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THE WOOD ANATOMICAL RANGE IN ILEX (AQUIFOLIACEAE) AND ITS ECOLOGICAL AND PHYLOGENETIC SIGNIFICANCE

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CONTENTS

SUMMARY

The wood anatomy of 81 species of *Ilex* is described in detail. The wood anatomical range encountered is presented in a generic description (p. 196). Data on ontogenetic changes in vessel member length and number of bars per perforation are given for three species.

The great amount of variation in mainly quantitative but also in some qualitative features is hardly or not related with subgeneric classification but with latitudinal and altitudinal distribution. In both the northern and southern hemisphere and in both the Old and New World, temperate and subtropical species are characterized by conspicuous growth rings, numerous narrow vessels, relatively short vessel members and few bars per perforation plate, conspicuous spiral thickenings on both vessel and fibre walls, and the fibre-tracheids are frequently provided with rather numerous conspicuously bordered tangential wall pits. In tropical lowland species growth rings are absent or less marked, the vessels are scanty and wide, the vessel members are long and the number of bars per perforation plate is high. Spirals are lacking or faint, or occur only in a minor part of the axial elements. The fibre-tracheids have usually few pits with more reduced borders on the tangential walls. Tropical montane species resemble the temperate ones to a great extent, but this does not apply to growth rings, spiral thickenings, and frequency and size of fibre-tracheid pits.

The only wood sample of a climbing *Ilex* species from the tropics studied deviates from the general trend in having few bars per perforation plate. The two temperate species *I. serrata* and *I. verticillata* are exceptional in lacking spiral thickenings. In all wood characters they resemble the genus *Nemopanthus* (also *Aquifoliaceae*) very closely.

Comparisons with data from literature and original observations on *Prunus, Symplocos, Vaccinium, Viburnum,* and to some extent also on *Hydrangea,* support the view that the gradual differences between temperate and tropical *Ilex* species conform to a general trend also present in other taxa. Therefore a major climatic influence on wood structure is indicated. This is discussed with reference to the major trends of phylogenetic wood specialization. The fact that within *Ilex* and *Symplocos* the tropical lowland species have perforations with the most numerous bars cannot be brought in agreement with the general phenomenon of a rare occurrence of scalariform perforations in tropical lowland floras.

Other items such as the parallel between the absence of spiral thickenings and the presence of entire leaf margins, the lack of a clear taxonomic pattern in the wood anatomical variation in *Ilex,* and observations by former students of *Ilex* wood anatomy are also discussed.

INTRODUCTION

While in search for possible relatives of the genera *Sphenostemon* and *Oncotheca,* which had been thought to be allied to *Aquifoliaceae* by several taxonomists in the past, I felt the need for a more comprehensive study of the wood anatomical range within that family. The genus *Ilex,* with a roughly estimated number of 400 species, constitutes the bulk of the family. The other genera are *Nemopanthus* from North America, and *Phelline* from New Caledonia.

Ilex occurs in all tropical areas of the world and extends into temperate regions up to 65° N (America, Eurasia) and 35° S (America, Africa). In the tropics a number of species is montane but a fair number occurs in the lowland forests. Because of this wide latitudinal and altitudinal, and consequently climatic, range of habitats, a survey of the wood anatomical range within this genus became all the more attractive in order to analyse any relationship that might exist between provenance and wood anatomy. I am aware that for conclusive evidence on correlations between climate or other ecological factors and wood structure, the study of many wood samples belonging to a single well defined species should be carried out in the first place in order to be more certain about genetical homogeneity in the material used for comparison. Preferably such a study should include specimens cultivated outside their natural geographic range. Sufficient material to afford such an analysis was, however, not available for this study.

This paper will report on the results of a study of 126 wood samples belonging to 78 identified species and 3 unidentified, but different, species of *Ilex* from all major distribution areas and from most of the important taxonomic groups recognized by Loesener (1901, 1908, 1942). A subsequent paper will deal with the affinities of *Ilex, Nemopanthus, Phelline (Aquifoliaceae),Oncotheca,* and *Sphenostemon* in the light of the whole range in characters from both wood and leaf.

In previous studies some common species have been described wood anatomically by several authors with a varying amount of detail. The most elaborate study is by Pennington (1953), whose thesis is, however, not easily accessible. She studied 54 species of *Aquifoliaceae,* 51 of which belonged to *Ilex.* Her material was derived from specimens 'evidencing secondary growth' and from her quantitative data it becomes clear that she used small twigs for most tropical species and both twigs and mature wood samples for the temperate species. In her discussion Pennington did not take these differences in sampling method into account, and all her painstaking measurements and conclusions based on these (and in complete disagreement with my results) are therefore unfortunately without value. Solereder (1899 and 1908) and Metcalfe and Chalk (1950) comprehensively summarized the older literature. Additional more recent publications are scanty and fragmentary. Hu (1967) reported on evolutionary trends in the xylem of *Ilex.* Ingle and Dadswell (1961) included quantitative data of 5 *Ilex* species in their discussion of the affinities of *Nouhuysia* (= *Sphenostemon*). More general publications by Abbate (1970), Barghoorn (1940), Brazier and Franklin (1961), Chattaway (1956), Greguss (1959), Jane (1970), Panshin, De Zeeuw and Brown (1964), Purkayastha (1963), Sarlin (1954), Sudo (1959), and Versteegh (1968) also contain data on several species of *Ilex*. The results of these previous studies will only be referred to in the discussion as far as is relevant for the present study.

MATERIALS AND TECHNIQUES

Wood samples were obtained from a number of institutional wood collections or from the wood collection of the Rijksherbarium. These institutions will be referred to using Stern's (1967) abbreviations, at the end of each specific description. The amount of detail in collection data appeared to be very variable in the material received, and the method of listing specimens can therefore not be uniform.

Herbarium vouchers are listed when known; collection numbers only referring to wood specimens are given between brackets. Mature wood samples (diam. of main stem or branch at least 5 cm; see p. 197) are listed without special indications, immature samples (diam. of main stem or branch between 1.5 and 5 cm) are marked with an asterisk.

Wood anatomical features were studied in transverse, radial, and tangential sections, and macerations. The latter were obtained using Franklin's method (Anonymous, 1968) and mounted in glycerin jelly.

For each sample 25 measurements were made for vessel member length, vessel diameter, number of bars per perforation plate, and fibre length. Vessel member length was measured including the tails. Data on vessel frequency and ray frequency are based on at least 3 counts in each specimen in areas of 1 square mm, and tangential distances of 1 mm respectively. For vessel frequency due attention was paid to include equal portions of early and late wood in temperate species. Pit sizes were measured in a few pits of the most frequently occurring size class, and pits of some extreme sizes.

Presence or absence of spiral thickenings was confirmed for several species with the scanning electron microscope. Clean cut tangential, transverse and oblique surfaces as well as radially split surfaces were examined after coating with carbon and gold.

Reliability and comparability of the material studied

The most recent monograph of the genus *Ilex* was published in 1901 and 1908 by Loesener, who recognized 279 species, distributed over 4 subgenera, numerous sections, subsections, and series. Later, in 1942, he added a fifth subgenus. Much more material has become available since Loesener's time, many new species have been published, and at present the genus is in need of a comprehensive new revision. This implies that the naming of the wood specimens I used for this study may be partly incorrect, which is all the more serious since a rather high proportion consisted of unvouchered specimens. Therefore, one should be aware that the names of the specimens studied are not always entirely reliable, though no doubt can exist about the provenance and the fact that all material described here belongs to the genus *Ilex*. On wood specimens data on localities are usually extremely undetailed. In assigning a degree of latitude to a specimen from 'Japan', 'China' or 'New Guinea' one therefore has to take an arbitrary decision, which will always be incorrect to some extent. However, such mistakes cannot have influenced the general results seriously. Altitudinal data are usually lacking, and the analysis of a direct or indirect effect of altitude on wood structure has therefore been limited to those specimens and species of which reliable data on altitude were available.

All *Ilex* species are woody, but the whole range from small shrubs to tall trees exists. Wood specimens may have been collected from main stems or branches, from a part high up the tree or close to the soil. Such data are usually lacking for the wood specimens studied, yet it is well known that distance from the pith and height in the tree (or shrub) may influence wood anatomical characters, particularly quantitative ones, to a great extent. Of these, distance from the pith is the most important factor, and to increase the comparability of data on specimens from both shrubs and trees, only material with a diameter of 5 cm or more was considered in the comparisons of quantitative features. Such material is referred to as 'mature', and it is assumed that beyond this diameter the increase in cambial initial length and changes in cambial products are negligible for this study. Arguments to substantiate this will be given on p. 197—199.

RESULTS AND DISCUSSIONS

Generic description of the wood of Ilex

Qualitative features based on 81 species. Quantitative values are given for mature wood samples only. Only the ranges of means for individual samples are given.

General features: Wood light and soft to fairly heavy and hard. Colour white to greyish brown. Growth rings absent to distinct. Vessels visible to the naked eye in some tropical lowland species only. Broad rays visible to the naked eye, usually prominent. Heartwood not differentiated.

Microscopic features: Wood diffuse to semi-ring porous. *Growth rings* absent to distinct. *Vessels* 13—220/mm^2, solitary and in radial multiples ranging from short to very long (over ten vessels), percentage of solitary vessels 8—70, angular to oval in T.S., mean tangential diameter 30—113 μm, mean vessel member length 600—1920 μm. Inter-vessel pits usually opposite, but in some species tending to alternate, in others sometimes transitional to scalariform; pits round to rounded rectangular or strongly flattened, tangential diameter 5 to over 20 μm, with minute circular to slit-like apertures, enclosed within the pit borders, in few species seemingly vestured. Vessel—ray and vessel—parenchyma pits scalariform to alternate, fully bordered, half bordered or tending to large and simple, sometimes unilaterally compound. Perforations scalariform in very oblique end walls with 13—58 bars. Helical thickenings ('spirals') well developed, faint, or absent. Warts noted in two species only. *Tyloses* and vessel *contents* (probably traumatic) noted in a few specimens only. Ground tissue composed of thin- to thick-walled *fibre-tracheids* with minute to fairly large bordered pits. Pits frequent on radial walls, infrequent to frequent on tangential walls, average diameter 3—7 μm, pit apertures slit-like and confined within the pit borders to extending several microns beyond the pit borders. Mean fibre-tracheid length 890—2830 μm. Helical or annular thickenings ('spirals') well developed, faint, or absent. Fibre-tracheids rarely gelatinous. *Parenchyma* diffuse and/or diffuse in aggregates, very scanty to fairly abundant. Parenchyma strands of 4—13, mostly of 7 or 8 cells. *Rays* mostly heterogeneous II, rarely heterogeneous I or III, uniseriate rays 6—16/mm; broad rays 1—7/mm, 2—25 cells wide, tallest rays 0.8—6.0 mm high, often with sheath cells.

Crystals present or absent, usually solitary and in ordinary, chambered erect, or idioblastic thick-walled and/or bulging ray cells; rarely irregularly clustered. *Silica* absent.

Pith flecks (traumatic) occasionally present.

Ontogenetic changes in vessel member length and number of bars

Three stems of widely different species from different geographical origin were analysed for the variation in vessel member length and number of bars per perforation plate with respect to the distance from the pith. This was important in order to establish at which stem diameter these characters become more or less stable and consequently when we can speak of 'mature' wood. Figures 1 and 2 give the curves for vessel member

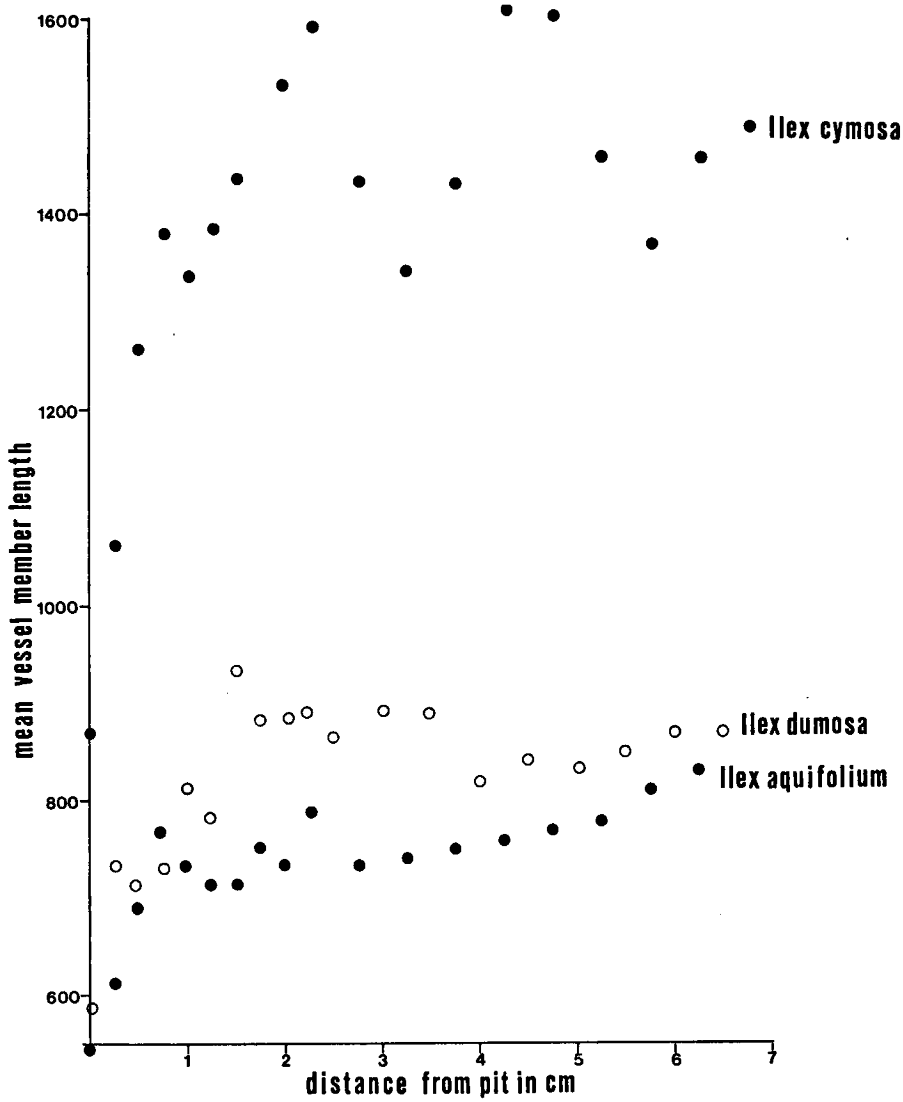

Fig. 1. Vessel member length (in μm) in relation to distance from the pith in *I. cymosa*, *I. dumosa*, and *I. aquifolium*.

length and number of bars respectively. For vessel member length the classical curves, frequently reported for both vessels and fibres are obvious: a strong increase in length in the first centimetre from the pith and the curve leveling off towards the periphery.

In *I. aquifolium* (*UN 163*, cult. Holland) the most important increase has been completed within the first 7.5 mm from the pith; vessel member length gradually, but very slightly increases beyond this point. In *I. dumosa* (*Lindeman & Hecking 1916*, Brazil, Parana) the length attains a maximum at 15 mm from the pith and fluctuates beyond here. In *I. cymosa* (*Ridley s.n.*, Singapore) is a strong increase up to 22.5 mm from the pith, beyond which there is a very strong fluctuation. If we define mature wood as secondary xylem from those parts of the stem, where there is no important increase in length with respect to further distance from the pith, we may conclude that for these *Ilex* species the mature stage is more or less reached in stems of which the xylem cylinder is just over 1.5, 3.0, and

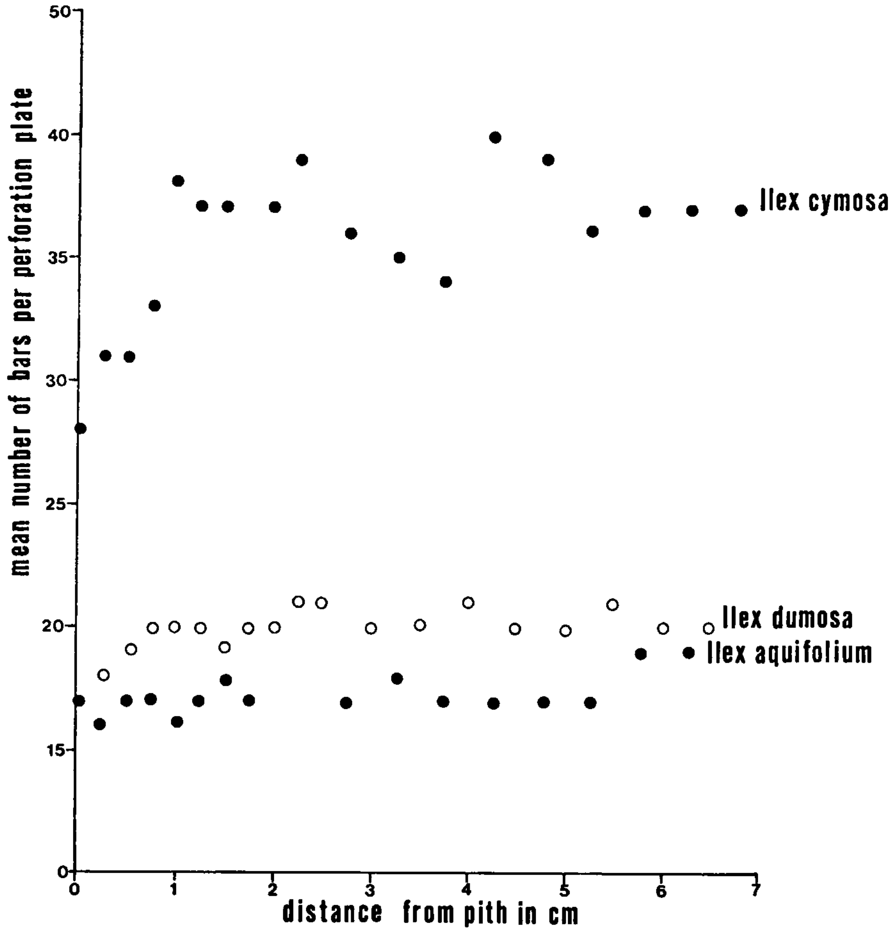

Fig. 2. Number of bars per perforation plate in relation to distance from the pith in *I. cymosa*, *I. dumosa*, and *I. aquifolium*.

4.5 cm in diameter. With the 5 cm limit, arbitrarily chosen for mature wood in samples of *Ilex* (cf. p. 195) I am therefore on safe grounds.

The number of bars per perforation plate is virtually constant in regard to distance from the pith in both *I. aquifolium* and *I. dumosa.* In *I. cymosa* there is a considerable increase in the first centimetre from the pith and a rather strong fluctuation beyond. No data from literature are available for comparison, and it is impossible to conclude from the present data whether the curve for *I. cymosa* is an exception to the rule or not. In those species of which I studied both mature and immature samples no consistent trend in differences in number of bars per perforation could be found. In five species the immature wood sample had slightly more or about the same number of bars per perforation as the mature wood sample(s); in three species this number was considerably lower for the immature specimens. In most cases exact diameters of the stems of the samples were unknown, which decreases comparibility.

It is, however, justified to conclude from our graphs that xylem of samples more than 5 cm in diameter is also mature with respect to number of bars per perforation. Further study is necessary to establish whether any general trends in the ontogenetic changes of number of bars per perforation plate exist in *Ilex* and other woody plants.

Diagnostic value of the characters used

From the generic description it appears that only very few wood anatomical characters are diagnostic at the genus level. Values for size and frequency of the different elements show an enormous range, which makes them useless for diagnostic purposes. Qualitative features such as growth rings, vessel distribution, pitting of the vessel walls, spiral thickenings and crystals are also variable within *Ilex.* The only characters which are constant at the genus level are: vessel perforations scalariform, ground tissue composed of fibre-tracheids, parenchyma diffuse or diffuse in aggregates, rays heterogeneous, broad and narrow. This character complex is also present in a fairly great number of other families with primitive wood structure (cf. Metcalfe and Chalk, 1950).

At the species level quantitative values also exhibit a considerable range in those species of which I studied sufficient material (cf. *I. cymosa, I. mitis* and *I. spec.* from New Guinea). Accordingly in the 63 species of which mature wood samples were available there is a great amount of overlap, so that species are not separable on quantitative wood anatomical features. For a number of qualitative features the same applies. Semi-ring porosity is not constant within e.g. *I. integra,* inter-vessel pit arrangement usually varies considerably within a single tangential section (Plate II, 6 & 7), and different specimens of the same species may show a different range (e.g. *I. anomala*). Spiral thickenings, if well developed are constant within the species, but in tropical species with only some faint spirals in the fibre tips, spirals may be entirely lacking as well (e.g. *I. cymosa*). Presence or absence of crystals has long been known to be variable at the species level and *Ilex* makes no exception to this rule.

From the fact that even within the restricted number of species of which I studied more than one wood specimen the majority of anatomical features proved to be variable, one may conclude that it is impossible to separate *Ilex* species using wood anatomy.

Discussion of the individual characters

Growth rings

Virtually all temperate and subtropical species of *Ilex* show distinct growth rings; most tropical species have faint growth rings or lack these entirely. In this respect the genus

Ilex follows a well known general rule. In some tropical species where more or less distinct growth ring boundaries occur this is probably due to a seasonal climate with pronounced dry periods (e.g. *I. crenata* and *I. quercetorum*). In other species (e.g. *I. curranii* and *I. volkensiana*) no apparent climatic reason for the occurrence of distinct growth rings can be given.

Vessel distribution (Plate I)

Most *Ilex* species possess diffuse porous wood, but in a few temperate and subtropical species the wood is semi-ring porous. This feature is not restricted to the deciduous subgenus *Prinus*, as one might expect, but also occurs in a number of evergreen species (e.g. *I. dipyrena*, *I. ficoidea*, *I. integra*, *I. latifolia*, and *I. perado*). In some species there is a transition between the diffuse-porous and semi-ring-porous condition (e.g. *I. aquifolium*).

There is a considerable range of variation in the extent to which the vessels are arranged in radial multiples. This is only very incompletely covered in the descriptions where percentages of solitary vessels are given. The length of radial multiples may vary considerably and strongly alter the impression the wood gives as seen in transverse section. It would be very time consuming to express such differences quantitatively. Moreover, the intraspecific variability is very considerable: for instance in *I. anomala* the range in percentage of solitary vessels in mature specimens is 31—64; in the specimen with the lowest percentage of solitary vessels, the radial multiples are not only more frequent, but on average also longer than in the other specimens. There is no clear relationship between taxonomic subdivision of the genus Ilex and vessel grouping, nor is there a very strong correlation with latitudinal or altitudinal distribution. In all distribution areas the range is very large. The *Ilex* species with the strongest tendency for vessel grouping (few solitary vessels, long radial multiples) are, however, from the temperate regions, and those with the shortest multiples and highest percentage of solitary vessels are from the tropics.

Vessel frequency and vessel diameter (Plate I)

The great range of variation in vessel frequency within the genus *Ilex* was found not to be related to its taxonomic subdivision. The same applies to vessel diameter. Both characters are inversely correlated, and are both related to latitudinal distribution (see fig. 3, 4, and 5). Temperate species are characterized by numerous narrow vessels, tropical species are characterized by few relatively wide vessels per unit surface area of the transverse section. All intermediates occur. Within the tropics, the lowland species tend to have the wider vessels, and the montane species have narrower vessels. Vessel frequency in tropical montane species does not differ much from that of the lowland species (fig. 6), and is much lower than in temperate species growing under comparable temperature regimes.

Intraspecific variation in vessel frequency and diameter may be considerable (e.g. in *I. cymosa*, *I. havilandii*, and *I. integra*).

For the latitudinal trends in vessel frequency and vessel diameter *Ilex* follows a more or less general rule. In general wood of temperate diffuse-porous trees has narrower vessels than that of tropical trees.

Versteegh (1968) has provided evidence that tropical montane species are frequently microporous, whilst their lowland relatives may be megaporous. This suggests that the altitudinal trend in tropical *Ilex* for vessel diameter also follows a general trend. Abbassova (1969) showed that both vessel diameter and vessel frequency decreased with increasing altitude in *Quercus*. This does not apply to *Ilex* as far as vessel frequency is concerned.

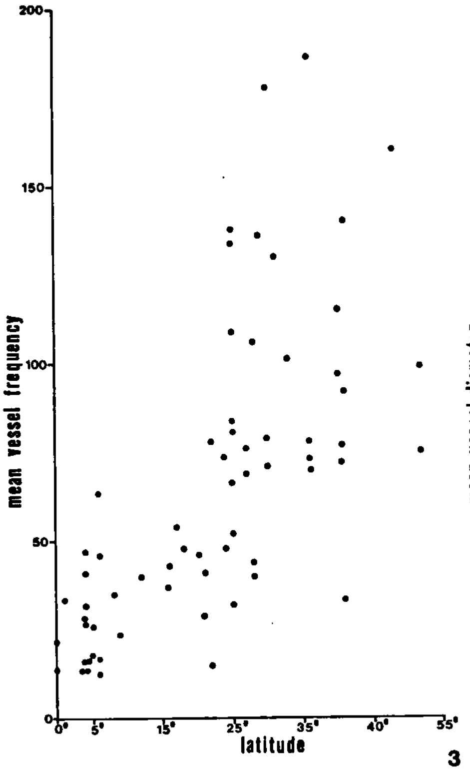

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Fig. 3. Vessel frequency and latitude in 64 species of *Ilex* (*I. crenata* plotted at 17° and 52°).

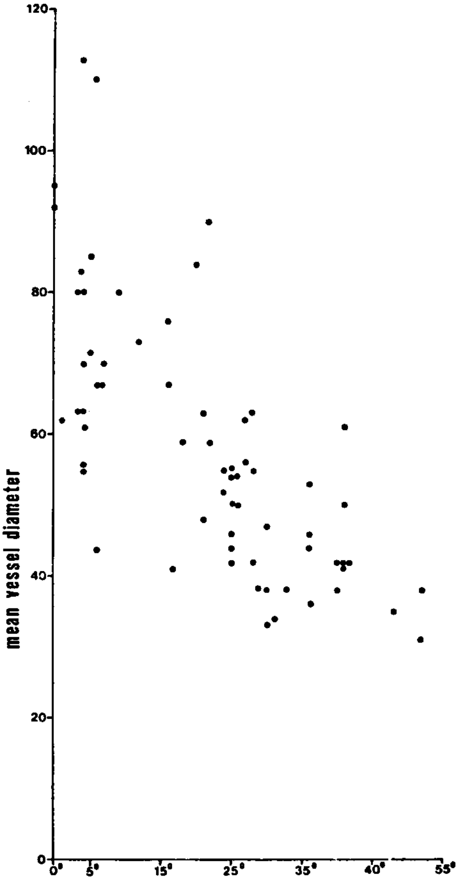

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Fig. 4. Vessel diameter (in μm) and latitude in 64 species of *Ilex* (*I. crenata* plotted at 17° and 52°).

