the petiole vascularization type and frequent (though slightly different) cork warts. Cork warts similar to those in *I. coriacea* occur in *I. macfadyenii* from Jamaica, which differs, however, in several minor leaf anatomical characters.
    Thévenard (1906) reported an almost continuous hypodermis for *I. coriacea* (under the synonym *I. lucida* Torr & Gray), but in *Beyrick 926* there are only sporadic subdivisions with mucilage cells in the epidermis.

Ilex cornuta Lindl. & Paxt. 'Burfordii' (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Oxyodontae*)
    Lamina 400 μm. Adaxial cuticle 12 μm; abaxial cuticle 5—6 μm. Sparse unicellular hairs on midrib and petiole. Stomata cyclocytic and bicyclic, 28 × 27 μm. Few irregular sclereids associated with, but tending to be detached from sclerenchyma caps of veins. Marginal sclerenchyma strand. Petiole with simple open vascular system (type 3).

Material studied. EGYPT. Cairo, cult. Wight nurseries: *Boom 38771.*

N o t e . This species clearly belongs to one group with *I. altaclarensis, I. aquifolium, I. bioritsensis, I. dipyrena, I. integra, I. perado,* and *I. pernyi,* all from subsection *Oxyodontae.* There are also similarities with *I. fargesii* from section *Lemurensis,* and with species having foliar sclereids.

Ilex crenata Thunb. (subg. *Euilex,* series B, sect. *Polyphyllae*)
Lamina 230 μm. Adaxial cuticle 8 μm; abaxial cuticle 7 μm. Sparse unicellular hairs on midrib and petiole. Stomata cyclocytic, 27 × 27 μm. Adaxial epidermis with periclinal subdivisions and bulging mucilage cells. Cork warts. Petiole with simple open vascular system (type 3).

Material studied. NETHERLANDS: cult. hort. Leiden; see also below.

N o t e . Besides the cultivated specimen cited above, 10 others were studied (of 9 specimens macerations only), because one deviating specimen of *I. crenata* var. *luzonica* Loes. (Moluccas, Ceram, *Eyma 2044*) showed lignified epidermal cells and also differed in a number of other leaf characters. In the remaining material no lignified epidermal cells were found, which indeed casts doubt on the identification of *Eyma 2044.* All specimens were constant for the occurrence of cork warts. The stomatal type ranged from almost exclusively cyclocytic, to anomo- to cyclocytic, or aniso- to cyclocytic. Remarkably enough the aberrant Eyma collection resembles the other species studied of section *Polyphyllae: I. dumosa* from Brazil, mainly through the shared lignified cells in the abaxial epidermis.

Ilex curranii Merr., Philip. J. Sc. 17 (1920) 273 (subg. *Euilex,* series C, sect. *Microdontae,* subsect. *Repandae*)
Lamina 230 μm. Adaxial cuticle 6 μm; abaxial cuticle 4 μm. Sparse unicellular hairs on midrib and petiole. Stomata cyclocytic, occasionally bicyclic, 38 × 28 μm. Bundle sheaths partly fibrous and lignified. Sclereids fusiform and moderately branched, partly associated with sclerenchyma caps of veins, abundant in adaxial part of mesophyll. Petiole with simple open vascular system (type 3).

Material studied. PHILIPPINES. Luzon: *PNH 7569.*

N o t e . Merrill (l.c.) originally placed *I. curranii* in section *Rugosae,* but Loesener (1942) rightly treated it as a member of subsection *Repandae,* where this species obviously belongs with its abundant foliar sclereids and many other features witnessing affinity.

Ilex cymosa Bl.; *I. pleiobrachiata* Loes. (subg. *Byronia,* series A)
Lamina 150—270 μm. Adaxial cuticle 1—5 μm; abaxial cuticle 1—4 μm. Indumentum absent or of sparse to fairly numerous unicellular hairs over whole abaxial surface, and on adaxial side of midrib and on petiole. Stomata mainly anisocytic, but a variable proportion tending to cyclocytic, 21 × 18 to 29 × 23 μm. Adaxial epidermis with or without periclinal subdivisions, usually but not in all specimens with mucilage cells. Bundle sheaths lignified. Part of spongy tissue usually lignified, except in *Kep. Field No. 71108.* Petiole usually with simple open vascular system (type 4), but with complex closed system in *Wirawan 194* (type 8).

Material studied. MALAYA: *Kep. Field No. 71108; Sinclair 10813.* — SINGAPORE: *Sing. Field No. 38887 (coll. Sinclair).* — BORNEO: *Kostermans 9235; SAN 48518.* —JAVA: *Wirawan 194.* — SUMATRA: *Dumas 1650.*

N o t e. The variation encountered in these seven specimens is very large. Hardly any of the characters is constant. Because of this strong variability it is possible to indicate many species with a high degree of similarity to *I. cymosa* specimens, but the distribution of those species over the different subgenera recognized by Loesener is virtually random, suggesting that these similarities have no taxonomic significance. This is what one would expect, since none of the leaf anatomical characters predominantly occurring in *I. cymosa* are unusual within *Ilex*. Within subgenus *Byronia*, there are good similarities with *I. ledermannii*, *I. macrophylla*, *I. sclerophylloides*, and *I. wallichii*.

The identity of the material studied was kindly checked by Prof. Van Steenis. The leaf anatomical variation is not correlated with the grouping of specimens as belonging to *I. cymosa* or *I. pleiobrachiata* according to Loesener's specific delimitation. The most striking example of variability is offered by the vascularization of the petiole, which is of a complex type in one specimen only.

Ilex danielis Killip & Cuatrec., Trop. Woods 101 (1955) 14 (subg. *Euilex*, series C, sect. *Micranthae*, subsect. *Epunctatae*)

Lamina 600 μm. Adaxial cuticle 14 μm; abaxial cuticle 4 μm. sparse unicellular hairs on adaxial side of midrib and major veins. Stomata cyclocytic, sometimes tending to anomocytic, 25 × 22 μm. Adaxial epidermis with occasional periclinal subdivisions and idioblastic bulging mucilage cells. Petiole with simple open vascular system (type 4).

Material studied. Colombia: *Hatheway 1602.*

N o t e. This species shows no features outstanding in *Ilex*, and the anatomical evidence is therefore rather neutral with regard to the systematic placement adopted here, following Killip and Cuatrecasas' (l.c.) suggestion of close affinities with *I. guianensis*. From the latter species and other species of subsection *Epunctatae* studied, *I. danielis* differs, however, in stomatal type.

Ilex decidua Walt. (subg. *Prinus*, series B)

Lamina 140 μm. Adaxial cuticle 2—3 μm; abaxial cuticle 1—2 μm. Sparse 2-cellular hairs with fairly broad base and thick basal partition wall on midrib and petiole. Stomata mainly anomocytic, occasionally tending to cyclocytic or anisocytic, 27 × 21 μm. Adaxial epidermis with occasional periclinal subdivisions, possibly also with mucilaginous cells. Petiole with simple open vascular system (type 1 in basal part, type 3 in distal part).

Material studied. U.S.A. Texas: *Heller & Heller 2414.*

N o t e. As most species of subgenus *Prinus*, this mesomorphic species does not show outstanding anatomical features.

Ilex dipyrena Wall. (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Oxyodontae*)

Lamina 400 μm. Adaxial cuticle 8—9 μm; abaxial cuticle 7—8 μm. Sparse unicellular hairs on petiole and midrib. Stomata cyclocytic and bicyclic, 31 × 29 μm. Epidermal cells with straight anticlinal walls. Marginal sclerenchyma strand. Petiole with simple open vascular system (type 3).

Material studied. Himalaya: *Heybroek 173.*

N o t e. With its partly bicyclic stomata and well-developed marginal sclerenchyma

strand, *I. dipyrena* clearly belongs to the same group of species as *I. aquifolium, I. bioritsensis, I. cornuta, I. integra, I. perado,* and *I. pernyi.*

Ilex divaricata Mart. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Sideroxyloides*)

Lamina 300 μm. Adaxial cuticle 9 μm; abaxial cuticle 4—5 μm. Sparse unicellular hairs on petiole and midrib. Stomata mainly cyclocytic, occasionally tending to anisocytic or anomocytic, 29 × 23 μm. Epidermal cells with straight anticlinal walls. Adaxial epidermis with periclinal division walls and bulging mucilage cells. Cork warts. Petiole with simple open vascular system (type 4).

Material studied. VENEZUELA: *Maguire, Rowan & Wurdack 30735* (U).

N o t e . According to Loesener this species is close to *I. sideroxyloides*. This is not supported by leaf anatomy, mainly because of differences in stomatal type and occurrence of regular cork warts. Similarities with other species (e.g. *I. coriacea, I. danielis, I. theezans,* and *I. tuerckheimii*) are not based on any unusual characters and therefore do not provide strong evidence of mutual affinity.

Ilex dubia (Don) Trel. var. **mollis** (Gray) Loes.; *I. montana* Torr. & Gray (subg. *Prinus*, series B)

Lamina 110 μm. Adaxial and abaxial cuticle *c.* 1 μm. Indumentum of long unicellular, occasionally septate, hairs with a striated cuticle abundant on adaxial side of midrib and lateral veins, also present on petiole. Stomata cyclocytic to anomocytic, 27 × 25 μm. Adaxial epidermis with bulging (probably mucilaginous) cells. Petiole with simple open vascular system (type 4).

Material studied. U.S.A. N. Carolina: *Stauffer c.s. 5958.*

N o t e . As in most other species of subgenus *Prinus* the leaves are mesomorphic and without outstanding anatomical features.

Ilex dumosa Reiss. (subg. *Euilex*, series B, sect. *Polyphyllae*)

Lamina 190 μm. Adaxial cuticle 6 μm; abaxial cuticle 3 μm. Sparse unicellular hairs on petiole. Stomata anomocytic to cyclocytic, 28 × 23 μm. Abaxial epidermis with lignified unspecialized cells. Bundle sheaths strongly birefringent. Petiole with simple open vascular system (type 3).

Material studied. BRAZIL. Parana: *Dusén 11076.*

N o t e . Through its lignified abaxial epidermis, this species resembles the aberrant specimen of *I. crenata* var. *luzonica*. Similarities are also present with *I. amara* and *I. boliviana* of different sections and series.

Ilex fargesii Franch. (subg. *Euilex*, series C, sect. *Lemurenses*)

Lamina 280 μm. Adaxial cuticle 6 μm; abaxial cuticle 4—5 μm. Stomata cyclocytic, occasionally bicyclic, 29 × 28 μm. Petiole with simple open vascular system (type 1 in basal part; type 3 in distal part).

Material studied. NETHERLANDS. cult. Wageningen: *Boom 30300.*

N o t e . Although this species lacks foliar sclereids, there are good leaf anatomical similarities with *I. mitis*, which Loesener regarded to be a related species.

Ilex ficoidea Hemsl. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Repandae*)

Lamina 210 & 230 μm. Adaxial cuticle 4—6 μm; abaxial cuticle 2—4 μm. Indumentum absent or of sparse unicellular hairs on midrib and petiole. Stomata cyclocytic, tending to bicyclic, 29×27 & 31×30 μm. Sclereids fusiform and moderately branched, partly associated with sclerenchyma caps of veins, abundant in adaxial part of mesophyll. Petiole with simple open vascular system (type 3).

Material studied. CHINA. Kwantung: *Tsang 20343, 20824.*

N o t e. Loesener's and Hu's (1950) suggestions of a close affinity with *I. buergeri* are fully supported by leaf anatomy. *I. cornuta, I. curranii, I. formosana, I. glomerata,* and *I. mitis* are also very similar to *I. ficoidea* through the common occurrence of, amongst others, foliar sclereids. *I. goshiensis* and *I. integra* lack this feature but are similar in many other respects.

Ilex formosana Maxim. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Repandae*)

Lamina 250 μm. Adaxial cuticle 5—6 μm; abaxial cuticle 3—4 μm. Sparse unicellular hairs on petiole and midrib. Stomata cyclocytic, tending to bicyclic, 31×29 μm. Adaxial epidermis with periclinal subdivisions. Sclereids fusiform or moderately branched, partly associated with sclerenchyma caps of veins, abundant in adaxial part of mesophyll. Concentration of fusiform sclereids in leaf margin. Petiole with simple open vascular system (type 3).

Material studied. TAIWAN: *Taiwan Herb. 11132.*

N o t e. Almost identical as it is to *I. ficoidea,* this species has the same anatomical affinities. Hu's (1950) remarks about close affinities with *I. ficoidea* are thus fully supported by leaf anatomy, as well as her treatment of *I. glomerata* and *I. buergeri* in the same series.

Ilex glabra (L.) Gray (subg. *Euilex*, series A, sect. *Cassinoides*)

Lamina 310 μm. Adaxial cuticle 3—5 μm; abaxial cuticle 6—7 μm. Sparse unicellular hairs on petiole and midrib. Stomata cyclocytic, 24×23 μm. Adaxial epidermis with infrequent anticlinal subdivisions. Cork warts. Petiole with 'double' vascular system (type 10).

Material studied. U.S.A. New Yersey: *Lawrence & Dress 269.*

N o t e. The arrangement of vascular tissue in the petiole is rather unusual for *Ilex* and is shared by *I. coriacea.* This, together with some other resemblances, strongly supports Loesener's suggestion of close affinities between the two species. Other overall similarities with some species are not based on special character complexes, and are probably not relevant for judging natural affinities. Thévenard (1906) reported a locally mucilaginous epidermis for this species, but no trace of this could be found in *Lawrence & Dress 269.*

Ilex glomerata King (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Repandae*)

Lamina 180 μm. Adaxial cuticle 2—3 μm; abaxial cuticle 2 μm. Stomata cyclocytic and bicyclic, 32×29 μm. Epidermal cells with strongly undulating anticlinal walls. Sclereids fusiform and moderately branched, partly associated with sclerenchyma caps of veins, abundant in adaxial part of mesophyll. Petiole with simple open vascular system (type 3).

Material studied. BORNEO. Mt. Kinabalu: *Clemens 28843.*

N o t e. Bicyclic stomata and fusiform foliar sclereids indicate affinities with *I. buergeri*, *I. curranii*, *I. ficoidea*, *I. formosana*, and *I. mitis*. *I. fargesii*, *I. integra*, *I. bioritsensis*, *I. dipyrena*, and *I. latifolia* also share many characters with *I. glomerata*.

Ilex goshiensis Hayata, Mat. Fl. Formosa (1911) 54 (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Sideroxyloides*)

Lamina 310 μm. Adaxial cuticle 7 μm; abaxial cuticle 3—4 μm. Sparse unicellular hairs with fairly broad bases on midrib and petiole. Stomata cyclocytic and bicyclic, 28 × 25 μm. Adaxial epidermis with infrequent anticlinal subdivisions. Solitary crystals present in midrib. Petiole with simple open vascular system (type 1).

