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RECUEIL DE TRAVAUX DE GEOBOTANIQUE / REVIEW OF GEOBOTANICAL MONOGRAPHS

7

AN ECOMORPHOLOGICAL STUDY
OF THE EVERGREEN LEAF

Manuela de Lillis

1991

CAMERINO-BAILLEUL

PUBBLICATION DU DEPARTEMENT DE BOTANIQUE ET ÉCOLOGIE DE L'UNIVERSITÉ DE CAMERINO ET DE LA STATION INTERNATIONALE DE PHYTOSOCIOLOGIE DE BAILLEUL SOUS L'ÉGIDE DE L'ASSOCIATION AMICALE DE PHYTOSOCIOLOGIE ED DE L'ASSOCIATION INTERNATIONALE POUR L'ÉTUDE DE LA VÉGÉTATION

BRAUN-BLANQUETIA

Un héritage est enrichissant et ouvre de nouvelles possibilités créatrices. Mais il en découle en contre partie l'obligation de ne pas gaspiller le patrimoine reçu.

Ceux qui, aujourd'hui étudient la végétation grâce à la phytosociologie peuvent utiliser des méthodologies bien au point et tirer profit d'un ensemble cohérent de connaisances.

C'est le résultat du travail méthodique de nombreux chercheurs de qualité pendant plusieurs décennies. Aujord'hui, nous trouvons face à des problémes qui ne sont sans doute pas tout à fait nouveaux mais qui paraissent infiniment plus graves que dans le passé: primauté de la technique, spécialisation, pénurie de matières premières, d'énergie et d'espace, crise de l'environnement...

Il se développe ainsi des problèmes spécifiques divers pour lesquels il est nécessaire de trouver des réponses nouvelles. Les chercheurs sont placés devant un véritable défi et il dépend de leur savoir et de leur imagination de montrer si la Science de la végétation est capable d'apporter une contribution appréciable à la solution de ces problèmes.

La tradition phytosociologique dans ce contexte constitue une base essentielle. La conception typologique de la végétation et la clarté du système qui en découle, l'habitude des cherchurs de vivre en contact étroit avec la végétation, les recherches basées sur l'observation condition antithétique de l'expérimentation, sont les traits caractéristiques de la phytosociologie.

Les lignes directrices qui nous ont été transmises par les maîtres de la Science de la végétation, Josias Braun-Blanquetia et Reinhold Tüxen avant tout, constituent actuelement une part importante de notre patrimoine d'idées. Notre but est de valoriser cet héritage et d'honorer la mémorie du premier de ces maîtres et fondateur de la phytosociologie moderne par une nouvelle série de publications.

Pourront y trouver place des monographies étudiant concrètement la végétation selon les enseignements de J. Braun-Blanquet et R. Tüxen qui, à travers la créativité des auteurs, produiront de nouveaux fruits.

Disciples nous-mêmes de J. Braun-Blanquet et ayant collaboré à son activité, nous pensons qu'à travers cette série de publications son héritage restera vivant dans l'esprit originel et avec de nouvelles idées.

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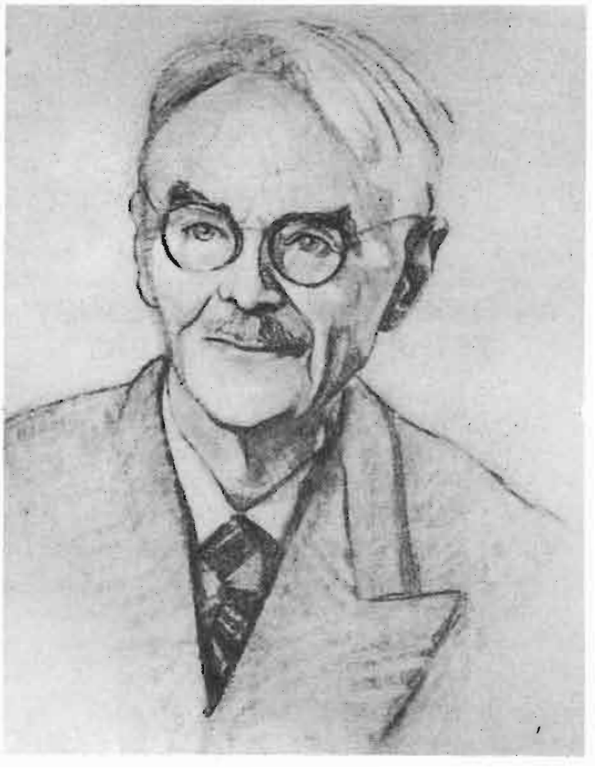

J. BRAUN-BLANQUET, 1954
Drawn form a photograph by Françoise M. Dansereau

To Alessandro Pignatti,
an inspiring teacher, dedicated scientist
and generous person.

ERRATA

p.5 3rd para, 4th from end "is presented" reads "are presented"
p.7 1st col., 3rd para, 4th line "has been evolved" reads "has evolved"
p.8 1st col., 3rd para., 7th line "decreases transpiration" reads "decrease transpiration"
p. 9 2nd col., 1st para., 4th from end "major biogeographical" reads "major biogeographical"
p.10 1st col., 1st para., 7th line and 4th para., 2nd line, "Fhan" reads "Fahn"; 2nd col., 2nd para., 8th from end " or were hand-cutted under stereomicroscope" reads "or were hand-cut under a stereo-microscope"; 3rd col., 2nd para., 5th line "this enables to refer the cuticle to the glaucous" reads "this enables us to refer to the cuticle as glaucous"
p.17 Tab. 2, 1st line "error standard" reads "standard error"; 2nd line "mechanichal" reads "mechanical"; "moderatly" reads "moderately"; 3rd, 4th, and 6th line "lenght" reads "length"
p.28 *Podocarpus latifolius*, 2nd col., 3rd para., 1st line "Vessels markedely lignified are" reads "Vessels, markedly lignified, are"
p.29 *Castanopsis cuspidata*, 3rd col., 1st para., last line "of the all genus" reads "of the entire genus"
p.31 *Quercus hui*, 3rd col., 2nd para., 4th from end "(21.6 µm thick) glaucous type." reads "(21.6 µm thick)."
p.33 *Gironniera subaequalis*, 3rd col., 1st para., 2nd last line "sheat-extensions" reads "sheath-extensions"
p.35 *Adenanthos cuneatus*, 2nd col., 3rd para., 2nd line "slerenchyma" reads "sclerenchyma"
p.42 *Leucadendron gandogeri*, 3rd col., 1st para., 6th line "does not exceeds" reads "does not exceed"
p.45 *Leucospermum hypophyllocarpodendron*, 1st col., last para., 2nd line "spongy as wide" reads "spongy parenchyma as wide"; last line "schereids" reads "sclereids"
p.47 *Petrophile ericifolia*, 2nd col., 3rd para., 3rd from end "and extends" reads "and extend"
p.48 *Protea amplexicaulis*, 2nd col., 1st para., 3rd line "two double layers" reads "two double or triple layers"
p. 49 *Protea longifolia*, 2nd col., 6th line "two double layers" reads "two double or triple layers"; 3rd col., 2nd para., 1st line "simular" reads "similar"; 2nd line "rime" reads "rima"
p.52 *Peumus boldus*, 2nd col., 4th para., 1st line "brunish masses" reads "brownish masses"
p.53 *Cryptocarya chinensis*, 1st col., 2nd para., 2nd line "smooth the lower" reads "smooth as the lower"
p.58 *Ternstroemia japonica*, 1st col., 1st para., 4th line "dorsiventral in" reads "dorsiventral symmetry in"
p. 59 *Adenostoma fasciculatum*, 1st col., 1st para., 3rd line "with radiate" reads "with radial"
p.63 *Brachysema sericeum*, 2nd col., last line "boundle sheat estensions" reads "bundle sheath extensions"
p.64 *Antidesma venosum*, 1st col., 1st para., last line "dorsiventral in" reads "dorsiventral symmetry in"; *Aporosa yunnanensis*, 1st col., 1st para., last line "dorsiventral in" reads "dorsiventral symmetry in"
p.70 *Ceanothus megacarpus*, 3rd col., 2nd last line "and is densely" reads "and are densely"
p.74 *Tetrastigma planicaule*, 3rd col., 1st para., last line "3.9 Em thick" reads "3.9 µm thick"
p.82 *Kunzea recurva*, 1st col., 2nd para, 4th line "is composed" reads "and is composed"
p.84 *Syzgium yambos*, 2nd col., 3rd para., 1st line "tissue occur" reads "tissue occurs"; 3rd col., 2nd para., 4th line "in thick" reads "thick"; *Blastus cochinchinensis*, 3rd col., last para., 4th from end "1324,440" reads "124,440"
p.91 *Ardisia sieboldii*, 3rd col., 2nd para., 1st line "Large glaudular" reads "Large glandular"
p.95 *Olea europaea L. ssp. africana*, 3rd copl., 2nd para., last line "unicellular hairs" reads "pluricellular hairs"
p.97 *Phillyrea media*, 1st col., 1st para., 3rd line "dorsiventral in" reads "dorsiventral symmetry in"
p.101 *Vernonia sp.*, 2nd col., 1st para., 2nd last line "consist of" reads "consists of"
p.104 *Rhaphydophora angustifolia*, 1st col., 1st para., 5th line "(17 mm thick" reads "(17 µm thick"
p.115 Fig. 6 caption "during Giurassic" reads "during Jurassic"
p.117 2nd col., last para., 8th from end "are related" reads "is related"
p.120 Résumé, 1st col., 1st para., 2nd line "peut considérés" reads "peut considéré"

FOREWORD

The analysis of vegetation, a long and painstaking task that describes the specific combinations identifiable in the field, has been the main focus of interest of phytosociology for decades. The study of plant adaptations as a function of their distribution in the environment is a subject to which even Braun-Blanquet often turned his attention; his fundamental contribution in "L'origine et le développement des flores dans le massif Central de la France" (1923) is a more than sufficient demonstration of that interest. As early as the first edition of his "Pflanzensoziologie" Braun-Blanquet insisted on the eco-physiological importance of adaptations like xeromorphism and hygromorphism. The successive influence of Schimper and Walter was fundamental in guiding the development of certain concepts in phytosociology.