Vessel member length and number of bars

(Plate II, 1—5; III, 5 & 6)

In fig. 7 the correlation between vessel member length and latitude of provenance is shown for mature wood samples of 64 species of *Ilex*. Although there is a considerable variation in all latitudinal zones, the trend is evident: the tropical species have considerably longer vessel members than the temperate ones. The number of bars per perforation plate is also inversely correlated with latitude (fig. 8). Accordingly, vessel member length and number of bars are positively correlated (fig. 9).

The lumping of data on vessel member length and number of bars of all species as done in figs. 7, 8, & 9 is justified. There is no obvious correlation of these features with taxonomic subdivision, and the general correlations apply equally well in the southern and northern hemisphere, and in the Old and the New World.

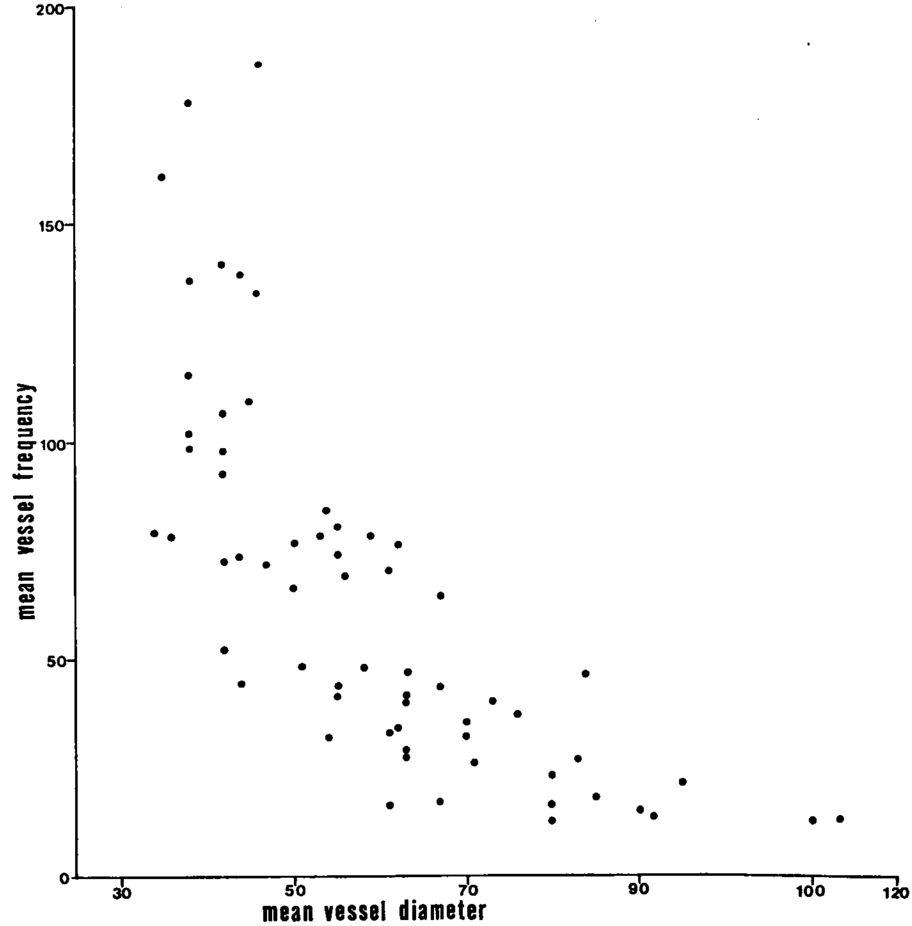

Fig. 5. Vessel frequency and vessel diameter (in μm) in 64 species of *Ilex*.

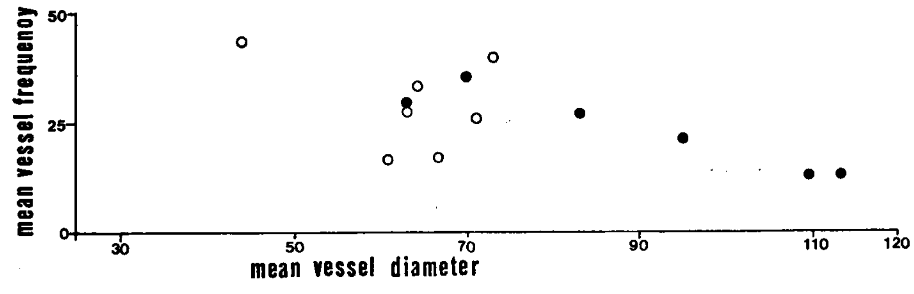

Fig. 6. Vessel diameter (in μm) and vessel frequency in tropical montane (o) and tropical lowland species (●).

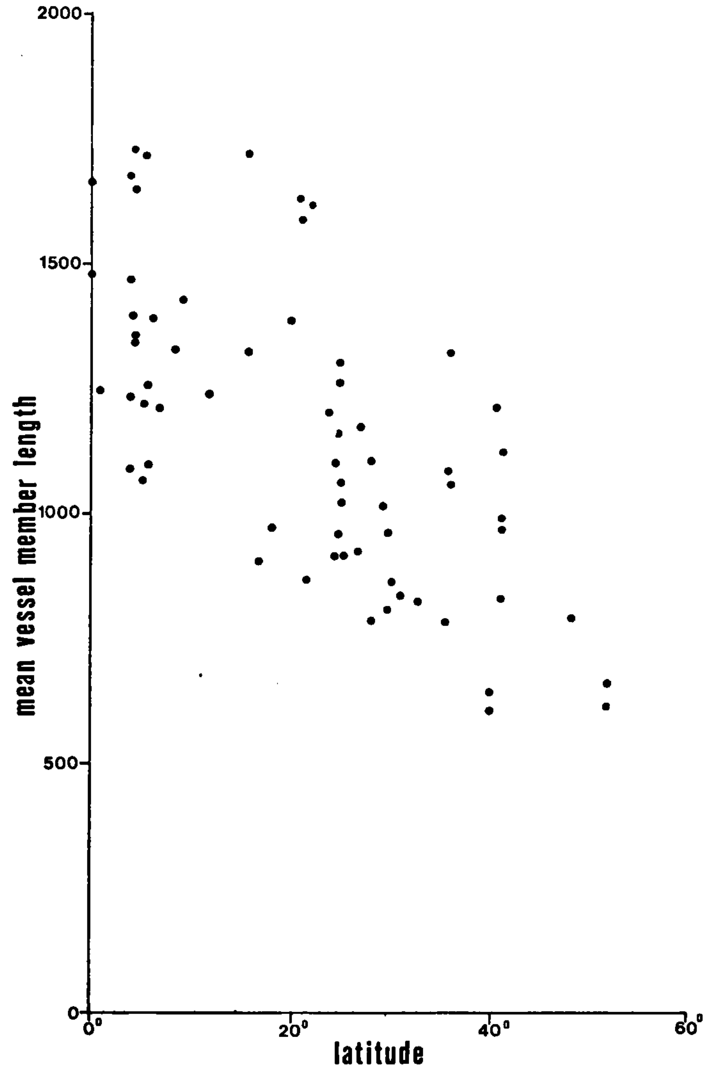

Fig. 7. Vessel member length (in μm) and latitude in 64 species of *Ilex* (*I. crenata* plotted at 17° and 52°).

Within the tropics the montane species studied have shorter vessel members and less bars per perforation plate than the lowland species (fig. 10). For the analysis of the 'altitudinal' effect only those specimens and species were taken into account on which reliable data on altitude were available. Of the species in fig. 10, eight are represented by specimens from sea level to well below 1000 m, one is from an altitude between 1000 and 2000 m, and the remaining seven species are from altidudes over 2000 m. There is only little overlap in the values for vessel member length, and the number of bars is consistently

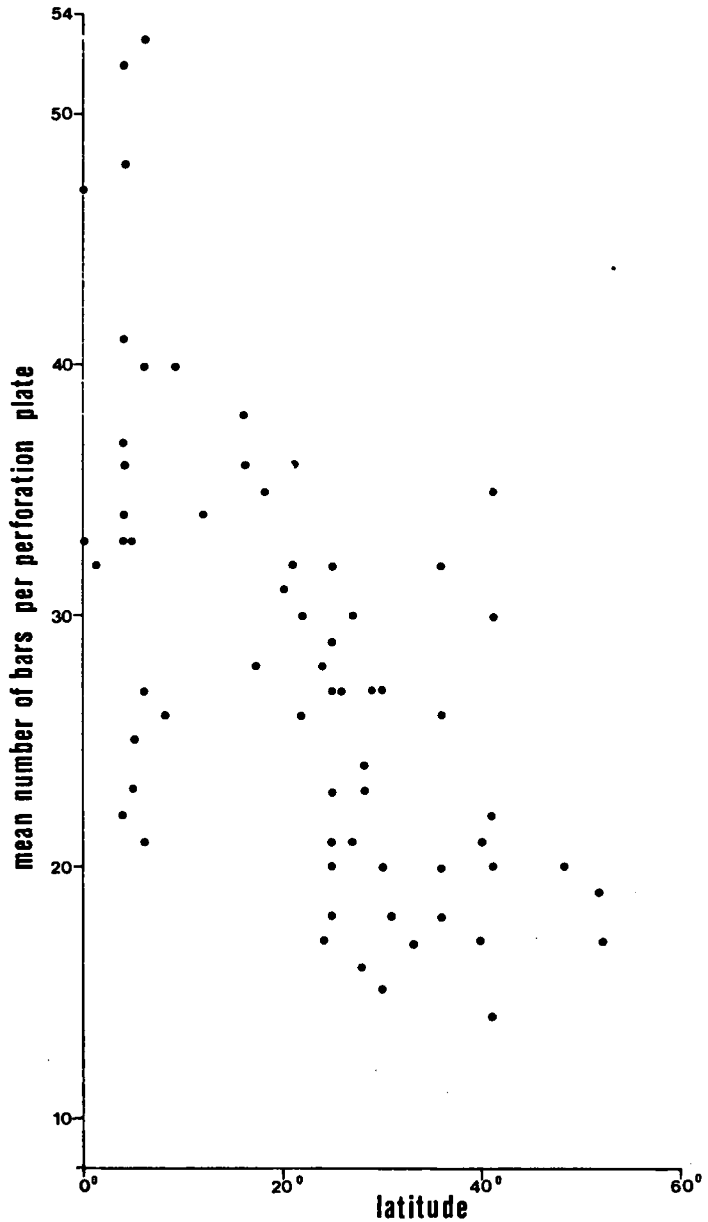

Fig. 8. Number of bars per perforation plate and latitude in 64 species of *Ilex (I. crenata* plotted at 17° and 52°).

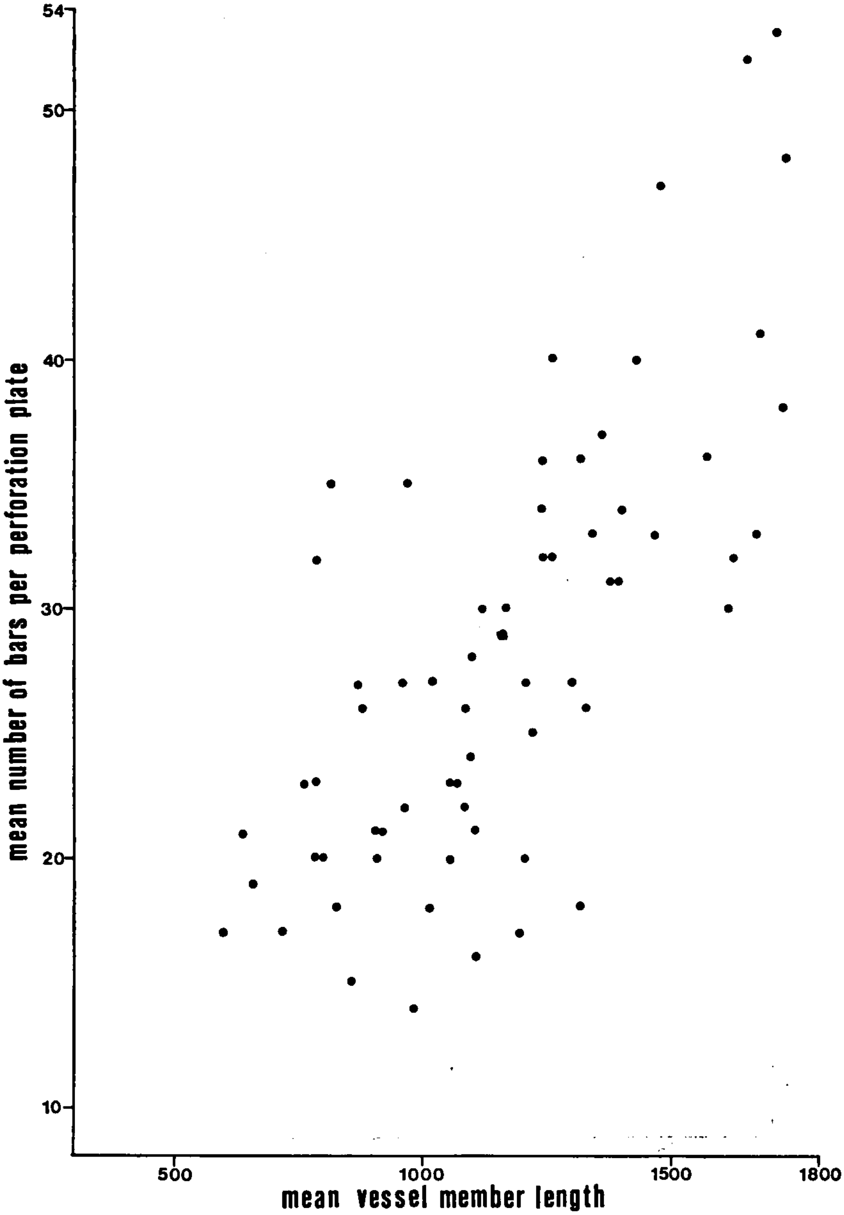

Fig. 9. Vessel member length (in μm) and number of bars per perforation plate in 64 species of *Ilex*.

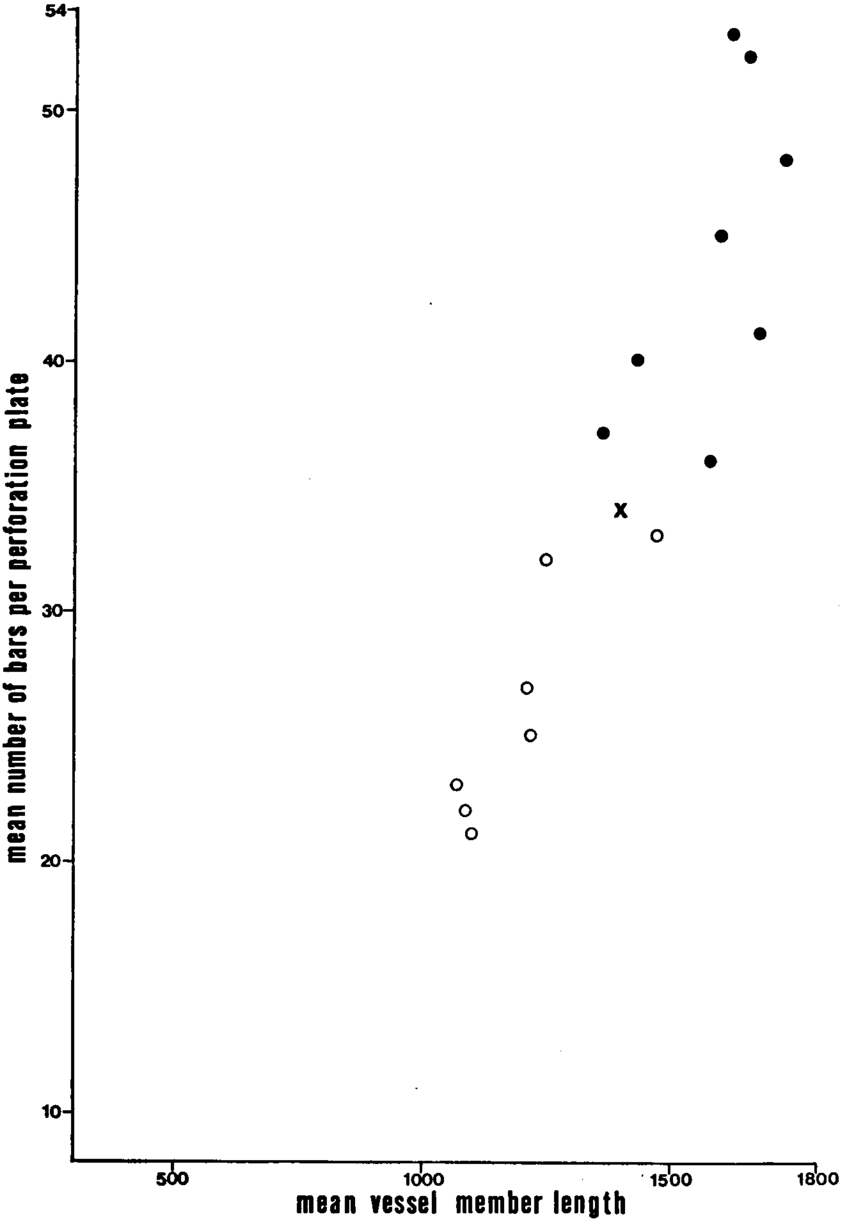

Fig. 10. Vessel member length (in μm) and number of bars in tropical lowland and tropical montane species of *Ilex*; — o = montane species (altitude over 2000 m); — x = from altitude between 1000 and 2000 m; — ● = lowland species (altitude below 1000 m).

lower in the montane than the lowland species from both the Old and New World tropics.

Fig. 11 gives a comparison of microtherm tropical montane species (wood samples from altitudes higher than 1600 m) with microtherm temperate species (from latitudes over 35°). These species groups can be considered to grow under comparable temperature regimes (not taking into account seasonal influences), according to the altitude—latitude scheme proposed by Van Steenis (1962). It is clear that the tropical montane species tend to have longer vessel members than their temperate counterparts, and that the number of bars does not differ considerably in the two categories (26 and 23 on average respectively).

In order to explore whether the correlation trends of vessel member length and number of bars per perforation plate with latitude and altitude in *Ilex* is an example of a general rule or not, two methods can be applied. One possibility is to compare data for 'whole' woody floras from different latitudes and altitudes; the other is to compare species from different latitudes and altitudes within other eurytherm genera.

As for the first possibility one must bear in mind that vessel member length is a character which may be much less variable for higher taxa such as genera and families than for instance vessel frequency and vessel diameter. Therefore it is not justified to compare our data on *Ilex* with data for whole woody floras available for e.g. Japan, Formosa, and the

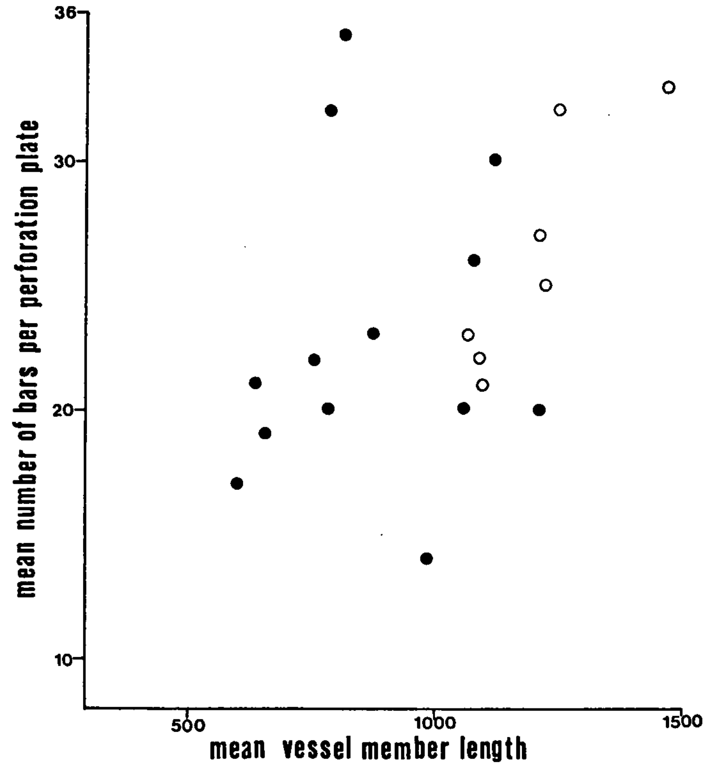

Fig. 11. Vessel member length (in μm) and number of bars per perforation plate in microtherm species from temperate regions (latitude over 35°: ●), and from tropical montane sites (altitude over 1600 m: ○).

Philippines (Kanehira 1921 a & b, 1924). Making a frequency distribution for maximum vessel member length classes of the species described by Kanehira, one finds hardly any difference between tropical and subtropical to temperate floras. However, the frequency distribution for the Philippines is highly influenced by the comparatively high proportion of *Dipterocarpaceae*, *Guttiferae*, *Leguminosae*, and *Meliaceae*, which are characterized by rather short vessel members. These families are very poorly represented in Formosa and Japan. On the other hand, families with comparatively long vessel members like e.g. *Magnoliaceae* and *Theaceae* are better represented in the materials studied by Kanehira. If one compares the species of those genera of which Kanehira studied material from all three countries it appears that in *Albizia*, *Cinnamomum*, *Litsea*, and *Quercus* the 'more tropical' species have the longer vessel members. For *Ficus* this is not very evident, and for *Melia* and *Diospyros* no clear differences can be found in Kanehira's data for the different localities.

Of *Prunus* I studied 12 species from widely different regions (Table I). The results clearly demonstrate that in *Prunus* too tropical species tend to have the longer vessel members and temperate species the shorter ones. In table II a similar phenomenon is shown for *Viburnum*, *Vaccinium*, *Symplocos*, and *Hydrangea*. For *Prunus* and *Symplocos* table I and II also contain some evidence that within the tropics montane species have shorter vessel members than the lowland species.

In the literature I found some more support for the idea that within taxa with representatives in both the tropics and subtropical to temperate regions the tropical species have the longer vessel members. Schweitzer (1971) showed this to hold for *Celtis (Ulmaceae)*, Carlquist (1966) for woody *Compositae*. For *Nothofagus*, Dadswell and Ingle (1954) showed that species belonging to the temperate sections had the shorter vessel members than those belonging to the single tropical subsection. If one equates vessel member length with fusiform cambial initial length, as is generally accepted to be valid, one may draw an interesting parallel with data on conifers. Dinwoodie (1963) showed that tracheid length in Sitka Spruce *(Picea sitchensis)* decreased with increasing latitude of provenance (41—63° N). In seedling cultures he could also establish that tracheid length was genetically fixed in the different populations from different latitudinal origin. He tentatively ascribed these differences to a 'long term effect' of temperature on cambial initial length.

Reviewing all these data on latitudinal variation in vessel member length, it seems fully justified to accept as a general rule that within taxa the tropical representatives have the longer vessel members and the species from higher latitudes have the shorter ones. The same probably applies to altitudinal variation in vessel member length.

Data on number of bars per perforation plate in relation to latitude and altitude are hardly available in the literature. One may cite my own results on young twigs of *Platanus* species (Baas, 1969), and interpret the higher percentage of scalariform perforation plates and the higher number of bars in the tropical species from Laos and Mexico as comparable to the latitudinal trends observed in *Ilex*. Novruzova (1968) compared for some species specimens from different altitudes in Soviet Azerbaijan, and found similar altitudinal trends as I found in *Ilex*: the number of bars per perforation plate decreased with increasing altitude. Original observations on *Symplocos* and *Viburnum* (Table II) are also suggestive that the latitudinal variation of number of bars per perforation plate as found in *Ilex* is a general phenomenon. The two species of *Hydrangea* studied seem to contradict this, but here we deal with wood from climbers which may be so strongly modified that they cannot be compared in this respect. The only wood specimen from an *Ilex* climber I studied, also does not follow the latitudinal trends (see p. 248). Tabata's (1964) data on

Table I. Vessel member length and spiral thickenings in 12 species of Prunus

	Origin and specimen studied	altitude	vessel member length (full range & means) in μm	spiral thickenings
A. TROPICAL SPECIES				
P. africanum (Hook. f.) Kalkman	Burundi, Lewalle s.n. (IF 21598)	?	310—480— 650	very fine
P. arborea (Bl.) Kalkman	New Guinea, BW 9680	35 m	390—710— 910	absent
P. ceylanica (Wt.) Miq.	East Pakistan, (MADw 24491)	?	290—580— 770	absent
P. grisea (C. Muell.) Kalkman	New Guinea, Kalkman 5173	2780 m	310—530— 700	very faint
P. javanica Bl.	New Guinea, BW 9217	100 m	360—580— 780	absent
P. myrtifolia Urb.	Surinam, Stahel 229	?	340—460— 660	very fine
P. pullei (Koehne) Kalkman	New Guinea, Van Balgooy 327	3600 m	270—400— 590	absent or very faint
P. schlechteri (Koehne) Kalkman	New Guinea, BW 1918	50 m	410—710—1030	absent
B. TEMPERATE SPECIES				
P. avium L.	Austria, (Vienna 053)	?	270—390— 510	well developed
P. cerasus L.	England, (Kw s.n.)	low	270—360— 440	fairly well developed
P. lusitanica L.	England, (Kw s.n.)	low	330—470— 640	well developed
P. virginiana L.	Belgium, cult. Tervuren	low	190—290— 380	fairly well developed

Table II. Vessel member length and number of bars per perforation plate in some miscellaneous genera

Species	Origin and specimen studied	altitude	vessel member length (full range & means) in µm	number of bars (full range & means) in µm
Viburnum				
V. tinus L.	Portugal, Barkorda 588, (U 6521)	?	590— 990—1440	13—19—26
V. prunifolium L.	U.S.A., Maryland, (USw 30653)	?	450— 860—1100	11—18—25
V. glaberrimum Merr.	Philippines, Jacobs 7435	2000 m	1190—1690—2270	28—39—60
Vaccinium				
V. arboreum Marsh.	Texas (USw 19399)	?	440— 550— 670	2— 6—11*
V. barandanum Vidal	Philippines, Jacobs 7026	2400 m	490— 640— 860	1— 7—13*
Symplocos				
S. tinctoria l'Hérit.	U.S.A., Maryland (USw 18849)	?	720—1040—1450	15—24—38
S. tenuifolia Brand.	Brazil, Santa Catharina, Reitz 23539	?	720—1090—1340	11—19—34
S. spec.	New Guinea, Kalkman 4870	3140 m	790—1320—1800	21—34—64
S. arborea Brongn.et Gris	New Caledonia, Sarlin (CTFT 6080)	low	1130—1490—1750	19—35—54
Hydrangea				
H. petiolaris Sieb.et Zucc.	Netherlands, cult. (UN 276) (climber)	low	480— 720— 980	7—17—34
H. durifolia Briq.	Venezuela, Breteler 3407 (climber)	?	1000—1100—1240	2— 4— 8

* predominantly simple

Japanese species of *Betula* also seem to be contradictory to those obtained on *Ilex* and some other genera. He found that the lowest number of bars per perforation occurred in species with a preference for wet sites in the valleys. For some high-montane species, partly also from higher latitudes, he recorded much higher numbers of bars. One has to be cautious with Tabata's data since he obtained them from twigs 5 mm in diameter, and from his paper it is not clear whether he studied the peripheral part of the secondary xylem or all of the xylem formed. He also did not give exact data on altitude, and his general conclusion that a low number of bars is associated with species growing in sites with a high moisture content seems to be contradicted by his own results on *Betula platyphylla* var. *japonica*. In this variety he found the specimens from marshy sites to have more bars per perforation plate than the specimens from well-drained sites.