Material studied. JAPAN. Ryukyu Islands, Okinawa: *Moran 5131*.

N o t e. The treatment of *I. goshiensis* in subsection *Sideroxyloides* follows Hayata's (l.c.) suggestions of affinities with *I. championii* of that subsection. There are, however, several anatomical differences between *I. sideroxyloides* and *I. divaricata*. *I. celebensis* of subgenus *Byronia* resembles *I. goshiensis* leaf anatomically in many respects, but since no special features are involved this cannot be taken as proof of close mutual affinity.

Ilex grandifolia Merr., Pap. Mich. Ac. Sc. 19 (1933) 163 (subg. *Byronia*, series A)

Lamina 400 μm. Adaxial and abaxial cuticle 3—4 μm. Stomata cyclocytic to anomocytic, 32 × 26 μm. Adaxial epidermis with anticlinal subdivisions and bulging mucilage cells. Bundle sheaths and spongy tissue lignified. Petiole with complex open vascular system (type 9).

Material studied. SUMATRA: *De Voogd 1134*.

N o t e. According to Merrill (l.c.) this species belongs in the same group as *I. cymosa*, and is probably most closely related to *I. macrophylla* Wall.; hence its treatment in subgenus *Byronia* here. The main difference between these species and *I. grandifolia* is the stomatal type, other characters being roughly similar. The complex vascularization of the petiole and the very conspicuous cuticular striations of the abaxial epidermis recall *I. cymosa p.p.* and *I. hypoglauca* from the same subgenus. There are also some similarities with species from section *Indico-Malaicae* of subgenus *Euilex*, series D.

Ilex guianensis (Aubl.) O. Ktze, incl. var. **arimensis** Loes.; *I. panamensis* Standl. (subg. *Euilex*, series C, sect. *Micranthae*, subsect. *Epunctatae*) — **Fig. 16**

Lamina 240—300 μm. Adaxial cuticle 3—5 μm; abaxial cuticle 1—3 μm. Stomata predominantly anisocytic, sometimes cyclocytic in *Broadway 4052*, predominantly cyclocytic, sometimes anomocytic or anisocytic in *Allen 3570*, cyclocytic to anisocytic in *Lanjouw & Lindeman 1495*, 22 × 19—26 × 21 μm. Adaxial epidermis with periclinal subdivisions and bulging mucilage cells. Petiole with simple open vascular system (type 4).

Material studied. PANAMA: *Allen 3570* (U). — SURINAM: *Lanjouw & Lindeman 1495* (U). — TRINIDAD: *Broadway 4052*.

N o t e. Leaf anatomically this species is not very unusual, and bears resemblance with a great number of *Ilex* species of different sections or even subgenera. Of all these *I. jenmanii* of the same subsection is closest leaf anatomically. *I. inundata* and *I. umbellata* are also quite similar, suggesting that subsection *Epunctatae* constitutes an anatomically rather homogeneous assemblage.

Ilex hanceana Maxim. (subg. *Euilex*, series B, sect. *Vacciniifoliae*)

Lamina 300 μm. Adaxial cuticle 8—9 μm; abaxial cuticle 3—4 μm. Sparse unicellular hairs on midrib and petiole. Stomata cyclocytic, occasionally anisocytic, 25 × 25 μm. Adaxial epidermis with occasional anticlinal subdivisions. Solitary crystals in ground tissue of petiole and midrib. Petiole with simple open (type 2) to almost closed vascular system; in midrib with completely closed system (type 6).

Material studied. JAPAN. Iriomote I.: *Gressitt 600* (U).

N o t e. The solitary crystals in addition to clustered ones constitute the only distinctive character of this species. Affinities with other species studied are not clear.

Ilex hypoglauca (Miq.) Loes. (subg. *Byronia*, series A) — **Plate I, 6; III, 6; fig. 8**

Lamina 210—400 μm. Adaxial cuticle 4—15 μm; abaxial cuticle 3—7 μm. Indumentum of broad-based hairs with numerous basal septs present on both surfaces (Plate I, 6; fig. 8). Stomata mainly cyclocytic (*Anderson 8536, Hallier B 2875*, and *Haviland 2872*) or cyclocytic to anisocytic (other 2 specimens), 26 × 22—31 × 27 μm. Adaxial epidermis with periclinal subdivisions and bulging mucilage cells in varying frequencies. Bundle sheaths and part of spongy tissue lignified. Petiole usually with complex closed vascular system (type 8), but with simple open system (type 4) in *Kostermans 4704*.

Material studied. BORNEO: *Anderson 8536, Hallier B 2875, Haviland 2872, Kostermans 4704.* — SUMATRA. Banka: isotype ('P.P. 21', ?*Horsfield*).

N o t e. Peculiar hairs with a broad basal part, subdivided by thin septs characterize this species. *I. zygophylla* has an indumentum of hairs which slightly resemble those of *I. hypoglauca*, but septs occur only sporadically in the hairs of that species, and are always few per hair if present. The variability of the vascular complex in the petiole in *I. hypoglauca* is remarkable. Besides with *I. zygophylla* there are anatomical affinities with several Malesian species of subgenus *Byronia*, and also with several other Malesian species of subgenus *Euilex: I. brunnea, I. versteeghii, I. archboldiana, I. laurifolia*, and also with *I. oppositifolia* of subgenus *Rybonia*. All these species share some scleromorphic features (thick cuticle, lignified bundle sheaths and partly lignified spongy tissue).

Ilex insignis Hook. *f.* (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Insignis*)

Lamina 380 μm. Adaxial cuticle 7—8 μm; abaxial cuticle 4—6 μm. Stomata cyclocytic, partly bicyclic, 27 × 28 μm. Adaxial epidermis with infrequent periclinal subdivisions, containing mucilage cells. Bundle sheaths strongly birefringent. Tendency for marginal sclerenchyma strand through reduction of vascular tissue in marginal vein, or through splitting off thin sclerenchyma strand from massive sclerenchyma cap of this marginal vein. Petiole with simple open vascular system (type 4).

Material studied. INDIA. Sikkim: *J. D. Hooker s.n.* (Herb. Ind. Or. Hook. *f.* & Thomson).

N o t e. As in *I. latifolia* of the same subsection the appearance of marginal sclerenchyma is variable in this species. Affinities are also with species from subsection *Oxyodontae*.

Ilex integerrima (Vell.) Reiss. var. **ebenacea** (Reiss.) Loes. (subg. *Euilex*, series C, sect. *Megalae*, subsect. *Pedicellatae*) — **Plate II, 3**

Lamina 320 μm. Adaxial cuticle 7—8 μm; abaxial cuticle 1—2 μm. Stomata mainly anisocytic, occasionally cyclocytic, 26 × 22 μm. Adaxial epidermis with anticlinal and

periclinal subdivisions, probably containing mucilage cells. Petiole with simple open vascular system (type 4).

Material studied. BRAZIL. Parana: *Hatschbach 7550.*

N o t e . Close affinities with *I. theezans* as advocated by Loesener, are supported by anatomical resemblances in most characters, though these are not very distinctive, so that affinities with other taxa could also be advocated. *I. brasiliensis* of the same subsection differs in a number of leaf anatomical features.

Ilex integra Thunb. (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Oxyodontae*)

Lamina 330 μm. Adaxial cuticle 7 μm; abaxial cuticle 5 μm. Stomata cyclocytic and bicyclic, 33 × 29 μm. Tendency for marginal sclerenchyma strand through reduction of vascular tissue in marginal vein, and through lateral extension of sclerenchyma cap of marginal vein. Petiole with simple open vascular system (type 3).

Material studied. JAPAN. Hondo: *N.S.M. 527.*

N o t e . This species closely resembles those of the same subsection (*I. aquifolium* etc.). There are also similarities with species of subsection *Repandae* having foliar sclereids and with species from subsection *Insignis*.

Ilex inundata Poepp. (subg. *Euilex*, series C, sect. *Micranthae*, subsect. *Epunctatae*)

Lamina 200 μm. Adaxial cuticle 3—4 μm; abaxial cuticle 1 μm. Sparse unicellular hairs on midrib. Stomata anisocytic to cyclocytic, 23 × 20 μm. Adaxial epidermis with anticlinal and periclinal subdivisions, containing mucilage cells. Petiole with simple open vascular system (type 4).

Material studied. BRAZIL: *Kappler 182.*

N o t e . According to Loesener this species is close to *I. umbellata.* This can be supported by a good overall leaf anatomical similarity. None of the leaf anatomical characters in *I. inundata* is, however, very distinctive, so that affinities with many other species could be supported.

Ilex jenmanii Loes. (subg. *Euilex*, series C, sect. *Micranthae*, subsect. *Epunctatae*)

Lamina 400 μm. Adaxial cuticle 4—6 μm. abaxial cuticle 3 μm. Stomata anisocytic to cyclocytic, 27 × 23 μm. Anticlinal walls of epidermis strongly undulated. Abaxial and adaxial epidermis containing bulging mucilage cells. Spongy tissue partly birefringent, probably unlignified. Petiole with simple open vascular system (type 4).

Material studied. SURINAM: *Lindeman 704* (U).

N o t e . As the previous species of the same subsection *I. jenmanii* is without outstanding characters and, although similar to several species of this subsection, similarities with other miscellaneous species are present as well.

Ilex kleinii Edwin in Reitz, Fl. ilustr. Catar. I, Aquifol. (1967) 41 (not assigned to a subgenus or section)

Lamina 110 μm. Adaxial cuticle 3 μm; abaxial cuticle 1—2 μm. Stomata mainly cyclocytic, occasionally anomocytic or anisocytic, 22 × 19 μm. Adaxial epidermis with infrequent anticlinal subdivisions. Petiole with simple open vascular system (type 4).

Material studied. BRAZIL. Santa Catarina: *Reitz & Klein 3966* (U).

N o t e. There are no distinctive anatomical characters in this species to afford a suggestion about systematic affinities.

Ilex krugiana Loes. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Eumicrodontae*)

Lamina 180 μm. Adaxial cuticle 4—6 μm; abaxial cuticle 3 μm. Stomata cyclocytic, occasionally bicyclic or complex, 30 × 25 μm. Adaxial epidermis with frequent anticlinal and periclinal subdivisions, containing mucilage cells. Petiole with simple open vascular system (type 4).

Material studied. BAHAMAS: *Eggers 4462.*

N o t e. In the absence of outstanding leaf anatomical features, the leaf microstructure is neutral with respect to Loesener's suggestion of an affinity with *I. brevicuspis*, from which *I. krugiana* differs in a few minor anatomical aspects.

Ilex kwantungensis Merr., J. Arn. Arb. 8 (1927) 8 (subg. *Euilex*, series A, sect. *Excelsae*)

Lamina 190 μm. Adaxial cuticle 3—5 μm; abaxial cuticle 2 μm. Indumentum of rather long unicellular hairs with thick walls and recurved tips present on both sides of lamina. Stomata cyclocytic, 24 × 22 μm. Adaxial epidermis with periclinal subdivisions, containing mucilage cells. Petiole with simple open vascular system (type 4); simple closed (type 6) in midrib.

Material studied. CHINA. Hunan: *Fan & Li 259.*

N o t e. Merrill (l.c.) doubtfully referred *I. kwantungensis* to section *Excelsae*. Hu (1950) treated the species together with *I. chinensis* in her series *Chinensis*, which contains many species not known to Loesener, except *I. chinensis* (syn. *I. purpurea*) and *I. lonicerifolia* which Loesener (1942) both referred to subsection *Umbelliformes* of section *Excelsae*. To conform to the Loesener system I therefore treat *I. kwantungensis* in this section, which finds good support in leaf anatomy; *I. chinensis* and *I. kwantungensis* are leaf anatomically alike, particularly in the midrib vascularization.

Ilex latifolia Thunb. (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Insignis*)

Lamina 600 μm. Adaxial cuticle 4—6 μm; abaxial cuticle 3—4 μm. Stomata cyclocytic and bicyclic, 37 × 34 μm. Epidermal cells with straight anticlinal walls. Tendency for marginal sclerenchyma strand through reduction of vascular tissue in marginal vein, or lateral extension of sclerenchyma cap of the latter. Petiole with simple open vascular system (± intermediate between type 3 and 4).

Material studied. FRANCE. cult. Orléans: *Boom 15484.*

N o t e. This species is anatomically very close to subsection *Oxyodontae (I. aquifolium, I. bioritsensis, I. cornuta, I. dipyrena, I. integra, I. perado,* and *I. pernyi)* although the marginal sclerenchyma is still associated with a vascular bundle in *I. latifolia*. Similarities with *I. insignis* of the same subsection are also present, as well as with *I. fargesii* and *I. glomerata* of other subsections. Thévenard (1906) recorded short hairs for this species, but these were absent from the specimen studied by me, indicating the variability of this character below the species level.

I. latifolia is native in Japan.

Ilex laurifolia Zipp. *ex* Loes. (subg. *Euilex*, series A, sect. *Excelsae*, subsect. *Laxae*)

Lamina 440 μm. Adaxial cuticle 7—8 μm; abaxial cuticle 4—5 μm. Stomata mainly anisocytic, rarely cyclocytic, 30 × 23 μm. Adaxial epidermis with anticlinal and periclinal subdivisions, containing mucilage cells. Bundle sheaths and part of spongy tissue lignified. Some fusiform sclereids in ground tissue of midrib. Minute solitary crystals in adaxial epidermis. Petiole with simple open vascular system (type 4).

Material studied. NEW GUINEA: *Van Royen 5415.*

N o t e. With mainly anisocytic stomata and leaf scleromorphy expressed in partly lignified mesophyll and a lignified bundle sheath, this species resembles several Malesian species, notably those of subgenus *Byronia*, series A, and some species of subgenus *Euilex*. *I. amplifolia*, from the same subsection but native in S. America differs in several characters. Loesener's remark about similarities with *I. cymosa* finds support in the anatomical character complex. There is also a very striking similarity with *I. brassii* also from New Guinea, with which species it shares the, for *Ilex* unusual, sclerified cells in the abaxial ground tissue of the midrib.

Ilex ledermannii Loes., Bot. Jahrb. 59 (1925) 81 (subg. *Byronia*, series A)

Lamina 180 μm. Abaxial and adaxial cuticle *c.* 1 μm. Stomata anisocytic to cyclocytic, 28 × 21 μm. Adaxial epidermis with bulging mucilage cells. Bundle sheaths and part of spongy tissue lignified. Petiole with simple open vascular system (type 4).

Material studied. NEW GUINEA: *Koster BW 7135.*

N o t e. Like several species from subgenus *Byronia*, *I. ledermannii* has scleromorphic leaves with lignified mesophyll and bundle sheaths. Several other Malesian species from subgenus *Euilex* (*I. archboldiana*, *I. laurifolia*, and *I. stapfiana*) are also rather similar.