The identification of adaptations that play an important role in determining water balance is, however, more often than not influenced by preconceived notions and ideas; demonstrating whether the various forms are also functionally efficient has been work often left undone. For example, I have examined the ecological significance of spininess in mountain shrubs found in mediterranean mountain areas; once considered an adaptive defence against browsing by herbivores, spininess is instead linked to the condensing and extraction of atmospheric humidity by plants.

The present study is concerned with what can be considered the most important eco-physiological adaptation of mediterranean woody flora, sclerophylly. In the mediterranean environment the ability to economize water is the winning factor in plant succession, and consequently sclerophylly is generally considered as an adaptation to avoid water loss. It is demonstrated here that the problem of sclerophylly is much more complex than was once thought and that there are many solutions, each of them functionally valid. An impressive amount of data gathered from the coordinated study of the eco-structure of mediterranean plants are presented here, as are data from plants in similar ecological conditions in other continents and, on a more general level, from tropical flora. From the conclusions presented here it is possible to reformulate the problem of climax in mediterranean environments in new terms.

I therefore think that this study can hold its own in a series of publications inspired by Braun-Blanquet even without presenting phytosociological data as such.

S.Pignatti

ACKNOWLEDGEMENTS

I would like to thank all those people who contributed to the success of this effort, especially my husband and my lovely daughter, for their endless patience and for willingly taking part in botanical expeditions that brought us to different continents and places all of us under sometimes difficult conditions.

I also very much appreciate the valuable discussions and encouragement of Erika and Sandro Pignatti, who had faith in my ability to conduct this study, even in those times I doubted I could continue. They also generously provided me with many samples from their herbarium collected in Japan, Chile, southwestern Australia and Southern Africa.

I would also like to thank Dr. K. Dixon from the King's Park and Botanical Garden of Perth and Prof. S. Salleo from the University of Messina for critical readings of an early draft.

INTRODUCTION

THE GENERAL PROBLEM

Plant anatomy is one of the oldest fields of botanical investigation; it was promoted to the ranks of a scientific discipline by the microscopical studies of Grew and Malpighi in 1671 (Morton, 1981). An advantage of such a long history is that many fundamental aspects of anatomy have been discovered and interpreted long ago; today's research can focus on fine details and applications centred on the knowledge accumulated over three centuries (Eames, 1947; Black, 1954; Carlquist, 1961; Metcalfe, 1961, 1963, 1979; Ayensu, 1972; Mauseth, 1987).

One of the main goals of contemporary anatomical studies is to understand the function of structures rather than simply catalogue and describe them; this means intimately connecting plant anatomy to physiology, and both of these in turn to ecology (Esau, 1967; Baas, 1973; Metcalfe, 1983; Jurko, 1983; Carlquist and Hockman, 1985; Körner et al., 1986; Shultz, 1986; Lausi et al., 1989).

Considerations on the adaptive significance of plant structures generally suggest that optimum form and function has been evolved by natural selection (Lewontin, 1977; Maynard Smith, 1977; Gould and Lewontin, 1979; Horn, 1979; Givnish, 1986). Leaves, one of the three basic organs of higher plants, are the most plastic structure in evolutionary terms, and several types have evolved in response to various selection pressures (Hickey, 1984). Although they play a vital role in photosynthesis – certainly the main function fulfilled by plants – and despite the great diversification of phyllome, anatomical studies of the leaf have been rather neglected, excluding the contributions of Nobs (1963), Pyykko (1966) and Montenegro (1984); most of the literature has focused on the conducting system, particularly on wood anatomy (Webber, 1936; Carlquist, 1975, 1985; Baas, 1982).

Environmental changes on a geological time scale have undoubtedly led to the development of particular leaf features that may have been adaptive for a certain period; these, however, may no longer be optimum but are sometimes still present in plants. Hence, it is therefore particularly important to consider the biology of individual species in terms of its leaf anatomy, keeping in mind the evolutionary history of the species as well as the ancestry of its anatomy. Given this, a dynamic approach becomes much more difficult a line of enquiry, yet it presents a challenging opportunity to draw forth new hypotheses and considerations on the adaptive significance of leaf structures from a synthetic point of view, one based on anatomical, biogeographical and phylogenetic evidence.

ON EVERGREENNESS

The availability and seasonality of environmental resources strongly affects the success of evergreen or deciduous growth forms (Stoker, 1971; Pool and Miller, 1975). Even though the ecological significance of leaf longevity was discussed in an earlier time by Schimper (1989) and Grisebach (1982), its functional significance has only been recently assessed (Schulze et al., 1977; Zwölfer, 1980; Schulze et al., 1980). The latter argue that all environmental conditions which tend to reduce the photosynthetic rate – mainly low nutrient and water availability – will promote evergreen leaf biomass. Indeed, a photosynthetic gain, weighed against the mantainance cost of non-photosynthesizing tissue, can only be achieved under these limiting factors by reducing the allocation of photosynthates for leaf growth and is only fulfilled if leaf biomass persists for a prolonged period of time.

It has also been suggested that the present geographical distribution of evergreen and deciduous growth forms has evolved since the Cretaceous (Axelrod, 1960; 1966). In fact, evergreenness is one of the most ancient features of vascular flora. It is characteristic of the primitive gymnosperms and angiosperms from which modern vegetation has evolved (Seward, 1917; Banks, 1970, 1981; Ogura, 1972; Stewart, 1983). In broad outline, the evergreen leaf can be conceived as a primitive result of the interaction between growth form and the uniform climate that was typical of the period preceding the late Cretaceous, when angiosperm flora under warm and humid environmental conditions reached world-wide diffusion through intensive speciation and occupation of new ecological niches (Axelrod, 1970; Pignatti 1984; Nimis, 1990).

Broad-leaved woody plants that dominated the evergreen tropical and subtropical forest continued to evolve and diffuse throughout the Tertiary until the Pliocene. Later on, mainly in the Pleistocene and following a thermal crisis, a new growth form appeared. It arose from seasonality, which induced heavy changes in the physical environment; its effects were clearly reflected in dramatic changes in the phenological cycle, in leaf longevity, in energetic balance and in the maintenance cost of photosynthetic tissue. Deciduous broad-leaved plants expanded chiefly in the ecological space that was part of the temperate evergreen forest, which was partly reabsorbed as a subordinate element in the mixed forest type (Pignatti, 1979 b).

Though these paleoclimatic events certainly favoured malacophyllous rather than evergreen species, this growth form not only did not disappear but actually survived in largely discontinuous areas located between the desert and the temperate zone characterized by summer aridity, as well as surviving in the tropics. Evergreens also thrived in the warm temperate humid forest, with a discontinuous distribution in Asia and the Canary Islands (Axelrod, 1975; Meusel, 1971).

Based on paleo-ecological inferences and a comparison of different flora, a progressive series of reductions in the life cycle as well as of size can be noted, at least in the northern hemisphere, for several groups of mediterranean flora: from evergreen to semi-deciduous and summergreen species such as *Quercus, Limonium, Euphorbia, Cistus,* etc. This step, even if it cannot be considered necessary from an evolutionary viewpoint, is still a matter of historical record; it seems to have been a general tendency that reached an extreme point in the Mediterranean Basin, where annual species became more and more diffused (Pignatti, 1979 c, 1989).

Despite this evidence, it is generally agreed that the evergreen broad-leaved forest be defined as the climax vegetation in mediterranean environments (Braun-Blanquet, 1936, 1953; Tomaselli, 1981; Pignatti, 1979 a). Evergreenness also occurs in most conifers, whose needle leaf is particularly adapted to coping with the hydric stress imposed by low temperatures.

A discrepancy seems to emerge when the ancestral habitat – in which the evergreen growth form was probably 'planned' and where water availability must not have been a problem – is compared to the present environment, where water is a limiting factor in mediterranean and boreal zones. Evergreen species, therefore, should have developed a tolerance to water deficit. Environmental tolerance expresses the genetic adaptation accumulated through successive generations that were exposed to long-term modifications (Riklefs, 1973). In order to adapt to environmental variations, plants react through morphological and functional changes that can be passed on in the population's genetic inheritance.

Environmental changes that occur very slowly in terms of a single organism's lifespan determine evolutionary response, i.e., changes in evolutionary fitness. The evolutionary response to prolonged conditions of water stress leads to a series of structural and physiological modifications in evergreen leaves (Killian et al., 1956; Oppenheimer, 1960).

ON SCLEROPHYLLY

Numerous observations have shown that many plants under arid conditions have structural peculiarities in leaf anatomy. Monfort (1918) coined the term "xeromorphism" to describe these adaptations as mechanisms that decreases transpiration – this view appears to be a concept typical of a mentality that had been influenced by traditional Darwinism –. Sclerophylly is a particular case of xeromorphism; it characterises evergreen species in mediterranean environments. The term "sclerophyll" was introduced by Schimper (1903) to describe rigid leathery leaves, and by extension, to designate trees and shrubs that possess this type of leaf. Sclerophylly implies an increase in leaf consistency, i.e., a "leaf hard and coriacious, breaking when folded" (Cowling and Campbell, 1983). Sclerophylly is identified by a low surface-to-volume ratio in leaves (Orshan, 1986); this external surface reduction promotes the structural changes in the leaf anatomy. Smaller cell size and thicker cellular walls, a bigger development of nervature per unit of leaf area, a thicker cuticle, a higher stomatal frequency and increased palisade development are some of the frequently found features in leaves thought to be sclerophyllous (Diamantoglou and Mitrakos, 1981; Christodoulakis and Mitrakos, 1987; Magnum Shields, 1950); another feature is leaf sclerification due to a large number of sclerenchyma cells within the mesophyll (Esau, 1965; Schulze, 1982).