If one nevertheless accepts that within taxa with scalariform perforations there is a general trend for the number of bars per perforation to decrease with increasing latitude and altitude, one would expect the tropical lowland habitat to be a favourable environment to foster species with elaborate scalariform perforation plates and the montane tropical and temperate environment to be better suited for species with reduced scalariform perforations viz. simple perforations. An analysis of the abundance of species with simple or scalariform perforations in different woody floras does not support this idea. Kanehira (1921a) showed that Japan houses a much higher percentage (32.6%) of genera with scalariform perforations than the Philippines (5.7%), Formosa being intermediate with 19.4%. A comparison of the European woods with woods from Java (Greguss, 1959, and Janssonius, 1906—1936) also gives a higher percentage of genera with scalariform perforations for temperate and subtropical Europe (23%) than for tropical Java (13%). In a comparison of the woody montane flora with the lowland woody flora of Indonesia, Versteegh (1968) showed that scalariform perforation plates were of more common occurrence in the mountains than in the lowland. The low frequency of taxa with scalariform perforation plates in tropical lowland forests is well known to wood anatomists. Therefore the trends reported for *Ilex*, *Symplocos*, *Viburnum*, and for *Platanus* and some species from Azerbaijan seem to be contradictory to the general distribution of species with scalariform and simple perforations. This will be further discussed in relation to phylogenetic implications (p. 218). *See also Addendum on p. 251.*

Vessel wall pitting (Plate II, 6—13; III, 1, 3—9)

The range in type and size of vessel wall pitting within *Ilex* is considerable. In many species there is also a considerable range within each individual specimen, restricting the diagnostic value of this character. Particularly the ranges transitional to opposite, and opposite to alternate inter-vessel pits frequently occur within one sample. Other species may even show the whole range from scalariform to alternate (e.g. *I. aquifolium* and *I. berteroi*). Usually one type predominates, however. Of the species studied, *I. anomala*, *I. berteroi*, *I. casiquiariensis*, *I. chinensis*, *I. coriacea*, *I. cornuta*, *I. decidua*, *I. glabra*, *I. longipes*, and *I. volkensiana* have a fairly high proportion of scalariform inter-vessel pits. These species are from all three subgenera of *Ilex* studied, and are distributed haphazardly over the various series and sections recognized by Loesener. Surprisingly enough, there is therefore no correlation between type of inter-vessel pits and subgeneric classification. A correlation of type of pits with latitude or altitude of provenance is also absent, nor is there any relationship with vessel member length or number of bars per perforation plate. This is contrary to what one would expect, since in general analyses it has been established for Dicotyledons as a whole that type of pitting is strongly correlated with vessel member length: the scalariform type of pitting being far more frequent in woods with long vessel members, and opposite to alternate pitting being more in evidence in woods with short vessel members (Metcalfe and Chalk, 1950: XLIII—XLV).

Vessel—ray pits are usually similarly arranged as the inter-vessel pits. Often the arrangement is slightly disturbed, however. Unilaterally compound pits are of frequent occurrence within the genus. Sometimes one ray pit corresponds with more than two bordered vessel wall pits, which are usually in horizontal rows. Occasionally the pits on the vessel wall side are arranged in small clusters of 3 or 4 ('complex unilaterally compound', Plate III, 6). The extent to which the pits on both vessel- and ray-side are overarched by borders varies also considerably within the genus. In some species with scalariform to transitional vessel—ray pits the borders are much reduced, resulting in almost simple pits.

Spiral thickenings (Plate III, 2; IV, V; 1 & 2)

Plate IV shows the range of vessel and fibre wall sculpturing. All possibilities from absence of spirals to spirals well developed are realized within *Ilex*. In some species only faint spirals occur in a number of fibre-tracheid tips. In others the vessels are devoid of spirals but most fibre-tracheids have fairly well developed spirals. Yet another possibility is the presence of very faint spiral thickenings on the walls of both vessels and fibre-tracheids. Very rare is the combination of spirals faint and infrequent in the fibre-tracheids and well developed in the vessels. (*I. curranii* and *I. dumosa*). The more or less continuous range from well developed spirals to very faint or no spirals includes at least two of the types recognized by Parham & Kaustinen (1973). Therefore, and probably also because of the small number of different woods studied, their classification of types of spiral thickenings is rather artificial.

Fig. 12 shows the proportional distribution of species with or without well developed spiral thickenings, as well as intermediate species over different latitudinal zones. Almost all species without spiral thickenings appear to be confined to the tropical zone between 12°30′ S and N. The two temperate species without spiral thickenings are exceptional (see p. 225). Most species with well developed spiral thickenings in both vessels and fibre-tracheids are to be found in the subtropics and temperate regions. Those species with well developed spirals from the latitudinal zones between 13° and 25° N or S are in fact mostly from the transitional zones between tropics and subtropics (20°—25°). Species with faint spirals in vessels and fibres, or with spirals well developed in only one category of these elements are mainly confined to the tropics. Of these the species growing closest to the equator have the faintest spirals, usually wholly confined to a few fibre-tracheid tips. This condition is therefore much closer to 'spirals absent' than to 'spirals well developed'. The temperate *I. montana* with its faint spirals in the vessels is exceptional for the temperate regions, where development of spiral thickenings is usually most conspicuous. Summarizing, there is a very obvious tendency of spiral thickenings to be rare in the tropics and to become very common and conspicuous in the subtropics and temperate regions.

For the tropical *Ilex* species a further attempt was made to analyse the variation encountered. Table III gives the distribution of species with well developed spirals, no spirals, and intermediate species in relation to altitude and seasonal or everwet climate.

Total absence of spiral thickenings seems to be more common in montane species than in lowland species. The climatic condition as expressed in seasonal or everwet also seems to have some bearing on the matter. All tropical *Ilex* species without spirals grow in

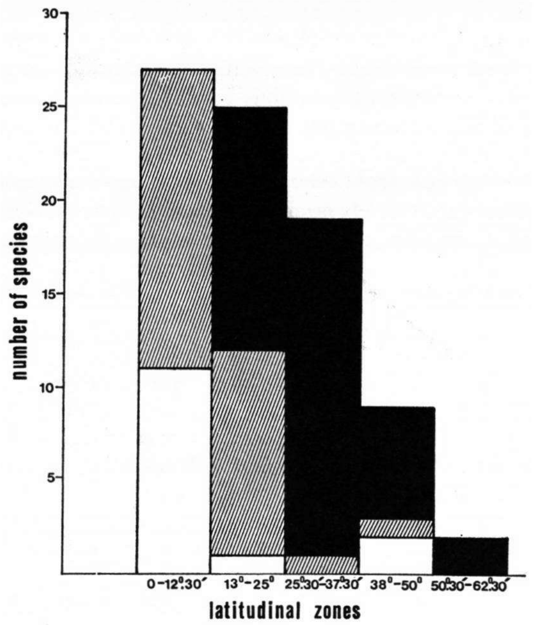

Fig. 12. Occurrence of spiral thickenings in 81 species of *Ilex*, and latitudinal distribution (*Ilex crenata* plotted at 17° and 52°). — white = spirals absent; — hatched = spirals faint or restricted to part of vessels and/or fibre-tracheids; — black = spirals well-developed.

habitats with an everwet climate or in a climate with a very short dry season. Climatic data used for this analysis were taken from Walther and Lieth (1960). Because the number of stations for which meteorological data are recorded is restricted, only those species could be considered of which locality data were suitable for comparison with Walther and Lieth's data.

From the fact that in exceptional cases well developed spiral thickenings occur both everwet and montane habitats, one must conclude that rain fall and temperature cannot

Table III. The occurrence of spiral thickenings in the wood of lowland and montane tropical Ilex species in relation to climate and altitude

	Number of species with:		
	well developed spirals	faint or rare spirals	no spirals
CLIMATE			
everwet	1	10	7
wet with short dry season	-	7	1
with pronounced dry season	1	9	-
ALTITUDE			
lowland (below 1000 m)	-	12	2
montane (over 1600 m)	1	4	6

be considered as entirely responsible for the presence or absence of spiral thickenings. Because of this one must assume that the character 'spiral thickenings' has to a great extent become genetically fixed in the species involved. The absence of spirals in the temperate species *I. serrata* and *I. verticillata* also points in this direction. Moreover, in general, presence or absence of spiral thickenings remains a valid diagnostic feature within temperate woody floras. For instance some *Viburnum* species are characterized by spiral thickenings, whilst others lack them (Greguss, 1959), also if they grow under the same conditions. Temperature can certainly not be held responsible for favouring either presence or absence of spirals. In the cool tropical montane habitats absence of spirals is the most frequent condition in *Ilex*; in regions of higher latitudes with comparable temperature regimes absence of spirals is very rare. Novruzova (1968) reported that spiral thickenings were of more common occurrence in mesic species than in xeric species in Soviet Azerbaijan. Whatever the climatic correlations found, however, from the foregoing it is clear that the environmental conditions cannot fully explain presence or absence of spiral thickenings, and one has therefore to assume that the evolutionary background plays an important role in the distribution of this character over the different species of *Ilex*. However, I have been unable to find a taxonomic pattern behind the variation encountered.

The more frequent occurrence of spiral thickenings in fibres and/or vessels in plants growing in subtropical and temperate regions as compared with tropical plants is a general phenomenon, recognized before (Kanehira, 1921a; Janssonius 1906—1936; Panshin, De Zeeuw & Brown, 1970), though it has not received much attention by students of wood anatomy. The general trend becomes clear if one compares the percentages of genera with spiral thickenings in the European flora (Greguss, 1959) and in the Javanese flora (Janssonius, 1936, index p. 31). In European trees and shrubs 91 genera out of 153 studied have spiral thickenings, that is 60% of all genera. For Java only 54 out of 377 genera (15%) have spirals. Moreover, these 54 genera have usually faint or infrequent spiral thickenings occurring in only a minority of the species. Kanehira (1921a) reported percentages of genera with spirals of 40.7, 22.3, and 4.7 for Japan, Formosa, and the Philippines respectively. For the United States Record (1919) noted spiral thickenings in 47 genera out of 122 studied, resulting also in a fairly high percentage: 38.5. In both tropical America and Africa the occurrence of spiral thickenings is a rare phenomenon (Mennega and Dechamps, private communications).

The general trend of spiral thickenings to be less common towards the tropics can also be demonstrated within a number of genera. *Celtis* (Schweitzer, 1971), *Gleditsia* and *Elaeocarpus* (Kanehira, 1921a & b, 1924), *Euonymus* (Moll and Janssonius, 1911), *Prunus* (Moll and Janssonius, 1914, and my own results in table I), *Koelreuteria* and *Symplocos* (original observations) are a few examples.

There is an interesting parallel between the diminishing frequency of spiral thickenings towards the tropics and the higher percentage of species with entire leaf margins in the tropics as compared with temperate floras.

Bailey and Sinnott (1916) gave percentages of species with entire leaf margins in tropical and temperate floras. Ferguson (1971) gave further percentages and discussed the value of the percentage of species with entire margins in assessing the climatic conditions of the past in paleobotanical studies.

Within *Ilex* too, leaf margin characters behave similar as presence or absence of spiral thickenings (see table IV). From the table it appears that in *Ilex* leaf margin characters are related to latitude to a considerable extent, but that the occurrence of spiral thickenings is even more strongly related to latitude. One cannot conclude from this parallel between spiral thickenings and leaf margin characters, that sculpturing of the vessel and/or fibre

Table IV. Leaf margin characters in 77 species and wall sculpturing in 81 species of Ilex

	Tropics (between 23°30' N & S)	Subtropics and temperate regions
LEAF MARGIN*		
Number of species with entire leaf margins	20	5
Number of species with subentire leaf margins (weakly dentate or crenulate)	11	10
Number of species with dentate leaf margins or with spines	5	26
WALL SCULPTURING		
Number of species without spirals	12	2
Number of species with faint spirals or with spirals confined to part of vessels and/or fibres	26	3
Number of species with well developed spirals	2(3)**	36

*Data from Loesener's monograph and from later specific descriptions available for 77 of the 81 species studied.

**If I. crenata is treated under both tropical and temperate the number here should be 3.

wall has the same potentiality of predicting climatic conditions of the past, using fossil woods. In doing so one would ignore the diversity in climatic conditions in the tropics due to differences in altitude. Moreover, comprehensive surveys of the wood anatomy in many different floras would be needed in order to have a firmer statistical basis to work with.

Fibre-tracheids (Plate V)

In *Ilex* fibre-tracheid length shows the same relationships with latitude and altitude as vessel member length. It decreases with increasing latitude and/or altitude. The ratio fibre length/vessel member length ranges from 1.2 to 2.2 (on average 1.6), the most frequent range is between 1.4 and 1.8. This means that the amount of intrusive growth of the differentiating xylem elements is fairly constant within *Ilex*. Part of the variation, possibly responsible for the extremes, may also be ascribed to differences within individual growth rings of temperate species. Many authors have shown fibre length to vary considerably from early to late wood within one growth ring, the vessel members being rather constant in length throughout the ring (e.g. Süss, 1967). No special attention was devoted to sampling chips for macerations from special parts of the growth rings in this study, so that it is likely that part of the variability was indeed caused by the different positions within the rings.

No relation exists between the elongation factor and vessel member length (regarded as more or less identical with cambial initial length) in *Ilex*. Chattaway (1936) had shown that in general the shorter the vessel members the stronger the elongation of the differentiating xylem elements developing into fibres. However, for the range of cambial initial length of 600—1900 μm (which is the range of *Ilex*) the differences she recorded in the ratios of fibre length to cambial initial length are only small and range between 1.3 and 1.8, which is almost the same as in *Ilex*.

Usually the bordered pits of the fibre-tracheids are more numerous on the radial than on the tangential walls, but on the latter they may vary from very infrequent to abundant and from having conspicuous borders enclosing the slit-like apertures to having much reduced borders with the slit-like apertures extending far beyond.

There is no clear correlation between the diversity in fibre-tracheid pitting and the classification by Loesener. In looking for a correlation with latitudinal zonation a considerable range in pit size and pit frequency is found in all latitudinal zones. Yet there is an obvious tendency for the tropical species to be characterized by small bordered pits in low frequencies, whilst the bordered pits are larger and more numerous in subtropical and temperate species (fig. 13). In the restricted number of tropical species of which sufficient data on altitude were available I could not find any trend of correlation in pit size and frequency with altitudinal distribution.

No adequate data from other plant groups or from the literature were at my disposal to establish whether the latitudinal trend in fibre characters found in *Ilex* is a general one. Two references may be significant here. Novruzova (1968) concluded that primitive fibre elements (fibre-tracheids) were more frequently observed in plants growing under conditions of adequate water supply, and that specialization towards libriform fibres depends on atmospheric dryness. Versteegh (1968) concluded that fibres with bordered pits were more in evidence in the tropical mountains than in the tropical lowland. My data are insufficient to support or reject either view.

Gelatinous fibres in irregular groups or partial concentric bands are present in *I. laurina*, *I. myricoides*, and *I. rimbachii*. They have hitherto not been recorded for *Ilex* (Höster and Liese, 1966).

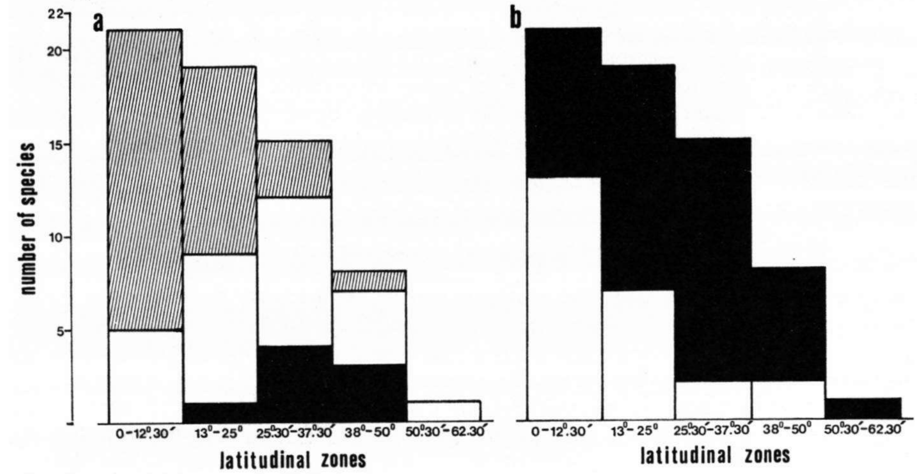

Fig. 13. a. Frequency of bordered pits on tangential walls of fibre-tracheids in 64 species of *Ilex* and latitudinal distribution. — hatched = pits infrequent; — white = pits rather infrequent to rather frequent; — black = pits frequent.

b. Diameter of bordered pits on tangential walls of fibre-tracheids in 64 species of *Ilex*, and latitudinal distribution. — white = pit borders less than 5 μm in diameter; — black = pit borders 5 μm or more in diameter.

Hu (1967) reported the presence of *septate fibres* in *I. hawaiensis* and *I. cymosa*. She must have mistaken the thin-walled parenchyma strands for these, because septate fibres are absent from all material I studied of *I. cymosa* and from the other *Ilex* material, except for some infrequent septate-like fibre-tracheids in *I. martiniana* (see p. 240, and Plate V, 3). The septate fibres she pictured for *I. hawaiensis* are clearly parenchyma strands.

Parenchyma

The range in parenchyma abundance from very scanty to fairly abundant shows a correlation with latitude. Temperate species have very scanty diffuse parenchyma, subtropical and tropical species have more abundant parenchyma which is both diffuse and diffuse in aggregates. This applies to lowland as well as to montane species.

Rays (Plate VI, 1—6)

There is a tremendous variation in ray size and frequency within *Ilex*. Since the variation is continuous no relationships could be established with taxonomic grouping, and an analysis of the latitudinal distribution of different size classes of rays only resulted in a vague trend for the higher rays to be more abundant in the tropics and the lower rays to be more in evidence in the temperate regions. Ray width does not show any correlations with latitude. Only in the case of *I. verticillata* and *I. serrata*, narrow ray width has been used as an additional character supporting their mutual close affinities (p. 225).

Crystals (Plate VI, 7—10)

Although virtually all crystals recorded here for *Ilex* belong to the solitary type, the variation is larger than previously realized (cf. Chattaway, 1956). Crystals in idioblasts are reported for the first time. About 30% of the species studied lack crystals. Of the crystalliferous species, the majority is to be found in the tropics.

The irregularly clustered crystals reported for few species may possibly be regarded as fragmented solitary crystals.

Wood phylogeny and ecological wood anatomy (see also p. 251)

Much of the variation in wood anatomy in *Ilex* and in some miscellaneous genera reported above concerns characters which are regarded as important indicators of phylogenetic specialization. In the context of this paper the following specialization trends are relevant (see Carlquist, 1961, for a general summary of mainly Bailey's and Frost's work).

1. Short vessel members are derived from long vessel members.
2. Perforation plates with few bars are derived from perforation plates with numerous bars.
3. Decrease of size and frequency of bordered pits on fibre walls means specialization.

Trend 1 and 2 in particular have often been regarded to represent irreversible evolutionary processes. Of interest here is also the generally accepted view that increase in vessel diameter, and a higher degree of vessel grouping in multiples may be interpreted as specialization, though most authors are aware of the fact that particularly vessel diameter may be easily affected by environmental conditions, which opens possibilities for reversibility of the specialization series.

After all the work that has been done on large and representative samples of Dicotyledonous woods, and from what can be deduced from the vesselless ancestry of the angiosperms, there can be no doubt about the validity of the general trends of xylem specialization established by Bailey and confirmed by many wood anatomists after him. This applies in particular to the three specialization trends listed above. It should be pointed out that the wording of trend 2 is my own, and that it represents only a part of the evolutionary pathway from a tracheid with crowded scalariform pits, via a vessel with scalariform perforations to a vessel with simple perforations.

From my own results some trends can also be deduced:

1a. Within taxa (genera) the longer vessel members are found in the tropical lowland species, the shorter vessel members in the temperate regions, and to a certain extent also in tropical high montane species.

2a. In trees and shrubs with scalariform perforations the number of bars is highest in the tropical lowland and decreases with increasing latitude and altitude.

3a. In tropical species of *Ilex* there is some tendency for fibre-tracheids to have more reduced and fewer bordered pits than in the temperate regions.

The question arises which is the significance of these correlations between wood structure and climate for the general phylogenetic trend, or reversely, which part phylogenetic wood specialization has played in these ecological correlations. Because of the evolutionary aspects of these questions the discussion must unfortunately remain highly speculative.

Trends 1/1a and 2/2a concerning vessel member length and reduction of bars per perforation plate could be harmonized by stating that within eurytherm genera the tropical lowland species have retained the most primitive wood structure, and that species of higher latitudes or altitudes are more specialized in their wood anatomy. For *Ilex* this would imply that primitive *Ilex* occurs in tropical lowland Asia, Africa, and South America. However, if one accepts Loesener's assumption that the cradle area of *Ilex* is somewhere in the northern hemisphere, and that the genus originated under mild climatic conditions ('mildes See-Klima', 1908, p. 246), this assumption is not very likely. Moreover, Loesener regarded most of the tropical species as derived rather than as primitive, and a number of species which he regarded as very primitive (belonging to series *Lioprinus* of subgenus *Euilex*) have for *Ilex* a relatively highly 'specialized' wood anatomy (e.g. *I. canariensis, I. chinensis, I. montana, I. rotunda,* and *I. uniflora*), in accordance with their latitudinal distribution. Whether one accepts Loesener's view or not, one has to assume some cradle area for *Ilex*, and this makes it hard to understand that there is a similar very low specialization level in the tropical lowland of three, now widely seperated, continents. Accepting the purely phylogenetic interpretation of trends 1a and 2a, would also imply that *all* tropical montane species should be regarded as specialized; this does not sound very likely to me, and finds no support in other morphological features. With respect to these montane species, I mention in passing that the wood anatomical evidence supports the idea that they are more closely related to tropical lowland species than to temperate or subtropical species. They have longer vessel members than temperate species growing under comparable temperature regimes (see p. 207), and they are charactarized by the absence of spirals or by very faint and infrequent spirals, as in the tropical lowland species. One can, however, not entirely exclude the possibility that some tropical montane species are more closely related to temperate species than to tropical lowland ones.

The trend for fibre-tracheids to be less specialized in the temperate and subtropical species than in the tropical species calls for opposite reasoning, viz. that the more specialized species are to be found in the tropics and the more primitive ones in subtropical and temperate regions. This argument, derived from fibre-tracheid specialization is, however, not a very strong one, because the correlations with latitude are here much weaker than for vessel specialization. Moreover, mixtures of advanced and primitive characters are of quite common occurrence in the wood and other parts of higher plants. For *Icacinaceae* Bailey and Howard (1941) found fibre specialization to parallel vessel specialization in trees and shrubs, but in scrambling and climbing *Icacinaceae* the fibre-tracheids or even tracheids were provided with numerous large bordered pits in spite of the very high specialization level of the vessel elements. According to Bailey and Howard this indicated that the specialization of the imperforate tracheary elements 'lagged behind'. In my opinion this phenomenon can just as well be explained by a reversal of the general specialization series. In *Ilex* a similar sort of reversal might have occurred in temperate shrubs and trees.

In passing, I mention that Hu (1967) suggested that the primitive *Ilex* species are found in the Pacific area (N. Borneo, Philippines, Cochinchina, Formosa, and Hawaii); she based this conclusion also on the primitive wood characters of those species. Although her results on the xylem specialization in some Pacific species of *Ilex* agree with mine, her suggestions cannot be upheld by wood anatomy. From the study of more species, presented here, it is clear that equally primitive wood is found in Central and South America.

On balance, I find the interpretation of the correlation of vessel member length and number of bars per perforation plate with altitude and latitude, in terms of phylogenetic specialization of the species concerned, not very satisfactory. One may also take another view and assume that the latitudinal and altitudinal correlations found in several eurytherm genera simply mean that climate has some sort of effect (long term or short term) on vessel member length and number of bars. This does not necessarily contradict the phylogenetic interpretation but puts emphasis on climatic influence as a factor of primary importance.

It also implies that the wood anatomy of a eurytherm genus is easily modified by climate and that 'independent' specialization trends, if any, can easily be obscured by the dominant effect of climate. For vessel member length this would nicely agree with Dinwoodie's results on tracheid length in Sitka Spruce (see p. 208). Moreover, it implies that with the wanderings of the genus *Ilex* over the globe in the past, reversals of the general specialization trends may have occurred, and that the change from a subtropical or temperate to a tropical climate (through major changes in situ, or through extensions of the distribution area of *Ilex*) may have resulted in elongation of the vessel members and an increase in the number of bars per perforation plate. This would then be an argument against the view strongly upheld by Bailey (1953) that the general trends of wood specialization are irreversible, a statement which I consider to be a belief rather than a biological law. In the literature some recent papers also indicate correlations of climate and wood structure which can hardly be incorporated in the general phylogenetic specialization series. These studies mainly refer to influence of water supply on wood structure. Carlquist (1970) showed an almost perfect correlation of rain fall and vessel member length in comparing several Hawaiian species of *Euphorbia* (ranging on average from 206—600 μm). For *Compositae* he found similar correlations between vessel member length and mesic or xeric conditions (1966). Novruzova (1968) analysed the woody flora in Soviet Azerbaijan and found 'primitive woods' characterized by scalariform or mixed scalariform and simple perforations to be more in evidence in sites with mesic conditions than in xeric habitats. Her analysis of 196 species led her to the following conclusions which are relevant for this discussion:

1. Plants in drought areas have specialized structural elements.
2. Primitive fibres in the conducting system are observed in plants with adequate water supply. Specialization would depend on atmospheric dryness.
3. Under drought conditions all fusiform elements become much shorter.
4. Quantitative and qualitative changes occur when mesophytes colonize xeric conditions, or when mesic conditions change into xeric.
5. In specimens of the same species with scalariform perforation plates, the number of bars decreases with increasing altitude.