Ilex longipes Champ. (subg. *Prinus*, series B)

Lamina 160 μm. Adaxial cuticle 1—2 μm; abaxial cuticle *c.* 1 μm. Indumentum of short but rather broad-based hairs on midrib and petiole. Stomata predominantly ano-mocytic, sometimes anisocytic or cyclocytic, 26 × 22 μm. Unspecialized abaxial epidermal cells with strongly undulated anticlinal walls. Adaxial epidermis with periclinal sub-divisions. Both epidermides containing bulging mucilage cells. Petiole with simple open vascular system (type 1).

Material studied. U.S.A. Tennessee: *Biltmore Herb. 4063.*

N o t e. As most species of subgenus *Prinus*, the leaf anatomy is typically mesomorphic with no distinctive characters, except for the rather sparse broad-based hairs and the fact that both abaxial and adaxial epidermides are mucilaginous and contain bulging cells.

Ilex macfadyenii (Walp.) Rehd., J. Arn. Arb. 3 (1922) 215; *I. montana* (Sw.) Griseb. (subg. *Euilex*, series A, sect. *Excelsae*, subsect. *Laxae*)

Lamina 190 μm. Adaxial cuticle 2—3 μm; abaxial cuticle 3 μm. Sparse unicellular hairs on midrib and petiole. Stomata cyclocytic, rarely complex, 26 × 22 μm. Adaxial epidermis with anticlinal subdivisions and mucilage cells. Cork warts with characteristic outlines. Petiole with simple open vascular system (type 4).

Material studied. JAMAICA: *Krug & Urban 5813.*

N o t e. The sunken cork warts with angular outlines together with other similarities recall the situation in *I. coriacea* of section *Cassinoides* of the same series. The leaf anatomy of *I. amplifolia* of the same subsection also resembles *I. macfadyenii* in many characters.

Ilex macrophylla Wall. *ex* Hook. *f.* (subg. *Byronia*, series A)
Lamina 210 μm. Adaxial cuticle 2—3 μm; abaxial cuticle 1 μm. Stomata anisocytic, rarely cyclocytic or complex, 23 × 24 μm. Adaxial epidermis with strongly undulating anticlinal walls, with periclinal subdivisions, and containing mucilage cells. Bundle sheaths and part of spongy tissue lignified. Petiole with simple open vascular system (type 4).

Material studied. SUMATRA: *Achmad 991.*

N o t e. Affinities with *I. pleiobrachiata* (=*I. cymosa*) as suggested by Loesener are supported by the leaf anatomy of this rather scleromorphic species. There are also similarities with several other tropical species sharing the scleromorphic character complex, but lacking distinctive anatomical features.

Ilex martiniana D. Don (subg. *Euilex*, series D, sect. *Thyrsiflorae*)
Lamina 260 μm. Adaxial and abaxial cuticle 5 μm. Sparse unicellular hairs on abaxial surface and adaxially of midrib. Stomata mainly anisocytic, occasionally cyclocytic, 26 × 23 μm. Epidermal cells with strongly undulating anticlinal walls. Abaxial epidermal cells (including subsidiary cells and guard cells) with lignified walls. Adaxial epidermis with infrequent anticlinal subdivisions. Cork warts. Locally developed hypodermis over midrib lignified. Bundle sheaths lignified. Spongy tissue strongly birefringent. Petiole with simple open vascular system (type 4).

Material studied. BRITISH GUIANA: *Schomburgk 385.*

N o t e. Frequent cork warts and a lignified abaxial epidermis characterize this species, which shares these features with *I. ovalifolia* of the same section. *I. retusa* from S. America and *I. triflora* from Malesia, each from different series, also resemble *I. martiniana* rather closely.

Ilex micrococca Maxim. (subg. *Byronia*, series B) — **Fig. 2**
Lamina 100 μm. Adaxial cuticle 3—4 μm; abaxial cuticle 2—3 μm. Indumentum of fairly long, partly septate, hairs on petiole, and on adaxial side of midrib and lateral veins. Stomata mainly anomocytic, often tending to cyclocytic, occasionally anisocytic, 31 × 21 um. Adaxial epidermis composed of bulging mucilage cells; abaxial epidermis also containing some bulging cells. Petiole with simple open vascular system (type 4).

Material studied. CHINA. Kweichow: *Steward, Chiao & Cheo 713.*

N o t e. With its mesomorphic leaves, mainly anomocytic stomata, and partly septate hairs this species recalls subgenus *Prinus* rather than other species of subgenus *Byronia*.

Ilex microdonta Reiss. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Eumicrodontae*)
Lamina 300 μm. Adaxial and abaxial cuticle *c.* 2 μm. Sparse unicellular hairs on midrib. Stomata mainly cyclocytic, rarely anisocytic or complex, 26 × 21 μm. Petiole with simple closed vascular system (type 7).

Material studied. BRAZIL. Santa Caterina: *Reitz & Klein 8400.*

N o t e. Loesener's suggestion of an affinity with *I. brevicuspis* cannot be supported by leaf anatomy. The two species differ mainly in petiole anatomy. In the absence of very distinctive features, the existing overall leaf anatomical similarities with *I. hanceana* from Japan and with *I. chinensis* from China may be systematically quite irrelevant.

Ilex mitis (L.) Radlk. (subg. *Euilex*, series C, sect. *Lemurenses*)
Lamina 360 μm. Adaxial cuticle 9 μm; abaxial cuticle 4—5 μm. Stomata cyclocytic, tending to bicyclic or complex, 28 × 26 μm. Slender undulating unbranched sclereids, sparse throughout mesophyll. Minute solitary crystals in adaxial epidermis. Petiole with simple open vascular system (type 4).

Material studied. KENYA: *Maas Geesteranus 5977.*

N o t e. By its infrequent foliar sclereids, in combination with a number of other less distinctive anatomical features, this species approaches the group of *I. buergeri, I. curranii, I. ficoidea, I. formosana,* and *I. glomerata,* all of subsection *Repandae* from Asia. *I. mitis* stands out, however, by the possession of minute rod- to needle-shaped crystals in the adaxial epidermis. Similarities with *I. fargesii* from section *Lemurensis* are also present.

Ilex opaca Ait. (subg. *Euilex*, series A, sect. *Cassinoides*)
Lamina 310 μm. Adaxial cuticle 9 μm; abaxial cuticle 4—5 μm. Stomata bicyclic, sometimes cyclocytic, 37 × 35 μm. Epidermal cells with strongly undulating anticlinal walls. Abaxial epidermis with lignified unspecialized cells and guard cells. Bundle sheaths and part of spongy tissue lignified. Petiole with simple closed vascular system (type 6).

Material studied. U.S.A. New Jersey: *Lawrence & Dress 246;* some other specimens for testing lignification of epidermal cells.

N o t e. Lignified abaxial unspecialized epidermal cells, bicyclic stomata, and a simple closed vascular system make this species rather outstanding. This combination of characters has not been encountered in any other *Ilex* species. *Ilex canariensis* and *I. cassine* from the same section share the lignified epidermis but have simply monocyclic or cyclocytic to anisocytic stomata and an open vascular system. *Ilex glabra* and *I. coriacea* also of section *Cassinoides* share none of the crucial characters of *I. opaca.* Loesener's remark that *I. opaca* is similar in several respects to *I. cassine* can be supported by leaf anatomy, in the absence of other species resembling *I. opaca* more closely.

Ilex oppositifolia Merr., J. Arn. Arb. 20 (1939) 222 (subg. *Rybonia*)
Lamina 660 μm. Adaxial cuticle 18—28 μm; abaxial cuticle 4—5 μm. Unicellular rather broad-based, thick-walled hairs on both sides of lamina. Stomata irregularly cyclocytic, 37 × 31 μm. Adaxial epidermis with anticlinal and periclinal subdivisions. Hypodermis differentiated adaxially in several parts of lamina. Bundle sheaths and part of spongy tissue lignified. Midrib of ± sessile leaves with complex closed vascular system (type 8).

Material studied. BORNEO: *Clemens 31895.*

N o t e. As the single representative of Loesener's (1942) subgenus, this species shares anatomical characters with *I. hypoglauca* of subgenus *Byronia* and with *I. archboldiana* and *I. versteeghii* of subgenus *Euilex*, section *Rugosae.* The complex closed arrangement of the vascular tissue of the midrib (petioles are ± absent) is a distinctive feature of this species, which has a very scleromorphic leaf anatomy.

Ilex ovalifolia Mey. (subg. *Euilex*, series D, sect. *Thyrsiflorae*) — **Plate III, 3**

Lamina 320 μm. Adaxial cuticle 4—6 μm; abaxial cuticle 3 μm. Stomata mainly anisocytic, occasionally cyclocytic, 33 × 28 μm. Epidermal cells with strongly undulating anticlinal walls. Abaxial epidermis with lignified unspecialized cells. Adaxial epidermis with periclinal subdivisions, containing mucilage cells. Cork warts. Bundle sheaths and part of spongy tissue lignified. Petiole with simple open vascular system (type 4).

Material studied. SURINAM: *B.B.S. 179* (U).

N o t e. Lignified abaxial unspecialized epidermal cells, mainly anisocytic stomata, and regular, frequent cork warts together with scleromorphic features such as partly lignified spongy tissue and lignified bundle sheaths of this species recall the situation in *I. martiniana* of the same section but also of *I. triflora* and *I. retusa*, each of different sections.

Ilex paraguariensis St. Hil. var. **sincorensis** Loes. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Repandae*) — **Plate III, 4**

Lamina 440 μm. Adaxial and abaxial cuticle 7—9 μm. Unicellular hairs on whole adaxial surface, on abaxial surface confined to midrib and major veins. Stomata cyclocytic, 32 × 21 μm. Abaxial unspecialized epidermal cells with straight very thick anticlinal walls; those of adaxial epidermis less markedly so. Cork warts. Minute solitary crystals in adaxial epidermis. Petiole with simple closed vascular system (type 6).

Material studied. BRAZIL. Bahia: *Ule 7082.*

N o t e. Thick-walled unlignified abaxial epidermal cells, a simple closed vascular system in the distal end of the petiole, and frequent cork warts are remarkable features of this species. Within subsection *Repandae*, *I. repanda* is the only one of the species studied which shares the petiole vasculature with *I. paraguariensis*. *I. paraguariensis* is furthermore characterized by minute prismatic to needle-like crystals in the adaxial epidermis, which character is also encountered in several unrelated species. I. find it impossible to indicate close affinities of *I. paraguariensis*, and leaf anatomically it is anyway rather aberrant within subsection *Repandae* and also within section *Microdontae* as a whole.

Ilex peduncularis F. v. Muell. (subg. *Byronia*, series A)

Lamina 270 μm. Adaxial cuticle 3—4 μm; abaxial cuticle 2 μm; Stomata irregularly cyclocytic, anisocytic, ± anomocytic or tending to complex, 26 × 23 μm. Adaxial epidermis with frequent anticlinal and periclinal subdivisions and containing some mucilage cells (multiple epidermis). Part of spongy tissue and bundle sheaths lignified. Petiole with simple open vascular system (type 4).

Material studied. AUSTRALIA: *Brass 20237.*

N o t e. This species is without outstanding anatomical features. The anatomy agrees fairly well with several other species from the same series (e.g. *I. cymosa*).

Ilex pedunculosa Miq. (subg. *Euilex*, series A, sect. *Excelsae*, subsect. *Umbelliformes*)

Lamina 190 μm. Adaxial cuticle 3—5 μm; abaxial cuticle 2—3 μm. Sparse unicellular hairs on midrib and petiole. Stomata cyclocytic, occasionally anisocytic, 30 × 27 μm. Petiole with simple open vascular system (type 2).

Material studied. JAPAN: *A. P. Wilson s.n.*

N o t e. Lack of latero-dorsal wing bundles in the petiole is the only noteworthy leaf anatomical feature of this species. There are several points of difference with both *I. chinensis* and *I. rotunda* from the same subsection. Similarities with some other species cannot be positively used to support mutual affinities.

Ilex perado Ait.; *I. platyphylla* Webb. (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Oxyodontae*) — **Plate IV, 7**

Lamina 410—470 μm. Adaxial cuticle 4—10 μm; abaxial cuticle 3—12 μm (thicker than adaxial cuticle in *Hunt 45* only). Sparse unicellular hairs on petiole of sheet *909.67—700* only. Stomata cyclocytic and bicyclic, 34 × 33—36 × 35 μm. Adaxial epidermis with frequent anticlinal subdivisions. Hypodermis of 1—2 cell layers. Marginal sclerenchyma strand. Petiole with simple open vascular system (type 3 or 4).

Material studied. AZORES: *Hunt 45* (U). — CANARY ISLANDS. Teneriffe: *Lems 2722*; sine nomine, Leiden herb. sheet *909.67—700*.

N o t e. Marginal sclerenchyma strands, bicyclic stomata together with almost all other less distinctive anatomical features indicate affinities with the species group of *I. aquifolium, I. bioritsensis, I. cornuta, I. dipyrena, I. integra,* and *I. pernyi*. There are also similarities with *I. fargesii*. The species is also more or less anatomically identical to *I. altaclarensis*, which is the hybrid between *I. perado* and *I. aquifolium*.

Ilex pernyi Franch. (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Oxyodontae*) — **Plate V, 4; fig. 1**

Lamina 510—530 μm. Adaxial cuticle 9—16 μm; abaxial cuticle 5—8 μm. Sparse, fairly broad-based, unicellular hairs on midrib and petiole. Stomata cyclocytic and bicyclic, 27 × 29 & 30 × 28 μm. Adaxial epidermis with infrequent anticlinal subdivisions. Marginal sclerenchyma strand. Petiole with simple open vascular system (type 3).

Material studied. GERMANY. cult. hort. Munich: *Boom 27299*. — NETHERLANDS: cult. hort. Leiden.

N o t e. *I. pernyi* belongs with the previous species to the same group which is characterized by marginal sclerenchyma strands, bicyclic stomata, and several other leaf anatomical characters. *Ilex fargesii* and *I. integra* also resemble *I. pernyi* to a considerable extent. *I. pernyi* is native in China.

Ilex pubescens Hook. & Arn. (subg. *Euilex*, series C, sect. *Prinifoliae*) — **Plate I, 5**

Lamina 150 μm. Adaxial and abaxial cuticle *c.* 1 μm. Indumentum of long septate hairs on both leaf surfaces. Stomata anisocytic, 21 × 19 μm. Adaxial epidermis with periclinal subdivisions. Both epidermides containing bulging mucilage cells. Petiole with simple open vascular system (type 3).

Material studied. CHINA. Kwantung: *S. Y. Lan 20137*.

N o t e. Abundant long uniseriate hairs characterize this mesomorphic species, which shows some anatomical affinities with species from subgenus *Prinus*, particularly *I. amelanchier*. The exclusively anisocytic stomata of *I. pubescens* plead, however, against inclusion in subgenus *Prinus*. Loesener's remark that this species is intermediate between subgenus *Euilex* and subgenus *Prinus* can be fully confirmed by the anatomical evidence.