Sclerophylly also appears to be associated with nutrient deficiencies (Loveless, 1961; Larcher, 1977). It has been hypothesised that under these conditions carbon is produced in excess, since any other growth would require additional nutrients; excess carbohydrates are deposited in cell walls or in cutin and waxes, which do not require nutrients. The result is sclerophylly. Therefore, both evergreenness and sclerophylly appear to be adaptive mechanisms under nutrient-deficient conditions (Shulze, 1982).

Although the functional significance of the sclerophyllous habitus is still a matter of discussion (Loveless, 1962; Kummerow, 1973; Pool and Miller, 1975; Lo Gullo and Salleo, 1988), it is commonly argued that sclerophyllous leaves enable plants to control transpiration (Killian et al., 1956; Mooney, 1983). Walter (1983) argued that the ecological advantage of sclerophylly should be seen not in the ability of the leaf to conduct active gas exchange in the presence of an adequate water supply but in its ability to dramatically reduce transpiration, even by closing stomata under water stress. This should enable sclerophyllous leaves to survive summer drought; when the rainy season starts again plants increase production. According to this view, sclerophyll plants should also be able to compete successfully with malacophyllous-deciduous species in winter-rain regions.

Drought avoidance as a component of drought resistance in vascular plants has been extensively discussed by Levitt (1980, 1985) and defined by Tyree (1976) in terms of the water relations involved. Since most mediterranean sclerophyllous species exhibit a "water saving" strategy (Mooney and Dunn, 1970; Mooney, 1982), they are often regarded as a physiologically homogeneous group (Kummerow, 1973; Salleo and Lo Gullo, 1985). And in vegetation studies leaf sclerophylly is considered a diagnostic characteristic in the physiognomic approach and recognized as the basis of the structural uniformity of mediterranean evergreen vegetation.

Indeed, sclerophylly is mainly considered as the most important physiognomic feature involved in the evolutionary convergence of the five, largely disjunct mediterranean ecosystems. This opinion goes back to the earliest ecological literature (Grisebach, 1884; Schimper, 1903; Warming, 1909). Convergence, formulated in a more evolutionary context as a major theme of comparative research on plant form and function in central Chile and in California (Mooney, 1977), has gained great momentum during the last few decades. As a result of these studies a number of paradigms that emphasize the significance of the convergent versus the non-convergent features of sclerophyllous mediterranean vegetation has been put forth (Cody and Mooney, 1978).

Despite these efforts and the large body of eco-physiological literature that deals with sclerophyllous species, sclerophylly is still an empirical term which, in practice, implies that any plants with leaves hard to the touch should be included in the sclerophyllous category. In fact, hard-leaved plants are also found outside mediterranean climates: in wet tropical zones (Freitag, 1982) and even beyond the arctic circle (e.g., *Rhododendron lapponicum*).

This problem has also intrigued biogeographers (Meusel, 1971), who, in the careful attempt to resolve the question, have tried to contrast the sclerophylly of evergreen mediterranean species with the laurophylly of evergreen tropical species. These efforts have introduced a new concept, formulated more on appearance than on an effective investigation of anatomical structure; unfortunately, this viewpoint has not clarified the concept of sclerophylly. However, the basis of this argument is extremely logical: i.e., starting from the evidence of the large climatic differences between the two biomes, a subsequent divergence in leaf anatomy would normally be expected. Such a difference should represent the ecological expression of drought adaptation within tropical species that have evolved into sclerophylls. However, even this simple paradigm did not prove true when leaf structure of evergreen woody species from the Mediterranean Basin were compared to evergreen laurophylls from the Canary Islands (De Lillis and Valletta, 1985); it is evident that the underlying ideas on sclerophylly must be completely reworked.

The surprising uniformity of anatomical data observed in the first step of our analysis made it impossible to draw a clear boundary between the two leaf types and induced a wider investigation into evergreen species from tropical to humid subtropical zones, and from warm temperate humid zones to the five mediterranean regions of the world.

The purpose of the present work is to provide a general picture of leaf structure as it relates to biogeographic distribution of broad-leaved evergreen species. The main objectives are to clarify the characteristics of sclerophylly and laurophylly to test if sclerophylly can be assumed as the basis for the identification of the mediterranean climax community; to gain a better understanding of eco-morphological convergence among mediterranean ecosystems; and to assess phylogenetic constraints on tropical and mediterranean evergreen flora.

EVERGREEN VEGETATION IN MEDITERRANEAN ECOSYSTEMS

The vegetation of the Mediterraean basin was first examined and interpreted from the syndynamical point of view by Braun-Blanquet, (1931, 1933, 1936). In his experience *Quercetum ilicis galloprovinciale* should be considered as the climax vegetation of the western portion of this zone; a similar community (*Orno-Quercetum ilicis*) was described some years later for Dalmatia (Horvatic, 1934), providing a climax model for the eastern part of the Mediterranean Basin. In both cases the final stage of vegetational succession in an evergreen forest is identified with the dominance of *Quercus ilex*. Most components are also evergreen (*Arbutus unedo, Pistacia lentiscus, Phillyrea latifolia, Smilax aspera, Rubia peregrina, Asparagus acutifolius, Myrtus communis*, etc.), and some deciduous elements (*Fraxinus ornus*) appear to have a distribution limited to the eastern zone.

On this basis, climax communities in Europe can be ordered along an altitudinal gradient (reflecting the variation of thermic conditions) in the following sequence:

- *PICEETUM*
  evergreen, needle-leaved;
- *FAGETUM*
  deciduous, broad-leaved;
- *MIXED OAK FOREST*
  deciduous, broad-leaved;
- *QUERCETUM ILICIS*
  evergreen, broad-leaved.

The occurence of evergreen types at both temperature extremes (warmest for *Quercetum ilicis* and coldest for the *Piceetum* appears difficult to explain because of the general correspondence between morphology and ecology in higher plants; however, it can be explained because of the large taxonomical difference between *Quercus ilex* (a broad-leaved Angiosperm) and *Picea* (a needle-leaved Gymnosperm). In fact, similarities between *Quercetum ilicis* and *Piceetum* are not limited to the evergreenness of the dominant trees: in both communities elements with tropical affinities are markedly present: e.g., *Ericaceae* (also largely evergreen) or orchids. Despite these unanswered questions, the existence of an evergreen climax community dominated by *Quercus ilex* for the mediterranean region was accepted as an axiom, and in most cases the limits of this vegetation were used as the mayor biogeographical boundary between the Mediterranean Basin and central Europe (Braun-Blanquet, 1936).

In the decades following Braun-Blanquet, similar vegetation types were described for other parts of the world having a mediterranean climate:

the chaparral vegetation in California (Axelrod, 1975; Barbour and Major, 1977)

the association between *Lithraea caustica* and *Quillaja saponaria* in central Chile (Schmithüsen, 1954; Oberdorfer, 1960)

the fynbos formation in southern Africa (Acocks, 1975)

the kwongan vegetation in southwestern Australia (Diels, 1906; Beard, 1984)

Consequently, evergreenness seems to be the general feature of vegetation growing under mediterranean climate conditions, and the coincidence of aspect was one of the most impressive pieces of evidence for the theory of convergent evolution in mediterranean-type ecosystems.

In the studies on the phytosociology of woody vegetation in Italy, the distinction between evergreen mediterranean vegetation (*Quercetum ilicis*) and deciduous temperate forests (*Quercetum pubescentis, Querco-Carpinetum*, etc.) is very sharp (Lucchese and Pignatti 1990). The floristic composition is completely different, so that *Quercetum ilicis* belongs to the class *Quercetea ilicis* whereas deciduous forests are included in *Querco-Fagetea*. Intermediate types are almost non-existent or of limited significance: e.g., near Trieste the *Seslerio-Ostryetum quercetosum ilicis* has been described, but this is a clear *Seslerio - Ostryetum* (deciduous) with *Quercus ilex* in the tree layer, occurring in the area of topographical contact between mediterranean and temperate vegetation (Poldini, 1989); on the other hand, such communities as *Orno-Quercetum ilicis* (the Adriatic coast) or *Ostryo-Quercetum ilicis* (Mt. Conero near Ancona) exhibit the normal composition of evergreen vegetation, with only one deciduous species present (Horvatic, 1934; Pignatti, 1960).

In general, evergreen species are either completely lacking or very rare in the forests of temperate climate regions in Europe. A regular zonation of evergreen and deciduous vegetation types appears only in Europe, whereas the situation is different under similar conditions on other continents. In Japan and generally in eastern Asia evergreen vegetation is also present under temperate climates and in areas where sufficient rainfall is available year-round; e.g., *Ardisio-Castanopsidetum* sieboldii and *Quercetum myrsinaefoliae* in the Tokyo area (Numata, 1974). The same situation can be observed in North America (Box, 1981). In South America and in particular, in the southern portion of the Andean Cordillera, it appears impossible to distinguish separate spaces for evergreen and deciduous tree species: even the austral beech (*Nothofagus*) has evergreen species in both the basal belt and near the treeline, and there are deciduous examples in between (Boelcke et al., 1985). In the western portion of the Australian continent all forest types are always evergreen (Beard 1990).