Though these results are not directly comparable with the altitudinal and latitudinal variation reported in this paper, Carlquist's and Novruzova's data on correlations between water supply and wood structure present interesting parallels. Drought conditions seem to have the same effect on fusiform element length as lower temperatures (as extrapolated from higher altitude or latitude). Specialized fibres found under both dry conditions and at tropical latitudes would, however, suggest a similar effect of drought and of the hot, mostly very wet, tropical climate.

I find it impossible to understand all the implications of the relationships existing between climatic conditions and the predominance of certain wood anatomical features. Yet it is obvious that such relationships exist, and the simplest interpretation would be in terms of climatological effects on wood structure. Whether climate only acts on the phenotypic variation of wood structure or influences a long term selection process in evolution so that functionally best fitted anatomical features are favoured, cannot be assessed with the data available now. I would be inclined to take the latter view. There can be little doubt that the characters found to be correlated with altitude and latitude are genetically fixed to a certain extent (cf. Dinwoodie, 1963). Moreover, characters like vessel member length and fibre specialization will certainly play an important role in the functions of water transport and water storage (Braun, 1970) and natural selection may favour certain combinations of anatomical characters for each major type of environment.

All within the possibilities of the genome, still witnessing affinities with relatives in the expression of certain wood anatomical features.

Much remains to be done on the correlations of wood structure and environmental conditions. Numerous examples have been cited above, suggesting a major role of the environment. Other studies, however, do not indicate any relation between environment and wood structure. Hawaiian *Metrosideros polymorpha* growing at widely different altitudes and under different conditions of water supply did not show any appreciable relation of wood structure with altitude or rainfall (Sastrapradja and Lamoureux, 1969). Apparently the variational range following environmental conditions also depends on the plant group. Novruzova (1968) also indicated this by concluding that different genera exhibit different degrees of variability in the water conducting system.

Though I have abandoned the purely phylogenetic interpretation of the altitudinal and latitudinal 'effects' on wood structure, this does not imply that the results on *Ilex* and some other eurytherm genera have no significance for wood phylogeny in general. The view that climatic factors have an influence on characters such as vessel member length, number of bars per perforation, and also in fibre specialization, may indicate that the same factors have played a role in directing the general phylogenetic specialization trends of secondary xylem, leaving possibilities open for reversals of these trends. If my results really represent examples of a general rule, this would mean that the tropical lowland is the best environment for the retention, or if reversals of specialization have occurred, the promotion, of primitive vessel characters. This, however, is contradicted by the majority of wood structure types in the tropical lowland floras. As mentioned before (p. 211) scalariform perforations are rare in the tropical lowland, and many of the dominant families are characterized by rather short vessel members. The attempt to bring these facts in harmony with the hypothesis that the tropical lowland favours primitive wood structure would involve fantastic speculations, like the assumption of an evolution outside the hot tropical environment for those families now constituting the bulk of the tropical flora. Obviously more facts are needed to reach a more sensible synthesis.

Wood anatomy and the classification of Ilex

The only comprehensive systematic subdivision of the genus *Ilex* is that proposed by Loesener (1901, 1908, and 1942), and although his system may be 'out of date' because of the availability of much more material from areas underexplored up to his time, there is no reason to challenge Loesener's claim that his subdivision in subgenera, series, sections, and subsections reflects natural grouping and that the arrangement of the infrageneric taxa reflects natural affinity. His system rests on the use of character complexes from inflorescence, merousness of the floral whorls, ovary, ovules, and leaves and was based on the investigation of about 2000 specimens (for c. 280 species). In this part I therefore follow Loesener's system adopting his nomenclature, including his intercalation of a rank 'series' between that of subgenus and section. It will appear that most sections, series, and subgenera are wood anatomically very heterogeneous, except those infrageneric taxa of which the species I studied are from similar habitats (tropical lowland or mountains, subtropical or temperate regions). In only a few sections the common occurrence of certain anatomical features is independent of latitude and altitude, and seems to point to natural affinity. On the grounds of this lack of correlation between wood anatomical diversity and Loesener's classification, it should not be concluded that his system is weak. This would be so if wood anatomically one could propose an alternative classification based on a consistent combination of wood anatomical characters for different infrageneric groups. From the continuous variation in all relevant wood anatomical features as recorded in the descriptive part it follows that such an alternative system cannot be proposed.

Notes on the wood anatomy of Loesener's sections, series, and subgenera

Subgenus RYBONIA

No material was available of the opposite-leaved species of this subgenus. According to Merrill (J. Arn. Arb. 20, 1939, 222) the wood anatomy is like that of other *Ilex* species.

Subgenus BYRONIA

Series A. EUBYRONIA

Species studied: *I. anomala, I. cymosa, I. hypoglauca, I. ledermannii, I. sclerophylloides.*

The quantitative features and most of the qualitative wood anatomical characters agree very well for these five species. *I. anomala* stands out by its scalariform and transitional inter-vessel pits and large vessel—ray pits. Except for *I. anomala* from the Pacific islands Tahiti and Hawaii, all other species are from the tropical lowland of Malesia.

Series B. MICROCOCCA

Species studied: *I. micrococca.*

This Japanese species differs from the foregoing series in having all features similar to the subtropical and temperate type of wood anatomy.

Subgenus *Byronia* is wood anatomically heterogeneous. The two wood anatomical types encountered coincide with the two series recognized by Loesener; they also coincide with geographical distribution: one type being restricted to the tropics, the other type to a temperate region.

Subgenus YRBONIA

No material was available of the only species *I. teratopsis.*

Subgenus EUILEX

Series A. LIOPRINUS

Section **Excelsae**

Species studied: subsection *Umbelliformes: I. chinensis, I. godajam, I. rotunda*; subsection *Laxae: I. amplifolia, I. kwantungensis, I. laurifolia, I. macfadyenii, I. nayana, I. sebertii.*

This section has a wide range in both the tropical, subtropical, and temperate New and Old Worlds. Generally the large wood anatomical variation follows the latitudinal zonation. It may be significant that the three tropical species from the Old World (*I. godajam, I. laurifolia,* and *I. sebertii*) lack spirals in their vessels and have only very faint spirals in some of the fibre tips, whilst the New World species from the tropics (*I. amplifolia, I. macfadyenii,* and *I. nayana*) have well developed spirals in the fibre-tracheids and *I. amplifolia* and *I. macfadyenii* weak spirals in the vessels as well.

Section **Cassinoides**

Species studied: *I. canariensis, I. cassine, I. coriacea, I. glabra, I. opaca, I. quercetorum.*

Except for the tropical-montane Mexican *I. quercetorum,* all species studied are from subtropical and temperate regions on the northern hemisphere. The anatomical variation is fairly small accordingly, though the average number of bars varies from 15—36. Of *I. quercetorum* I only studied an immature specimen; the presence of fairly well developed spirals in the vessels of this tropical montane species suggests that it may be derived from a subtropical or temperate ancestor.

Series B. PALTORIA

Section **Rupicolae**

Species studied: *I. uniflora.*

This tropical montane species follows the altitudinal trend of *Ilex* in showing short vessel members and a low number of bars per perforation plate. Presence of spirals in the vessels combined with their frequent absence from the fibre-tracheids is unusual for *Ilex.*

Section **Polyphyllae**

Species studied: *I. crenata, I. dumosa, I. myricoides.*

The three species differ widely from each other. *I. crenata* has all characteristics of a temperate to subtropical *Ilex,* also in the tropical montane specimen from the Philippines. *I. dumosa* stands out like *I. uniflora* in having more conspicuous spirals in the vessels than in the fibre-tracheids, and *I. myricoides* has a wood anatomical character complex typical for tropical lowland species, in spite of its high altitude. Thus part of the heterogeneity within this section cannot be explained by the latitudinal and altitudinal trends in *Ilex.*

Series C. AQUIFOLIUM

Section **Lemurensis**

Species studied: *I. fargesii, I. mitis.*

The two species differ widely in quantitative features, following the latitudinal variation in *Ilex.*

Section **Aquifolioides**

Species studied: subsection Oxydontae: *I. aquifolium, I. cornuta, I. dipyrena, I. integra, I. perado*; subsection *Insignis: I. insignis, I. latifolia.*

The species studied of this section are all rather similar in exhibiting typically temperate to subtropical wood anatomical features. In all species tangential fibre wall pits are fairly frequent.

Section **Microdontae**

Species studied: subsection *Eumicrodontae: I. brevicuspis, I. krugiana*; subsection *Repandae: I. argentina, I. buergeri, I. cinerea, I. ficoidea, I. formosana, I. liukiuensis, I. paraguariensis, I. repanda, I. toluccana, I. volkensiana*; subsection *Vomitoriae: I. caroliniana*; subsection *Sideroxyloides: I. divaricata, I. goshiensis, I. sideroxyloides, I. wilsonii.*

Section *Microdontae* has a pantropical and pansubtropical distribution. The species I studied are mainly from subtropical regions, and those from the tropics were only represented by immature specimens. Anatomically the wood agrees with what one would except in the subtropical species. *I. krugiana* stands out, however, by the absence of spirals from the vessels. The tropical species conform to the latitudinal trend in lacking spirals in their vessels, and have only faint or few spirals in the fibre-tracheids.

Section **Daphnophyllae**

Species studied: *I. caliana, I. laurina.*

These two species resemble each other very closely, and clearly conform to the altitudinal effect in tropical montane *Ilex.* They moreover share the large gash-like vessel—ray pits, which is a rather unusual character in *Ilex.*

Section **Megalae**

Species studied: subsection *Pedicellatae: I. brasiliensis, I. theezans.*

In quantitative values and the presence of well developed spirals these two species conform to what one would expect of subtropical *Ilex* species.

Section **Micranthae**

Species studied: subsection *Punctatae: I. petiolaris;* subsection *Epunctatae: I. berteroi, I. guianensis, I. inundata, I. jenmanii, I. umbellata.*

All species studied are from the tropical lowland. Accordingly the wood shows rather long vessel members and fairly numerous bars per perforation plate, though the values are distinctly lower than for instance for the tropical lowland species of subgenus *Byronia. I. berteroi* from Cuba stands out with very few bars and short vessel members. The occurrence of faint to well developed spirals in the fibre-tracheids is shared by all species.

Section **Rugosae**

Species studied: *I. curranii, I. versteeghii.*

Both species studied grow in the tropical montane habitat. Yet they differ in the presence (*I. curranii*) or absence (*I. versteeghii*) of spirals.

Series D. THYRSOPRINUS

Section **Racemosae**

Species studied: *I. havilandii.*

This species conforms to the tropical montane type of *Ilex* wood anatomy.

Section **Indico-Malaicae**

Species studied: *I. cissoidea.*

The wood anatomy of this species is similar to that of *Ilex* species from the lowland tropics, as for instance those belonging to subgenus *Byronia.*

Section **Thyrsiflorae**

Species studied: *I. casiquiariensis, I. martiniana, I. ovalifolia.*

The three species studied are all from the lowland of tropical South America and are very similar wood anatomically. They also resemble other species of the tropical lowland (cf. section *Indico-Malaicae*) with their long vessel members, numerous bars and absence of spirals.

Subgenus *Euilex* is, in this study, the best represented one: 61 species from all major distribution areas of the genus. Accordingly the wood anatomical variation encountered within this subgenus is almost as large as within the whole genus. Frequently the variation related with latitude and altitude is also very considerable within the individual sections or even subsections. In some sections one finds an indication of systematic affinity based on wood characters, as for instance in sections *Daphnophyllae* and *Aquifolioides.* Yet, in other sections (*Rugosae* and *Polyphyllae*) the wood anatomical diversity is considerable and cannot be entirely correlated with the general latitudinal and altitudinal trends.

Subgenus PRINUS

Series A. EUPRINUS

Species studied: *I. serrata, I. verticillata.*

The two species resemble each other very closely in their semi-ring-porousness, short vessel members, few bars per perforation, rather narrow rays and the — for temperate species unique — absence of spirals from the vessel- and fibre walls. This whole character complex put these species together in a rather isolated position within the genus. According to Loesener (1901, p. 501) the species of series *Euprinus* are closest to the North American genus *Nemopanthus*. The wood anatomy of *Nemopanthus* is ± identical to that of *I. serrata* and *I. verticillata* and very strongly supports Loesener's suggestion.

Series B. PRINOIDES

Species studies: *I. chapaensis*, *I. decidua*, *I. dubia*, *I. longipes*, *I. montana*.

The three former species share the presence of numerous tangential wall pits in the fibre-tracheids, whereas *I. montana* has infrequent fibre-wall pits. Other characters vary considerably, partly in relation to the latitudinal trend (20°—41 °N).

Subgenus *Prinus* can be split into two groups, as based on wood anatomy. Series *Euprinus* stands out by its absence of spirals, and series *Prinoides* simply follows latitudinal trends with its fairly faint spirals in the tropical *I. chapaensis* and the well developed spirals in the subtropical to temperate species. Subgenus *Prinus* is composed of deciduous species, in contrast to the remaining evergreen subgenera. The heterogeneity of this deciduous subgenus indicates that there is no relationship between wood anatomical characters and the deciduous or evergreen habit in *Ilex*.

Specific wood anatomical descriptions

Explanatory notes. — The specific descriptions are as short as possible. Data on average and maximal number of vessels per radial multiple, frequency of different size classes of radial vessel multiples, abundance of parenchyma, length of parenchyma strands etc. are not included in the specific descriptions because of the great variation below the species level of the vessel distribution characters, and the time consuming nature of measuring parenchyma frequency. For these characters the general statements in the generic description and in the discussion of the characters must suffice. Abbrevations and very condensed sentences have been used to shorten the descriptions even further. The general descriptive scheme adopted is as follows:

Vessel distribution. Growth rings. Average vessel frequency(ies), average percentage(s) of solitary vessels, tangential vessel diameter (full range and range of means; in case of two specimens studied both means are given as e.g. 800 & 1000, with more specimens the extreme means are connected by a hyphen), vessel member length (ibid.), inter-vessel pits and vessel—ray pits (arrangement and size), number of bars per perforation plate (full range and range of means), helical and annular thickenings (spirals). Fibre-tracheid length (full range and range of means), frequency and size of tangential wall pits, helical and annular thickenings (spirals). Average frequencies of broad and narrow rays, ray type (following Kribs), maximum height and width of the broad rays, sheath cells. Crystals. Peculiarities (if any).

The *abbreviations* used are: alt. = alternate; diam. = tangential diameter; freq. = frequent; het. = heterogeneous; infreq. = infrequent; length = vessel member length; occ. = occasionally; opp. = opposite; scal. = scalariform; sol. = solitary; spirals = helical or annular thickenings of the cell wall; tang. = tangential; unil. comp. = unilaterally compound; v—r pits = vessel—ray pits; v—v pits = inter-vessel pits.

Ray frequency is expressed in two figures, e.g. 3+8/mm. This means that the total number of rays per millimetre is 11, and that 3 of these are multiseriate and 8 are uniseriate.

For the *citation* of specimens and meaning of the terms *mature* and *immature*, see p. 195 and 196.

Ilex amplifolia Rusby (subg. *Euilex*, series *A*, sect. *Excelsae*, subsect. *Laxae*)

Latitude in graph 16 °S.

Diffuse porous. *Growth rings* faint. *Vessels* 43/mm^2, 47% sol., diam. 42—67—88 μm, length 1130—1720—2270 μm, v—v pits trans. to opp., 7—10 μm, v—r pits similar and sometimes unil. comp., bars 26—38—52, spirals very faint to hardly present. *Fibre-tracheids* 1260—2500—3420 μm, tang. wall pits infreq., 6 μm, spirals well developed. *Rays* 1 (2) + 10/mm, het. II, up to 4.1 mm high, to 11 cells wide, sheath cells occ. present. Sol. crystals in ordinary ray cells.

Material studied. BOLIVIA. *Krukoff 11198 (SJRw 39912).*

Note. The presence of well developed spirals in the fibre-tracheids in this species, which shows the typically tropical character complex in its other wood anatomical features, is noteworthy and curious.

Ilex anomala Hook. & Arn., incl. **f. sandwicensis** (Endl.) Loes. and **f. taitensis** (Gray) Nadaud (subg. *Byronia*, series *A*. *Eubyronia*) — **Plate III, 3.**

Latitude 17 °S and 19—22 °N; in graph 21°.

Diffuse porous. *Growth rings* rather indistinct to absent. *Vessels* 33—48 (27—50)/mm^2, 31—64 (28—62)% sol., diam. 29—50—76 (55—68)—97 μm, length 1050—1570—1690 (960—1350)—2160 μm, v—v pits mainly scal., seemingly vestured in some specimens, ranging to opp., v—r pits similar and large and gash-like, sometimes unil. comp., bars 19—28—35 (29—37)—51, spirals absent. *Fibre-tracheids* 1740—2180—2580 (1450—1950) —3230 μm, tang. wall pits infreq. in mature specimens, freq. in immature specimens, 3—5 (4—6) μm, spirals absent. *Rays* 1—2 + 8—10/mm, het. II to het. I, up to 3.5 mm high, to 8 cells wide, sheath cells often present. Sol. crystals, sometimes slightly elongated, present in ordinary ray cells in 8 out of 9 specimens studied.

Material studied. HAWAII (f. *sandwicensis*). *(BISHw 24)*; *Bryan Jr et al. s.n. (BISHw 2758*)*, alt. 1040 m; *MacDaniels 84 (SJRw 24945*)*, alt. 750 m; *MacDaniels 116 (SJRw 24977*)*, alt. 50 m; *MacDaniels 161 (SJRw 25019*)*, alt. 1300 m; *Rock & Homer s.n. (BISHw 46)*; *Thrum s.n. (BISHw 140)*. — TAHITI (f. *taitensis*). *Van Balgooy 1689**, alt. 850 m; *MacDaniels 653 (SJRw 43839)*, alt. 1300 m.

Note. In its qualitative and most of its quantitative wood anatomical features this species is rather constant. The scalariform v—v pits and large, gash-like, v—r pits are striking features.

Ilex aquifolium L. (subg. *Euilex*, series *C*, sect. *Aquifolioides*, subsect. *Oxydontae*) — **Plate IV, 1 & 2.**

Latitude 39—54 °N, in graph 48 °N.

Diffuse to semi-ring porous. *Growth rings* distinct. *Vessels* 128—192/mm^2, 8—23% sol., diam. 17—31—38—51 μm, length 520—690—890—1130 μm, v—v pits trans. to opp., rarely also scal. or alt., v—r pits opp. to alt., very rarely unil. comp., bars 12—19—21—32, spirals well developed. *Fibre-tracheids* 490—990—1320—1840 μm, tang. wall pits freq., 4—6 μm, spirals well developed. *Rays* 3—4 + 7—9/mm, het. II, up to 0.9—2.1 mm high, to 5—7 cells wide, sheath cells absent. Crystals absent.

Material studied. GREECE. *(MADw 17874)*. — BELGIUM. *(IF 14473)*. NETHERLANDS. cult. *UN 163* (Uw) low alt.

Note. The three samples studied are very similar.

Ilex argentina Lillo, An. Soc. Cient. Argent. 72 (1910) 171 (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Repandae*)
Latitude *c.* 27°S.

Diffuse porous. *Growth rings* distinct. *Vessels* 69/mm^2, 26% sol., diam. 38—56—76 μm, length 670—920—1190 μm, v—v pits trans. to opp., 6—9 μm, v—r pits similar and sometimes unil. comp., bars 15—21—34, spirals well developed. *Fibre-tracheids* 1100—1740—2290 μm, tang. wall pits infreq., 6 μm, spirals well developed. *Rays* 3+8/mm, het. II, up to 2.0 mm high, to 10 cells wide, sheath cells abundant. Sol. crystals infreq. in ordinary ray cells.

Material studied. ARGENTINA. (*Molfino s.n.*, presented by Prince of Wales no 392 to FHOw), alt. *c.* 1200 m.

Note. According to Lillo l.c. this species is closely related to *I. paraguariensis*. I have therefore included it in subsection *Repandae*.

Ilex berteroi Loes. *ex*. Urb. (subg. *Euilex*, series *C*, sect. *Micranthae*, subsect. *Epunctatae*)
Latitude *c.* 21°N.

Diffuse porous. *Growth rings* faint. *Vessels* 29/mm^2, 52% sol., diam. 38—55—71 μm, length 520—880—1210 μm, v—v pits opp. to alt., 6—8 μm, v—r pits scal. to alt. and sometimes unil. comp., bars 8—15—21, spirals absent. *Fibre-tracheids* 890—1370—1760 μm, tang. wall pits freq., *c.* 5 μm, spirals fairly well developed. *Rays* 3+8/mm, het. II, up to 1.8 mm high, to 10 cells wide, sheath cells present. Sol. crystals in ordinary ray cells.

Material studied. CUBA. *Bucher s.n. (SJRw 19290*)*.

Note. The number of bars per perforation plate is remarkably low in this tropical species. This can only partly be due to the fact that the specimen studied was immature.

Ilex brasiliensis (Spreng.) Loes. (subg. *Euilex*, series *C*, sect. *Megalae*, subsect. *Pedicellatae*)
Latitude *c.* 25°S.

Diffuse porous. *Growth rings* distinct. *Vessels* 104/mm^2, 13% sol., diam. 25—46—59 μm, length 470—820—1180 μm, v—v pits opp. to alt., 7—9 μm, v—r pits similar and occ. unil. comp., bars 15—27—43, spirals well developed. *Fibre-tracheids* 1080—1320—1500 μm, tang. wall pits rather freq., 6 μm, spirals well developed. *Rays* 1—2+9/mm, het. II, up to 1.1 mm high, to 10 cells wide, sheath cells rarely present. Sol. crystals in ordinary and chambered erect ray cells.

Material studied. BRAZIL. Parana: *Lindeman & Hecking 873 (Uw 12774*)*.

Ilex brevicuspis Reiss (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Eumicrodontae*)
Latitude *c.* 28°S.

Diffuse to semi-ring porous. *Growth rings* distinct. *Vessels* 105/mm^2, 10% sol., diam. 25—42—59 μm, length 520—800—1130 μm, v—v pits opp. to alt., 6—9 μm, v—r pits similar and sometimes unil. comp., bars 13—19—30, spirals well developed. *Fibre-tracheids* 740—1100—1370 μm, tang. wall pits rather infreq., *c.* 6 μm, spirals well developed.

Rays 2+10/mm, het. II, up to 2.6 mm high, to 14 cells wide, sheath cells rare. Sol. crystals in ordinary and chambered erect ray cells.

Material studied. BRAZIL. Santa Catharina: *Herb. Barb. Rodr. Sant. Cat. 31568**, high alt.

Ilex buergeri Miq. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Repandae*)
Latitude in graph 41° N.

Diffuse porous. *Growth rings* distinct. *Vessels* 140/mm^2, 30% sol., diam. 29—42—59 μm, length 510—1120—1470 μm, v—v pits opp. to alt., 6—8 μm, v—r pits similar and sometimes unil. comp., bars 18—30—53, spirals well developed. *Fibre-tracheids* 1050—1970—2550 μm, tang. wall pits rather infreq., 5—7 μm, spirals well developed. *Rays* 3+8/mm, het. II, up to 1.9 mm high, to 8 cells wide, sheath cells occ. present. Sol. crystals in idioblastic thick-walled and bulging square ray cells.

Material studied. JAPAN. (*IF 23288 = Jap. Govt. Exp. Sta. 756*, Tervuren).

Ilex caliana Cuatr., Lloydia 11 (1948) 213 (subg. *Euilex*, series *C*, sect. *Daphnophyllae*)
Latitude in graph 4° N.

Diffuse porous. *Growth rings* faint. *Vessels* 21/mm^2, 33% sol., diam. 42—71—92 μm, length 550—980—1540 μm, v—v pits opp. 6—8 μm, v—r pits similar and occ. unil. comp., also tending to large and gash-like, bars 18—23—34, spirals absent. *Fibre-tracheids* 1500—1860—2370 μm, tang. wall pits infreq., 3—4 μm, spirals absent. *Rays* 3+8 /mm, het. II, up to 2.5 mm high, to 9 cells wide, sheath cells occ. present. Sol. crystals abundant in ordinary ray cells.

Material studied. COLOMBIA. *Cuatrecasas 18281*, type (*SJRw 43277**), alt. 2160 m.

Note. This species is closest to *I. laurina* according to Cuatrecasas, and is therefore included in section *Daphnophyllae* here.

The low quantitative values for vessel member length and number of bars per perforation are probably due to both the immature nature of the specimen and the high altitude of its habitat.

Ilex canariensis Poir. (subg. *Euilex*, series *A*, sect. *Cassinoides*) — **Plate VI, 6.**
Latitude *c.* 28° N.

Diffuse porous. *Growth rings* rather vague. *Vessels* 43 & 45/mm^2, 47 & 63% sol., diam. 29—50 & 59—80 μm, length 620—1030 & 1190—1500 μm, v—v pits trans. to opp., 6—10 μm, v—r pits similar and sometimes unil. comp., bars 10—15 & 16—22, spirals well developed. *Fibre-tracheids* 1130—1600 & 2000—2500 μm, tang. wall pits freq., 6 μm, spirals well developed, absent in some fibres. *Rays* 2 & 5 + 5 & 6/mm, het. II, up to 1.5 & 1.7 mm high, to 8 cells wide, sheath cells present, remainder of ray cells also bigger than usual. Sol. and irregularly clustered crystals in ordinary ray cells.

Material studied. CANARY ISLANDS. *Baas & Ridsdale 8*, alt. 600 m; *Bourgeau s.n.* (K-Jw).

Note. The rather vague growth ring boundaries and the unusually large ray cells are noteworthy in this subtropical species. I also studied an unvouchered specimen (*IF 18236*, Tervuren) which does not show these peculiarities, and moreover differs in quantitative features: Vessels 105/mm^2, 29% sol., v—v pits opp. to alt., 6—7 μm, bars 20—28—36. Rays 3+9/mm. This specimen fully agrees with the two specimens of *I. perado* I studied, also from the Canaries. I suspect therefore that *IF 18236* is misnamed.