Ilex pulogensis Merr., Philip. J. Sc. Bot. 5 (1910) 358 (subg. *Euilex*, series D, sect. *Indico-Malaicae*) — **Plate II, 5**

Lamina 300 μm. Adaxial cuticle 3 μm; abaxial cuticle 4—5 μm. Stomata cyclocytic and bicyclic, 32 × 23 μm. Adaxial epidermis with periclinal subdivisions, containing strongly bulging mucilage cells. Cork warts. Bundle sheaths lignified. Petiole with simple open vascular system (type 4).

Material studied. PHILIPPINES: *Conklin & Buwaya PNH 79634.*

N o t e. Frequent cork warts constitute the most outstanding leaf anatomical feature of this species. which Merrill (l.c.) assigned to section *Indico-Malaicae*. In the species studied and belonging to that section it is impossible to find sufficient resemblance with *I. pulogensis* to support Merrill's treatment. In view of the rather 'unspecialized' leaf anatomy of *I. pulogensis*, it is, however, impossible to indicate alternatives. Loesener (1942) listed *I. pulogensis* as a species 'ohne Punkte' (without cork warts), but the 2 specimens present in the Rijksherbarium (*PNH 79634; BS 31855*) both have frequent regular cork warts.

Ilex repanda Griseb. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Repandae*)

Lamina 290 μm. Adaxial cuticle 4—6 μm; abaxial cuticle 3—5 μm. Stomata cyclocytic, 29 × 27 μm. Adaxial epidermis with periclinal subdivisions and bulging mucilage cells. Bundle sheaths birefringent, possibly lignified. Petiole with simple closed vascular system (type 7).

Material studied. BAHAMAS: *Curtiss 88.*

N o t e. Through its petiole type *I. repanda* somewhat resembles *I. microdonta* of the same section from Santa Catarina. In the absence of other distinctive characters no other suggestions can be made about its affinities.

Ilex retusa Klotsch (subg. *Euilex*, series A, sect. *Crassifoliae*)

Lamina 480 μm. Adaxial cuticle 15—19 μm; abaxial cuticle *c.* 15 μm. Sparse unicellular hairs on midrib and petiole. Stomata cyclocytic and anisocytic, 34 × 32 μm. Abaxial epidermis with lignified unspecialized cells and guard cells. Adaxial epidermis with periclinal subdivisions and bulging mucilage cells. Cork warts. Bundle sheaths lignified. Petiole with simple open vascular system (type 4).

Material studied. BRITISH GUIANA. *Maguire & Fanshawe 32483* (U).

N o t e. Well-developed and frequent cork warts together with a lignified abaxial epidermis and other features suggest affinities of this species with *I. ovalifolia* and *I. triflora* of different sections.

Ilex revoluta Stapf (subg. *Euilex*, series C, sect. *Rugosae*)

Lamina 330 μm. Adaxial cuticle 10—12 μm; abaxial cuticle 6—8 μm. Moderately long, curved, unicellular hairs on midrib and petiole, also infrequent over whole abaxial surface. Stomata cyclocytic, sometimes tending to anomocytic, 33 × 29 μm. Adaxial epidermis with infrequent anticlinal and periclinal subdivisions, possibly containing mucilage cells. Cork warts. Petiole with simple open vascular system (type 3).

Material studied. BORNEO: *Meyer SAN 29253.*

N o t e. The species differs from the others studied of the same section. Affinities with species of other sections cannot be suggested because of the lack of enough distinctive characters.

Ilex rotunda Thunb. (subg. *Euilex*, series A, sect. *Excelsae*, subsect. *Umbelliformes*)

Lamina 220 μm. Adaxial and abaxial cuticle 2 μm. Stomata cyclocytic and anisocytic, occasionally tending to complex, 33 × 28 μm. Adaxial epidermis with periclinal subdivisions and bulging mucilage cells. Very minute solitary crystals in adaxial epidermis. Petiole with simple open vascular system (type 4).

Material studied. CHINA. Kwantung: *Lan 20237.*

N o t e. This species shows no unusual anatomical features. There are several points of difference with *I. chinensis* and *I. pedunculosa* of the same subsection.

Ilex sclerophylloides Loes. (subg. *Byronia*, series A)

Lamina 380 μm. Adaxial cuticle 4—5 μm; abaxial cuticle 2—3 μm. Stomata mainly anisocytic; occasionally cyclocytic, 26 × 21 μm. Adaxial epidermis with straight anticlinal walls. Bundle sheaths and part of spongy tissue lignified. Petiole with simple open vascular system (type 4).

Material studied. BORNEO: *Herb. For. Dept. Sarawak 4381.*

N o t e. Except for a strong expression of scleromorphic features such as lignification of spongy tissue and bundle sheaths, there are no unusual features in this species. There are good overall similarities with several other species of subgenus *Byronia* (*I. brassii*, *I. cymosa*, *I. macrophylla*) but also with some species of subgenus *Euilex*.

Ilex scrabidula Merr. & Perry, J. Arn. Arb. 22 (1941) 258 (? subg. *Euilex*, series D, sect. *Indico-Malaicae*)

Lamina 320 μm. Adaxial cuticle 2—3 μm; abaxial cuticle 1—2 μm. Stomata mainly cyclocytic, occasionally anisocytic, 28 × 24 μm. Cork warts. Bundle sheaths lignified. Petiole with simple open vascular system (type 3).

Material studied. NEW GUINEA: *Brass 10502.*

N o t e. Merrill & Perry (l.c.) remarked that this species somewhat resembles *I. spicata*; hence its treatment in section *Indico-Malaicae* here. Leaf anatomically there are no very remarkable characters, except abundant cork warts. Similar anatomies can be found in some species, notably *I. spicata*, supporting Merril & Perry's suggestions. *I. spicata* differs, however, in its complex vascular supply of petiole and midrib.

Ilex sebertii Panch. & Séb. (subg. *Euilex*, series A, sect. *Excelsae*, subsect. *Laxae*)

Lamina 330 μm. Adaxial cuticle 8—9 μm; abaxial cuticle 6—8 μm. Stomata mainly cyclocytic, occasionally anisocytic, 36 × 31 μm. Adaxial epidermis with anticlinal and periclinal subdivisions, containing mucilage cells. Part of spongy tissue birefringent, possibly weakly lignified. Petiole with simple open vascular system (type 4).

Material studied. NEW CALEDONIA: *McKee 2562.*

N o t e. There are no distinctive anatomical features in this species, and the anatomical evidence is rather neutral with regard to Loesener's suggestion of an affinity with *I. laurifolia*.

Ilex serrata Thunb., incl. var. **sieboldii** (Miq.) Loes. (subg. *Prinus*, series A) — **Fig. 3**
Lamina 110—130μm. Adaxial and abaxial cuticle *c.* 1μm. Unicellular broad-based hairs numerous on both leaf surfaces. Stomata anomocytic, 24 × 17μm. Abaxial epidermis with strongly undulating anticlinal walls forming an interlocking pattern. Petiole with simple open vascular system (type 2).

Material studied. NETHERLANDS. cult. Wageningen: *Rijksarboretum 946 (=Boom 6165).* —JAPAN: Leiden herb. sheet *904.134—327.*

N o t e. Strongly undulating anticlinal epidermal walls, anomocytic stomata, together with a mesomorphic leaf anatomy, are well in line with the characters of most species of subgenus *Prinus*, notably *I. verticillata* of the same series. The difference in indumentum between these two species would not hold if more material had been studied, because Loesener recorded both glabrous and puberulous forms or varieties for the two species.

Ilex sideroxyloides (Sw.) Griseb. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Sideroxyloides*)
Lamina 300μm. Adaxial cuticle 2—3μm; abaxial cuticle 1—2μm. Stomata mainly anisocytic, occasionally cyclocytic, 28 × 20μm. Epidermal cells with strongly undulating anticlinal walls. Adaxial epidermis with periclinal subdivisions; both epidermides containing bulging mucilage cells. Petiole with simple open vascular system (type 4).

Material studied. WEST INDIES: Lesser Antilles. *Eggers 6234.*

N o t e. There are no distinctive leaf anatomical features in this species to justify meaningful systematic suggestions. There are rather important differences with *I. divaricata* from the same subsection.

Ilex sikkimensis Kurz (subg. *Euilex*, series C, sect. *Aquifolioides*, subsect. *Insignis*)
Lamina 170μm. Adaxial cuticle 7—8μm; abaxial cuticle 3—5μm. Stomata irregularly cyclocytic, sometimes anomocytic, 29 × 27μm. Petiole with simple open vascular system (type 4).

Material studied. SIKKIM. Sinchal: *Thomson s.n.*

N o t e. This species is without distinctive leaf anatomical characters. There are some differences with *I. insignis* and *I. latifolia* of the same subsection.

Ilex spicata Bl. (subg. *Euilex*, series D, sect. *Indico-Malaicae*)
Lamina 350μm. Adaxial and abaxial cuticle 2—3μm. Stomata cyclocytic, 29 × 24μm. Adaxial epidermis containing some bulging mucilage cells. Cork warts. Bundle sheaths lignified. Part of spongy tissue birefringent, possibly lignified. Petiole with complex closed vascular system (type 8).

Material studied. JAVA: *Van Ooststroom 13113.*

N o t e. *I. stapfiana* of section *Indico-Malaicae* resembles *I. spicata* in many respects but lacks regular cork warts. *I. cissoidea* of the same section differs more strongly from *I. spicata.*

Ilex stapfiana Loes. (subg. *Euilex*, series D, sect. *Indico-Malaicae*)
Lamina 400μm. Adaxial cuticle 5—7μm; abaxial cuticle 4—6μm. Stomata anomocytic

to cyclocytic, 29×20 μm. Adaxial epidermis with periclinal subdivisions and strongly bulging mucilage cells. Bundle sheaths lignified. Spongy tissue with mucilaginous cell walls. Petiole with complex closed vascular system (type 8).

Material studied. BORNEO. Sarawak: *Haviland 3557.*

N o t e. Loesener's suggestion about affinities with *I. spicata* are largely supported by leaf anatomy (see above). Besides showing a strongly mucilaginous adaxial epidermis with large bulging subdivided cells, part of the spongy tissue in *I. stapfiana* has mucilaginous cell walls. The species shows also similarities with some other Malesian species from subgenus *Byronia* and with *I. oppositifolia* from subgenus *Rybonia.*

Ilex theezans Mart. (subg. *Euilex*, series C, sect. *Megalae*, subsect. *Pedicellatae*) — **Fig. 11 and 12**

Lamina 300—320 μm. Adaxial cuticle 4—6 μm; abaxial cuticle 2—3 μm. Indumentum absent or of sparse unicellular hairs on midrib. Stomata anisocytic and cyclocytic in different ratios in the 2 specimens studied, 25×21 & 29×23 μm. Adaxial epidermis with anticlinal and periclinal subdivisions, containing few or many bulging mucilage cells. Abaxial epidermis also with some bulging cells. Part of spongy tissue birefringent, possibly lignified. Petiole with simple open vascular system (type 4).

Material studied. BRAZIL: *Dusén 10608*; Santa Catarina: *Reitz & Klein 3222* (U).

N o t e. The two specimens studied differ from each other in some characters. Because of this, and in the absence of distinctive leaf anatomical features this species shares its leaf anatomy with a large number of species from many sections and different subgenera. *I. brasiliensis* and *I. integerrima* of the same subsection belong to these similar species.

Thévenard (1906) recorded several mucilaginous hypodermal layers for *I. theezans* (as in *I. anomala*), and furthermore described a midrib vascularization different from that in the material studied here. Possibly his material was misidentified.

Ilex tolucana Hemsl. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Repandae*)

Lamina 380 μm. Adaxial cuticle 6 μm; abaxial cuticle 2 μm. Indumentum of thick-walled, slender, fairly long, unicellular hairs over whole lamina. Stomata cyclocytic, tending to complex, 27×27 μm. Guard cells lignified (?). Adaxial epidermis with anticlinal subdivisions. Petiole with simple open vascular system (type 4). Midrib with simple closed system (type 6).

Material studied. MEXICO: *Meyer & Rogers 2942* (U).

N o t e. Indumentum, guard cells, and midrib vascularization are distinctive in this species. Within subsection *Repandae* I have not seen species with a similar leaf anatomy. There are some similarities with *I. microdonta* of section *Microdontae.*

Ilex triflora Bl. (subg. *Euilex*, series C, sect. *Microdontae*, subsect. *Stigmatophorae*)

Lamina 130—210 μm. Adaxial cuticle 3—8 μm; abaxial cuticle 2—8 μm. Sparse unicellular hairs on midrib and petiole, rarely also on abaxial side of lamina. Stomata cyclocytic and anisocytic in different proportions in different specimens, 25×24—32×29 μm. Guard cells lignified. Unspecialized cells of abaxial epidermis mostly lignified; very few cells lignified only in *Forbes 2901.* Adaxial epidermis with periclinal subdivisions and bulging mucilage cells in very variable frequencies. Cork warts. Spongy tissue partly lignified. Petiole with simple open vascular system (type 3).

N o t e. In spite of its variability the species remains outstanding with its lignified (at least *pro parte*) abaxial epidermis and frequent cork warts. This in combination with the partly anisocytic stomata would suggest affinities with the New World species *I. martiniana* and *I. ovalifolia* from section *Thyrsiflorae* of series D. *Thyrsoprinus.*

Ilex tuerckheimii Loes.; Symb. Antill. (Ed. Urban) 7 (1912) 268 (subg. *Euilex*, series A, sect. *Excelsae*, subsect. *Laxae*)
Lamina 280 μm. Adaxial and abaxial cuticle 2—3 μm. Sparse unicellular hairs on midrib and petiole. Stomata anisocytic and cyclocytic, 24 × 21 μm. Hypodermis of 1—2 layers of partly bulging cells, probably containing mucilage. Spongy tissue with abaxial ligni-fied layer, remainder composed of thick-walled ± collenchymatous cells. Petiole with simple open vascular system (type 4).

N o t e. A mucilaginous 'true' hypodermis, comparable to that in *I. anomala* and some strongly lignified cells of the spongy tissue in the layer adjacent to the abaxial epidermis are the only distinctive characters of this species. Within subsection *Laxae* none of the species studied resembles *I. tuerckheimii* very closely, nor have I found evidence of closer affinities with species from other sections or subsections.

Ilex umbellata Kl. var. **humirioides** (Reiss.) Loes. (subg. *Euilex*, series C, sect.*Micranthae*, subsect. *Epunctatae*) — **Fig. 14**
Lamina 310 μm. Adaxial and abaxial cuticle 1—2 μm. Sparse unicellular hairs on petiole, midrib, and major veins. Stomata anisocytic and cyclocytic, 18 × 16 μm. Adaxial epidermis with periclinal subdivisions and strongly bulging mucilage cells. Petiole with simple open vascular system (intermediate between type 3 and type 4).