The sharp distinction between thermophilous evergreen and temperate deciduous vegetation appears to be peculiar to southern Europe, and it may be considered as a consequence of the Pleistocene Ice Age (Pignatti, 1977). In fact, evergreen temperate elements also exist in southern European flora, such that Di Martino et al., (1977) proposed the relictic Colchic Belt for the mountain vegetation of Sicily.

SOURCE OF STUDY MATERIALS AND METHODS

Various features are related to leaf scleromorphism, but in this investigation only the features that are most affected by high temperature, strong illumination and hydric deficit have been considered (Esau, 1965; Kummerow, 1973; Fhan, 1982). The following characteristics have been examined in relation to their function under conditions of water stress:

the development and shape of the upper and lower cuticle (Priestley, 1943; Stace, 1965; Eglinton and Hamilton, 1967; Holloway and Baker, 1970; Martin and Juniper, 1970; Hartmann, 1979; Edwards et al., 1982). These are linked to the regulation of cuticular transpiration and light absorption (Cutler et al., 1982);

mechanical structures and the occurrence of collenchyma (Duchaigne, 1955; Chafe, 1970; Pilet and Roland, 1974; Calvin and Null, 1977) or sclerenchyma (Foster, 1946; Rao, 1951a, 1951b; Arzee, 1953; De Ronn, 1967; Rao and Das, 1979; Harris, 1983, 1984). As well as their support function, these serve to limit dehydration damage:

decreasing size of epidermic cells (Fhan and Dembo, 1964; Heide-Jorgensen, 1978; Lawton, 1980; Lyshede, 1982; Thomas and Masarati, 1982) under hydric stress and the thickening of epidermic cell walls which have a support function (Magnum Shields, 1950);

palisade development, which is related both to the protective function exerted on the chloroplast under strong illumination (Magnum Shields, 1950) and to high photosynthetic activity. The latter is related to increased transpiration in conditions of water availability (Grieve and Hellmuth, 1970). By diminishing intercellular spaces (Sifton, 1957), a large palisade development reduces the diffusion of water and facilitates the movement of cellular liquid within the mesophyll (Margaris and Vokou, 1982);

position, size and density of stomata (Kenda, 1952; Pant and Banezji, 1965; Srivastava and Singh, 1972; Stevens and Martin, 1978) engaged in the control of transpiration (Killian at al., 1956);

leaf hairs (Carolin, 1971; Dickinson, 1974; Johnson, 1975; Theobald et al., 1975; Heide-Jorgensen, 1980), which in arid conditions exert some influence on the control of transpiration and maintain boundary layer conductance (Magnum Shields, 1950).

Of the most representative species in the five mediterranean areas of the world and in the tropical, subtropical and warm temperate zones, 146 evergreen species (Munz, 1959, 1974; Dyer, 1975; Pignatti, 1982; Ohwi, 1984; Green, 1985) were selected for inclusion in this study (Tab. 1). The specimens were personally collected during field investigations in the Mediterranean Basin, western Australia, California and the Canary Islands in the Spring, and in southern China in Summer; other material was received from collaborators or derived from modern dried collections which had also been collected during Spring. Dried material sometimes shows considerable resistance to dissection, especially in specimens that are already noted for their toughness in the fresh state. In order to make this material more suitable for cutting, specimens were rehydrated through exposure to water vapour for a few minutes; this process does not alter the anatomical structures of leaves (Dop and Gautié, 1928; Johansen, 1940). About 30 transverse sections (25 μm - 40 μm thick) from 25 to 30 selected mature leaves were cut with a TC-Sorval tissue sectioner or were hand-cutted under stereomicroscope. Sections were treated with dyes and observed under an optical microscoscope. Pictures were also taken by an optical microscope. Dimensions were measured using a micrometrical eyepiece.

The thickness of the lamina was measured as well as the thickness of the upper and lower cuticle, of the upper and lower epidermis, of the palisade and spongy parenchyma and of the undifferentiated mesophyll. The percentage of palisade with respect to total thickness was also calculated.

Qualitative characteristics of the leaf anatomy, such as the presence of hairs and mechanical structures, were evaluated using a scale of abundance (from 0 to +++) corresponding to their absence, presence and abundance; the position of stomata was marked (from + to ++ and +++), corresponding to the epidermic, intermediate and sunken levels. Impressions of the epidermis (Hilu and Randall, 1984) were made with cellulose acetate in order to measure stomata size – width, length and surface – on both sides of the leaf; stomata density per mm² was estimated with a micrometrical reticle. The corresponding transpiring surface and its percentage with respect to leaf area was calculated. Finally, the length and width of the leaf was measured.

The cuticle layer was also examined and photographed under a scanning electron microscope after sections were coated with gold (Exley et al. 1974); this enables to refer the cuticle to the "glaucous" or "glabrous" type according to the presence of waxes and papillae (Culter et al., 1982). The standard error for the mean values of the measurements relating to each character was calculated (Tab. 2). The average value of each measurement was assigned to numerical classes (Orshan, 1986); i.e., the range of variation of each character among all the species considered was expressed as a percentage of the maximum value measured. Qualitative characteristics were also processed converting their abundance value to a percentage scale (from 30% to 60%, 100%).

Micrometrical data made possible the construction of a matrix composed of 23 characteristics for 146 species. The matrix was processed using Wildi-Orloci (1983) software. Several calculations were carried out: first, considering all characteristics and all species (23 x 146 matrix, Fig. 1, 2); then, the number of characteristics was reduced from 23 to the 6 characteristics (6 x 146 matrix) – leaf thickness, leaf width and length, mechanical structures and upper and lower transpiring surface – that essentially express leaf xeromorphism (Fig. 3); finally, the number of species was reduced from 146 to 92 (23 x 92 matrix) and then to 51 (23 x 51 matrix) – i.e., mediterranean species were processed separately from tropical and subtropical species (Figs. 4, 5).

SPECIES	FAMILY	DISTRIBUTION
Hemigramma decurrens (Hook.) Copel	*Gleicheniaceae*	S. China
Hicriopteris chinensis (Ros.) Ching	*Aspidiaceae*	S. China
Podocarpus latifolius R. Br.	*Podocarpaceae*	S. Africa
Castanopsis chinensis Hance	*Fagaceae*	S. China
Castanopsis cuspidata Schottky	*Fagaceae*	Japan
Castanopsis fissa R. & W.	*Fagaceae*	S. China
Quercus agrifolia Neé.	*Fagaceae*	S. California
Quercus chrysolepis Liebm	*Fagaceae*	S. California
Quercus hui Chun	*Fagaceae*	S. China
Quecus ilex L.	*Fagaceae*	Medit. Basin
Quercus myrsinaefolia Blume	*Fagaceae*	Japan
Quecus serrata Thunb.	*Fagaceae*	Medit. Basin
Quercus suber L.	*Fagaceae*	Medit. Basin
Gironniera subaequalis Planch.	*Ulmaceae*	S. China
Ficus nervosa Heyne	*Moraceae*	S. China
Celtis sinensis Willd.	*Urticaceae*	Japan
Adenanthos cuneatus Labill.	*Proteaceae*	SW. Australia
Banksia grandis Willd.	*Proteaceae*	SW. Australia
Banksia littoralis R. Br.	*Proteaceae*	SW. Australia
Banksia quercifolia R. Br.	*Proteaceae*	SW. Australia
Conospermum caerulem R. Br.	*Proteaceae*	SW. Australia
Conospermum crassinervium Meissner	*Proteaceae*	SW. Australia
Faurea saligna Harv.	*Proteaceae*	S. Africa
Grevillea pulchella (R. Br.) Meissner	*Proteaceae*	SW. Australia

Tab. 1 - List of the species under study.

SPECIES	FAMILY	DISTRIBUTION
Isopogon attenuatus R. Br.	*Proteaceae*	SW. Australia
Lambertia multiflora Lindley	*Proteaceae*	SW. Australia
Leucadendron gandogeri Bourke	*Proteaceae*	SW. Africa
Leucadendron linoides Knight	*Proteaceae*	S. Africa
Leucadendron nervosum Phill. & Hutch.	*Proteaceae*	SW. Africa
Leucadendron salignum R. Br.	*Proteaceae*	S. Africa
Leucospermum calligerum Knight	*Proteaceae*	S. Africa
Leucospermum hypophyllocarpodendron (L.) Druce	*Proteaceae*	S. Africa
Persoonia longifolia R. Br.	*Proteaceae*	SW. Australia
Petrophile ericifolia R. Br.	*Proteaceae*	SW. Australia
Petrophile linearis R. Br.	*Proteaceae*	sw. Australia
Protea amplexicaulis R. Br.	*Proteaceae*	S. Africa
Protea cynaroides L.	*Proteaceae*	S. Africa
Protea latifolia R. Br.	*Proteaceae*	S. Africa
Protea longifolia R. Br.	*Proteaceae*	SW. Africa
Protea welwitschii R. Br.	*Proteaceae*	S. Africa
Stirlingia latifolia R. Br.	*Proteaceae*	SW. Australia
Synaphaea petiolaris R. Br.	*Proteaceae*	SW. Australia
Xylomelum occidentale R. Br.	*Proteaceae*	SW. Australia
Peumus boldus Molina	*Monimiaceae*	Chile
Cryptocarya alba R. Br.	*Lauraceae*	Chile
Cryptocarya chinensis (Hance) Hemsl.	*Lauraceae*	S. China
Cryptocarya concinna Hance	*Lauraceae*	S. China
Laurus azorica (Seub.) Franco	*Lauraceae*	Canary Islands