The fact that two species growing together in the same islands in the same habitat show rather clear differences in their wood anatomy is remarkable for *Ilex*, where usually differences between unrelated species growing in similar habitats are very slight or fully absent.

Ilex caroliniana (Lam). Loes.; *I. vomitoria* Ait. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Vomitoriae*) — **Plate II, 4 & 12; III, 9; VI, 2.**

Latitude 15—34° N, in graph 30° N.

Diffuse porous. *Growth rings* distinct. *Vessels* 135—220/mm², 9—16% sol., diam. 21—34—42—50 µm, length 410—800—910—1130 µm, v—v pits opp., rarely tending to alt., 6—8 µm, v—r pits similar, occ. unil. comp., bars 9—14—16—21, spirals well developed. *Fibre-tracheids* 740—1160—1490—1840 µm, tang. wall pits fairly infreq., 5—6 µm, spirals well developed. *Rays* 2—4 + 10—12/mm, het. II, up to 1.6—2.7 mm high, to 15 cells wide, sheath cells abundant in specimens of smallest diameter, rarely present in other two specimens. Sol. crystals in ordinary ray cells of *MADw 751* only.

Material studied. MEXICO. Chiapas: *Page 9643 (MADw 23880*)*. — U.S.A. Texas: *(IF 18236*); (MADw 751)*.

Note. The quantitative values for the mature and immature specimens do not differ widely. The tropical specimen from Chiapas is probably from a montane locality, which would explain the low values for vessel member length and number of bars per perforation plate.

Ilex casiquiariensis Loes. (subg. *Euilex*, series *D*, sect. *Thyrsiflorae*)

Latitude in graph 6° N.

Diffuse porous. *Growth rings* faint. *Vessels* 64/mm², 19% sol., diam. 38—67—80 µm, length 1000—1260—1700 µm, v—v pits scal. to opp., 6—8 µm, v—r pits similar and sometimes unil. comp., bars 29—40—67, spirals absent. *Fibre-tracheids* 1390—1840—2370 µm, tang. wall pits infreq., 4 µm, spirals absent. *Rays* 2 + 14/mm, het. II, up to 2.5 mm high, to 8 cells wide, sheath cells occ. present. Crystals absent.

Material studied. VENEZUELA. Amazonas: *Wurdack & Adderley ?43197 (SJRw 54122)*.

Ilex cassine L.; *I. myrtifolia* Walt. (subg. *Euilex*, series *A*, sect. *Cassinoides*)

Latitude in graph 30° N.

Diffuse porous. *Growth rings* distinct. *Vessels* 62 & 80/mm², 18 & 20% sol., diam. 21—44 & 50—71 µm, length 640—910 & 1020—1290 µm, v—v pits opp. to alt., 5—6 µm, v—r pits similar, rarely unil. comp., bars 12—24 & 29—40, spirals well developed. *Fibre-tracheids* 840—1320 & 1550—1950 µm, tang. wall pits infreq. in *MADw 2634*, freq. in *MADw 11284*, 5—6 µm, spirals well developed. *Rays* 3 & 4 + 8 & 9/mm, het. II, or het. II + III *(MADw 2634)*, up to 1.7 & 1.9 mm high, to 8 cells wide, sheath cells absent. Crystals absent.

Material studied. U.S.A. Florida: *(MADw 2634); Marts 4 (MADw 11284)*.

Note. The differences in tangential pit frequency in the fibres and in ray histology between the two specimens, raise the question whether one of the samples is misnamed, or whether *I. cassine (MADw 2634)* is indeed synonymous with *I. myrtifolia (MADw 11284)*.

Ilex chapaensis Merr., J. Arn. Arb. 21 (1941) 373 (subg. *Prinus*, series *B*, *Prinoides*) — **Plate III, 1 & 2; IV, 3.**

Latitude *c.* 20° N.

Diffuse porous. *Growth rings* very faint. *Vessels* 46/mm^2, 28% sol., diam. 50—84—101 μm, length 880—1380—1660 μm, v—v pits opp. to alt., 6—8 μm, v—r pits similar and sometimes unil. comp., bars 20—31—38 μm, spirals faint, warts noted with SEM. *Fibre-tracheids* 1390—2550—2890 μm, tang. wall pits rather freq., 5 μm, spirals fairly well developed. *Rays* 2+7/mm, het. II, up to 3.0 mm high, to 7 cells wide, sheath cells infreq. Sol. crystals in enlarged erect ray cells with much thickened walls.

Material studied. NORTH VIETNAM. *Chevalier 30129 (CTFT 11009,* CTFw).

Note. According to Merrill l.c. this species is closets to *I. henryi*, which Loesener included in series *Prinoides*. Therefore *I. chapaensis* is included in this section here.

Merrill's type is from 1500 m alt. Our specimen clearly shows some 'tropical trends' in vessels member length and number of bars, although the presence of spiral thickenings is more in line with a subtropical habitat. This agrees well with latitudinal and altitudinal distribution of this species.

The small warts are present on the vessel walls, including the inside of the borders overarching the half-bordered vessel—parenchyma pits (Plate III, 1 & 2).

Ilex chinensis Sims; *I. purpurea* Hassk. (subg. *Euilex*, series *A*, sect. *Excelsae*, subsect. *Umbelliformes*) — **Plate II, 9; V, 2.**

Latitude in graph 41° N.

Diffuse porous. *Growth rings* distinct. *Vessels* 72/mm^2, 29% sol., diam. 39—42—55 μm, length 670—990—1490 μm, v—v pits scal. to opp., opp. pits 7—9 μm, v—r pits similar and often complex unil. comp., bars 10—14—17, spirals well developed. *Fibre-tracheids* 1000—1760—2240 μm, tang. wall pits freq., 6—7 μm, spirals well developed. *Rays* 3+8/mm, het. II, up to 1.3 mm high, to 8 cells wide, sheath cells infreq. Sol. crystals in thick-walled idioblastic erect ray cells, often elongated.

Material studied. JAPAN. *(IF 17637,* Tervuren = *Jap. Govt. Exp. Sta. 2254).*

Note. Hu (J. Arn. Arb. 30, 1949, 299) proposed the reduction of *I. purpurea* to *I. chinensis.*

Ilex cinerea Champ. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Repandae*) — **Plate V, 1.**

Latitude *c.* 22° N.

Diffuse porous. *Growth rings* distinct. *Vessels* 78/mm^2, 50% sol., diam. 38—59—63 μm, length 560—880—1280 μm, v—v pits opp. to alt., 6 μm, v—r pits similar, rarely unil. comp., bars 19—26—33, spirals well developed. *Fibre-tracheids* 1000—1470—2100 μm, tang. wall pits fairly freq., *c.* 5 μm, spirals well developed. *Rays* 2+7/mm, het. II, up to 1.9 mm high, to 15 cells wide, sheath cells occ. present. Sol. crystals infreq. in ordinary ray cells.

Material studied. HONGKONG. *Ford s.n.* (K-Jw).

Ilex cissoidea Loes. (subg. *Euilex*, series *D*, sect. *Indico-Malaicae*)

Latitude in graph 0°.

Diffuse porous. *Growth ring* fairly distinct (one in sample studied). *Vessels* 14/mm^2, 30% sol., diam. 50—92—120 μm, length 1290—1670—2160 μm, v—r pits opp. to alt., 6 μm, v—r pits similar and often unil. comp., bars 22—33—44, spirals absent. *Fibre-tracheids* 1760—2550—3160 μm, tang. wall pits very infreq., 3—5 μm, spirals absent. *Rays* 2+7/mm, het. II, up to 2.0 mm high, to 7 cells wide, sheath cells occ. present. Crystals absent.

Material studied. Indonesia. *bb. 2119 (RTIw 2564).*

Note. The presence of a distinct growth ring in this typically tropical representative is remarkable. The small size of the wood sample studied leaves the question unanswered whether growth rings are formed periodically or whether the ring boundary in our specimen is due to an unusual dry spell.

Ilex coriacea (Pursh.) Chapm. (subg. *Euilex*, series *A*, sect. *Cassinoides*)
Latitude *c.* 32° N.

Diffuse porous. *Growth rings* distinct. *Vessels* 140/mm^2, 15% sol., diam. 21—34—50 μm, length 430—850—1060 μm, v—v pits scal. to opp., v—r pits opp. and sometimes unil. comp., *c.* 6 μm, bars 17—35—48, spirals well developed. Fibre-tracheids 710—1100—1550 μm, tang. wall pits freq., 5—6 μm, spirals well developed. *Rays* 1+7/mm, het. II, up to 2.5 mm high, to 15 cells wide, sheath cells very rare. Crystals absent.

Material studied. U.S.A. Florida: *MADw 4567**.

Note. The number of bars per perforation plate is very high for this immature wood sample of fairly high latitude.

Ilex cornuta Lindl. & Paxt. (subg. *Euilex*, series *C*, sect. *Aquifolioides*, subsect. *Oxydontae*)
Latitude *c.* 30° N.

Diffuse porous. Growth rings distinct. Vessels 61 & 97/mm^2, 29 & 44% sol., diam. 17—30 & 35—50 μm, length 420—750 & 850—1130 μm, v—v pits scal. to opp., v—r pits opp., rarely unil. comp., bars 13—19 & 21—29, spirals well developed. *Fibre-tracheids* 600—1360 & 1660—2180 μm, tang. wall pits fairly freq., 6 μm, spirals well developed. *Rays* 4 & 5+6 & 7/mm, het. II, up to 1.2 & 1.9 mm high, to 8 cells wide, sheath cells occ. present. Sol. crystals in chambered erect and ordinary ray cells.

Material studied. U.S.A. Florida: *NYSCF 8701 (MADw 1108); (IF 22715*).*

Note. The immature specimen does not appreciably deviate from the mature wood sample. *I. cornuta* is native in China.

Ilex crenata Thunb., incl. var. **typica** Loes. f. **luzonica** (Rolfe) Loes. (subg. *Euilex*, series *B*, sect. *Polyphyllae*)
Latitude 17—52° N, in graph plotted both under 17° and 52°.

Diffuse to semi-ring porous. *Growth rings* distinct. *Vessels* 54—82/mm^2, 21—60%, sol., diam. 21—31—41—55 μm, length 300—620—900—1130 μm, v—v pits trans. to opp., occ. scal., v—r pits similar and unil. comp., bars 13—17—28—43, spirals well developed. *Fibre-tracheids* 790—1100—2050 μm, tang. wall pits rather freq., 5—8 μm, spirals well developed. *Rays* 2—4+7—9/mm, het. II, up to 0.8—2.0 mm high, to 10 cells wide, sheath cells occ. present. Crystals absent.

Material studied. Netherlands. cult. *UN 215* (Uw), low alt. — China. Makai: *(IF 23290*, Tervuren), montane. — Philippines (var. *typica* f. *luzonica*). Mountain Province: (*BF 18040*, CLPw), high alt.

Note. The three collections studied allow for a comparison of samples from widely different latitudes and altitudes. The montane sample from the Philippines exhibits all characteristics of a typically temperate representative of *Ilex*. The specimen from the Netherlands shows the lowest values for number of bars per perforation plate and vessel member length. The wide range in % of sol. vessels is noteworthy. The fact that all samples exhibit the same type of intervascular pitting supports the view that the material studied here all belongs to one species.

Ilex curranii Merr., Philip. J. Sci. 17 (1920) 273 (subg. *Euilex*, series *C*, sect. *Rugosae*)
Latitude 17° N.

Diffuse porous. *Growth rings* fairly distinct. *Vessels* 69/mm^2, 41% sol., diam. 25—49—63 μm, length 460—1030—2060 μm, v—v pits opp. to alt., 5—7 μm, v—r pits similar and sometimes unil. comp., bars 18—34—50, with rather well developed spirals. *Fibre-tracheids* 1240—1800—2300 μm, tang. wall pits infreq., 5—6 μm, faint spirals only present in some of the fibres. *Rays* 2+9/mm, het. II, up to 2.1 mm high, to 10 cells wide, sheath cells occ. present. Sol. crystals in ordinary ray cells.

Material studied. PHILIPPINES. Luzon, Mountain Province: *Stern & Rojo 2290**, high alt.

Note. This species grows in the mossy forest. The low values for vessel member length and number of bars per perforation are in line with the montane habitat and immature nature of this specimen. The presence of well developed spirals in the vessels, but less so in the fibres is noteworthy.

Ilex cymosa Bl.; *I. bogoriensis* Loes., *I. pleiobrachiata* Loes. (subg. *Byronia*, series *A. Eubyronia*) — **Plate I, 6; II, 8; III, 7; V, 5.**
Latitude 10° S—12° N, in graph 0°.

Diffuse porous. *Growth rings* only distinct in *CSIRO 4993*, indistinct or absent in remainder. *Vessels* 12—30/mm^2, 17—66% sol., diam. 42—76—113—139 μm, length 740—1040—1920—2630 μm, v—v pits opp., occ. tending to alt., 5—6 μm in *CSIRO 4993* and *Elmer 12806*, 7—9 μm in remainder, seemingly vestured in some specimens, v—r pits opp., occ. unil. comp., bars 19—36—58—101, spirals absent. *Fibre-tracheids* 1050—1630—2710—3160 μm, tang. wall pits rather freq., 3—4 μm in *CSIRO 4993*, *KEPw 2337* and *Elmer 12806*, 5—6 μm in remainder, spirals absent in all samples except for some faint ones in *Ridley s.n.* *Rays* 1—4+6—9/mm, het. II, up to 1.5—5.0 mm high, to 25 cells wide, sheath cells only present in few specimens. Sol. crystals in chambered erect ray cells.

Material studied. PHILIPPINES. Palawan: *Elmer 12806*. — MALAYA. *H 3792* (*CSIRO 4993*, FPAw); *(KEPw 2337)*. — SINGAPORE. *Ridley s.n. (K-Jw 59. 1901)*. — BORNEO. Sarawak: *S 9789*, alt. 3 m; *S 13480*, alt. 100 m. — INDONESIA. *bb 8494* (*Ind. 8082*, RTIw). Java: *(SFCw R 575—12)*. New Guinea: *BW 339*, alt. 100 m; *BW 611*, alt. 50 m; *BW 1067*, alt. 10 m.

Note. The material examined shows a great deal of variation in quantitative characters of vessels, pits, and rays. The lowest values for vessel member length were recorded in *Elmer 12806*, *CSIRO 4993*, and *S 9789*.

Ilex decidua Walt. (subg. *Prinus*, series *B. Prinoides*) — **Plate I, 3.**
Latitude *c.* 33 °N.

Diffuse to semi-ring porous. *Growth rings* distinct. *Vessels* 88 & 113/mm^2, 52 & 56% sol., diam. 21—38—50 μm, length 440—780 & 860—1210 μm, v—v pits scal. to opp., v—r pits similar and sometimes unil. comp., bars 10—16 & 17—21, spirals well developed. *Fibre-tracheids* 870—1180 & 1260—1840 μm, tang. wall pits freq., 6—7 μm, spirals well developed. *Rays* 3+10 & 13/mm, up to 1.4 mm high, to 7 & 12 cells wide, sheath cells infreq. Sol. crystals infreq. in ordinary ray cells or absent.

Material studied. U.S.A. North Carolina: *E.S. Harrar NYSCF 8575 (MADw 849)*, Texas: *Nogle-Wilson T-40 (MADw 15611)*.

Note. The two specimens are very similar wood anatomically. Although I could not determine the exact diameter of the stems from which the small specimens were taken, the curving of the growth rings suggested almost or just mature wood.

Ilex dipyrena Wall. (subg. *Euilex*, series *C*, sect. *Aquifolioides*, subsect. *Oxydontae*)
Latitude 31°N.

Semi-ring porous. *Growth rings* distinct. *Vessels* 130/mm², 21% sol., diam. 21—34—54 µm, length 680—830—1060 µm, v—v pits opp. to alt., 5 µm, v—r pits similar, rarely unil. comp., bars 10—18—26, spirals well developed. *Fibre-tracheids* 920—1420—1970 µm, tang. wall pits fairly freq., 3—4 µm, spirals well developed. *Rays* 3+7/mm, het. II, up to 1.3 mm high, to 7 cells wide, sheath cells abundant. Crystals absent.

Material studied. INDIA. Natigana Simla (*Ind. For. Dept. 1878*, K-Jw), 2300 m alt.

Ilex divaricata Mart. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Sideroxyloides*)
Latitude *c.* 4°N.

Diffuse porous. *Growth rings* faint. *Vessels* 55/mm², 18% sol., diam. 34—55—67 µm, length 680—1050—1440 µm, v—v pits opp. to alt., 6—7 µm, v—r pits similar and sometimes unil. comp., bars 16—32—50, spirals absent. *Fibre-tracheids* 1000—1470—1710 µm, tang. wall pits rather infreq., 4—5 µm, spirals very faint. *Rays* 2+8/mm, het. II, up to 2.6 mm high, to 10 cells wide, sheath cells occ. present. Sol. crystals in ordinary and chambered erect ray cells.

Material studied. VENEZUELA. Amazonas: *Wurdack & Alderly (SJRw 5448*)*, low alt.

Note. The low value for average vessel member length is here probably entirely due to the immature nature of the specimen (diam. 1.5 cm). The presence of weak spirals in the fibres is noteworthy in this species from the hot tropics.

Ilex dubia (Don) Trel. var. *macropoda* (Miq). Loes. (subg. *Prinus*, series *B*. *Prinoides*)
Latitude 36°N.

Diffuse to faintly semi-ring porous. *Growth rings* distinct. *Vessels* 186/mm², 17% sol., diam. 21—46—71 µm, length 450—790—1080 µm, v—v pits opp., 5—6 µm, v—r pits similar and sometimes unil. comp., bars 21—32—46, spirals well developed. *Fibre-tracheids* 1000—1310—1630 µm, tang. wall pits rather freq., 5 µm, spirals well developed. *Rays* 3+7/mm, het. II, up to 2.5 mm high, to 11 cells wide, sheath cells occ. present. Sol. crystals (occ. slightly elongated) in erect marginal and sheath cells.

Material studied. JAPAN. Mt. Fujioka: *(MADw 8135)*.

Ilex dumosa Reiss. (subg. *Euilex*, series *B*, sect. *Polyphyllae*)
Latitude *c.* 25°S.

Diffuse porous. *Growth rings* distinct. *Vessels* 138/mm², 25% sol., diam. 34—44—59 µm, length 670—910—1080 µm, v—v pits opp., 6 µm, v—r pits similar and sometimes unilaterally compound, bars 15—21—25, spirals well developed. *Fibre-tracheids* 1240—1710—

2100 µm, tang. wall pits infreq., 5 µm, spirals absent or faint in fibre tips. *Rays* 2+10/mm, het. II, up to 2.3 mm high, to 14 cells wide, sheath cells abundant. Crystals absent.

Material studied. BRAZIL. Parana: *Lindeman & Hecking 1916 (Uw 13412).*

Note. This species usually grows at fairly low altitudes (*cf.* Reitz, Flora ilustr. Catarinense 1, Aquifol., 1967). The absence of spirals in the majority of the fibre tracheids is remarkable.

Ilex fargesii Franch. (subg. *Euilex*, series *C*, sect. *Lemurensis*) — **Plate I, 1.**
Latitude 52 °N.

Diffuse porous. *Growth rings* distinct. *Vessels* 99/mm², 9% sol., diam. 29—38—50 µm, length 410—660—1040 µm, v—v pits opp. to alt., 6—7 µm, v—r pits similar and sometimes unil. comp., bars 15—19—33, spirals well developed. *Fibre-tracheids* 840—1450—1790 µm, tang. wall pits fairly freq., 5 µm, spirals well developed. *Rays* 3+8/mm, het. II, up to 1 mm high, to 6 cells wide, sheath cells rare. Sol. crystals very infreq. in ordinary ray cells.

Material studied. NETHERLANDS. cult. *UN 162* (Uw).

Note. *I. fargesii* is native in China.

Ilex ficoidea Hemsl. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Repandae*)
Latitude in graph 25 °N.

Semi-ring porous. *Growth rings* distinct. *Vessels* 84/mm², 33% sol., diam. 29—54—67 µm, length 870—1160—1440 µm, v—v pits opp. to alt., 6 µm, v—r pits similar and occ. unil. comp., bars 20—29—40, spirals well developed. *Fibre-tracheids* 1390—1890—2370 µm, tang. wall pits infreq., 4—5 µm, spirals well developed. *Rays* 2+6/mm, het. II, up to 2.8 mm high, to 12 cells wide, sheath cells almost absent. Sol. crystals in chambered erect and ordinary ray cells.

Material studied. CHINA. *(SJRw 21930).*

Ilex formosana Maxim. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Repandae*)
Latitude *c.* 24 °N.

Diffuse porous. *Growth rings* rather faint. *Vessels* 74/mm², 40% sol., diam. 29—55—80 µm, length 630—1100—1550 µm, v—v pits opp. to alt., 6—8 µm, v—r pits similar, rarely unil. comp., bars 22—28—39, spirals well developed. *Fibre-tracheids* 1180—2000—2840 µm, tang. wall pits rather infreq., *c.* 6 µm, spirals fairly well developed. Rays 3+5/mm, het. II, up to 2.6 mm high, to 10 cells wide, sheath cells abundant. Sol. crystals in ordinary and chambered erect ray cells, crystalliferous cells often with thickened bulging walls.

Material studied. TAIWAN. *(MADw 3266).*

Ilex glabra (L.) Gray (subg. *Euilex*, series *A*, sect. *Cassinoides*)
Latitude 36 & 52 °N.

Diffuse porous. *Growth rings* distinct. *Vessels* 124 & 135/mm², 29 & 34% sol., diam. 17—29 & 34—42 µm, length 500—790 & 830—1180 µm, v—v pits scal. to opp., v—r pits similar and sometimes unil. comp., bars 22—34 & 36—46, spirals well developed. *Fibre-tracheids* 600—950 & 1000—1390 µm, tang. wall pits freq., 5 µm, spirals well developed. *Rays* 2 & 3+11 & 18/mm, het. II, up to 1.3 & 1.7 mm high, to 14 cells wide, sheath cells absent. Sol. and clustered crystals in ordinary ray cells of *MADw 2628.*

Material studied. U.S.A. North Carolina: *MADw 4567**. — NETHERLANDS. cult. *UN 374** (Uw).

Note. As in *I. coriacea*, the high number of bars is noteworthy for these immature temperate specimens.

Ilex godajam Colebr. (subg. *Euilex*, series *A*, sect. *Excelsae*, subsect. *Umbelliformes*)

Latitude *c.* 22 °N.

Diffuse porous. *Growth rings* absent. *Vessels* 15/mm², 60% sol., diam. 59—90—122 μm, length 1130—1620—2370 μm, v—v pits opp. to alt., 6—7 μm, v—r pits similar and often unil. comp., bars 23—30—37, spirals absent, warts noted with SEM. *Fibre-tracheids* 2240—2950—3420 μm, tang. wall pits infreq., 3—4 μm, spirals absent or very faint in some of the fibre tips. *Rays* 3+6/mm, het. II, up to 2.1 mm high, to 7 cells wide, sheath cells present. Crystals absent.

Material studied. EAST PAKISTAN. *Majumdar & Islam 35 (MADw 24486).*

Note. The warts on some of the vessel walls are similar to those of *I. chapaensis*. The number of species studied with SEM is too low to know whether we deal here with a unique feature for *I. godajam* and *I. chapaensis*, or whether a warty layer is of more common occurrence in *Ilex*.

Ilex goshiensis Hayata, Mater. Flora Formosa (1911) 54; *I. hanceana sensu auct. Jap. non* Maxim. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Sideroxyloides*) — **Plate VI, 7.**

Latitude *c.* 36 °N.

Diffuse porous. *Growth rings* distinct. *Vessels* 73 & 82/mm², 21 & 25% sol., diam. 29—46 & 59—76 μm, length 720—1040 & 1130—1530 μm, v—v pits opp. to alt., 6—8 μm, v—r pits similar, not unil. comp., bars 15—23 & 29—50, spirals well developed. *Fibre-tracheids* 950—1760 & 1970—2210 μm, tang. wall pits infreq., 5—6 μm, spirals well developed. *Rays* 2+6 & 7/mm, het. II, up to 1.6 & 2.2 mm high, to 12 cells wide, sheath cells occ. present. Sol. crystals in idioblastic thick-walled or chambered erect ray cells, or absent.

Material studied. JAPAN. *(IF 23291)*; Mt. Fujioka, *(MADw 8535).*

Note. According to Hayata l.c., this species is closely related to *I. championii* which belongs to subsection *Sideroxyloides*. I therefore treat *I. goshiensis* in this subsection.

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

Latitude 2—15 °N, in graph 8 °N.

Diffuse porous. *Growth rings* faint. *Vessels* 20 & 50 (49 & 57)/mm², 30 (30 & 39)% sol., diam. 42—54 & 86 (32 & 56)—122 μm, length 740—1220 & 1440 (840 & 1420)—2210 μm, v—v pits trans. to opp., v—r pits similar and sometimes unil. comp., bars 11—21 & 30 (26 & 32)—45, spirals absent. *Fibre-tracheids* 1450—2050 & 2520 (1530 & 2000)—3100 μm, tang. wall pits infreq., 4—5 μm, spirals very faint to fairly well developed. *Rays* 2+7 & 12 (7 & 8)/mm, het. II, up to 1.6 (2.2) mm high, to 9 (10) cells wide, sheath cells present. Sol. crystals in ordinary ray cells and/or in chambered erect ray cells. Crystals sometimes sheathed with thick layer (presumably cell wall material).

Material studied. HONDURAS. *SJRw 7565**. — NICARAGUA. *(IF 20780)*. — SANTA DOMINGO. Jovero: *Abott 2521 (SJRw 7102*)*, var. *macoucoua*. — SURINAM. *Lanjouw & Lindeman 1474 (Uw 1502).*

Note. Loesener (1942) treated *I. panamensis* as belonging to *I. guianensis*.

Ilex havilandii Loes. (subg. *Euilex*, series *D*, sect. *Racemosae*)
Latitude 6 °N.

Diffuse porous. *Growth rings* absent or extremely faint. *Vessels* 34 & 51/mm², 29 & 61% sol., diam. 30—42 & 46—83 μm, length 310—1050 & 1150—1520 μm, v—v pits opp., rarely scal. to trans., 5—6 μm, v—r pits opp. to scal. and occ. tending to large and gash-like, bars 14—20 & 22—29, spirals absent. *Fibre-tracheids* 1180—1810 & 2080—2370 μm, tang. wall pits rather infreq., 3—4 μm, spirals absent. *Rays* 2+12/mm, het. I and II, up to 2.0 mm high, to 6 cells wide, sheath cells abundant. Crystals absent. Pith flecks abundant in *SAN 76642*.