N o t e. This species shows no outstanding anatomical features. Affinities with *I. inundata, I. guianensis,* and *I. sideroxyloides* as suggested by Loesener could be supported by leaf anatomy, as well as affinities with several other species from different infrageneric taxa recognized by Loesener.

Ilex versteeghii Merr. & Perry, J. Arn. Arb. 22 (1941) 259 (subg. *Euilex*, series C, sect. *Rugosae*)
Lamina 530 μm. Adaxial and abaxial cuticle 6 μm. Stomata cyclocytic, 38 × 30 μm. Unspecialized abaxial epidermal cells with very thick anticlinal walls. Adaxial epidermis with anticlinal and periclinal subdivisions, containing bulging mucilage cells. Bundle sheaths and part of spongy tissue lignified. Minute solitary crystals in adaxial epidermis. Petiole with simple open vascular system (type 4).

N o t e. Except for thick-walled unspecialized epidermal cells and a scleromorphic leaf anatomy (partly lignified spongy tissue, lignified bundle sheaths), this species lacks distinctive features. Of section *Rugosae, I. archboldiana* is very close to *I. versteeghii. I.*

revoluta of the same section differs in having regular cork warts and in some other characters as well. Overall similarities with several species of subgenus *Byronia* and of other series and sections of subgenus *Euilex* are also present.

Ilex verticillata (L.) Gray (subg. *Prinus*, series A) — **Plate II, 2**
Lamina 160 μm. Adaxial and abaxial cuticle *c.* 1 μm. Stomata anomocytic, 35 × 21 μm. Unspecialized abaxial epidermal cells with strongly undulating anticlinal walls forming an interlocking pattern. Adaxial epidermis with infrequent periclinal subdivisions and slightly bulging, possibly mucilaginous cells. Petiole with simple open vascular system (type 4).

Material studied. CANADA. Quebec: *Roland Germain 6216.*

N o t e . With its mesomorphic leaf anatomy, anomocytic stomata, and strongly undulating epidermal abaxial anticlinal cell walls this species resembles *I. serrata* and several other species of subgenus *Prinus*.

Ilex vitiensis Gray (subg. *Euilex*, series A, sect. *Excelsae*, subsect. *Laxae*)
Lamina 270 μm. Adaxial cuticle 3—4 μm; abaxial cuticle 2—3 μm. Unicellular hairs on abaxial side of midrib, petiole and major veins. Stomata anomocytic to cyclocytic, 26 × 21 μm. Hypodermis of 1 layer of small cells. Bundle sheaths lignified. Part of spongy tissue strongly birefringent. Petiole with simple open vascular system (type 4), but median strand composed of several discrete bundles.

Material studied. FIJI: *Degener 14592.*

N o t e . A small-celled hypodermis is the only outstanding feature of this species, which according to Loesener resembles amongst others *I. laurifolia.* However, the latter species differs from *I. vitiensis* in several leaf anatomical characters. The only species of subsection *Laxae* with hypodermal development is *I. tuerckheimii,* but the type of hypodermis is different. The anatomical evidence for indicating close affinities is therefore inconclusive.

Ilex wallichii Hook. *f.* (subg. *Byronia*, series A)
Lamina 320 μm. Adaxial cuticle 5—6 μm; abaxial cuticle 3—4 μm. Stomata mainly anisocytic, rarely cyclocytic, 19 × 18 μm. Adaxial epidermis with infrequent bulging mucilage cells. Bundle sheaths and part of spongy tissue lignified. Petiole with simple open vascular system (type 4).

Material studied. MALAYA: *Md. Nur SFN 33996.*

N o t e . Loesener's suggestion of a close affinity with *I. cymosa* can be supported by leaf anatomy: *I. wallichii* is more or less within the anatomical range of *I. cymosa.* There is also a resemblance with some other species from subgenus *Byronia* (*I. brassii, I. ledermannii,* and *I. sclerophylloides*) and with several species from subgenus *Euilex* (*I. guianensis, I. inundata, I. jenmannii,* and *I. laurifolia*).

Ilex zygophylla Merr., J. Arn. Arb. 20 (1939) 222 (subg. *Euilex*, series B, sect. *Vacciniifoliae* or subg. *Byronia*, series A) — **Plate IV, 9; fig. 7**
Lamina 700 μm. Adaxial cuticle 18—22 μm; abaxial cuticle 14—16 μm. Indumentum of thick-walled hairs, sometimes rather broad-based and with several basal septs (as in

I. hypoglauca), often unicellular, present over whole lamina. Stomata mainly cyclocytic, rarely anisocytic, 42 × 34 μm. Adaxial epidermis with straight anticlinal walls, with infrequent anticlinal subdivisions. Hypodermis of 1 cell layer, lignified. Petiole with simple open vascular system (type 4).

Material studied. N. Borneo: *Meijer SAN 38459.*

N o t e. When Merrill (l.c.) described this species as opposite-leaved he mentioned that both *I. zygophylla* and *I. oppositifolia* might belong to either subgenus *Byronia* series A, or subgenus *Euilex*, section *Excelsae*. Loesener (1942), however, corrected Merrill's observation on *I. zygophylla* and recorded leaves alternate or in whorls of three. He referred the species to section *Vacciniifoliae*. Anatomically the species is rather outstanding with its — for *Ilex* unique — lignified adaxial hypodermis, its indumentum of broad-based hairs which are partly septate as in *I. hypoglauca*, and the unusually large-sized stomata. The leaves are moreover highly scleromorphic with strongly lignified spongy tissue and bundle sheaths. Anatomically the affinities are with subgenus *Byronia* (*I. hypoglauca*) rather than with section *Excelsae* or *Vacciniifoliae* of subgenus *Euilex*. However, the species remains anatomically rather isolated.

Lists of Ilex species with certain leaf anatomical characters

For easy reference and identification purposes lists are given of the distribution of the more important leaf anatomical characters over the different species studied. Because of considerable overlapping between species it will be impossible to key out individual *Ilex* species on leaf anatomical characters, but combinations of characters from the lists can be used to narrow down the possibilities and find indications for the identification.

In intermediate or doubtful cases the species name is followed by ±. If more than one specimen has been studied, the species name may be followed by *p.p.* (*pro parte*) indicating that the feature involved is not constant for that species.

Hairs long and/or uniseriate

I. amelanchier	I. decidua	I. kwantungensis (±)	I. pubescens
I. brasiliensis	I. dubia	I. micrococca (±)	I. revoluta (±)
I. cassine			

Hairs unicellular with broad septate base

I. hypoglauca	I. zygophylla (±)

Abaxial epidermis (at least partly) lignified

I. amara	I. canariensis *p.p.*	I. dumosa	I. ovalifolia
I. argentina	I. cassine	I. martiniana	I. retusa
I. boliviana	I. crenata *p.p.?*	I. opaca	I. triflora

Adaxial epidermis with anticlinal division walls

I. altaclarensis	I. cassine	I. inundata	I. pernyi
I. amplifolia	I. cissoidea	I. krugiana	I. revoluta
I. anomala	I. coriacea	I. laurifolia	I. sebertii
I. aquifolium	I. formosana	I. macfadyenii	I. theezans
I. archboldiana	I. goshiensis	I. martiniana	I. tolucana
I. argentina	I. grandifolia	I. oppositifolia	I. versteeghii
I. brasiliensis	I. hanceana	I. peduncularis	I. zygophylla
I. brassii	I. integerrima	I. perado	

Adaxial epidermis containing mucilage cells

I. amelanchier
I. amplifolia
I. archboldiana
I. argentina
I. asprella
I. brassii
I. brunnea
I. canariensis
I. caroliniana
I. cassine
I. chinensis .
I. clemensiae
I. coriacea

I. crenata
I. cymosa *p.p.*
I. danielis
I. decidua (±)
I. divaricata
I. dubia (±)
I. grandifolia
I. guianensis
I. hypoglauca
I. insignis
I. integerrima (±)
I. inundata
I. krugiana

I. kwantungensis
I. laurifolia
I. ledermannii
I. longipes
I. macfadyenii
I. macrophylla
I. micrococca
I. ovalifolia
I. peduncularis
I. pulogensis
I. repanda
I. retusa

I. revoluta (±)
I. rotunda
I. sebertii
I. sideroxyloides
I. spicata
I. stapfiana
I. theezans
I. triflora
I. umbellata
I. versteeghii
I. verticillata (±)
I. wallichii

At least part of the stomata bicyclic

I. altaclarensis
I. aquifolium
I. argentina
I. bioritsensis
I. buergeri
I. celebensis

I. chinensis
I. cornuta
I. curranii
I. dipyrena
I. fargesii
I. ficoidea

I. formosana
I. glomerata
I. goshiensis
I. insignis
I. integra

I. krugiana
I. latifolia
I. opaca
I. perado
I. pernyi

Stomata predominantly anomocytic

I. amara
I. decidua

I. longipes

I. serrata

I. verticillata

Stomata mainly anomocytic to cyclocytic

I. amelanchier
I. anomala
I. archboldiana

I. asprella
I. brasiliensis
I. coriacea

I. dubia
I. dumosa
I. grandifolia

I. micrococca
I. stapfina

Stomata predominantly anisocytic

I. brassii
I. brunnea
I. cymosa *p.p.*

I. integerrima
I. laurifolia
I. macrophylla

I. martiniana
I. ovalifolia
I. pubescens

I. sclerophylloides
I. sideroxyloides
I. wallichii

Stomata mainly anisocytic to cyclocytic

I. cissoidea
I. clemensiae
I. confertiflora
I. cymosa *p.p.*
I. guianensis *p.p.*

I. hypoglauca *p.p.*
I. inundata
I. jenmannii
I. ledermanii

I. peduncularis
I. retusa
I. rotunda
I. theezans *p.p.*

I. triflora *p.p.*
I. tuerckheimii
I. umbellata
I. vitiensis

Stomata predominantly cyclocytic

I. amplifolia
I. argentina
I. boliviana
I. brevicuspis
I. buergeri
I. canariensis
I. caroliniana
I. cassine
I. celebensis
I. chinensis
I. crenata

I. curranii
I. danielis
I. divaricata
I. fargesii
I. ficoidea
I. formosana
I. glabra
I. hanceana
I. hypoglauca *p.p.*
I. insignis
I. integra

I. kleinii
I. krugiana
I. kwantungensis
I. macfadyenii
I. microdonta
I. mitis
I. oppositifolia
I. paraguariensis
I. pedunculosa
I. pulogensis
I. repanda

I. revoluta
I. scrabidula
I. sebertii
I. sikkimensis
I. spicata
I. theezans *p.p.*
I. tolucana
I. triflora *p.p.*
I. versteeghii
I. zygophylla

Guard cell pairs 20 μm long or shorter

I. amelanchier

I. umbellata

I. wallichii

Guard cell pairs 35 μm long or longer

I. altaclarensis
I. aquifolium *p.p.*
I. asprella
I. canariensis

I. clemensiae
I. latifolia
I. opaca

I. oppositifolia
I. perado *p.p.*
I. sebertii

I. versteeghii
I. verticillata
I. zygophylla

Regular cork warts

I. amara
I. amplifolia
I. boliviana
I. caroliniana
I. clemensiae

I. coriacea
I. crenata
I. divaricata
I. glabra
I. macfadyenii

I. martiniana
I. ovalifolia
I. paraguariensis
I. pulogensis
I. retusa

I. revoluta
I. scrabidula
I. spicata
I. triflora

Continuous hypodermis present

I. altaclarensis
I. anomala
   (mucilaginous)

I. aquifolium
I. brasiliensis
   (mucilaginous)

I. perado
I. tuerckheimii
   (mucilaginous)

I. vitiensis
I. zygophylla
   (lignified)

At least part of spongy tissue lignified or strongly birefringent

I. amara
I. archboldiana
I. brassii
I. confertiflora
I. cymosa *p.p.*
I. grandifolia

I. hypoglauca
I. laurifolia
I. ledermannii
I. macrophylla
I. martiniana
I. opaca

I. oppositifolia
I. ovalifolia
I. peduncularis
I. sclerophylloides
I. sebertii
I. triflora

I. tuerckheimii
I. versteeghii
I. vitiensis
I. wallichii
I. zygophylla

Bundle sheaths lignified or at least strongly birefringent

I. amara
I. anomala
I. archboldiana
I. argentina (±)
I. boliviana
I. brassii
I. buergeri
I. celebensis
I. cissoidea (±)

I. clemensiae
I. cymosa
I. dumosa
I. grandifolia
I. hypoglauca
I. insignis
I. laurifolia
I. ledermannii
I. macrophylla

I. martiniana
I. opaca
I. oppositifolia
I. ovalifolia
I. peduncularis
I. pulogensis
I. repanda (±)
I. retusa

I. sclerophylloides
I. scrabidula
I. spicata
I. stapfiana
I. versteeghii
I. vitiensis
I. wallichii
I. zygophylla

Foliar sclereids present throughout lamina

I. buergeri
I. confertiflora (±)

I. cornuta (±)
I. curranii

I. ficoidea
I. formosana

I. glomerata
I. mitis

Marginal sclerenchyma strands

I. altaclarensis
I. aquifolium
I. bioritsensis

I. confertiflora (±)
I. cornuta
I. dipyrena

I. insignis (±)
I. integra (±)
I. latifolia (±)

I. perado
I. pernyi

Minute solitary crystals in adaxial epidermis

I. celebensis
I. laurifolia

I. mitis
I. paraguariensis

I. rotunda

I. versteeghii

Vascular system of petiole simple open without wing bundles (types 1 & 2)

I. amelanchier	I. caroliniana	I. longipes	I. serrata
I. asprella	I. celebensis	I. pedunculosa	

Vascular system of petiole simple closed (types 6 & 7)

I. chinensis (±)	I. microdonta	I. opaca	I. repanda

Vascular system only closed in midrib

I. anomala p.p.	I. hanceana	I. kwantungensis	I. tolucana
I. chinensis			

Vascular system of petiole complex open to closed (types 8 & 9)

I. cymosa p.p.	I. hypoglauca p.p.	I. spicata	I. stapfiana
I. grandifolia	I. oppositifolia		

Vascular system of petiole interrupted open (type 5)

I. clemensiae

Vascular system of petiole 'double' (type 10)

I. coriacea	I. glabra

Comparison of leaf anatomical data with Loesener's system

In this section the leaf anatomical ranges of variation of the individual infrageneric taxa recognized by Loesener will be discussed. Suggestions will be made about the affinities of these taxa in cases where the leaf anatomical evidence has obvious taxonomic implications.

The number of species of which each individual section is composed is given between brackets, and is taken from Loesener (1942).

Subgenus RYBONIA

(1 species in Borneo)

1 species studied: *I. oppositifolia*.