SPECIES	FAMILY	DISTRIBUTION
Laurus nobilis L.	*Lauraceae*	Medit. Basin
Lindera chunii Merr.	*Lauraceae*	Japan
Neolitsea sericea Koidz.	*Lauraceae*	Japan
Hibbertia cuneiformis (Labill.) Smith	*Dilleniaceae*	SW. Australia
Hibbertia hypericoides (D.C.) Benth.	*Dilleniaceae*	SW. Australia
Eurya japonica Thunb.	*Theaceae*	Japan
Ternstroemia japonica Thunb.	*Theaceae*	Japan
Itea chinensis Hook. et Arn.	*Saxifragaceae*	S. China
Pittosporum viridiflorum Sims.	*Pittosporaceae*	S. Africa
Adenostoma fasciculatum Hook. & Arn.	*Rosaceae*	S. California
Heteromeles arbutifolia M. Roem. L. C.	*Rosaceae*	S. California
Prunus ilicifolia Walp.	*Rosaceae*	S. California
Prunus lusitanica L.	*Rosaceae*	Canary Islands
Quillaja saponaria Molina	*Rosaceae*	Chile
Acacia podalyriaefolia A. Cunn.	*Leguminosae*	SW. Australia
Acacia rostellifera Benth.	*Leguminosae*	SW. Australia
Brachysema sericeum (Smith) Domin	*Leguminosae*	SW. Australia
Ceratonia siliqua L.	*Leguminosae*	Medit. Basin
Antidesma venosum E. Mey.	*Euphorbiaceae*	S. Africa
Aporosa yunnanensis Metc.	*Euphorbiaceae*	S. China
Glochidion obovatum Sieb. et Zucc.	*Euphorbiaceae*	Japan
Boronia crenulata Smith	*Rutaceae*	SW. Australia
Diplolaena microchephala Bartl.	*Rutaceae*	SW. Australia
Mischocarpus pentapetalus (Roxb.) Radlk.	*Sapindaceae*	S. China

SPECIES	FAMILY	DISTRIBUTION
Lithraea caustica Hook. & Horn.	*Anacardiaceae*	Chile
Pistacia atlantica Desf.	*Anacardiaceae*	Canary Islands
Pistacia lentiscus L.	*Anacardiaceae*	Medit. Basin
Rhus excisa Thunb.	*Anacardiaceae*	S. Africa
Ilex aquifolium L.	*Aquifoliaceae*	Medit. Basin
Ilex canariensis Poiret	*Aquifoliaceae*	Canary Islands
Ilex rugosa F. Schmidt	*Aquifoliaceae*	Japan
Ceanothus megacarpus Nutt.	*Rhamnaceae*	S. California
Ceanothus oliganthus Nutt.	*Rhamnaceae*	S. California
Ceanothus spinosus Nutt.	*Rhamnaceae*	S. California
Rhamnus alaternus L.	*Rhamnaceae*	Medit. Basin
Rhamnus californica Esch.	*Rhamnaceae*	S. California
Rhamnus crenulata Ait.	*Rhamnaceae*	Canary Islands
Rhamnus glandulosa Ait.	*Rhamnaceae*	Canary Islands
Tetrastigma planicaule Gagnep.	*Vitaceae*	S. China
Elaeocarpus sylvestris Poiret	*Tiliaceae*	Japan
Urena lobata L.	*Malvaceae*	S. China
Pterospermum lanceaefolium Roxb.	*Sterculiaceae*	S. China
Xylosma monospora Harv.	*Bixaceae*	S. Africa
Agonis flexuosa (Spreng.) Schauer	*Myrtaceae*	SW. Australia
Agonis hypericifolia Schauer	*Myrtaceae*	SW. Australia
Beaufortia decussata R. Br.	*Myrtaceae*	SW. Australia
Calothamnus quadrifidus R. Br.	*Myrtaceae*	SW. Australia
Calothamnus sanguineus Labill.	*Myrtaceae*	SW. Australia

SPECIES	FAMILY	DISTRIBUTION
Darwinia lejostyla (Turcz.) Domin	*Myrtaceae*	SW. Australia
Eucalyptus calophylla Lindley	*Myrtaceae*	SW. Australia
Eucalyptus caesia Benth.	*Myrtaceae*	SW. Australia
Eucalyptus marginata Donn.	*Myrtaceae*	SW. Australia
Hypocalymma angustifolium Endl.	*Myrtaceae*	SW. Australia
Kunzea recurva Schauer	*Myrtaceae*	SW. Australia
Melaleuca acerosa Schauer	*Myrtaceae*	SW. Australia
Melaleuca huegelii Endl.	*Myrtaceae*	SW. Australia
Syzygium jambos (L.) Alston	*Myrtaceae*	Japan
Blastus cochinchinensis Loureiro	*Myrtaceae*	S. China
Melastoma candidum D. Don	*Melastomaceae*	S. China
Melastoma dodecandrum Loureiro	*Melastomaceae*	S. China
Melastoma sanguineum Sims	*Melastomaceae*	S. China
Schefflera octophylla (Lour.) Harms	*Araliaceae*	S. China
Heteromorpha trifoliata Eckl. & Zeyh.	*Umbelliferae*	S. Africa
Arbutus canariensis Duham.	*Ericaceae*	Canary Islands
Arbutus menziesii Pursh	*Ericaceae*	S. California
Arbutus unedo L.	*Ericaceae*	Medit. Basin
Arctostaphylos glandulosa Lindl.	*Ericaceae*	S. California
Arctostaphylos glauca Lindl.	*Ericaceae*	S. California
Erica multiflora L.	*Ericaceae*	Medit. Basin
Erica plukenetii L.	*Ericaceae*	S. Africa
Ardisia sieboldii Miq.	*Myrsinaceae*	Japan
Myrsine africana L.	*Myrsinaceae*	S. Africa

SPECIES	FAMILY	DISTRIBUTION
Rapanea melanophloeos Mez	*Myrsinaceae*	S. Africa
Sideroxylon inerme L.	*Sapotaceae*	S. Africa
Diospyros morrisiana Hanae	*Ebenaceae*	S. China
Euclea divinorum Hiern	*Ebenaceae*	S. Africa
Euclea racemosa Murr.	*Ebenaceae*	S. Africa
Euclea undulata Thunb.	*Ebenaceae*	SW. Africa
Olea europaea L.	*Oleaceae*	Medit. Basin
O. europaea L. ssp. africana P.S. Green	*Oleaceae*	S. Africa
O. europaea L. ssp. cerasiformis Kuntk. et Sund.	*Oleaceae*	Canary Island
Phillyrea angustifolia L.	*Oleaceae*	Medit. Basin
Phillyrea media L.	*Oleaceae*	Medit. Basin
Psychotria capensis Vatke	*Rubiaceae*	S. Africa
Psychotria manillensis Bartl.	*Rubiaceae*	Japan
Psychotria zombamontana (Kuntze) E. Petit	*Rubiaceae*	S. Africa
Rosmarinus officinalis L.	*Labiate*	Medit. Basin
Viburnum rigidum Vent.	*Caprifoliaceae*	Japan
Viburnum rugosa Pers.	*Caprifoliaceae*	Canary Islands
Viburnum tinus L.	*Caprifoliaceae*	Medit. Basin
Vernonia sp. Schreb.	*Compositae*	S. China
Smilax aspera L.	*Liliaceae*	Medit. Basin
Smilax canariensis Willd.	*Liliaceae*	Canary Islands
Smilax china L.	*Liliaceae*	S. Japan
Caryota mitis Loureiro	*Palmae*	S. China
Pothos repens (Lour.) Druce	*Araceae*	S. China
Rhaphydophora angustifolia Schott	*Araceae*	S. China