Material studied. NORTH BORNEO. Mt. Kinabalu: *SAN 76642* & *76645*, alt. 2200 m.

Ilex hypoglauca (Miq.) Loes. (subg. *Byronia*, series *A. Eubyronia*) — **Plate IV, 6.**
Latitude *c.* 4 °N.

Diffuse porous. *Growth rings* faint but present. *Vessels* 13/mm², 31% sol., diam. 63—80—113 μm, length 1130—1730—2370 μm, v—v pits opp. or occ. alt., 6—8 μm, v—r pits similar, occ. unil. comp., bars 24—48—67, spirals absent. *Fibre-tracheids* 1710—2240—2550 μm, tang. wall pits infreq., 4—5 μm, spirals absent. *Rays* 2+10/mm, het. II, up to 4.2 mm high, to 10 cells wide, sheath cells absent. Sol. crystals in chambered erect ray cells and procumbent ray cells.

Material studied. BORNEO. Sarawak: *S 30197*, low alt.

Ilex insignis Hook. f. (subg. *Euilex*, series *C*, sect. *Aquifolioides*, subsect. *Insignis*)
Latitude 27° N.

Diffuse porous. *Growth rings* distinct. *Vessels* 76/mm², 32% sol., diam. 38—62—80 μm, length 850—1170—1580 μm, v—v pits opp. to alt., 7—8 μm, v—r pits similar and sometimes unil. comp., bars 17—30—42, spirals well developed. *Fibre-tracheids* 1160—1840—2370 μm, tang. wall pits freq., 4—5 μm, spirals well developed. *Rays* 1—2+8/mm, het. II, up to 2.0 mm high, to 11 cells wide, sheath cells occ. present. Crystals absent.

Material studied. INDIA. Darjeeling: *Ind. For. Dept. 1878* (K-Jw), alt. 2400 m.

Ilex integra Thunb.; *I. othera* Spreng. (subg. *Euilex*, series *C*, sect. *Aquifolioides*, subsect. *Oxydontae*)
Latitude 36 °N.

Diffuse or semi-ring porous. *Growth rings* distinct. *Vessels* 52 & 93/mm², 25 & 29% sol., diam. 29—42 & 46—63 μm, length 700—990 & 1130—1540 μm, v—v pits trans. to alt., v—r pits similar and sometimes unil. comp., bars 11—14 & 25—39, spirals well developed. *Fibre-tracheids* 1130—1790 & 1910—2450 μm, tang. wall pits infreq. or fairly freq., 5—6 μm, spirals well developed. *Rays* 3 & 3+5 & 7/mm, het. II, up to 1.4 & 1.9 mm high, to 10 cells wide, sheath cells occ. present. Sol. crystals infreq. in chambered erect and ordinary ray cells, or absent.

Material studied. JAPAN. *(IF 17254)*; Mt. Fujioka *(SJRw 9662)*, probably montane.

Note. The two specimens are rather different from each other in general wood anatomical appearance, and several quantitative features. Perhaps one of the identifications is erroneous.

Ilex inundata Poepp. (subg. *Euilex*, series *C*, sect. *Micranthae*, subsect. *Epunctatae*)
Latitude *c.* 6 °S.

Diffuse porous. *Growth rings* faint. *Vessels* 37/mm², 60% sol., diam. 46—56—96 μm, length 980—1390—1700 μm, v—v pits opp., 6—10 μm, v—r pits similar and sometimes unil. comp., bars 16—31—39, spirals absent. *Fibre-tracheids* 1580—2180—2700 μm, tang. wall pits rather infreq., 5 μm, spirals fairly well developed. *Rays* 2+8/mm, het. II, up to 2.2 mm high, to 12 cells wide, sheath cells occ. present. Sol. crystals in ordinary and thick-walled ray cells.

Material studied. BRAZIL. Para: *Maguire 51823 (MADw 21515*)*, low alt.

Ilex jenmanii Loes. (subg. *Euilex*, series *C*, sect. *Micranthae*, subsect. *Epunctatae*)
Latitude *c* 4 °N.

Diffuse porous. *Growth rings* faint to absent. *Vessels* 27 (71)/mm², 33 (24)% sol., diam. 50—83 (55)—100 μm, length 820—1360 (1370)—2160 μm, v—v pits opp. to alt., *c.* 6 μm, v—r pits similar and often until. comp., sometimes tending to gash-like, bars 24—37 (31)—50, spirals absent in mature specimen, present but faint in immature specimen. *Fibre-tracheids* 1420—2240 (2030)—2890 μm, tang. wall pits infreq., *c.* 4 μm, spirals absent or confined to fibre tips in mature specimen, well developed in immature specimen. *Rays* 2+6 (12)/mm, het. II, up to 3.2 (2.1) mm high, to 8 cells wide, sheath cells occ. present. Sol. crystals in ordinary ray cells.

Material studied. SURINAM. *Heyligers 704* (Uw 6737); Stahel 185*, low alt.

Note. The presence of conspicuous spirals in the fibre-tracheids of the immature specimen (quantitative values between brackets) and of hardly any spirals in the mature specimen of this tropical lowland species is remarkable.

Ilex kleinii Edwin in Reitz, Flora ilustr. Catarinense 1, Aquifol. (1967) 41 (not assigned to a subgenus or section)
Latitude 28 °S.

Diffuse porous. *Growth rings* distinct. *Vessels* 94/mm², 19% sol., diam. 14—26—38 μm, length 620—940—1290 μm, v—v pits alt. to opp., 7 μm, v—r pits similar and sometimes unil. comp., bars 14—26—38, spirals well developed. *Fibre-tracheids* 970—1500—1920 μm, tang. wall pits rather infreq., 5—6 μm, spirals well developed. *Rays* 2+12/mm, het. II, up to 1.6 mm high, to 12 cells wide, sheath cells present. Sol. crystals in ordinary and chambered, occ. thick-walled ray cells.

Material studied. BRAZIL. Santa Catarina: *Herb. Barb. Rodr. S. C. 30382**, alt. between 450 and 1200 m.

Ilex krugiana Loes. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Eumicrodontae*)
Latitude *c.* 28 °N.

Diffuse porous. *Growth rings* very faint. *Vessels* 40/mm², 38% sol., diam. 42—63—88 μm, length 650—1100—1550, v—v pits trans. to opp., occ. scal., v—r pits similar and sometimes unil. comp., bars 15—24—39, spirals absent. *Fibre-tracheids* 1270—1950—2310 μm long, tang. wall pits fairly freq., 5 μm, spirals fairly well developed to absent. *Rays* 1—2+10/mm, het. II, up to 3.5 mm high, to 12 cells wide, sheath cells common. Sol. crystals in chambered erect and ordinary ray cells.

Material studied. U.S.A. Florida: *(SFCw R 114—66)*.

Note. The absence of spirals from the vessels in this subtropical species is noteworthy. The quantitative values are well in line with latitude of provenance.

Ilex kwantungensis Merr., J. Arn. Arb. 8 (1927) 8 (subg. *Euilex*, series *A*, ? sect. *Excelsae*)
Latitude in graph 25 °N.

Diffuse porous. *Growth rings* distinct. *Vessels* 134/mm², 16% sol., diam. 34—46—55 μm, length 690—1020—1550 μm, v—v pits opp., 6—7 μm, v—r pits similar, bars 13—18—25, spirals well developed, tending to annular thickenings. *Fibre-tracheids* 1240—1760—2550 μm, tang. wall pits infreq., 3—5 μm, spirals well developed. *Rays* 3+9/mm, het. II, up to 1.2 mm high, to 6 cells wide, sheath cells very infreq. Sol. crystals in ordinary erect ray cells.

Material studied. CHINA. (*SJRw 21939*).

Note. Merrill l.c. placed *I. kwantungensis* in section *Excelsae*, but added that he was not sure that this was the proper place for it.

Ilex latifolia Thunb. (subg. *Euilex*, series *C*, sect. *Aquifolioides*, subsect. *Insignis*) — **Plate II, 13; III, 6.**
Latitude *c.* 41 °N.

Semi-ring porous. *Growth rings* distinct. *Vessels* 77/mm², 24% sol., diam. 29—50—71 μm, length 720—970—1140 μm, v—v pits opp. to alt., 6—8 μm, v—r pits similar, sometimes unil. comp., bars 14—22—29, spirals well developed. *Fibre-tracheids* 970—1660—2160 μm, tang. wall pits fairly freq., 6 μm, spirals well developed. *Rays* 2+9/mm, het. II, up to 1.7 mm high, to 8 cells wide, sheath cells occ. present. Crystals absent.

Material studied. JAPAN. (*MADw 5053*).

Ilex laurifolia Zipp. *ex* Loes. (subg. *Euilex*, series *A*, sect. *Excelsae*, subsect. *Laxae*) — **Plate VI, 10.**
Latitude *c.* 0°.

Diffuse porous. *Growth rings* extremely faint. *Vessels* 48/mm², 21% sol., diam. 46—68—105 μm, length 720—1330—1840 μm, v—v pits opp., 6—8 μm, v—r pits similar and often unil. comp., bars 28—43—55, spirals absent. *Fibre-tracheids* 1580—2050—2760 μm, tang. wall pits infreq., 3—4 μm, spirals typically absent, except for some weak spirals in some of the fibres. *Rays* 2+9/mm, het. II, rarely het. I, up to 1.9 mm high, to 7 cells wide, sheath cells not clearly differentiated. Sol. crystals extremely abundant in ordinary ray cells, occ. in chambered erect ray cells.

Material studied. NEW GUINEA. Waigeo Isl.: *Van Royen 5499**, low alt.

Note. In spite of the fact that we deal here with an immature specimen (diam. 1.5 cm), the quantitative values for vessel member length etc. are comparatively high and typical for a tropical lowland species.

Ilex laurina H.B.K. (subg. *Euilex*, series *C*, sect. *Daphnophyllae*) — **Plate II, 10.**
Latitude *c.* 5 °N.

Diffuse porous. *Growth rings* faint. *Vessels* 18/mm², 50% sol., diam. 25—85—118 μm, length 870—1220—1550 μm, v—v pits trans. to opp., 8—11 μm, v—r pits similar and often unil. comp., tending to large and gash-like, bars 18—25—34, spirals absent. *Fibre-tracheids* 2030—2310—2810 μm, occ. gelatinous, tang. wall pits infreq., *c.* 4 μm, spirals absent. *Rays* 2+9/mm, het. II, up to 6.0 mm high, to 13 cells wide, sheath cells occ. present. Crystals absent.

Material studied. VENEZUELA. *MADw 21223 (MERw 44).*

Note. In its absence of spirals this species conforms to the tropical type of wood anatomy, the values for vessel member length and number of bars per perforation plate are, however, comparatively low. This is probably due to the high altitude (2500—2900 m) at which this species occurs (Steyermark, Fieldiana, Bot. 28, 1957, 958—962).

Ilex ledermannii Loes. (subg. *Byronia*, series *A. Eubyronia*)

Latitude *c.* 6°S.

Diffuse porous. *Growth rings* faint. *Vessels* 11—15/mm², 27—38% sol., diam. 63—100—120—139 μm, length 930—1630—1800—2270 μm, v—v pits opp., 6—8 μm, v—r pits similar or horizontally more elongated, occ. unil. comp., bars 32—51—55—79, spirals absent. *Fibre-tracheids* 1660—2390—2830—3550 μm, tang. wall pits infreq., 4—6 μm, spirals typically absent, but a few spirals noted in fibre tips of 2 specimens. *Rays* 2+7—9/mm, het. II, up to 1.3—2.9 mm high, to 8 cells wide, sheath cells hardly or not differentiated. Sol. crystals abundant in chambered erect ray cells.

Material studied. New Guinea. *BW 1467*, alt. 6 m; *BW 7835*, alt. 630 m; *NGF 3295*.

Ilex liukiuensis Loes. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Repandae*) — **Plate VI, 8 & 9.**

Latitude 25°N.

Diffuse porous. *Growth rings* rather faint. *Vessels* 32/mm², 63% sol., diam. 29—54—76 μm, length 880—1260—1600 μm, v—v pits opp., 6—8 μm, v—r pits similar, rarely unil. comp., bars 25—32—40, spirals well developed. *Fibre-tracheids* 2130—2740—3020 μm, tang. wall pits infreq., *c.* 6 μm, spirals well developed. *Rays* 1—2+7/mm, het. II, up to 2.5 mm high, to 11 cells wide, sheath cells abundant. Crystals in thick-walled-idioblasts, chambered erect ray cells with thickened bulging walls, and in ordinary ray cells.

Material studied. Japan. Ryukyu Isl.: *Iriomote (MADw 12946)*.

Ilex longipes Chapm. (subg. *Prinus*, series *B. Prinoides*)

Latitude *c.* 30° N.

Diffuse to semi-ring porous. *Growth rings* distinct. *Vessels* 107/mm², 50% sol., diam. 17—38—55 μm, length 580—860—1180 μm, v—v pits scal. to opp., v—r pits similar and sometimes unil. comp., bars 11—17—25, spirals well developed. *Fibre-tracheids* 730—1260—1710 μm, tang. wall pits freq., 5—6 μm, spirals well developed. *Rays* 3+10/mm, het. II, up to 1.1 mm high, to 10 cells wide, sheath cells hardly differentiated. Sol. crystals in ordinary or enlarged ray cells.

Material studied. U.S.A. Texas: *(MADw 13271*)*.

Ilex macfadyenii (Walp.) Rehd.; *I. montana* (Sw.) Griseb. (subg. *Euilex*, series *A*, sect. *Excelsae*, subsect. *Laxae*) — **Plate I, 4; II, 11; III, 8.**

Latitude 18° N.

Diffuse porous. *Growth rings* faint. *Vessels* 48/mm², 60% sol., diam. 38—58—80 μm, length 500—970—1290 μm, v—v pits trans. to opp., v—r pits similar, occ. unil. comp., bars 26—35—46, spirals rather faint. *Fibre-tracheids* 1030—1680—1970 μm, tang. wall pits infreq., 3—5 μm, spirals well developed. *Rays* 2+9/mm, het. II, up to 1.3 mm high, to 6 cells wide, sheath cells occ. present. Crystals absent.

Material studied. Jamaica. *MADw 20901 (= USw 6112)*.

Ilex martiniana D. Don (subg. *Euilex*, series *D*, sect. *Thyrsiflorae*) — **Plate III, 5; V, 3; VI, 3.**

Latitude *c.* 4° N.

Diffuse porous. *Growth rings* very faint. *Vessels* 32/mm², 22% sol., diam. 50—70—84 µm, length 1170—1650—2010 µm, v—v pits opp., 6 µm, v—r pits similar and sometimes unil. comp. or gash-like, bars 36—52—71, spirals absent. *Fibre-tracheids* 1550—2310—2890 µm, tang. wall pits infreq., 4 µm, spirals absent. *Rays* 2—11/mm, het. II, up to 2.9 mm high, to 6 cells wide, sheath cells occ. present. Sol. crystals infreq. in ordinary ray cells.

Material studied. SURINAM. *Lindeman 6540 a (Uw 4466 a).*

Note. In very few of the fibre-tracheids I noted septa, staining blue with haematoxylin (Plate V, 3). These septa may occur at very irregular distances within a single fibre tracheid. I hesitate to refer to these as septate fibres and I am not certain whether the structures involved are artefactual in the sense that they were formed under unusual conditions (contraction of the protoplast followed by the deposition of a thin membrane at the periphery for instance). I have not noticed septate fibres in any other wood specimen of *Ilex.*

Ilex micrococca Maxim. (subg. *Byronia*, series *B. Micrococca*)

Latitude 36° N.

Diffuse porous to semi-ring porous. *Growth rings* distinct. *Vessels* 70/mm², 24% sol., diam. 34—61—70 µm, length 840—1320—1630 µm, v—v pits opp. to alt., 6 µm, v—r pits similar and often unil. comp., bars 10—18—24, spirals well developed. *Fibre-tracheids* 1050—1890—2630 µm, tang. wall pits infreq., 6 µm, spirals well developed. *Rays* 2+5/mm, het. II, up to 0.9 mm high, to 6 cells wide. Crystals absent.

Material studied. JAPAN. Fujioka: *(MADw 7419).*

Ilex mitis (L.) Radlk.; *I. capensis* Harv. & Sond., *I. monticola* Tul. (subg. *Euilex*, series *C*, sect. *Lemurensis*)

Latitude 25° S to 12° N, in graph plotted at 12°.

Diffuse porous. *Growth rings* extremely faint to rather distinct. *Vessels* 32–48/mm², 13—50% sol., diam. 38—70—76—105 µm, length 820—1130—1340—2060 µm, v—v pits opp. to alt., 5—8 µm, v—r pits similar and sometimes unil. comp., bars 16—25—43—52, spirals faint to almost absent. *Fibre-tracheids* 1320—1950—2680—3160 µm, tang. wall pits infreq., 3—6 µm, spirals fairly conspicuous to absent. *Rays* 2—3+7—10/mm, het. II, up to 1.8—2.7 mm high, to 13 cells wide, sheath cells occ. present. Sol. crystals in ordinary or chambered erect ray cells, or absent.

Material studied. BURUNDI. *Lewalle 3623 (IF 21963,* Tervuren). — CAMEROONS. *Mann s.n.* (K-Jw), high alt.; *Letouzey & M. C. 183 (CTFT 14646,* CTFw), high alt. — MADAGASCAR. *Thouvenot 15 (CTFT 1792,* CTFw); *(CTFT 13474).*

Note. Considering the fact that *I. mitis* is a widely distributed and variable species, the wood anatomical variation is rather limited. The species generally occurs in montane habitats, and the quantitative values well agree with what one would expect of a tropical species growing at higher altitudes. In our material, specimens from Madagascar showed the spirals most clearly (almost subtropical latitude!). Abbate (1970) pictured the wood of an *I. mitis* specimen from Eritrea (lat. *c.* 14° N) with very conspicuous spirals as one would expect in a subtropical species. Abbate's drawing of a vessel member is misleading and erroneous. However, his photomicrograph leaves no doubt that he has studied an

Ilex. His values for vessel frequency (63/mm^2) and diameter (50 μm) may possibly be due to his specimen being immature.

Ilex montana Torr. & Gray (subg. *Prinus*, series *B. Prinoides*)
Latitude in graph 18° and 41° N.

Diffuse to semi-ring porous. *Growth rings* faint to distinct. *Vessels* 48—98/mm^2, 46—60% sol., diam. 17—42—58—80 μm, length 440—760—970—1130 μm, v—v pits trans. to alt., v—r pits similar, not comp., bars 23—31—39—60, spirals rather faint. *Fibre-tracheids* 1030—1320—1680—1970 μm, tang. wall pits infreq., 4—5 μm, spirals well developed. *Rays* 3+6—9/mm, het. II, up to 1.7 mm high, to 14 cells wide, sheath cells absent or occ. present. Sol. crystals in thick-walled erect ray cells present in *SFRw R 151—7*, absent in other specimens.

Material studied. JAPAN. (*R 151—7*, SFRw). — U.S.A. Pennsylvania: *MADw 14603*.

Note. Loesener (1901) treated *I. montana* Torr . & Gray var. *mollis* as a variety of *I. dubia* (Don) Trel. Rehder (J. Arn. Arb. 3, 1922, 215), however, maintained the species. The wood specimens I studied of both *I. montana* and *I. dubia*, have a relatively high number of bars per perforation plate in common. In some qualitative features they differ (see p. 233).

Ilex myricoides H.B.K. var. **polyphylla** (Benth.) Loes. (subg. *Euilex*, series *B*, sect. *Polyphyllae*)
Latitude *c.* 4° N.

Diffuse porous. *Growth rings* virtually absent. *Vessels* 16/mm^2, 70% sol., diam. 46—61—80 μm, length 660—1470—2130 μm, v—v pits trans. to opp., 6—8 μm, v—r pits similar and often unil. comp. with wide slits on parenchyma cells extending over the whole radial wall, bars 15—33—42, spirals absent. *Fibre-tracheids* 1660—2390—2890 μm, occ. gelatinous, tang. wall pits infreq., *c.* 5 μm, spirals absent. *Rays* 2+10/mm, het. II, up to 1.5 mm high, to 7 cells wide, sheath cells occ. present. Crystals absent.

Material studied. COLOMBIA. *Cuatrecasas 19166 (SJRw 43288)*, alt. 2700 m.

Note. In spite of the high altitude of the locality of this specimen, the values for vessel member length and number of bars per perforation plate are high.

Ilex nayana Cuatr., Lloydia 11 (1949) 214 (subg. *Euilex*, ? series *A*, ? sect. *Excelsae*, subsect. *Laxae*)
Latitude 4° N.

Diffuse porous. *Growth rings* faint. *Vessels* 40/mm^2, 20% sol., diam. 50—84—114 μm, length 790—1080—1390 μm, v—v pits opp. to alt., 7—9 μm, v—r pits similar and sometimes unil. comp., bars 22—36—49, spirals absent. *Fibre-tracheids* 1450—1810—2160 μm, tang. wall pits infreq., 4—5 μm, spirals fairly well developed. *Rays* 3+6/mm, het. II, up to 2.5 mm high, to 7 cells wide, sheath cells present. Sol. crystals abundant in ordinary and chambered erect ray cells.

Material studied. COLOMBIA. *Cuatrecasas 14286*, type *(SJRw 42755*)*, alt. 3 m.

Note. Cuatrecasas l.c. mentioned that this species is closely related to *I. amygdifolia* (of this section) and to *I. laureola* (from section *Thyrsiflorae* of series *D* of subgenus *Euilex*). The short vessel members and fibres should be accounted for by the small diameter of the sample.

Ilex opaca Ait. (subg. *Euilex*, series *A*, sect. *Cassinoides*)
Latitude *c.* 29° N.

Diffuse to semi-ring porous. *Growth rings* distinct. *Vessels* 128 & 143 /mm^2, 9 & 12% sol., diam. 21—34 & 42—50 µm, length 720—1010 & 1020—1390 µm, v—v pits opp. to alt., 5—7 µm, v—r pits similar, rarely unil. comp., bars 11—26 & 27—38, spirals well developed. *Fibre-tracheids* 760—1390 & 1520—2050 µm, tang. wall pits infreq. to rather freq., 4—6 µm, spirals well developed. *Rays* 4 & 5+5 & 6/mm, het. II to III, up to 1.1 & 1.4 mm high, to 7 cells wide, sheath cells absent. Crystals absent.

Material studied. U.S.A. Florida: *(MADw 2636)*; Louisiana: (*IF 19728*, Tervuren).

Ilex ovalifolia Mey. (*sensu* Loes). (subg. *Euilex*, series *D*, sect. *Thyrsiflorae*)
Latitude *c.* 4° N.

Diffuse porous. *Growth rings* faint. *Vessel* 47/mm^2, 38% sol., diam. 29—63—84 µm, length 740—1340—1800 µm, v—v pits opp., 5—8 µm, v—r pits similar and sometimes unil. comp., bars 18—33—41, spirals absent. *Fibre-tracheids* 1230—2450—3160 µm, tang. wall pits fairly freq., 3—5 µm, spirals absent. *Rays* 4+7/mm, het. I to II, up to 1.7 mm high, to 5 cells wide, sheath cells abundant. Crystals absent.

Material studied. SURINAM. *Lindeman 4541 (Uw 3150).*

Ilex paraguariensis St. Hil. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Repandae*)
Latitude *c.* 25° S.

Diffuse porous. *Growth rings* father faint. *Vessels* 80/mm^2, 28% sol., diam. 38—55—80 µm, length 690—910—1340 µm, v—v pits opp. to alt., 6—8 µm, v—r pits similar and sometimes unil. comp., bars 14—20—25, spirals well developed. *Fibre-tracheids* 710—1810—2370 µm, tang. wall pits rather infreq., 4—5 µm, spirals well developed. *Rays* 2+9/mm, het. II, up to 3.5 mm high, to 15 cells wide, sheath cells infreq. Sol. crystals in chambered erect and ordinary ray cells.

Material studied. BRAZIL. Parana: *Lindeman & Hecking 2829 (Uw 13942).*

Ilex perado Ait.; *I. platyphylla* Webb (subg. *Euilex*, series *C*, sect. *Aquifolioides*, subsect. *Oxydontae*) — **Plate I, 2.**
Latitude *c.* 28° N.

Semi-ring porous. *Growth rings* distinct. *Vessels* 89—123/mm^2, 14—28% sol., diam. 21—39—44—63 µm, length 310—690—880—1240 µm, v—v pits trans. to opp., 6—9 µm, v—r pits similar and sometimes unil. comp., bars 16—20—25—39, spirals well developed. *Fibre-tracheids* 650—1130—1520—1810 µm, tang. wall pits infreq. to rather freq., 4—7 µm, spirals well developed. *Rays* 3—4+7—10/ mm, het. II, up to 0.9—1.4 mm high, to 8 cells wide, sheath cells occ. present. Crystals absent.

Material studied. CANARY ISLANDS. *(IF 22937)*; *Bourgeau s.n.* (K-Jw); *Baas & Ridsdale 9*, alt. 600 m.

Note. This species differs widely from two specimens I studied of *I. canariensis* growing in the same habitat; one probably misnamed specimen of *I. canariensis* is very similar to *I. perado*. See also the note under *I. canariensis*.

Ilex petiolaris Benth.; *I. parviflora* Benth. (subg. *Euilex*, series *C*, sect. *Micranthae*, subsect. *Punctatae*)
Latitude *c.* 4° S.

Diffuse porous. *Growth rings* very faint to absent. *Vessels* 16/mm^2, 56% sol., diam.

55—80—101 µm, length 930—1240—1730 µm, v—v pits opp., 6—8 µm, v—r pits similar and sometimes unil. comp., bars 27—36—47, spirals very faint. *Fibre-tracheids* 1390—1790—2160 µm, tang. wall pits infreq., 5—6 µm, spirals very faint. *Rays* 2+8/mm, het. II, up to 2.9 mm high, to 8 cells wide, sheath cells occ. present. Sol. crystals in ordinary ray cells.

Material studied. BRAZIL. Amazonas: *Krukoff 6561 (MADw 12529).*

Ilex quercetorum Johnston, J. Arn. Arb. 19 (1938) 122 (subg. *Euilex*, series *A*, sect. *Cassinoides*)

Latitude *c.* 16° N.

Diffuse porous. *Growth rings* distinct. *Vessels* 64/mm^2, 40% sol., diam. 25—42—59 µm, length 670—860—1060 µm, v—v pits opp. to alt., 6—7 µm, v—r pits similar and sometimes unil. comp., bars 16—24—35, spirals fairly well developed. *Fibre-tracheids* 870—1420—1920 µm, tang. wall pits infreq., 5—6 µm, spirals present but faint. *Rays* 5+8/mm, het. II, up to 1.1 mm high, to 6 cells wide, sheath cells absent. Sol. crystals rare in ordinary ray cells.