Loesener established this subgenus in 1942, without discussing its systematic position within the genus *Ilex*. From his placing of subgenus *Rybonia* at the beginning of the list of 5 subgenera, close to subgenus *Byronia*, one may conclude that he regarded *I. oppositifolia* as a primitive representative of *Ilex*. The leaf anatomy of this species indeed recalls that of some species of subgenus *Byronia*, and the complex vascular system in the midrib of the leaves can be used to support the idea that subgenus *Rybonia* is derived from the same ancestral stock as section *Indico-Malaicae* of subgenus *Euilex*, and as subgenus *Byronia*. There are also leaf anatomical similarities with some species treated as members of section *Rugosae* of subgenus *Euilex*.

Subgenus BYRONIA

Series A. EUBYRONIA (*c*. 20 species in tropical Asia, Australia, and Polynesia)

11 species studied: *I. anomala, I. brassii, I. celebensis, I. cymosa, I. grandifolia, I. hypoglauca, I. ledermannii, I. macrophylla, I. peduncularis, I. sclerophylloides, I. wallichii*.

The stomatal type may be predominantly anomocytic, anisocytic, or cyclocytic within

this series, whilst partly bicyclic stomata occur in *I. celebensis*. Stomatal size ranges from 19 × 18 to 34 × 29 μm. The indumentum varies from the unusual type in *I. hypoglauca* to consisting of short unicellular hairs, or it is absent. Cork warts are absent or at least never of regular outline and frequent occurrence. The adaxial epidermis may be entirely un-modified, or contain mucilage cells, or show periclinal and/or anticlinal subdivisions with or without mucilaginous daughter cells. A 'true' (mucilaginous) hypodermis occurs in *I. anomala* only. The bundle sheaths are lignified in all species. The vascular pattern in the distal end of the petiole covers the ranges from simple open (1—4) to the more complex types (7—9). Sclereids and marginal sclerenchyma strands are absent from all species. Most species show a number of scleromorphic features: all species (except *I. anomala* and *I. celebensis*) have partly lignified spongy tissue.

Series *Eubyronia* thus appears to be anatomically very heterogeneous with a great diversity in most leaf anatomical features relevant for the characterization of individual *Ilex* species. The heterogeneity would be somewhat reduced by expelling *I. anomala* and *I. celebensis* from this series, so that series *Eubyronia* would lack hypodermal differentiation and bicyclic stomata. *I. anomala* is also wood anatomically rather aberrant (Baas, 1973).

The only way to characterize series *Eubyronia*, and most of Loesener's other infrageneric taxa leaf anatomically, would be to record the most frequent occurrence of certain features like: bundle sheaths lignified; spongy tissue mostly partly lignified; often with anisocytic stomata, etc. As additional characterization one might use negative characters like: cork warts, sclereids, and marginal sclerenchyma strands absent, abaxial epidermis not lignified, etc.

Series B. MICROCOCCA (1 species in East Asia)
    1 species studied: *I. micrococca*.
    With its septate hairs, anomocytic to cyclocytic stomata, and simple mesomorphic leaf anatomy this species is very different from those of series *Eubyronia*. Similarities with subgenus *Prinus* are much stronger.

Subgenus Byronia as a whole
    The subgenus is leaf anatomically very heterogeneous. Similarities of some species with those of other subgenera (*Rybonia*, *Euilex*, section *Indico-Malaicae*, and *Prinus*) may indicate true affinities or be due to parallel or convergent evolution. The anatomical heterogeneity does not necessarily challenge Loesener's grouping, because he based this subgenus on the common occurrence of supposedly primitive characters of inflorescence and flower. One could accept that within such a group of species in which these primitive characters have been retained, other characters like those of leaf anatomy have become specialized in different ways.

<div align="center">Subgenus EUILEX</div>

Series A. LIOPRINUS
Section Excelsae (*c.* 31 species in East Asia, Polynesia, and Tropical America)
    10 species studied: subsection *Umbelliformes*: *I. chinensis, I. kwantungensis, I. pedunculosa, I. rotunda*; subsection *Laxae*: *I. amplifolia, I. laurifolia, I. macfadyenii, I. sebertii, I. tuerckheimii, I. vitiensis.*
    An indumentum is absent or consists of short unicellular hairs only, except in *I. kwan-tungensis* which has numerous long hairs. The stomata are usually aniso- and cyclocytic, one of the types is sometimes predominant or exclusive. Only *I. chinensis* has some partly

bicyclic to complex cyclocytic stomata. Stomatal size ranges from 22 × 21 to 36 × 31 μm. Regular frequent cork warts occur in *I. amplifolia* and *I. macfadyenii* only. The adaxial epidermis may be entirely unmodified, contain mucilage cells, or show periclinal sub-divisions with mucilaginous daughter cells, or anticlinal subdivisions. A small-celled hypodermis occurs in *I. vitiensis*, whilst a mucilaginous hypodermis of partly subdivided bulging cells occurs in *I. tuerckheimii*. The bundle sheaths and mesophyll are entirely unlignified or almost so in all species except *I. laurifolia* and *I. vitiensis*. The vascular system of the petiole is mainly of the common type 4, but a single strand (type 1) occurs in *I. pedunculosa* and a simple closed type 6 system in (at least the midrib of) *I. chinensis* and *I. kwantungensis*. Foliar sclereids and marginal sclerenchyma strands are absent from all species.

Section *Excelsae* is therefore also rather heterogeneous leaf anatomically, albeit less so than e.g. series *Eubyronia*. The range in epidermal and hypodermal differentiation in subsection *Laxae* is rather great, as well as the variation in vascular patterns in petiole and midrib in subsection *Umbelliformes*. *I. amplifolia* seems out of place because of its frequent cork warts. Some species, notably *I. laurifolia*, are similar to species of subgenus *Eubyronia*, and section *Indico-Malaicae* of subgenus *Euilex*.

Leaf anatomy does not provide good diagnostic characters to separate subsection *Umbelliformes* and subsection *Laxae*.

Section **Cassinoides** (*c.* 16 species in Macaronesia, America, and East Asia)

5 species studied: *I. canariensis, I. cassine, I. coriacea, I. glabra, I. opaca*.

In section *Cassinoides* the indumentum may be absent, consist of short unicellular hairs, or of long septate hairs (*I. cassine*). The stomata are mainly cyclocytic but occasionally anisocytic stomata or transitions to anomocytic stomata also occur, whilst *I. opaca* has predominantly bicyclic stomata. Stomatal size ranges from 24 × 23 to 39 × 35 μm. Regular cork warts are present in *I. coriacea* and *I. glabra* only. The abaxial epidermis of *I. canariensis* p.p., *I. cassine*, and *I. opaca* has lignified unspecialized cells. The adaxial epidermis is entirely unmodified or is mucilaginous with periclinal subdivisions. The bundle sheaths are lignified in *I. opaca* only. The mesophyll is generally unlignified though in *I. opaca* it is partly lignified. The vascular pattern of the petiole may be of type 4, 6, or 10 (*I. coriacea* and *I. glabra*). Sclereids and marginal sclerenchyma strands are absent from all species studied.

The anatomical heterogeneity of this section thus also appears to be considerable, with presence or absence of cork warts and of a lignified epidermis as the most striking variables. *I. canariensis* from Macaronesia resembles *I. cassine* from North America. *Ilex coriacea* and *I. glabra*, both from N. America, also seem mutually related. *I. opaca* from N. America appears rather isolated anatomically.

Section **Dasyneurae** (*c.* 3 species in S. America)

1 species studied: *I. boliviana*.

Anisocytic to cyclocytic stomata, long hairs, a lignified abaxial epidermis with frequent regular cork warts, and lignified bundle sheaths characterize this scleromorphic species. Apparently, cork warts are not a constant feature of this section, because Loesener (1942) recorded that the other 2 species have '*punktlose Blätter*'. Anatomical resemblance with *I. retusa* of the related section *Crassifoliae* seems systematically significant (cf. Loesener, 1908: 47—49). Affinities with *I. martiniana* and *I. ovalifolia* of series D, section *Thyrsiflorae* and with *I. triflora* of section *Microdontae* can also be advocated on the strength of anatomical similarities in rather unusual character complexes.

Section **Crassifoliae** (*c.* 11 species in tropical S. America)
    1 species studied: *I. retusa.*
    I. retusa is very similar to *I. boliviana* and the same characterization, except for the indumentum, would apply. Affinities would therefore also be indicated with section *Microdontae*, section *Thyrsiflorae*, and section *Dasyneurae.*

Series Lioprinus as a whole
    The series is anatomically very heterogeneous, and can only be characterized by the absence of some — elsewhere in *Ilex* unusual — features such as broad-based septate hairs, sclereids, and marginal sclerenchyma strands.

Series **B.** PALTORIA
    Section **Polyphyllae** (*c.* 20 species mainly in tropical S. America, *I. crenata* from East Asia and North Malesia)
    2 species studied: *I. dumosa, I. crenata.*
    Although *I. crenata* itself shows a considerable degree of variation, the two species from different geographical regions resemble each other. The material studied is, however, too limited to conclude whether all species of *Polyphyllae* are characterized by the character combination shared by *I. crenata* and *I. dumosa.* At least the occurrence of cork warts (cf. Loesener's accounts of species with '*unpunktierte Blätter*', 1942) and of a lignified abaxial epidermis (cf. variability of *I. crenata*) is not constant within this section. Other features for which the section appears to be heterogeneous are subdivision and mucilaginous nature of the adaxial epidermis and lignification of the bundle sheaths. Loesener's suggestion (1908) about possible links with section *Crassifoliae* of series *Lioprinus* could be supported because a lignified epidermis and frequent cork warts have also been found in *I. retusa* of that section.

Section **Vacciniifoliae** (*c.* 26 species in S. America, Malesia, and Ceylon)
    2 species studied: *I. hanceana, I. zygophylla.*
    The rather 'unspecialized' leaf anatomy of *I. hanceana* does not allow systematic discussions of relevance for this widely distributed section. *I. zygophylla* is entirely different and may be closer to subgenus *Byronia* series A than to this section and series.

Series Paltoria as a whole
    Only 4 species from two sections have been studied of this series. Inclusion of *I. zygophylla* makes series *Paltoria* anatomically very heterogeneous.

Series **C.** AQUIFOLIUM
Section **Lemurenses** (*c.* 12 species; 1 in Africa, the remainder in East Asia and Indo-Malesia)
    2 species studied: *I. fargesii, I. mitis.*
    According to Loesener (1908: 57) the two species used for study belong to the relatively advanced species of this section, which is said to represent an intermediate fase between series *Lioprinus* and series *Aquifolium.* Anatomically links are indicated with section *Aquifolioides* and *Microdontae* subsection *Repandae.* Within the small sample of species studied, the anatomical range is quite narrow; the diversity is restricted to presnece or absence of foliar sclereids and of bicyclic stomata, and to the degree of curving of the vascular bundle in the petiole.

Section **Aquifolioides** (*c.* 21 species, for distribution see under subsections)

Subsection O x y o d o n t a e (*c.* 14 species in Macaronesia, N. Africa, and Eurasia)

7 species studied + 1 hybrid: *I. altaclarensis* (hybrid), *I. aquifolium, I. bioritsensis, I. cornuta, I. dipyrena, I. integra, I. perado, I. pernyi.*

Subsection I n s i g n i s (*c.* 7 species in Indo-Malesia and East Asia)

3 species studied: *I. insignis, I. latifolia, I. sikkimensis.*

Most of the species of section *Aquifolioides* share a highly characteristic complex of leaf anatomical features. Except *I. sikkimensis* all species share at least partly bicyclic stomata, marginal sclerenchyma strands or a tendency towards this feature (*I. insignis, I. integra,* and *I. latifolia*), large stomata (27 × 27 to 38 × 36 μm), indumentum absent or composed of short unicellular hairs only, a simple open vascular system of the petiole of type 2 or 4, and the absence of lignification in the abaxial epidermis and mesophyll, and of frequent cork warts. *I. insignis* is the only species with a lignified bundle sheath. *I. sikkimensis* is aberrant with its cyclocytic to anomocytic stomata, and absence of marginal sclerenchyma strands.

The anatomical homogeneity of section *Aquifolioides* (excluding *I. sikkimensis*) is very exceptional for *Ilex*, and strongly supports the naturalness of this group of species. There are leaf anatomical links with section *Lemurenses* through *I. fargesii* and with a number of species from section *Microdontae* subsection *Repandae*. This agrees remarkably well with Loesener's ideas about mutual relationships of those sections. His statement (1908: 59) that section *Aquifolioides* represents a highly specialized evolutionary level within subgenus *Euilex*, could be used to support the rather intuitive belief that within *Ilex* characters like bicyclic stomata, marginal sclerenchyma strands and hypodermal development represent anatomical specializations. *I. sikkimensis* might represent a link with less specialized groups, although the leaf anatomy is not distinctive enough to indicate a particular section.

Section **Microdontae** (*c.* 50 species, for distribution see under subsections)

Subsection E u m i c r o d o n t a e (*c.* 6 species in tropical America)

3 species studied: *I. krugiana, I. brevicuspis, I. microdonta.*

Subsection R e p a n d a e (*c.* 35 species in tropical and subtropical America and Asia)

10 species studied: *I. argentina, I. buergeri, I. confertiflora, I. curranii, I. ficoidea, I. formosana, I. glomerata, I. paraguariensis, I. repanda, I. tolucana.*

Subsection V o m i t o r i a e (1 species in N. America)

1 species studied: *I. caroliniana.*

Subsection S t i g m a t o p h o r a e (*c.* 2 species in tropical and subtropical Asia)

1 species studied: *I. triflora.*

Subsection S i d e r o x y l o i d e s (*c.* 6 species in East Asia and tropical America)

3 species studied: *I. divaricata, I. goshiensis, I. sideroxyloides.*

The anatomical range in section *Microdontae* is very considerable, not only in the section as a whole but also in the individual subsections of which more than one species was studied.

In subsection *Repandae* an indumentum may be absent, consist of short unicellular hairs, or as in *I. tolucana* be represented by longer unicellular broad-based hairs. Stomata are always at least partly cyclocytic but in some species bicyclic stomata are present in various amounts, in others anisocytic stomata are present in addition. The guard cell pairs range in size from 23 × 23 to 38 × 28 μm. Regular cork warts are present in one species only (*I. paraguariensis*), the adaxial epidermis is usually unmodified but has periclinal subdivisions with mucilaginous daughter cells in two species. A hypodermis is never

fully developed; only some species show local hypodermal differentiation in the midrib. *I. argentina* has lignified abaxial epidermal cells, and in *I. paraguariensis* these cells have very thick unlignified walls. The bundle sheaths and spongy tissue of the mesophyll may be lignified or not. The petiole is usually supplied with a simple open vascular system (type 3 or 4) but a closed cylinder occurs in *I. repanda* and *I. paraguariensis*. Marginal sclerenchyma strands are usually absent, but five species are characterized by idioblastic foliar sclereids.