SPECIES	LEAF LENGTH	LEAF WIDTH	LEAF THICKNESS	UPPER CUTICLE	UPPER EPIDERMIS	MECHAN. STRUCT.	UNDIFF. MESOPHYLL	PALISADE	SPONGY	PAL/ LEAF %	LOWER EPIDERMIS	LOWER CUTICLE	HAIR	ST. PO.
Hemigramma decurrens	103±1.47	36±0.47	298.60±8.97	7.80±0.78	27.30±1.95	+	247.37±8.26	0	0	0	8.91±1.01	5.05±0.62	0	+
Hicriopteris chinensis	115±0.91	20±1.18	68.90±3.44	1.95±0.31	7.80±0.79	++	51.99±2.41	0	0	0	5.85±0.79	1.95±0.31	0	+
Podocarpus latifolius	95±1.30	10±1.30	236.99±2.06	15.75±1.11	12.37±0.39	+++	0	26.62±1.06	159.00±5.37	14	12.00±0.93	11.25±1.37	0	+
Castanopsis chinensis	93±2.18	25±0.47	117.00±2.65	9.09±1.17	15.60±0.89	++	0	41.59±1.48	35.30±2.41	54	15.60±0.57	7.80±0.98	0	+
Castanopsis cuspidata	72±1.18	26±1.56	213.00±6.39	13.50±1.63	16.50±1.63	++	0	72.00±7.20	85.50±3.19	45	13.50±1.63	16.50±1.63	0	++
Castanopsis fissa	110±0.47	27±1.18	212.00±2.90	21.10±1.30	16.90±0.76	++	0	69.00±1.45	62.97±2.07	53	12.80±0.69	20.70±0.83	+	++
Quercus agrifolia	34±2.20	28±2.60	221.97±2.06	8.15±0.50	8.48±0.50	++	0	104.32±8.72	88.02±4.75	47	7.50±0.70	5.50±0.45	0	+
Quercus chrysolepis	56±3.82	30±2.60	263.40±2.75	5.95±0.46	10.70±0.97	++	0	105.20±7.85	124.00±6.28	40	10.26±0.94	7.28±0.39	0	+
Quercus hui	82±0.47	20±0.47	220.00±2.11	13.84±1.21	16.43±0.72	++	0	75.50±1.21	78.70±2.52	34	14.70±1.41	21.60±2.21	0	+
Quercus ilex	64±0.91	30±0.99	312.00±7.00	11.76±1.10	13.14±1.29	++	0	132.17±1.21	107.95±1.52	42	11.07±1.01	9.68±0.21	+	+
Quercus mirsinaefolia	106±0.47	34±0.47	165.64±2.88	15.60±0.89	22.09±1.17	++	0	51.90±1.48	81.90±5.53	31	9.09±1.17	9.09±1.17	0	+
Quercus serrata	73±0.47	21±0.47	165.64±2.65	15.60±0.92	12.48±1.71	++	0	60.80±3.43	85.80±3.12	37	9.36±1.40	7.80±0.99	0	+
Quercus suber	36±1.91	21±1.01	161.92±2.00	5.88±0.38	13.49±1.00	++	0	77.85±2.50	44.29±3.05	48	10.72±0.96	10.03±0.92	+	+
Gironniera subaequalis	155±1.18	55±0.47	172.48±2.03	16.26±0.51	14.53±1.48	+	0	48.09±3.04	72.31±3.74	28	11.07±1.40	10.38±1.71	+	+
Ficus nervosa	105±0.47	41±0.27	119.68±5.89	8.30±0.51	17.60±1.07	+	0	21.79±0.69	58.12±3.73	18	11.07±1.45	6.22±1.55	0	+
Celtis sinensis	77±0.47	43±0.79	126.24±4.68	7.80±0.95	14.99±1.48	++	0	49.80±3.04	39.00±3.74	44	7.80±0.97	7.80±0.95	0	+
Adenanthos cuneatus	20±2.45	11±0.97	332.49±4.00	8.30±0.59	19.72±0.99	+++	279.91±6.00	0	0	0	16.26±0.50	8.30±0.98	++	++
Banksia grandis	196±1.91	54±0.46	359.50±5.02	9.20±0.63	8.06±0.94	+++	0	259.00±3.10	70.08±9.99	69	7.47±0.67	6.92±0.74	+	+++
Banksia littoralis	92±0.79	4±0.30	215.19±3.03	14.53±0.43	34.94±2.00	+++	0	70.93±4.00	68.85±3.59	33	14.18±1.00	11.76±0.99	+++	+++
Banksia quercifolia	25±2.00	7±0.60	418.57±4.01	12.80±1.03	77.36±4.90	+++	0	144.52±6.90	150.68±7.04	34	20.76±0.97	12.45±2.00	++	+++
Conospermum caeruleum	221±1.34	7±0.10	475.72±2.60	9.68±0.57	12.10±1.30	+	0	231.12±2.41	200.33±4.50	48	11.41±1.52	11.07±1.12	0	+++
Conospermum crassinervium	160±2.18	3±0.60	260.12±4.50	6.28±0.95	17.31±1.26	+	0	89.00±2.43	110.33±4.56	40	15.22±1.10	11.07±1.15	++	+++
Faurea saligna	97±0.88	16±1.30	344.83±4.75	6.31±0.27	24.92±2.19	+	0	148.45±4.46	134.40±6.28	43	25.66±1.86	5.29±0.59	0	+++
Grevillea pulchella	16±1.70	9±0.99	397.58±4.88	18.16±1.82	17.71±1.80	+	0	248.08±9.91	90.13±6.79	60	10.38±1.09	15.12±1.60	0	+++
Isopogon attenuatus	25±2.49	12±1.13	598.08±5.88	13.84±1.40	21.45±2.16	+++	0	142.19±4.44	388.08±6.12	24	19.72±2.00	12.80±1.87	0	+++
Lambertia multiflora	28±1.91	5±0.60	358.74±6.69	11.41±1.14	56.36±5.00	+++	0	154.31±8.99	101.03±7.98	43	21.10±2.00	14.53±1.30	0	+++
Leucadendron gandogeri	95±2.91	17±1.59	592.28±6.18	30.00±2.31	29.14±0.87	+	0	369.57±5.05	107.14±04.88	62	30.86+0.87	26.54±1.74	++	++
Leucadendron linoides	10±1.91	3±1.91	355.83±1.91	14.49±2.10	24.99±1.10	++	265.90±6.26	0	0	0	34.69±1.49	15.60+1.58	++	++
Leucadendron nervosum	45±2.3	15±0.59	560.37±4.75	42.89±2.29	18.99±1.88	++	0	302.57+12.5	133.71+5.28	54	18.00±2.33	44.57±1.58	++	++
Leucadendron salignum	62±2.6	19±1.30	319.88±6.61	15.60±2.31	15.64±0.87	+	257.40+2.00	0	0	0	15.86±0.87	26.57±1.23	++	+++
Leucospermum calligerum	15±1.91	5±2.50	338.57±2.20	18.86±2.47	12.86±0.87	+	0	222.85±4.60	55.71±5.28	66	12.80±1.33	16.27±1.23	++	++
Leucospermum hypophyll.	85±1.97	4±0.4	662.80±2.11	30.00±1.21	12.90±0.72	+++	0	397.20+4.33	186.00+6.10	60	10.30±1.41	26.40±2.00	++	+++
Persoonia longifolia	120±9.89	7±1.90	432.84±9.99	15.91±1.20	24.22±2.99	++	0	138.05±4.99	214.52±9.99	32	24.22±2.47	15.91±1.20	0	++

Tab. 2 - Measurements of the characters examined in each species. Values, given in μm, represent the average ± error standard. Qualitative characters such as mechanichal structures and hairiness are classified as moderatly present (+) abundant (++), very abundant or important (+++). Stomatal location at the epidermic level, weakly sunken, largely protected or cryptic are marked by +, ++, +++ respectively. Leaf lenght and width are given in mm.

See from p. 17 to p. 20 for leaf lenght, leaf width, leaf thickness, upper cuticle, upper epidermis, mechanical structures, undifferentiated mesophyll, palisade, spongy, palisade/leaf percentage, lower epidermis, lower cuticle, hairs, stomatal location.

See from p. 21 to p. 24 for lower stomatal density, lower stomatal lenght, lower stomatal width, lower stomatal surface, lower transpiring surface, lower transpiring surface/leaf surface percentage, upper stomatal density, upper stomatal length, upper stomatal width, upper stomatal surface, upper transpiring surface, upper transpiring surface/leaf surface percentage.