Material studied. MEXICO. Chiapas: *Page 9754 (MADw 23937*)*, probably high alt.

Note. According to Johnston l.c. this species should be included in section *Cassinoides*. The type specimen is a montane plant from 1860 m alt. The diameter of the present specimen must have been almost 4 cm, judged from the curving of the growth rings in the peripheral block I obtained. The low values for vessel member length are probably only partly due to the fact that this specimen was not fully mature, but also to the montane habitat of this species.

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

Latitude *c.* 21° N.

Diffuse porous. *Growth rings* faint. *Vessels* 42/mm^2, 60% sol., diam. 34—55—67 µm, length 670—1110—1490 µm, v—v pits opp. to alt., 6—7 µm, v—r pits similar and often extensively unil. comp., bars 9—22—33, spirals absent. *Fibre-tracheids* 1450—1940—2550 µm, tang. wall pits infreq., 5—6 µm, spirals present and rather faint. *Rays* 1+9/mm, het. II, up to 2.7 mm high, to 12 cells wide, sheath cells freq. Sol. crystals in ordinary and chambered erect ray cells.

Material studied. CUBA. *Bucher 243 (SJRw 21418*).*

Note. The low values of vessel member length and number of bars per perforation plate for this tropical species are probably due to the fact that the specimen for study was immature. The absence of spirals in the vessels is more in line with latitude.

Ilex rimbachii Standley, Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser. 17 (1937) 198. — **Plate II, 6 & 7; V, 7 & 8; VI, 5.**

Latitude *c.* 1° S.

Diffuse porous. *Growth rings* rather faint. *Vessels* 34/mm^2, 68% sol., diam. 30—62—80 µm, length 960—1250—1500 µm, v—v pits scal. to opp., v—r pits similar and often unil. comp., bars 19—32—37, spirals faint. *Fibre-tracheids* 1630—2100—2370 µm, occ. gelatinous, tang. wall pits infreq., *c.* 6 µm, spirals faint. *Rays* 2+9/mm, het. II, up to 5.5 mm high, to 15 cells wide, sheath cells occ. present. Crystals absent.

Material studied. ECUADOR. *Acosta Solis 6689 (MADw 16614)*, alt. 2500—3000 m.

Note. Standley l.c. did not give any indication about the affinity of this species with other *Ilex* species.

Ilex rotunda Thunb. (subg. *Euilex*, series *A*, sect. *Excelsae*, subsect. *Umbelliformes*) — **Plate V, 6.**

Latitude in graph 41° N.

Diffuse porous. *Growth rings* distinct. *Vessels* 33/mm^2, 40% sol., diam. 42—61—86 μm, length 850—1210—1600 μm, v—v pits opp., 6—8 μm, v—r pits similar and often unil. comp., bars 12—20—25, spirals well developed. *Fibre-tracheids* 1840—2290—2760 μm, tang. wall pits fairly freq., 6 μm, spirals well developed. *Rays* 3+5/mm, het. II, up to 1.4 mm high, to 6 cells wide, sheath cells very rare. Solitary crystals present in ordinary ray cells, occ. somewhat elongated.

Material studied. JAPAN. (*CSIRO 13255*, FPAw).

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

Latitude *c.* 4° N.

Diffuse porous. *Growth rings* faint. *Vessels* 13 (16)/mm^2, 44 (54)% sol., diam. 59—113 (62)—134 μm, length 360—1680 (1190)—2210 μm, v—v pits opp., 7—8 μm, v—r pits similar and often unil. comp., bars 22—41 (36)—58, spirals absent. *Fibre-tracheids* 1110—2740 (1940)—3420 μm, tang. wall pits infreq. to rather freq., 4—5 μm, spirals absent or rare and faint (in *S 20855*). *Rays* 2 & 3+8 & 9/mm, het. II, up to 1.9 & 6.0 mm high, to 9 cells wide, sheath cells present. Sol. crystals abundant in ordinary and chambered erect ray cells.

Material studied. BORNEO. Sarawak: *S 20855*; *?S* 16867 (*CSIRO 30222**, FPAw), low alt.

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

Latitude *c.* 21° S.

Diffuse porous. *Growth rings* very faint. *Vessels* 29/mm^2, 48% sol., diam. 38—63—84 μm, length 930—1580—2270 μm, v—v pits opp. to alt., 6—8 μm, v—r pits similar and unil. comp., bars 26—36—55, spirals absent. *Fibre-tracheids* 1960—2650—3450 μm, tang. wall pits infreq., 5—6 μm, spirals typically absent but a few weak spirals noted in some fibre tips. *Rays* 1 or 2+8/mm, het. II, occ. het. I, up to 2.2 mm high, to 8 cells wide, sheath cells occ. present. Sol. crystals infreq. in chambered erect ray cells.

Material studied. NEW CALEDONIA. *Sarlin 85* (*CTFT 6117*, CTFw), low alt.

Ilex serrata Thunb. (subg. *Prinus*, series *A. Euprinus*) — **Plate II, 3.**

Latitude 40° N.

Semi-ring porous. *Growth rings* distinct. *Vessels* 115/mm^2, 30% sol., diam. 21—38—46 μm, length 380—600—870 μm, v—v pits trans. to alt., 6—8 μm, v—r pits opp. and sometimes unil. comp., bars 10—17—24, spirals absent. *Fibre-tracheids* 670—1000—1320 μm, tang. wall pits rather freq., 3—4 μm, spirals absent. *Rays* 5+9/mm, het. II, up to 0.6 mm high, to 5 cells wide, sheath cells occ. present. Crystals absent.

Material studied. U.S.A. cult. Brooklyn Bot. Garden (*SJRw 40816*).

Note. This species is native in Japan. The absence of spirals in this temperate species is very remarkable (see also under *I. verticillata* and taxonomic discussions on p. 224 and 225).

Ilex sideroxyloides (Sw.) Griseb. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Sideroxyloides*) — **Plate II, 2.**

Latitude *c.* 16° N.

Diffuse porous. *Growth rings* faint. *Vessels* 37 (22)/mm^2, 51 (50)% sol., diam. 46—76 (59)—105 μm, length 1000—1320 (990)—1700 μm, v—v pits opp., 6—8 μm, v—r pits similar and sometimes unil. comp., bars 24—36 (23)—56, spirals absent. *Fibre-tracheids* 1200—2230 (1580)—3140 μm, tang. wall pits rather infreq., 4—5 μm, spirals faint. *Rays* 1—2 (2)+8 (9)/mm, het. II, up to 3.7 (3.0) mm high, to 15 cells wide, sheath cells occ. present. Sol. crystals abundant in ordinary and chambered erect ray cells.

Material studied. DOMINICA. *Stern & Wasshausen 2506 (MADw 24200*)*. — GUADELOUPE. (*HM 2279—53*, RTIw).

Ilex subrugosa Loes. in Sargent, Plantae Wilsonianae 1 (1911) 80 (subg. *Euilex*, series *C*, sect. *Microdontae*)

Latitude in graph 25° N.

Diffuse to semi-ring porous. *Growth rings* distinct. *Vessels* 109/mm^2, 43% sol., diam. 25—50—67 μm, length 550—960—1340 μm, v—v pits opp. to alt., 5—7 μm, v—r pits similar and sometimes unil. comp., bars 18—27—34, spirals well developed. *Fibre-tracheids* 1210—1810—2520 μm, tang. wall pits freq., *c.* 5 μm, spirals well developed. *Rays* 3+7/mm, het. II, up to 1.2 mm high, to 7 cells wide, sheath cells occ. present. Sol. crystals in ordinary ray cells.

Material studied. CHINA. *SJRw 21734*.

Note. Loesener doubtfully included *I. subrugosa* in section *Microdontae*, but he also remarked that it recalls section *Rugosae*. Wood anatomically it is closer to section *Microdontae* than to section *Rugosae*, but this may be entirely due to the fact that of the latter section I only examined tropical species and that no special characters apart from those following the general latitudinal trend are present in the wood of *I. subrugosa.*

Ilex theezans Mart. (subg. *Euilex*, series *C*, sect. *Megalae*, subsect. *Pedicellatae*)

Latitude *c.* 25° S.

Diffuse porous. *Growth rings* distinct. *Vessels* 66/mm^2, 20% sol., diam. 34—50—63 μm, length 1050—1300—1600 μm, v—v pits opp. to alt., 6—7 μm, v—r pits similar and sometimes unil. comp., bars 16—27—37, spirals well developed. *Fibre-tracheids* 1710—2390—2760 μm, tang. wall pits rather freq., 5 μm, spirals well developed. *Rays* 1—2+7/mm, het. II, up to 4.5 mm high, to 20 cells wide, sheath cells abundant. Crystals absent.

Material studied. BRAZIL. Parana: *Lindeman & Hecking 1152 (Uw 12923)*.

Ilex toluccana Hemsl. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Repandae*) — **Plate VI, 4.**

Latitude in graph 24° N.

Diffuse porous. *Growth rings* rather faint. *Vessels* 48/mm^2, 37% sol., diam. 38—52—72 μm, length 760—1200—1650 μm, v—v pits trans. to opp., 6—8 μm, v—r pits similar and sometimes unil. comp., bars 10—17—22, spirals well developed. *Fibre-tracheids* 1470—2160—2310 μm, tang. wall pits infreq., 6 μm, spirals well developed. *Rays* 2—3+10/mm, het. II, up to 1.5 mm high, to 8 cells wide, sheath cells abundant. Crystals absent.

Material studied. MEXICO. (*IF 19128*, Tervuren).

Ilex umbellata Kl. var. *humirioides* (Reiss.) Loes. (subg. *Euilex*, series *C*, sect. *Micranthae*, subsect. *Epunctatae*) — **Plate II, 1.**

Latitude *c.* 9° N.

Diffuse porous. *Growth rings* faint. *Vessels* 24/mm^2, 67% sol., diam. 50—80—101 μm, length 1030—1430—1870 μm, v—v pits trans. to opp., v—r pits similar and sometimes unil. comp., bars 25—40—58, spirals absent. *Fibre-tracheids* 1970—2600—3080 μm, tang. wall pits infreq., 6 μm, spirals faint. *Rays* 1 (2)+8/mm, het. II, up to 5.5 mm high, to 12 cells wide, sheath cells occ. present. Sol. crystals in ordinary ray cells.

Material studied. British Guiana. *Forest Dept. 3693 (SJRw 43839)*, probably low alt.

Ilex uniflora Benth. var. *panamensis* Cuatr., Lloydia 11 (1948) 206 (subg. *Euilex*, series *B*. sect. *Rupicolae*)

Latitude in graph 4° N.

Diffuse porous. *Growth rings* very faint. *Vessels* 28/mm^2, 57% sol., diam. 29—63—88 μm, length 430—1090—1440 μm, v—v pits trans. to opp., 6—8 μm, v—r pits similar and sometimes unil. comp., bars 16—22—30, spirals fairly well developed. *Fibre-tracheids* 1260—1920—2390 μm, tang. wall pits infreq., 4—5 μm, spirals absent or very faint. *Rays* 3+4/mm, het. II, up to 1.4 mm high, to 6 cells wide, sheath cells sometimes present. Sol. crystals infreq. in ordinary ray cells.

Material studied. Colombia. *Cuatrecasas 20565*, type *(MADw 17630)*, alt. 3400 m.

Note. The low values for vessel member length and number of bars per perforation plate, together with the presence of spirals in the vessels, make this species of high montane habitat resemble temperate representatives of *Ilex*.

Ilex versteeghii Merr. & Perry, J. Arn. Arb. 22 (1941) 259 (subg. *Euilex*, series *C*, sect. *Rugosae*)

Latitude *c.* 5° S.

Diffuse porous. *Growth rings* absent. *Vessels* 26/mm^2, 36% sol., diam. 40—71—97 μm, length 720—1070—1550 μm, v—v pits opp. to alt., 6—7 μm, v—r pits similar and sometimes unil. comp., bars 17—23—30, spirals absent. *Fibre-tracheids* 1000—1740—2160 μm, tang. wall pits rather infreq., 3—4 μm, spirals absent. *Rays* 2+7/mm, het. II, up to 1.1 mm high, to 7 cells wide, sheath cells occ. present. Crystals absent.

Material studied. New Guinea. *NGF 9460*, alt. 2200 m.

Note. *I. versteeghii* is said to be close to *I. archboldiana* (Merrill & Perry l.c.) which in turn is said to be close to *I. revoluta*. The latter species belongs to section *Rugosae*, and therefore *I. versteeghii* is treated under this section.

Values for vessel member length and number of bars per perforation plate are low in this tropical montane species. This is probably due to the altitudinal effect.

Ilex verticillata (L.) Gray (subg. *Prinus*, series *A*. *Euprinus*) — **Plate IV, 5; V, 4; VI, 1.**

Latitude *c.* 40° N.

Semi-ring porous. *Growth rings* distinct. *Vessels* 97/mm^2, 24% sol., diam. 25—42—80 μm, length 330—640—820 μm, v—v pits trans. to alt., 6—9 μm, v—r pits opp. and sometimes unil. comp., bars 12—21—36, spirals absent. *Fibre-tracheids* 780—890—1180 μm, tang. wall pits freq., 6—7 μm, spirals absent. *Rays* 6+10/mm, het. II, up to 1.0 mm high, to 3 (rarely 5) cells wide, sheath cells absent. Crystals absent.

Material studied. U.S.A. Ohio: *(SFCw R 206—14)* for detailed description; Michigan: *(MADw 2629)* for checking of absence of spirals.

Note. As in *I. serrata*, the absence of spirals in this temperate species with low values for vessel member length and number of bars per perforation plate is very remarkable (see taxonomic discussions on p. 224 and 225).

Ilex volkensiana (Loes.) Kaneh. & Hatus., Bot. Mag. Tokyo 50 (1936) 607; *I. mertensii* Maxim. var. *volkensiana* Loes. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Repandae*)
Latitude 7° N.

Diffuse to semi-ring porous. *Growth rings* fairly distinct. *Vessels* 31/mm^2, 30% sol., diam. 42—59—80 μm, length 700—1040—1390 μm, v—v pits scal. to opp., v—r pits similar and unil. comp., bars 21—28—36, spirals absent. *Fibre-tracheids* 1450—2060—2680 μm, tang. wall pits fairly freq., *c.* 6 μm, spirals faint. *Rays* 3+7/mm, het. II, up to 2.2 mm high, to 10 cells wide, sheath cells abundant. Sol. crystals in ordinary ray cells.

Material studied. MICRONESIA. Ponape: *Kanehira 802 (SJRw 20354*)*, alt. 650 m.

Note. This specimen is from the summit area of Mt .Tolotom, and the low value for vessel member length may be due to the immature nature of the specimen and the fact that the summits of the mountains of Ponape are exposed to frequent strong winds which results in stunted tree growth (Glassman, Bern. P. Bish. Mus. Bull. 209, 1952, 152 pp.).

Ilex wilsonii Loes. (subg. *Euilex*, series *C*, sect. *Microdontae*, subsect. *Sideroxyloides*)
Latitude in graph 25°N.

Diffuse porous. *Growth rings* distinct. *Vessels* 52/mm^2, 38% sol., diam. 25—42—63 μm, length 550—1060—1320 μm, v—v pits opp. to alt., 6—7 μm, v—r pits similar and sometimes unil. comp., bars 13—23—30, spirals well developed. *Fibre-tracheids* 1180—1810—2210 μm, tang. wall pits rather infreq., 4—6 μm, spirals well developed. *Rays* 2+6/mm, het. II, up to 1.8 mm high, to 8 cells wide, sheath cells rare. Sol. crystals infreq. in ordinary or chambered erect ray cells.

Material studied. CHINA. *Chow s.n. (SJRw 42563)*.

Ilex spec. (unidentified)
Latitude 6°S.

Diffuse porous. *Growth rings* absent. *Vessels* 17/mm^2, 59% sol., diam. 50—67—84 μm, length 520—1020 & 1390—1770 μm, v—v pits trans. to opp., 6—9 μm, v—r pits similar and sometimes unil. comp., bars 13—22 & 32—41, spirals absent. *Fibre-tracheids* 890—1500 & 2260—2680 μm, tang. wall pits infreq., 4—6 μm, spirals absent. *Rays* 2 & 3+5 & 7/mm, het. II, up to 1.8 mm high, to 9 cells wide, sheath cells present. Crystals absent.

Material studied. NEW GUINEA. *Kalkman 4863*, alt. 3140 m; *Kalkman 5136*, alt. 3350 m.

Note. The two specimens differ considerably in quantitative values in spite of the fact that both samples are from mature stems and from similar (very high) altitude. *Kalkman 5136* had the lowest values for vessel member length and number of bars per perforation plate, but occurs in a similar vegetation (mossy forest) as *Kalkman 4863*.

Ilex spec. (unidentified)
Latitude 4°N.

Diffuse porous. *Growth rings* faint to fairly distinct. *Vessels* 41/mm^2, 51% sol., diam.

38—55—71 µm, length 720—1400—1960 µm, v—v pits trans. to opp., occ. scal., v—r pits similar, sometimes unil. comp. or tending to gash-like, bars 20—34—41, spirals absent. *Fibre-tracheids* 1710—2340—2890 µm, tang. wall pits infreq., 5—6 µm, spirals faint or absent. *Rays* 2+9/mm, het. II, up to 3.3 mm high, to 16 cells wide, sheath cells occ. present. Sol. crystals in ordinary, chambered erect, and idioblastic thick-walled bulging ray cells.

Material studied. NORTH SUMATRA. *De Wilde 13020*, alt. 1300—1500 m.

Note. The presence of growth rings in this specimen from the montane rain forest is curious. Both the growth rings and the presence of spirals in some of the fibre-tracheids would suggest a climate with a dry season, but according to the collector dry spells are virtually absent in the habitat where this species was found.

Ilex spec. (unidentified) — **Plate I, 5; II, 5; III, 4.**

Latitude 15 °N.

Diffuse porous. *Growth rings* faint to absent. *Vessels* 25/mm^2, 44% sol., diam. 48—84—118 µm, length 470—1090—1440 µm, v—v pits opp., rarely trans., 7—10 µm, v—r pits similar or irregularly arranged and large and gash-like, occ. unil. comp., bars 4—13—29, spirals absent. *Fibre-tracheids* 1400—1830—2510 µm, tang. wall pits freq., 3—5 µm, spirals faint or absent. *Rays* 2+10/mm, het. II, up to 6.5 mm high, to 17 cells wide, sheath cells fairly common. Sol. crystals in ordinary ray cells.

Material studied. PHILIPPINES. *Jacobs 7928**, alt. 600—700 m (climber!).

Note. This specimen represents the only climbing species of *Ilex* available for this wood anatomical study. It shows some striking anatomical deviations, such as the very low number of bars per perforation plate (the lowest for the whole genus, and very strongly deviating from other tropical lowland species, which are all characterized by a high number of bars per perforation plate). The bars are, moreover, very widely spaced. The parenchyma, which is diffuse in aggregates, is unusually abundant. Although the specimen with its diameter of 3.5 cm was not yet fully mature, according to the arbitrary minimum size of stems used as a standard here, the vessel members and fibre-tracheids are remarkably short for tropical lowland *Ilex*. All deviations reported here are well in agreement with general anatomical tendencies in the wood of climbing plants.

The generic identity of this specimen was confirmed by pollen morphology.

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Prof. Dr. W. K. H. Karstens and Prof. Dr. C. Kalkman critically read the manuscript.

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ADDENDUM

While this paper was in the press data became available on the latitudinal and altitudinal variation in 19 other widely distributed genera, studied by Mr. N. van der Graaff in our institute. In most of these genera the latitudinal and altitudinal trends for vessel member length are the same as in *Ilex*, so there are very strong arguments to regard these trends to be of general validity. However, in the seven genera possessing scalariform perforations, the number of bars did not show the same altitudinal and latitudinal trends as in *Ilex*; on the contrary: six of the genera showed a trend for the tropical lowland species to have the lowest number of bars per perforation. This is in fact what one would expect, if one considers the rare occurrence of scalariform perforations in the woody flora of the tropical lowland. For *Ilex*, and perhaps also for *Symplocos* and *Viburnum*, this may imply that the possibly 'exceptional' latitudinal trends for scalariform perforations are, after all, of great phylogenetic significance within these genera. For *Ilex* the wood anatomy would then suggest a primitive status for tropical lowland species and a more derived one for tropical montane and subtropical and temperate species. Mr. Van der Graaff's data will be the subject of a separate publication.

Plate I. *Ilex*. Vessel frequency, arrangement, distribution, and diameter, all × 75. 1. *I. fargesii (UN 162)*, diffuse porous, long radial multiples; 2. *I. perado (Bourgeau s.n.)*, tending to semi-ring-porous, vessels numerous, mostly in long radial multiples; 3. *I. decidua (MADw 849)*, semi-ring-porous, high percentage of solitary vessels; 4. *I. macfadyenii (MADw 2090)*, diffuse porous, high percentage of solitary vessels; 5. *Ilex spec.* (climber, *Jacobs 7928*), diffuse porous; 6. *I. cymosa (KEPw 2337)*, diffuse porous, vessels wide.

Plate II. *Ilex*. 1—5. vessel perforations, all × 220. 1. *I. umbellata (SJRw 43839)*, maceration, over 50 bars; 2. *I. sideroxylodides (HM 2279—53)*, radial section, 38 bars; 3. *I. serrata (SJRw 40816)*, maceration, 23 bars; 4. *I. caroliniana (MADw 751)*, radial section, 15 bars; 5. *I. spec.* (climber, *Jacobs 7982*), radial section, 12 widely spaced bars. — 6—13. inter-vessel pits in tangential sections. 6 & 7. *I. rimbachii (MADw 16614)*, transitional and opposite pits in same section, × 550; 8. *I. cymosa (SFCw R 575—12)*, opposite, seemingly vestured pits, × 800; 9. *I. chinensis (IF 17637)*, scalariform to transitional pits, × 350; 10. *I. laurina (MADw 21223)*, transitional pits, × 350; 11. *I. macfadyenii (MADw 2090)*, opposite, small pits, × 350; 12. *I. caroliniana (MADw 751)*, opposite to alternate, ± polygonal pits, × 350; 13. *I. latifolia (MADw 5053)*, opposite to alternate, circular pits, × 350.

Plate III. *Ilex*. 1 & 2. SEM photographs in radial surface of *I. chapaensis (CTFT 11009)*. 1. half-bordered pits between parenchyma and vessel, note warts on overarching pit borders from vessel side, × 3300; 2. vessel wall with weak spirals and warty layer, × 1300. — 3—9. vessel—ray pits in radial section; 3—5, large and gash-like pits; 6—9, opposite and opposite to alternate. 3. *I. anomala (BISHw 140)*, × 550; 4. *I. spec.* (climber, *Jacobs 7928*), × 350; 5. *I. martiniana (Uw 4466 a)*, × 350; 6. *I. latifolia (MADw 5053)*, with some 'complex' unilaterally compound pits indicated by arrows, × 800; 7. *I. cymosa (SFCw R 575—12)*, × 350; 8. *I. macfadyenii (MADw 2090)*, × 350; 9. *I. caroliniana (MADw 751)*, × 350.

Plate IV. *Ilex*. Presence and absence of spiral thickenings. All SEM photographs. 1 & 2. *I. aquifolium (IF 14473)*, × 310; 1. transverse surface, broad spirals in vessels; 2. oblique tangential surface, broad spirals in vessels and narrow ones in fibre-tracheids (arrow); 3. *I. chapaensis (CTFT 11009)*, radial surface, faint spirals on vessel walls, × 290; 4. *I. guianensis (SJRw 7565)*, vessel without spirals, fibre-tracheid with faint spirals (arrow), × 290; 5. *I. verticillata (SFCw R 206—14)*, radial oblique surface, spirals absent from vessel- and fibre-tracheids, scalariform perforations with few bars, × 290; 6. *I. hypoglauca (S 30917)*, spirals absent, scalariform perforations with numerous bars, × 110.

Plate V. *Ilex*. Fibre-tracheids. 1—5. tangential sections. 1. *I. cinerea (Ford s.n.)*, helical thickenings, × 800; 2. *I. chinensis (IF 17637)*, annular thickenings, × 800; 3. *I. martiniana (Uw 4466 a)*, 'septa' (arrows) in fibre-tracheid; 4. *I. verticillata (SFCw R 206—14)*, tangential wall pits numerous and with conspicuous borders enclosing pit apertures, × 350; 5. *I. cymosa (KEPw 2337)*, tangential wall pits with minute borders (not visible in photograph) and extended slit-like apertures, × 350. — 6—8. transverse sections, × 350; 6. *I. rotunda (CSIRO 13255)*, thin-walled fibre-tracheids; 7 & 8. *I. rimbachii (MADw 16614)*, thick-walled fibre-tracheids in same transverse section, stained with safranin and haematoxylin; 7. normal fibre-tracheids; 8. gelatinous (tension wood) fibre-tracheids.

Plate VI. *Ilex*. Rays and crystals. 1—6. tagential sections, × 65. 1. *I. verticillata (SFCw R 206—14)*; 2. *I. caroliniana (MADw 751)*; 3. *I. martiniana (Uw 4466 a)*, with occasional sheath cells; 4. *I. toluccana (IF 19128)*, sheath cells abundant and conspicuous in ray on the right; 5. *I. rimbachii (MADw 16614)*; 6. *I. canariensis (Bourgeau s.n.)*, broad rays unusually abundant. — 7—10. × 265. 7. *I. goshiensis (IF 23291)*, radial section, crystal in thick-walled isioblast; 8 & 9. *I. liukiuensis (MADw 12946)*; 8. radial section, crystals in chambered bulging ray cells; 9. tagential section, crystal in thick-walled idioblast; 10. *I. laurifolia (Van Royen 5499)*, radial section, slightly elongate crystals in chambered ray cells.