The species of subsection *Eumicrodontae* are more or less within the leaf anatomical range of subsection *Repandae*. Cork warts, a lignified epidermis, or foliar sclereids have not been encountered in the species studied. Here too the stomata are always at least partly cyclocytic, but in one species (*I. krugiana*) bicyclic stomata also occur, and in *I. microdonta* anisocytic stomata are present in addition. Stomatal size ranges from 26×21 to $30 \times 25 \mu m$. The latter species also shows local hypodermal development in the midrib region.

I. caroliniana of subsection *Vomitoriae* with its frequent cork warts and lack of wing bundles in the petiole is not very close to any particular species of subsection *Repandae*, although most of its characters are present somewhere in that subsection.

I. triflora of subsection *Stigmatophorae* with its combination of lignified abaxial epidermis and regular cork warts is unique amongst the species studied of this section.

Subsection *Sideroxyloides* is anatomically heterogeneous, even in the small sample of 3 species studied. Stomatal type, presence or absence of cork warts and hairs are the main variables here. Through *I. sideroxyloides* the anatomical range of section *Microdontae* is again somewhat extended because stomata are predominantly anisocytic in this species.

The leaf anatomical heterogeneity of section *Microdontae* makes it impossible to indicate affinities with other sections for the whole group of species studied. Leaf anatomy only provides strong arguments to regard a group of 6 species from subsection *Repandae* as mutually closely related. This group is characterized by the presence of foliar sclereids, cyclocytic or cyclocytic to bicyclic stomata and numerous other less outstanding anatomical features. *I. buergeri*, *I. confertiflora*, *I. curranii*, *I. ficoidea*, *I. formosana*, and *I. glomerata* belong to this group. These species have anatomical links with *I. mitis* from section *Lemurensis* and with the species from section *Aquifolioides*. It is noteworthy that the latter species which are mainly provided with marginal sclerenchyma strands should share many features with species having another device to increase the scleromorphic nature of their leaves: foliar sclereids. *I. cornuta* and *I. confertiflora* are anatomically intermediate between these two groups. Affinities of section *Microdontae* with section *Lemurensis* and section *Aquifolioides* are well in line with Loesener's ideas about the derivation of this group. The anatomical heterogeneity also implies that links between several other sections can be suggested. For *I. microdonta* of subsection *Eumicrodontae* this would be section *Vacciniifoliae* and section *Excelsae*. For *I. argentina* of subsection *Repandae* affinities with section *Cassinoides* could be suggested because of resemblance with *I. canariensis* of that section. Anatomies similar to that of *I. caroliniana* of subsection *Vomitoriae* occur in section *Cassinoides* and section *Excelsae*. *Ilex triflora* of subsection *Stigmatophorae* shares many leaf characters with certain species of section *Thyrsiflorae*. Finally affinities could be suggested of *I. divaricata* of subsection *Sideroxyloides* with sections *Cassinoides*, *Micranthae*, *Megalae*, and *Excelsae*. However, since many of these similarities are based on rather indistinctive leaf anatomies, the value of these similarities for judging the natural affinities is probably highly restricted.

Section **Prinifoliae** (1 species in East Asia)
    1 species studied: *I. pubescens*.
    The anatomy of this mesomorphic species is suggestive of that of subgenus *Prinus* except for a difference in stomatal type.

Section **Megalae** (*c.* 13 species in tropical S. America)
    3 species studied: *I. brasiliensis, I. integerrima, I. theezans*.
    The only variables in the leaf anatomy of this group of species are in stomatal type and indumentum. *I. brasiliensis* stands out in both these characters with long septate hairs and cyclocytic to anomocytic stomata, instead of cyclocytic to anisocytic stomata occurring in the other two species. The characters shared by all three species are of very common occurrence within *Ilex*, so that affinities with many groups could be advocated without really contributing much to our understanding of the wider affinities of this section.

Section **Micranthae** (*c.* 27 species in tropical America)
    5 species studied: *I. danielis, I. guianensis, I. inundata, I. jenmanii, I. umbellata*.
    The variation within this section is quite small. An indumentum, if present, always consists of short unicellular hairs; the stomata are usually cyclocytic to anisocytic, with *I. danielis* as the only exception with cyclocytic to anomocytic stomata; stomatal size ranges from 18×16 (*I. umbellata*) to $27 \times 23 \mu m$; regular cork warts are absent; the epidermis is usually subdivided and is at least always partly mucilaginous. The abaxial epidermis and bundle sheaths are never lignified. The petiole vasculature is simple open, and sclereids and marginal sclerenchyma strands are always absent. As in section *Megalae* this anatomical character complex is rather unspecialized and of common occurrence throughout *Ilex*.

Section **Rugosae** (*c.* 5 species in Indo–Malesia and East Asia)
    3 species studied: *I. archboldiana, I. revoluta, I. versteeghii*.
    Of these three species, only *I. revoluta* was known by Loesener. *I. versteeghii* and *I. archboldiana* are treated here because of suggestions by Merrill & Perry (1941). The two latter species are very similar, but *I. revoluta* deviates in having frequent cork warts, an indumentum of moderately long hairs, and non-lignified spongy tissue.
    For this species no suggestions about affinities can be given. For the other two species there are links with subgenus *Byronia* and several sections of subgenus *Euilex*. These links rest on a scleromorphic anatomy without very characteristic features, and may therefore be of little systematic significance.

Series Aquifolium as a whole
    This large infrageneric taxon with over 100 species shows a tremendous leaf anatomical range in the sample of 44 species studied. Foliar sclereids and marginal sclerenchyma strands have only been found in species of this series, though they are absent from the majority of them. Not the entire anatomical range of *Ilex* is covered in series *Aquifolium*. Complex vascular systems and a mucilaginous hypodermis never occur. Bicyclic stomata are almost entirely confined to this series, but only three species outside it show this feature, whilst 14 species of series *Aquifolium* (belonging to section *Microdontae* and section *Aquifolioides*) have at least partly bicyclic stomata. Within the series two clearly defined anatomical groups can be distinguished: one with marginal sclerenchyma strands and another with foliar sclereids. These two groups are in other characters anatomically rather similar, and are at the same time linked through intermediates. They probably

represent the highest levels of leaf anatomical specialization in *Ilex*. The majority of species presents a rather heterogeneous assemblage, only infrequently showing distinctive anatomical features.

Series D. THYRSOPRINUS

Section **Indico-Malaicae** (*c.* 18 species in Malesia, Ceylon, and Papuasia)

7 species studied: *I. brunnea, I. cissoidea, I. clemensiae, I. pulogensis, I. scrabidula, I. spicata, I. stapfiana.*

In Loesener's system only *I. cissoidea, I. pulogensis, I. spicata,* and *I. stapfiana* are included; the other three species are treated here because of suggestions of affinity by their authors. '*Punktierte Blätter und Blätter ohne Punkte*' both occur within this section according to Loesener (1942); this is reflected in the variability in presence or absence of frequent regular cork warts recorded here.

The anatomical range of the four former species is as follows: indumentum absent or consisting of broad-based hairs (*I. cissoidea*), stomata cyclocytic, cyclocytic to anisocytic, cyclocytic to anomocytic, or cyclocytic to bicyclic (*I. pulogensis*), stomatal size ranges from 26 × 21 to 32 × 23 μm, regular cork warts frequent or absent, adaxial epidermis unmodified, containing mucilage cells, or subdivided with mucilaginous daughter cells. Petiole with complex closed vascular system (*I. spicata* and *I. stapfiana*) or with simple open system (*I. cissoidea* and *I. pulogensis*). The bundle sheaths are usually lignified, but sometimes very faintly so. Unusual features such as a hypodermis, sclereids, or marginal sclerenchyma strands are absent. The inclusion of the three other species, especially *I. clemensiae*, would extend the anatomical range to some extent: an indumentum of short unicellular hairs is present in *I. clemensiae*, stomatal size would range up to 38 × 29 μm (*I. clemensiae*), and the vascularization of the petiole would also include the unusual type 5 (*I. clemensiae*).

Regardless of the inclusion of the latter species in this section, *Indico-Malaicae* remains leaf anatomically a rather heterogeneous group, with indumentum, stomatal type, cork warts, and petiole vascularization as the main variables. Loesener's hypothesis that this section, together with subgenus *Byronia*, is derived from a common stock can be supported by leaf anatomy. Complex types of petiole vascularization of type 8 are entirely restricted to subgenus *Byronia* and section *Indico-Malaicae*. *I. oppositifolia* of subgenus *Rybonia*, with a similar midrib vascularization, could be derived from the same ancestors. Moreover, some species of section *Indico-Malaicae* share their overall leaf anatomy with several species of subgenus *Byronia*. It should, however, be stressed that similarities also exist with several species of subgenus *Euilex*, opening possibilities to advocate affinities with numerous sections.

Section **Thyrsiflorae** (*c.* 10 species in tropical S. America)

2 species studied: *I. martiniana, I. ovalifolia.*

These two species are anatomically very similar with the following characters shared: indumentum absent, stomata aniso- to cyclocytic, regular cork warts frequent, abaxial epidermis and bundle sheaths lignified, vascular bundle pattern in petiole simple open, and unusual features absent. The remaining diversity: stomatal size ranging from 26 × 23 to 33 × 28 μm, adaxial epidermis unmodified or mucilaginous and with periclinal subdivisions, is quite small in comparison with the overall similarities.

Loesener (1908) suggested a different ancestry for this section and the following section (*Brachythyrsae*) than for section *Indico-Malaicae* of the same series. Support for this suggestion may be advanced using a leaf anatomical character: lignified abaxial epidermal cells. This feature also occurs in section *Crassifoliae*, which was put 'at the base' of section

Thyrsiflorae by Loesener. In other sections of series A. *Lioprinus*, which according to Loesener's 'Stammbaum' are even more primitive, the lignified epidermis also occurs sporadically (in section *Dasyneurae* and section *Cassinoides*). Outside series D and A, lignified abaxial epidermides are only found in two species of section *Microdontae* (series C), one species of section *Rugosae* (series C), and in section *Polyphyllae* (series B); the latter section is regarded to be very close to some sections of series D by Loesener. Within series D a lignified epidermis characterizes also the only species studied of section *Brachythyrsae*.

The fact that within this part of the genus *Ilex*, an unusual anatomical feature like the occurrence of a lignified epidermis is strongly correlated with Loesener's ideas of classification as based on macromorphology is suggestive of a considerable systematic value of this anatomical character. This is also supported by Cador's observations on some other species of the same or closely related sections showing a lignified abaxial epidermis. Whether this has also implications for the systematic position of those species from series C having a lignified epidermis, remains uncertain until a new taxonomic revision of the whole genus is carried out.

Section **Brachythyrsae** (*c.* 6 species in Brazil)

1 species studied: *I. amara.*

With its frequent cork warts and lignified epidermis this species recalls those of the previous section. The main difference is the predominance of anomocytic stomata in *I. amara*. The anatomical resemblance of *I. amara* with species from section *Thyrsiflorae* and of sections *Polyphyllae* and *Crassifoliae* are in full agreement with Loesener's suggestions about affinities (see above).

Series Thyrsoprinus as a whole

From Loesener's derivation of the inflorescences in this series and his phylogenetic tree (fig. 31) follows a polyphyletic origin for the different sections of this series. Only a limited number of representatives of part of the sections has been studied anatomically, but the leaf anatomy may be used to support this hypothesis. Section *Indico-Malaicae* shows links with subgenus *Byronia*, and the other sections witness affinities with sections *Crassifoliae*, *Polyphyllae*, *Cassinoides*, and *Dasyneurae* of series *Lioprinus* and series *Paltoria* of subgenus *Euilex*. As with most series treated before, the anatomical diversity of *Thyrsoprinus* is very great.

Subgenus Euilex as a whole

This is Loesener's largest subgenus, numbering about 230 species out of the total number of 271 *Ilex* species recognized in 1908. It is not surprising therefore to note that the anatomical range of this subgenus virtually covers the whole range of the genus. The only character not occurring within this subgenus is the unusual hair type with septate base as occurring in *I. hypoglauca* of subgenus *Byronia*. If, however, Loesener's placing of *I. zygophylla* in section *Vacciniifoliae* would be correct, hairs resembling the 'hypoglauca' type would also occur in subgenus *Euilex*. The anatomical diversity of subgenus *Euilex* cannot be used to verify Loesener's classification and ideas of affinities. According to his derivations of several character complexes, the different series and sections present many diverse specializations in external morphology, and this may well be brought in agreement with a great anatomical diversity. The anatomical heterogeneity of several sections is, however, more problematic, and raises the question whether their arrangement and delimitation really reflects natural affinities.

Subgenus PRINUS

Series A. EUPRINUS (*c.* 6 species in N. America and East Asia)

2 species studied: *I. serrata, I. verticillata*.

Thin mesomorphic leaves and strongly undulating 'interlocking' anticlinal walls in the abaxial epidermis with anomocytic stomata, but without other outstanding anatomical features characterize the two species studied. Yet there is some anatomical heterogeneity in indumentum, stomatal size (24 × 17 & 35 × 21 μm), presence or absence of mucilage cells in the epidermis and presence or absence of wing bundles in the petiole. There are obvious links with several species of series B. *Prinoides*, and also with some species with a mesomorphic leaf anatomy from other subgenera, notably *I. micrococca* from subgenus *Byronia*.

Series B. PRINOIDES (*c.* 10 species in N. America, East Asia, and India)

5 species studied: *I. amelanchier, I. asprella, I. decidua, I. dubia, I. longipes*.

The species of this series share many characters with those of series *Euprinus*. The anatomical heterogeneity is quite restricted: an indumentum may be absent but is usually well-developed and consists of long septate hairs or non-septate broad-based hairs; the stomata are usually anomocytic or anomocytic to cyclocytic with very rarely anisocytic stomata in addition (*I. decidua*); stomatal size ranges from 20 × 19 to 37 × 29 μm; the adaxial epidermis always contains mucilage cells, and frequently shows periclinal sub-divisions; petiole vasculature is always simple open. Features such as cork warts, sclereids, lignified epidermis, marginal sclerenchyma strands, lignified spongy tissue, and lignified bundle sheaths are absent from all these mesomorphic species. The interlocking undulations of the abaxial anticlinal epidermis walls in *I. longipes* recall the situation in series *Euprinus*. Besides similarities with the latter series, there are anatomical resemblances with *I. micrococca* (of subgenus *Byronia*) and *I. pubescens* and *I. brevicuspis* (of subgenus *Euilex*). All these species are also characterized by a mesomorphic leaf anatomy, so that the anatomical similarities may reflect similar autecologies of the species involved (*in casu* deciduous habit ?) rather than true affinity.

Subgenus Prinus as a whole

Through its deciduous mesomorphic leaves, this subgenus constitutes anatomically a fairly homogeneous assemblage. There is a strong tendency for anomocytic stomata to be the predominant type, and all other characters except the indumentum tend to be rather 'unspecialized'. Although there are some species in the other subgenera with a similar leaf anatomy, it would be unjustified to use this as a strong argument in favour of mutual affinity since most of these characters are a direct consequence of the mesomorphic habit of the foliage in these species. As Loesener's suggestions of affinities with other species also largely rest on this mesomorphic appearence as a macromorphological feature, the use of the leaf anatomical characters for additional arguments would imply an overweighting of the same character complex.