SPECIES	LEAF LENGTH	LEAF WIDTH	LEAF THICKNESS	UPPER CUTICLE	UPPER EPIDERMIS ?????	MECHAN. STRUCT.	UNDIFF. MESOPHYLL	PALISADE	SPONGY	PAL/ LEAF %	LOWER EPIDERMIS	LOWER CUTICLE	HAIR	ST. PO.
Petrophile ericifolia	34±3.22	4±2.19	1115.8±8.89	12.16±1.55	20.76±2.00	+++	0	298.31±5.60	749.74±4.70	27	20.78±1.70	12.11±1.56	0	++
Petrophile linearis	41±1.30	7±1.18	846.50±1.91	16.26±2.31	20.75±1.90	+++	0	305.50±7.52	469.04±4.05	36	18.33±2.12	16.60±1.73	0	++
Protea amplexicaulis	57±1.30	35±1.30	618.00±1.91	30.08±1.74	28.50±2.19	+	0	340.50±7.59	180.00±13.73	55	24.02±3.05	15.00±1.73	0	++
Protea cynaroides	87±1.60	57±1.91	640.26±3.23	28.70±1.33	34.28±1.81	++	0	108.40±28.5	314.50±11.40	17	39.43±3.23	28.29±1.32	0	++
Protea latifolia	52±3.82	25±1.30	421.20±1.91	11.73±0.60	23.47±1.37	++	0	300.12±31.32	50.00±11.22	70	23.40±0.60	11.74±0.30	+	++
Protea longifolia	180±2.91	35±2.60	644.50±6.29	36.00±1.21	33.40±2.32	++	0	343.71±28.1	168.0±11.2	53	27.40±2.22	36.00±1.20	++	++
Protea welwitschii	93±9.89	14±0.4	316.14±8.90	7.92±1.51	21.12±2.47	++	0	141.15±7.90	118.82±9.88	45	19.42±2.40	7.61±1.64	+	++
Stirlingia latifolia	170±8.50	3±1.49	394.25±5.00	13.86±2.00	12.88±1.40	++	0	131.48±4.98	198.94±7.89	33	22.57±1.60	14.72±1.90	0	++
Synaphaea petiolaris	60±8.90	5±2.29	546.66±8.89	20.74±1.40	14.80±1.30	+++	0	233.87±9.89	242.56±9.99	43	15.59±2.20	19.70±1.50	0	++
Xylomelum occidentale	76±6.00	46±3.00	526.94±6.89	13.14±1.67	23.18±2.30	+++	0	223.50±7.94	233.55±9.67	42	19.03±2.00	13.84±1.40	0	++
Peumus boldus	64±6.00	34±2.30	237.64±8.76	7.32±0.89	27.90±2.60	+	0	62.20±5.55	120.70±4.60	26	17.08±1.49	2.44±0.12	+	++
Cryptocarya alba	42±4.00	26±1.98	277.27±9.00	4.88±6.98	33.34±2.45	++	0	123.62±4.44	103.24±5.56	45	8.94±0.90	3.25±0.23	0	++
Cyiptocarya chinensis	85±0.79	39±0.27	191.11±1.63	15.60±0.97	9.09±1.71	++	0	50:96±5.16	91.20±14.3	33	15.60±1.23	12.48±1.71	0	+
Cryptocarya concinna	102±1.18	30±0.27	191.44±2.26	11.70±1.56	14.29±1.17	++	0	44.30±2.43	100.71±9.40	29	9.09±1.17	11.70±1.56	++	+
Laurus azorica	63±0.47	61±0.27	204.45±4.40	5.61±0.50	16.34±1.54	++	0	71.49±6.09	93.20±7.89	35	13.42±4.98	4.39±0.34	+	+
Laurus nobilis	120±1.47	40±0.47	247.72±2.11	7.77±0.21	12.65±0.72	+	0	102.17±7.21	87.84±2.52	45	8.54±1.41	8.23±1.21	0	+
Lindera chunii	85±0.72	37±0.47	141.66±3.19	10.39±1.48	15.60±1.71	+	0	45.49±2.88	44.19±2.41	50	15.60±0.98	10.39±1.48	+	+
Neolitsea sericea	145±1.18	47±0.21	147.38±4.83	1.95±0.48	8.82±0.20	+	0	88.68±8.21	39.19±0.45	60	7.35±0.34	1.47±0.31	0	+
Hibbertia cuneiformis	26±2.00	8±0.20	413.40±9.98	15.60±1.00	23.40±2.00	+	0	109.20±8.97	234.00±9.00	26	23.40±1.90	7.80±0.45	0	++
Hibbertia hypericoides	8±0.54	3±0.23	280.80±7.89	15.60±1.00	31.20±2.98	+	0	124.80±9.23	85.80±8.00	44	15.60±1.23	7.80±0.43	+	++
Eurya japonica	61±1.18	19±0.25	252.0±15.9	3.75±0.78	12.75±2.10	+	0	70.50±1.63	148.50±4.21	27	12.75±2.10	3.75±0.78	0	+
Ternstroemia japonica	76±2.20	29±0.26	499.20±3.82	15.60±1.03	34.32±1.71	+	0	57.72±1.71	357.24±2.65	11	18.72±1.71	15.60±1.84	0	+
Itea chinensis	70±1.98	29±0.23	168.48±4.83	7.80±0.98	9.09±1.17	+	142.99±3.97	0	0	0	9.09±1.17	7.80±1.08	+	+
Pittosporum viridiflorum	95±1.30	33±1.91	179.33±1.91	9.70±0.60	25.28±1.45	++	0	50.57±1.76	64.09±0.73	28	22.34±0.73	7.35±0.47	0	+++
Adenostoma fasciculatum	7±0.24	3±0.09	581.11±7.89	9.17±0.91	10.07±1.00	+	0	100.70±9.78	441.90±9.99	17	10.07±1.01	9.17±0.78	0	++
Heteromeles arbutifolia	62±2.22	31±1.91	408.24±3.90	8.89±0.78	26.68±2.00	+	0	150.75±5.98	192.77±8.86	37	21.25±1.90	7.90±0.56	0	++
Prunus ilicifolia	42±3.00	31±2.78	296.20±8.90	10.38±1.02	16.43±1.50	+	0	132.34±7.90	116.77±8.95	45	11.67±1.13	8.65±0.81	0	++
Prunus lusitanica	24±2.00	24±1.99	346.80±9.91	7.66±0.56	20.21±2.00	+	0	108.75±4.40	188.57±4.56	31	14.29±1.00	7.32±0.54	0	+
Quillaja saponaria	36±2.29	18±1.47	502.60±9.54	12.20±1.10	23.18±2.00	+	452.58±17.3	0	0	0	9.76±0.89	4.88±0.39	0	+
Acacia podalyriaefolia	29±2.86	17±1.56	234.00±8.90	7.80±0.98	15.60±1.50	+	0	124.80±7.89	62.40±6.24	57	15.60±1.50	7.80±0.80	+	++
Acacia rostellifera	78±5.50	5±0.50	553.80±9.78	7.80±0.90	15.60±1.50	+	0	241.80±8.96	257.40±8.81	44	23.40±2.30	7.80±0.79	0	++
Brachysema sericeum	21±1.91	10±0.97	304.20±9.86	15.60±1.57	31.20±3.12	+	0	101.40±8.98	117.00±8.56	33	15.60±1.50	23.40±2.30	0	+++
Ceratonia siliqua	45±3.46	33±3.00	451.51±8.97	18.68±1.90	40.48±3.96	++	0	194.45±8.99	159.50±8.69	42	21.45±2.00	16.95±1.70	0	+
Aporosa yunnanensis	72±0.69	23±0.19	188.17±4.33	11.14±2.18	58.90±2.02	+	104.82±1.32	0	0	0	15.60±1.94	11.14±4.21	0	+
Antidesma venosum	90±1.47	27±1.18	146.99±2.20	7.59±0.25	16.17±0.87	+	0	57.82±4.44	49.00±4.99	40	12.74±1.53	3.67±0.43	0	+
Glochidion obovatum	32±0.36	19±0.21	265.50±6.16	15.00±1.95	19.50±1.63	+	0	64.50±3.19	141.00±8.42	24.4	16.50±1.63	9.00±1.32	0	+
Boronia crenulata	8±0.76	3±0.26	296.40±4.45	7.80±8.00	15.60±1.55	+	249.60±6.66	0	0	0	11.70±1.20	11.70±1.18	0	++
Diplolaena microchephala	17±1.65	7±0.66	265.20±5.56	7.80±7.78	15.60±1.55	+	0	78.00±7.80	140.40±8.78	29	15.60±1.60	7.80±0.76	++	++

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Mischocarpus pentapetalus	190±1.16	56±0.43	95.28±7.87	7.80±0.89	7.80±0.76	+	0	35.88±1.72	31.20±3.82	35.9	4.80±1.95	7.80±0.97	0	+
Lithraea caustica	39±3.87	19±1.85	317.10±9.97	10.50±1.05	14.64±1.50	++	0	135.82±8.77	135.00±9.87	42	13.82±1.40	7.32±0.73	+	++
Pistacia atlantica	31±3.00	32±2.99	253.90±8.97	4.90±0.46	30.00±0.50	+	0	115.30±7.90	91.50±9.00	45	7.30±0.70	4.90±0.39	0	+
Pistacia lentiscus	39±3.90	13±1.27	246.57±4.49	5.79±0.60	11.59±1.16	+	0	98.21±6.66	117.42±9.45	40	9.45±0.90	4.11±0.40	0	+
Rhus excisa	31±3.00	6±0.50	249.60±7.78	7.80±0.80	15.60±1.60	++	0	70.20±7.00	132.60±9.81	28	15.60±1.60	7.80±0.80	0	+++
Ilex aquifolium	71±6.00	42±4.23	556.61±6.89	10.98±1.98	35.83±2.22	+	0	162.26±5.54	320.86±6.43	29	13.72±1.32	12.96±1.30	0	+
Ilex canariensis	36±3.00	57±1.99	423.96±8.78	9.58±1.00	11.85±1.10	+	0	137.33±8.00	219.90±8.56	33	13.94±1.23	8.71±0.80	0	+
Ilex rugosa	28±1.95	8±0.73	313.20±10.6	12.00±0.98	22.80±1.40	+	0	74.40±4.75	170.40±4.75	24	20.40±1.7	12.00±0.90	0	+
Ceanothus megacarpus	15±1.45	6±0.50	582.22±9.73	12.68±1.30	16.15±1.64	++	484.40±8.89	0	0	0	13.84±1.40	16.15±1.60	++	+++
Ceanothus oliganthus	9±0.97	6±0.56	179.39±8.89	8.09±0.80	50.23±4.45	++	0	61.05±5.00	50.38±4.67	34	13.23±1.30	6.41±0.60	++	+++
Ceanothus spinosus	19±1.89	11±0.90	342.50±3.50	8.65±7.80	52.77±5.00	++	0	66.08±8.90	197.74±9.00	19	13.84±1.40	3.46±0.34	0	++
Rhamnus alaternus	31±3.00	19±1.50	253.80±6.90	8.70±0.81	17.70±1.45	+	0	88.80±6.00	116.00±9.87	35	10.80±1.01	11.80±1.15	0	+
Rhamnus californica	36±3.00	19±1.34	171.59±2.90	8.15±0.79	29.34±1.47	+	0	56.96±5.21	63.02±6.00	33	8.69±0.70	5.43±0.56	0	++
Rhamnus crenulata	34±2.99	19±1.30	253.64±7.89	4.88±0.44	19.00±1.90	+	0	66.60±6.00	144.40±3.99	31	15.86±1.50	2.90±0.20	0	+
Rhamnus glandulosa	36±3.55	20±1.91	285.80±8.85	6.62±0.45	18.12±1.10	+	0	81.56±8.00	158.25±7.99	34	16.03±1.45	5.22±0.54	+	+
Tetrastigma planicaule	152±1.75	49±0.78	135.72±5.69	3.90±0.45	5.46±0.85	+	0	17.00±2.03	100.00±5.30	14	5.46±0.85	3.90±0.31	0	+
Elaeocarpus sylvestris	54±1.18	15±0.29	295.50±1.63	8.25±0.78	19.50±1.63	+	0	114.00±2.73	133.50±3.19	38	16.50±1.63	7.50±0.93	0	+
Urena lobata	35±2.27	24±1.72	129.44±5.80	10.92±1.00	7.80±0.95	+	0	60.80±6.00	34.32±3.21	47	7.80±0.79	7.80±0.57	++	+
Pterospermum lanceaefolium	79±3.45	23±0.78	118.84±1.71	5.46±0.85	4.68±0.70	+	0	49.42±3.58	46.80±2.18	41	5.46±0.85	7.02±0.70	+++	+
Xylosma monospora	114±1.30	32±1.30	163.80±1.30	6.60±0.50	32.40±1.70	+	0	27.00±1.90	64.80±3.10	16	19.80±2.80	13.20±2.08	0	+
Agonis flexuosa	106±7.80	6±0.56	289.90±7.00	12.11±1.10	11.41±1.00	+	0	107.25±6.60	134.94±8.00	36	11.41±1.30	12.80±1.13	0	++
Agonis hypericifolia	10±0.90	6±0.45	306.88±7.99	11.76±1.10	17.30±1.55	+	0	116.60±6.66	135.28±4.99	38	14.87±1.40	11.07±1.10	0	++
Beaufortia decussata	9±0.80	6±0.55	346.32±9.56	13.84±1.29	8.65±0.77	++	0	86.49±8.00	210.36±8.99	25	15.22±1.23	11.76±1.12	+	++
Calothamnus quadrifidus	17±1.67	2±0.90	1126.1±10.0	28.86±2.67	23.84±2.20	+	0	253.87±9.90	766.83±9.99	22	28.86±2.00	23.84±2.10	0	++
Calothamnus sanguineum	18±1.77	2±0.89	667.07±8.99	14.18±1.40	17.30±1.67	+	0	211.05±9.71	393.40±7.99	32	15.57±1.44	15.57±1.10	0	++
Darwinia lejostyla	5±0.20	2±0.02	449.78±9.78	14.53±1.23	22.14±2.12	+	0	60.55±6.00	317.28±7.99	13	21.10±1.99	14.18±1.22	0	++
Eucalyptus caesia	80±7.00	34±2.99	616.72±7.99	29.65±0.80	18.06±1.54	+++	522.90±9.97	0	0	0	17.30±1.55	29.20±1.00	0	+++
Eucalyptus calophylla	77±0.77	35±0.32	311.66±7.99	8.65±2.02	17.64±1.22	+++	0	104.83±9.00	146.70±4.99	33	17.30±1.70	16.60±2.45	0	+++
Eucalyptus marginata	150±2.99	34±2.20	356.00±6.99	16.26±1.55	20.06±1.99	+++	0	93.76±9.00	189.60±9.00	26	19.37±1.76	16.95±1.54	0	+++
Hypocalymma angustifolium	13±1.00	2±1.02	667.40±6.99	11.41±1.10	15.57±1.12	+	0	274.02±9.02	339.77±8.96	41	15.22±1.50	11.41±1.09	0	+++
Kunzea recurva	3±0.22	2±0.11	347.69±9.03	12.45±1.11	17.64±1.60	++	286.82±21.50	0	0	0	14.87±1.33	15.91±1.49	0	++
Melaleuca acerosa	11±1.01	2±0.09	528.64±6.78	13.14±1.23	12.45±1.13	+	0	206.20±7.89	267.80±7.99	39	14.18±1.39	14.87±1.40	0	++
Melaleuca huegelii	5±0.29	2±0.08	461.02±7.99	11.24±1.10	21.62±1.91	+	0	96.01±9.00	298.42±9.00	21	19.89±1.78	13.84±1.22	0	++
Syzygium jambos	181±4.80	40±3.56	272.40±11.1	8.40±1.71	24.00±2.18	+	0	69.60±6.25	144.00±7.02	25	20.40±1.71	6.00±0.70	0	+
Blastus cochinchinensis	80±1.75	28±1.63	85.45±1.93	6.92±0.48	10.03±0.89	0	0	24.22±0.85	29.06±1.97	28	6.92±0.69	8.30±0.72	++	+
Melastoma candidum	53±1.24	18±1.47	143.70±2.65	7.80±0.37	20.05±1.48	+	0	49.02±2.02	44.57±2.02	34	14.48±1.01	7.80±0.31	++	+
Melastoma dodecandrum	79±4.75	30±1.93	156.00±6.78	7.80±0.15	22.09±2.18	+	0	44.19±3.58	51.99±3.04	28	22.09±1.17	7.80±1.18	0	+
Melastoma sanguineum	121±3.15	32±1.18	97.47±3.27	7.80±0.85	15.60±0.71	+	0	32.49±1.17	24.69±1.26	30	9.09±1.17	7.80±0.31	0	+