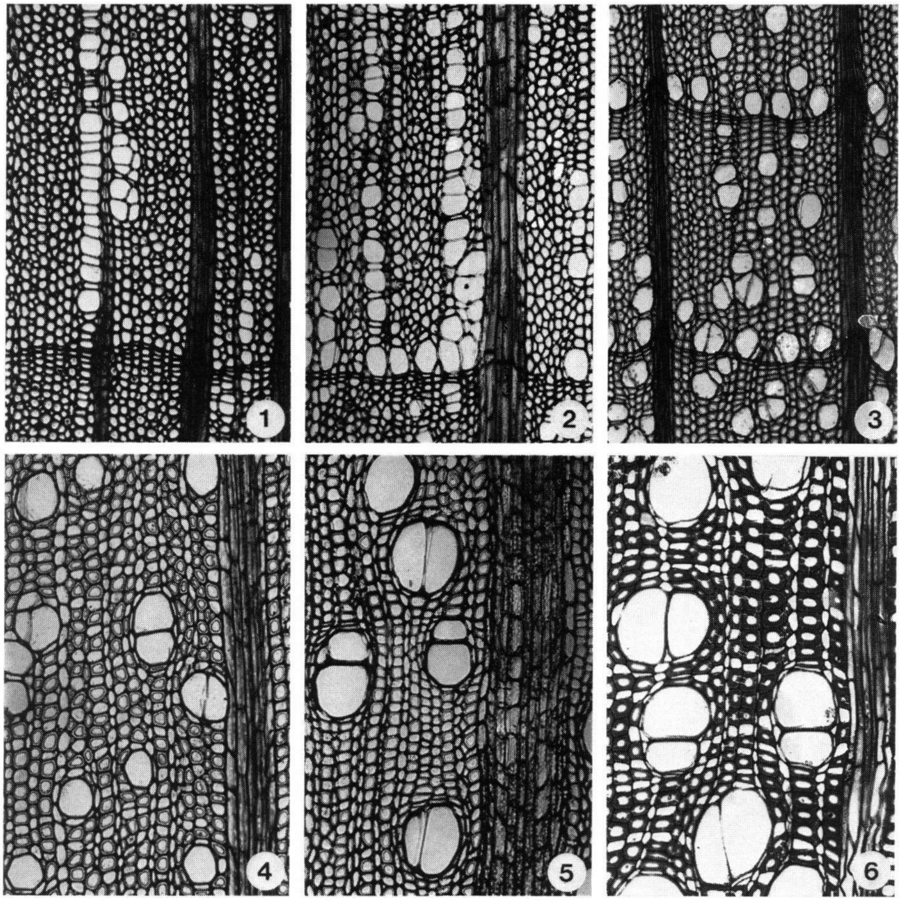


Plate I

(for legends of plates see p. 252)

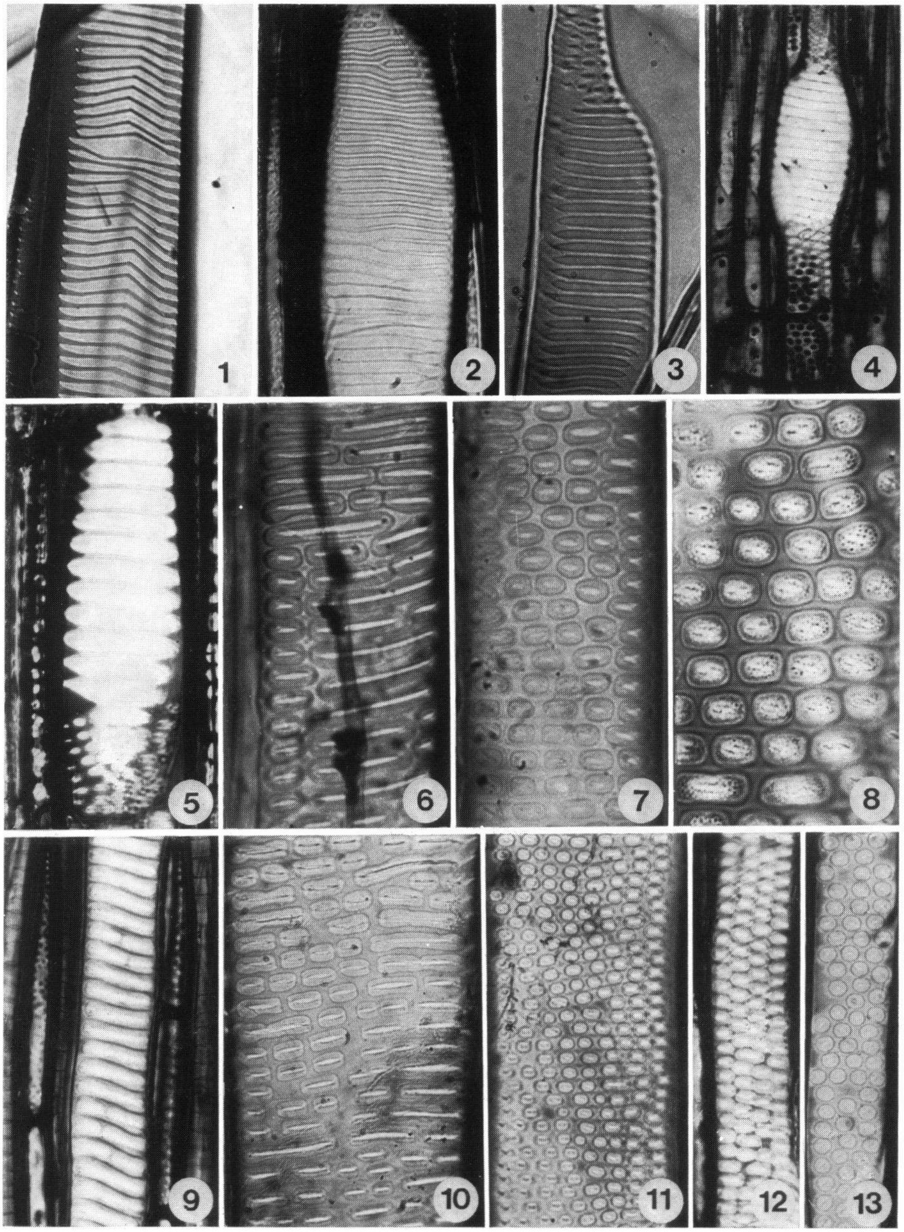


Plate II

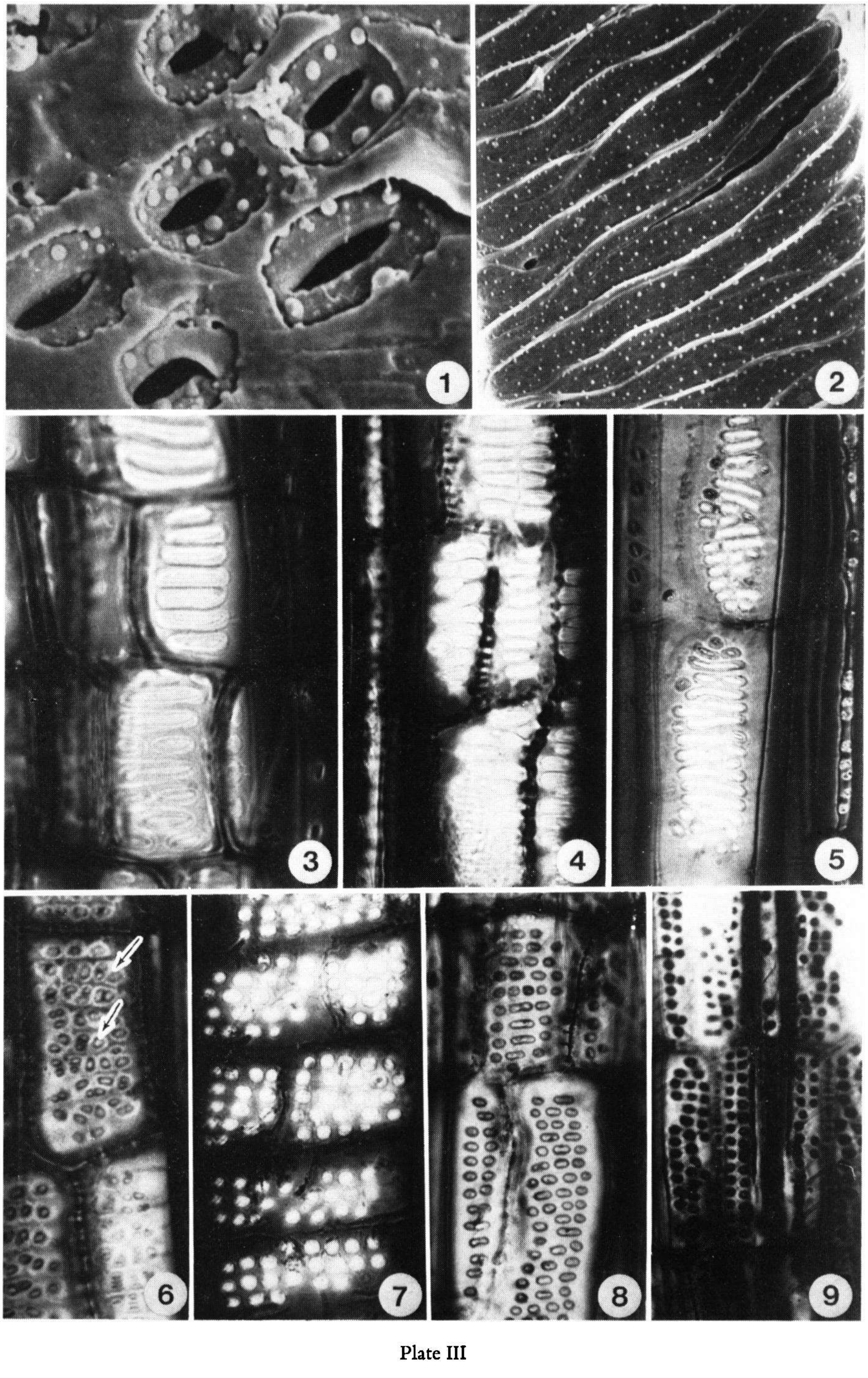
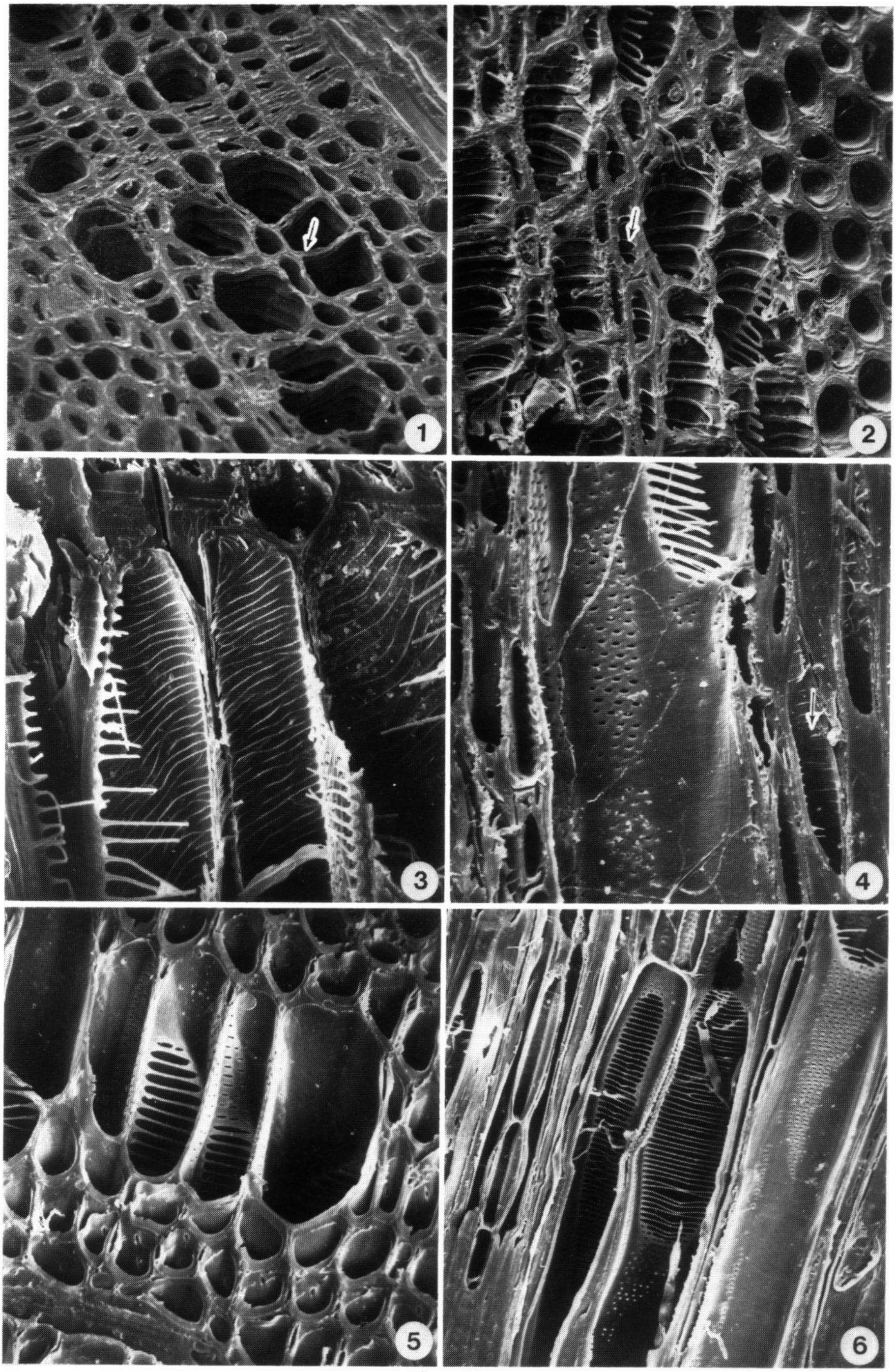


Plate III



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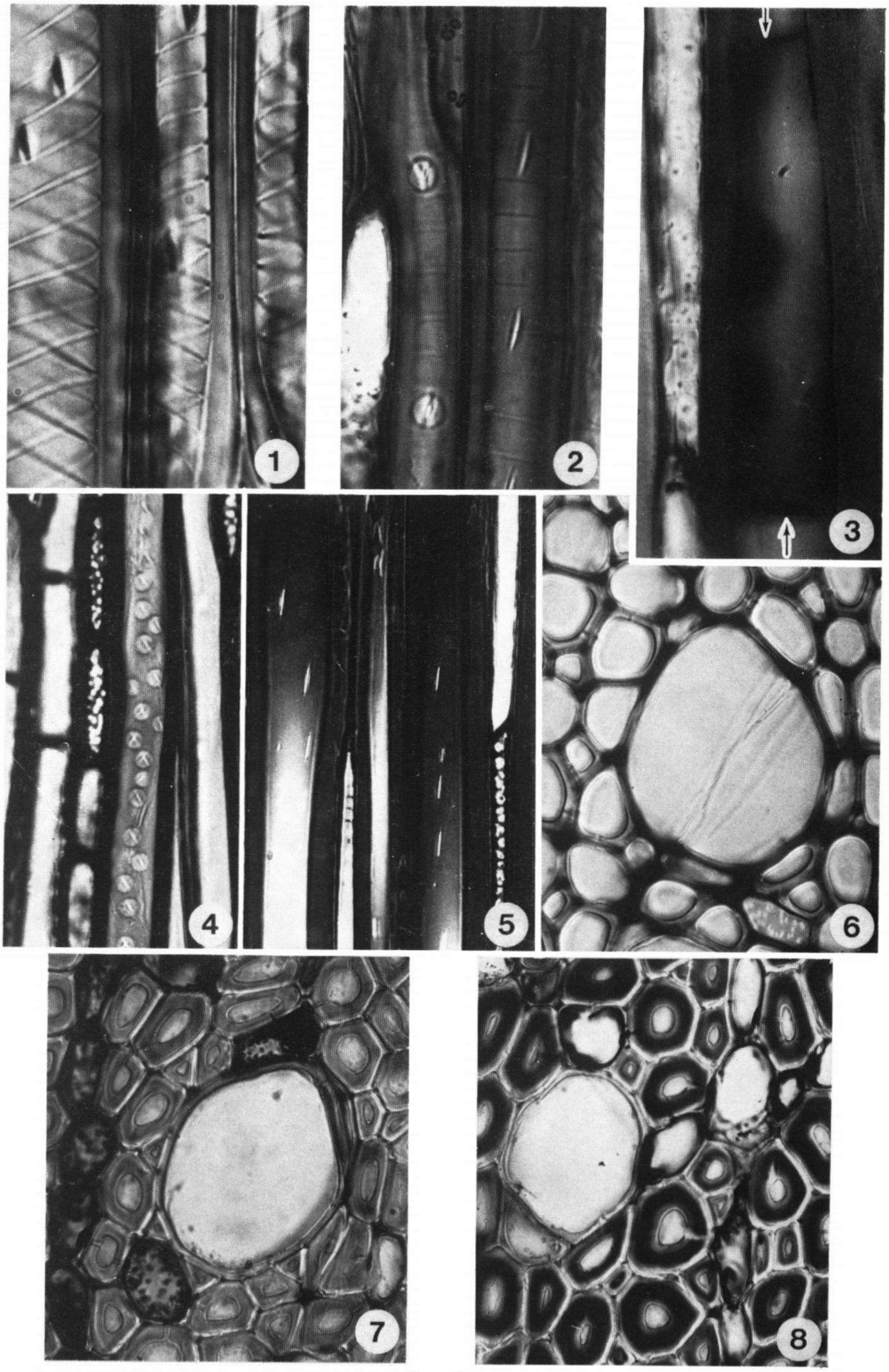


Plate V

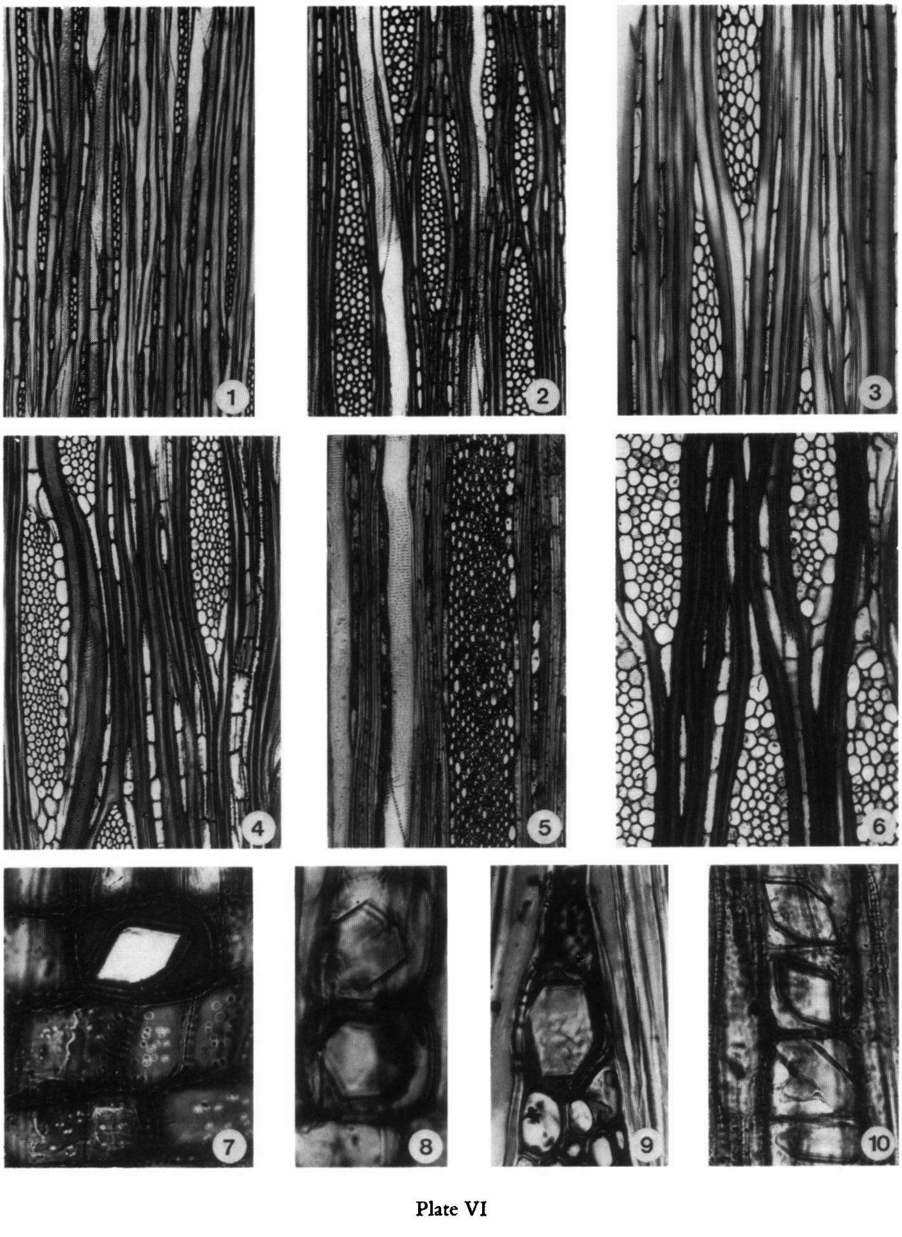
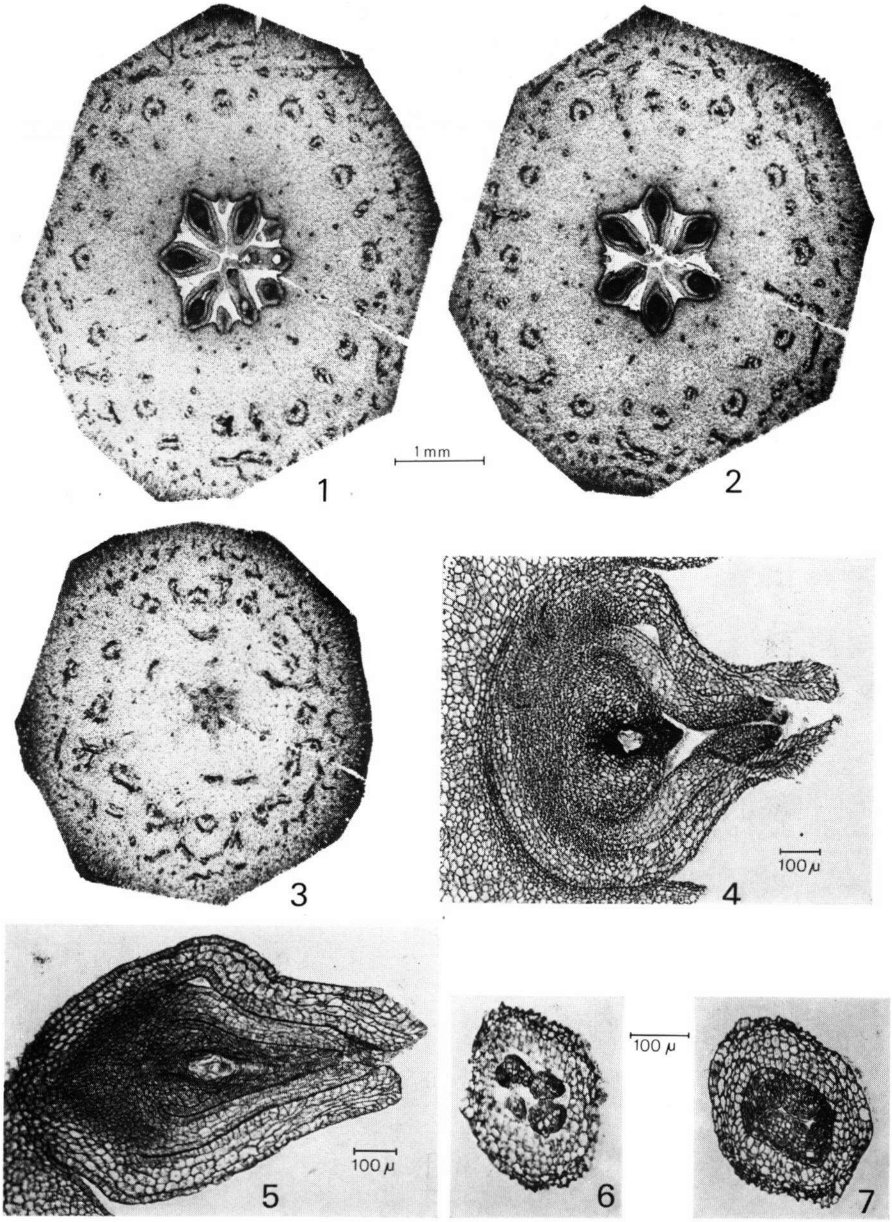


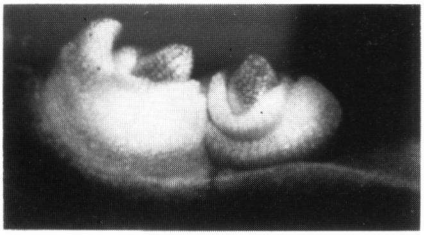
Plate VI



Scaphocalyx spathacea. — Photo 1—3. C.s. of pistil in upward sequence. — Photo 4. Ovule, ± median l.s. — Photo 5. Ovule, ± transverse l.s. — Photo 6 & 7. Ovule, subdistal c.s. showing separation of inner integument into four tips.

11

10



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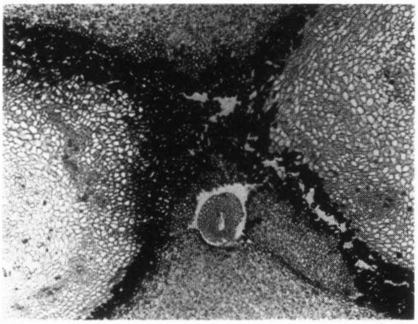

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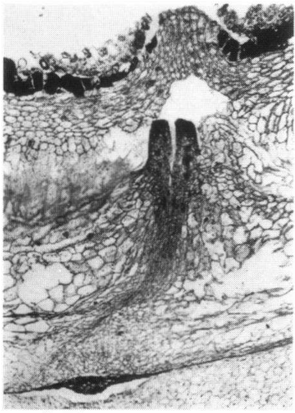

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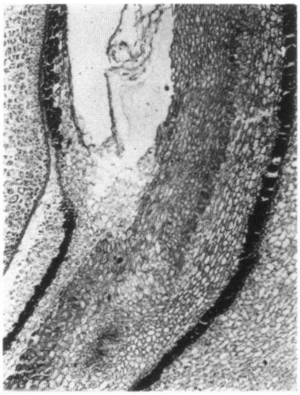

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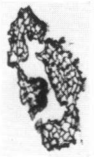

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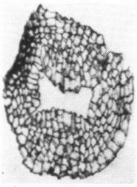

9

Scaphocalyx spathacea — Photo 8 & 9. Ovules, distal c.s. showing lobing of outer integument. — Photo 10. Halved ovary with five ovules. — Photo 11 & 12. Young ovules. — Photo 13. Micropylar region of seed, showing tips of inner integument. Exostome out off section. — Photo 14. Micropylar region of seed, showing ectostome and endocarp lobes. — Photo 15. Lateral base of seed, transverse l.s., showing the separation of inner cell layers of testa.