Taxonomic conclusions

The leaf anatomical heterogeneity of most infrageneric taxa recognized by Loesener raises the question about the naturalness of his classification. All subgenera show some or much overlapping in their leaf anatomical range with each other, and this also holds for most series, sections, and subsections.

As similar situation in wood anatomy (Baas, 1973) could not be used to challenge

Loesener's system, because latitudinal and altitudinal trends were strongly suggestive of ecological factors as directing agents in the evolution of wood anatomical diversity.

Leaf anatomy in general may also be correlated with ecological factors, but since *Ilex* shows different possibilities to arrive at xeromorphic or scleromorphic structures, the actual structures present may still be witness of natural affinities (see p. 404). However, the number of examples in which there is a correlation between leaf anatomy and Loesener's system is very limited. Attempts to make alternative groupings of *Ilex* species, based on combinations of anatomical characters have failed, with the few exceptions of small species groups characterized by rather distinctive leaf anatomies e.g. the species with marginal sclerenchyma strands and/or foliar sclereids.

The numerous *Ilex* species without distinctive anatomical characters do not provide suggestions about natural affinities, and the distribution of the remaining species with distinctive characters (special petiole types, hypodermal development, special features of the epidermis, stomatal types of infrequent occurrence etc.) over the different infrageneric taxa is suggestive of a much more complex pattern of relationships than suggested in Loesener's formal subdivision. This is in fact also what one would suspect when analyzing Loesener's rather vague characterizations of his infrageneric taxa.

Infraspecific variability in 15 species of Ilex

Of the following 15 species, more than one specimen was studied. The number of specimens studied is indicated between brackets: *I. anomala* (4); *I. aquifolium* (4); *I. bioritsensis* (2); *I. canariensis* (3); *I. crenata* (11); *I. cymosa* (7); *I. ficoidea* (2); *I. guianensis* (3); *I. hypoglauca* (5); *I. opaca* (3); *I. perado* (3); *I. pernyi* (2); *I. serrata* (2); *I. theezans* (2); *I. triflora* (6). In some cases infraspecific variability was only studied for certain anatomical characters, without considering the complete leaf anatomy: e.g. of *I. crenata* only macerations were studied to check the lignification of the cell walls of the abaxial epidermis.

Although the number of specimens studied for testing the diagnostic value of the anatomical characters was very limited, the results indicate a high degree of variability below the species level of most characters.

Lamina thickness varies between wide or narrow limits as can be seen in the descriptions of the species tested.

The presence or absence of an indumentum is variable in four species tested. This always concerns species with only sparse unicellular hairs. Species with a more distinctive hair type are constant in this respect.

The texture of the cuticle, caused by a granular or smooth structure of the cuticular layer (cf. Van Staveren & Baas, 1973) is variable in two of the species tested. Cuticular striations appeared to be variable in distinctness or even presence or absence in five species. Cuticular thickness always varies to a small or large extent, and is recorded in the specific descriptions.

The outline of the unspecialized epidermal cells, as affected by the anticlinal walls being straight, curved, or undulated is variable in seven of the species tested. The variation usually covers only part of the entire range in *Ilex*: viz. straight to curved, or curved to undulated. Whether the anticlinal cuticular flanges are pitted or not was found to be variable in five species. The shape of the epidermal cells overlying the midrib (flattened, square, or elongate) is variable in eight species. The venation pattern of the leaves usually causes little or no modification of the epidermal cell pattern; yet the degree to which this occurs varies in four of the species tested. The occurrence of thickened lignified cell walls in the abaxial epidermis is limited to few species of *Ilex* only, and of even fewer species

more than one specimen was studied: in *I. opaca* and *I. triflora* lignified epidermal cells are of constant occurrence, although in one specimen of *I. triflora* (*Hallier B 2471*) only a minor proportion of the unspecialized cells is lignified; *I. canariensis* and *I. crenata* were found to be variable for this character.

The stomatal type is also variable in seven of the species tested, but this only concerns a variability in the proportion of different types occurring in the same leaf. In for instance *I. triflora* some specimens show predominantly anisocytic and infrequent cyclocytic and intermediate stomata, and other specimens have predominantly cyclocytic stomata with infrequent anisocytic ones. In several other species the ratio of anisocytic and cyclocytic stomata is also variable. Species with cyclocytic and/or bicyclic stomata are usually constant in stomatal type. See also the specific descriptions. Stomatal size variations may be considerable, notably in *I. anomala* in which it amounts to 31% of the average maximum value. Length/width ratios of the guard cell pairs also vary, albeit usually within fairly narrow limits. *I. perado* is an exception with about 13% variation: from 0.93 to 1.07. Polar T-pieces (see Stace, 1965) are never very conspicuous in *Ilex*, and if sufficiently distinct their diagnostic value is limited because four species were found to vary in this respect. Peristomal rims, although virtually always present in *Ilex*, also vary somewhat in distinctness in four species.

Cork warts, if fairly frequent and of regular outline, are diagnostic for the few species (3) tested. Presence or absence and frequency of irregularly shaped, probably traumatic, cork warts (cf. Herridge, 1963) is always variable.

The degree of subdivision of the adaxial epidermis in those species which tend to form a multiple, largely mucilaginous, epidermis is highly variable in six of the species tested. The degree of bulging of the mucilaginous cells also varies in these species. The presence and type of hypodermis is constant in the species tested.

In all species tested the bundle sheaths are constant with respect to their cell walls being lignified or not. However, in some species it is not obvious in safranin/haematoxylin stained sections whether the bundle sheaths are lignified or not, which limits the applicability of this character for diagnostic purposes. The same applies to lignification of (part of) the spongy tissue. Here the proportion of lignified tissue varies in some species. In *I. cymosa* the cell walls of the spongy tissue may be lignified or not. In doubtful cases the bundle sheaths and spongy tissue are recorded to be strongly birefringent. It should be realized that unlignified cell walls also show birefringence, but secondary lignified wall thickenings are usually much more strongly birefringent. It is therefore likely that lignification has occurred in the more strongly birefringent walls, although the staining did not reveal this clearly. Wiesner's reaction (phloroglucinol and hydrochloric acid) has only sporadically been used for testing the presence or absence of lignin.

The midrib in *Ilex*, as seen in transverse sections, is usually grooved but in a fair number of species it is flattened to raised. However, in three of the species tested this is variable.

Vascularization of the midrib, but especially of the petiole varies in four of the species tested. This is particularly striking in *I. hypoglauca* and *I. cymosa*, where both simple open and highly complex types occur in the same species. This variability is not to be confused with the differences existing between the basal part of the petiole (which always has a simple system, if sectioned close enough to the place of attachment to the stem) and the distal part of the petiole.

Foliar sclereids are of rare occurrence in *Ilex* as a whole, and their diagnostic value has only been 'tested' in one species (*I. ficoidea*), of which both specimens studied possess them.

Marginal sclerenchyma strands were also found to be of constant occurrence in the four species tested. However, in the 'intermediate' species (*I. confertiflora, I. insignis,* and *I. latifolia*) their appearance varies along the leaf margin of a single leaf.

Frequency of crystals is variable in most species tested. In only one specimen of *I. theezans* no crystals were found at all. Probably the latter observation would need correction if a complete series of sections from leaf tip to petiole were made.

The considerable variation below the species level in many leaf anatomical characters is even stronger than the infraspecific variations reported of epidermal and leaf histological characters (Jansen & Baas, 1973; Bongers, 1973; Van Staveren & Baas, 1973; Van Vliet & Baas, 1975) in species of *Celastraceae, Winteraceae, Icacinaceae*, and *Crypteroniaceae* respectively, although most of the characters discussed above appeared to show some degree of variation below the species level in these families as well. It should be stressed that in *Ilex* probably an even higher degree of leaf anatomical infraspecific variability exists than reported above. The number of specimens studied was very limited for most species, and with more specimens the number of variable characters will no doubt increase for each species.

The infraspecific variability may be due to genetical variability or ecological factors. Yet it is likely that within *Ilex* species two other factors will also have contributed to the variational range. In the first place this may be the age of the persistent leaves. Although full-grown leaves have been selected for this study, no data on the actual age were available, and it is known that several leaf anatomical characters may change during the life span of persistent leaves (see Napp-Zinn, 1974, and literature cited by him). Cuticular thickness, degree of subdivision of the epidermis, lignification of epidermis and mesophyll may have been affected by this. In the second place, the lack of a recent taxonomic revision for *Ilex* implies the possibility of doubtful specific delimitation and erroneous identifications, which may well underly part of the variation recorded below the species level. However, in a number of cases the anatomical evidence almost excludes the possibility of misidentifications, because the species involved show a highly characteristic anatomical feature or combination of characters: *I. anomala, I. aquifolium, I. bioritsensis, I. ficoidea, I. hypoglauca, I. opaca, I. perado, I. pernyi,* and *I. triflora.* Even in this small group of nine species the infraspecific variability of several anatomical characters is very considerable. In those species studied for which infraspecific taxa are recognized no correlation has been found between anatomical variation and infraspecific classification.

The above results made it hardly useful to document all leaf anatomical characters in elaborate specific descriptions. I have therefore chosen the very condensed form of description in which data on cuticular granulation and striations, outline of the epidermal cells, etc. have usually been left out altogether.

Latitudinal and altitudinal trends; ecological and functional anatomy

Stimulated by the results of previous studies on wood anatomical variation (Baas, 1973; Van der Graaff & Baas, 1974) I have also searched for correlations between several leaf anatomical characters and latitude and altitude of provenance. For 76 of the 95 species studied, collection data were sufficient to do this. Four groups were distinguished: tropical high mountain species (altitude over 2500 m; 6 species); tropical mountain species from altitudes between 1000 and 2500 m (12 species); tropical lowland species (altitude below 1000 m; 18 species), and subtropical and temperate species (40 species).

All four groups appeared to be rather heterogeneous with respect to most quantitative and qualitative leaf anatomical characters. Exceptions to this lack of altitudinal and latitudinal trends are the following:

High mountain species in the tropics always have thick leaves, and mostly also thick

cuticles. Their anticlinal epidermal cell walls are usually straight to curved, and rarely undulated. The percentage of species with undulated walls increases with decreasing altitudes in the tropics: *c.* 17% for high mountain habitats; *c.* 45% for mountain habitats between 1000 and 2500 m altitude; and *c.* 60% for the tropical lowland (cf. Bongers, 1973, for comparable results in *Drimys piperita*). In the temperate and subtropical regions *c.* 60% of the species have undulated anticlinal epidermal cell walls.

Lignified bundle sheaths and lignified spongy tissue are of much more frequent occurrence in the tropics (more or less independent of altitude) than in temperate and subtropical regions. Remarkably enough there is a difference between the New World and Old World tropics in this respect. About 65% of 33 *Ilex* species from tropical Asia and the Pacific have lignified bundle sheaths; in tropical America only *c.* 27% of 18 species show this character. For temperate and subtropical species the percentage is *c.* 10. Comparable percentages for lignified spongy tissue are *c.* 50, 11, and 9 respectively.

The distribution of stomatal types also shows some peculiar correlations. Of the 22 species with bicyclic stomata only 3 are from the tropics, and these are restricted to Malesian mountain regions. The other 19 are mainly from subtropical and temperate Eurasia, with the exception of *I. argentina*, *I. krugiana*, and *I. opaca*. On the other hand, anisocytic stomata are much more in evidence in the tropics: of the tropical species studied 12 show predominantly anisocytic stomata, against 2 in subtropical and temperate regions. If we also include the species with anisocytic to cyclocytic stomata it appears that *c.* 50% of all tropical species studied have at least partly anisocytic stomata (independent of other geographical factors) against *c.* 10% for the subtropical and temperate species. For cyclocytic and anomocytic stomata there are no latitudinal trends.

Other characters like stomatal size and many qualitative characters which are limited to a minority of *Ilex* species only, are not clearly correlated with latitude or altitude of provenance.

It is not possible to give a satisfactory explanation of the trends in the percentages recorded above. In those cases where the latitudinal trends are due to the frequent occurrence of the characters in a special geographical area only (lignified bundle sheaths and mesophyll, bicyclic stomata), I suggest that these are only the consequence of restricted distributions of groups of closely related species; this implies that these trends are of no importance in ecological considerations but only stress the significance of the feature involved as a systematic character within *Ilex*. For the remaining trends any explanation is completely lacking.

Latitude and altitude are of course very poor and rough indicators of the ecological conditions of the species involved. Data from the literature and on herbarium labels were unfortunately insufficient to overcome this lack of ecological information for most species studied. Nevertheless the diversity in leaf anatomy in *Ilex* has induced me to give some general considerations about ecological and functional aspects.

For *Ilex* many leaf anatomical characters could be listed which are traditionally believed to be of importance for drought resistance of the plants involved. With the exception of the deciduous species, most *Ilex* species show such structural details in their leaves. Three main categories can be distinguished in this respect:

1. Structures to prevent the loss of water. Examples in *Ilex* are: thick cuticle and periclinal outer epidermal cell walls, and conspicuous outer stomatal ledges providing a sheltered stomatal front cavity.
2. Water storage tissue. Examples are: hypodermal development (different types in *Ilex*), and specialization of certain epidermal cells to large mucilage cells.

3. Mechanical reinforcement (scleromorphy) in order to prevent damage to protoplasts in case of wilting. Examples of these are manyfold: thick cuticle; thick epidermal and/or hypodermal cell walls; extra development of sclerenchyma adjacent to vascular bundles; foliar sclereids; marginal sclerenchyma strands; lignified epidermal cells; lignified bundle sheaths; and finally lignified spongy tissue.

Not a single *Ilex* species shows a combination of all characters mentioned above. Usually only few of the characters have been realized in a single species.

It should be stressed that the functions attributed to several anatomical features listed above, have only been assumed, and although generally accepted and logical (cf. Haberlandt, 1918, and Burström & Odhnoff, 1963), no factual evidence has been presented that these structures are necessary for the species to survive. In this respect it is of interest to note that many highly scleromorphic features occur in everwet Malesian lowland rain forest species or in species from montane mossy forests. In temperate evergreen species xeromorphic features seem to have a more obvious function: prevention of water loss in times of reduced water uptake at low temperatures (Windslow & Havis, 1967). It is well-known that several xeromorphic (including scleromorphic) features are induced by ecological conditions which are different from drought, such as light intensity (Martin & Juniper, 1970) and mineral deficiency of the soil (Loveless, 1961).

In view of such facts the diverse xeromorphic characters realized in the genus *Ilex* should not be interpreted as adaptive characters. For taxonomic studies these characters may have the same value as any other leaf anatomical characters.

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