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Schefflera octophylla	108±1.96	28±0.89	176.79±3.43	3.90±0.66	20.79±2.41	+	128.70±4.05	0	0	0	19.50±1.56	3.90±0.72	0	+
Heteromorpha trifoliata	45±3.23	17±1.30	113.63±3.67	9.66±0.63	17.12±1.20	++	0	34.52±2.28	39.72±1.21	30	5.20±0.50	7.41±1.37	++	+
Arbutus canariensis	45±2.28	28±1.75	243.98±7.99	9.76±0.56	12.20±1.19	+	0	101.43±6.66	102.82±8.09	41	11.50±1.12	6.26±0.55	0	+
Arbutus menziesii	46±3.00	28±2.00	237.43±7.99	6.92±0.55	18.59±1.13	+	0	102.93±7.00	91.69±8.00	43	6.92±0.54	10.38±1.00	0	++
Arbutus unedo	76±5.55	31±2.34	240.93±9.65	5.28±0.46	24.19±2.00	+	0	89.87±5.99	102.07±8.90	37	15.25±1.20	4.27±0.39	0	+
Arctostaphylos glandulosa	45±4.00	24±2.00	360.90±9.78	10.18±1.00	13.56±1.30	++	308.86±9.87	0	0	0	14.72±1.40	13.57±1.29	0	++
Arctostaphylos glauca	36±3.00	23±2.07	635.48±9.04	19.60±1.89	11.53±1.10	++	580.13±8.88	0	0	0	13.84±1.30	10.38±1.00	0	++
Erica multiflora	9±0.55	4±0.09	526.40±9.67	21.12±2.00	70.56±7.00	+	0	216.48±9.69	174.24±8.90	41	21.12±1.99	22.88±2.00	+	+++
Erica plukenetii	8±2.94	4±0.15	396.00±3.67	11.50±1.40	40.80±1.79	+	0	85.80±5.60	208.00±6.70	22	40.80±1.29	9.90±1.50	+	+++
Ardisia sieboldii	114±8.21	41±3.56	212.20±8.73	2.76±0.23	21.60±1.71	+	164.40±4.75	0	0	0	20.40±1.71	2.85±0.07	0	+
Myrsine africana	16±1.30	7±1.30	213.23±1.76	10.78±0.32	15.92±0.90	+	0	85.01±2.46	80.77±6.04	40	11.11±0.94	9.64±0.44	++	+
Rapanea melanophloeos	95±2.50	32±1.30	448.73±2.50	24.00±1.30	22.29±1.13	+	0	118.29±3.93	240.86±4.30	26	25.29±1.31	18.00±1.33	0	+
Sideroxylon inerme	55±3.23	30±1.91	556.50±3.67	19.50±1.50	52.5±2.66	++	0	271.50±7.50	163.50±6.65	49	31.50±1.50	18.00±2.45	0	+
Diospyros morrisiana	80±4.21	38±1.56	120.12±1.40	7.80±0.71	14.04±1.71	+	0	39.00±2.18	37.44±1.40	32	14.04±0.54	7.80±0.66	0	+
Euclea divinorum	42±1.89	21±1.30	221.34±1.90	7.60±2.56	21.17±1.99	++	0	55.86±9.00	110.25±9.76	25	19.11±1.83	7.35±2.30	0	+
Euclea racemosa	20±2.00	9±0.09	462.00±9.99	18.00±2.30	30.00±2.99	+	0	72.00±7.00	300.40±7.89	16	30.00±2.22	12.00±2.20	0	++
Euclea undulata	20±1.89	9±0.08	358.80±9.29	23.40±1.78	23.40±2.99	+	0	93.60±9.00	179.40±7.89	26	15.60±1.52	23.40±2.30	0	++
Olea europaea	74±7.20	15±1.30	451.20±6.20	12.54±1.20	15.68±1.59	++	0	136.98±6.99	268.05±8.90	30	11.85±1.63	6.10±0.60	++	+
Olea europaea ssp.africana	75±2.20	12±1.30	188.40±5.55	7.35±1.60	13.23±1.04	++	0	51.45±8.99	98.49±3.09	27	12.25±1.20	5.63±0.46	++	+
Olea europaea ssp.cerasif.	71±6.00	15±1.30	366.64±5.59	6.95±1.20	10.24±1.08	++	0	167.62±8.99	163.95±5.90	46	12.20±1.18	5.73±0.60	++	+
Phillyrea angustifolia	43±4.00	6±0.50	307.71±6.99	12.07±1.02	7.80±0.70	++	0	112.48±7.90	155.18±7.66	36	6.10±0.56	14.15±1.32	0	+
Phillyrea media	41±4.00	22±2.00	306.44±9.71	11.52±1.10	10.16±1.00	++	0	108.70±6.99	155.60±7.90	35	9.48±0.93	10.98±1.09	0	+
Psychotria capensis	115±1.20	32±2.60	186.66±1.18	6.98±0.38	24.31±1.67	+	0	50.52±1.03	85.68±2.25	27	11.60±0.89	7.57±0.39	0	+
Psychotria manillensis	190±1.18	65±5.61	191.10±1.21	7.35±0.48	22.05±1.35	+	132.30±1.87	0	0	0	22.05±1.15	7.35±0.42	0	+
Psychotria zombamontana	90±2.20	32±2.60	137.18±1.91	7.87±0.27	14.48±0.21	+	0	40.73±1.29	58.37±1.98	30	8.96±0.56	6.77±0.31	0	+
Rosmarinus officinalis	28±2.00	3±0.23	285.78±8.96	12.80±1.21	22.14±2.10	+	0	113.83±7.77	111.41±8.09	40	14.53±1.02	11.07±0.99	++	+
Viburnum rigidum	58±1.46	24±0.47	405.58±6.08	7.80±0.34	23.40±1.87	+	0	152.10±6.16	197.59±3.04	36	16.89±1.17	7.80±0.26	0	+
Viburnum rugosa	57±5.00	28±2.00	386.42±7.99	9.76±0.90	19.21±1.80	+	0	119.56±7.77	219.60±7.65	37	13.11±1.30	5.18±0.49	+	+
Viburnum tinus	59±4.44	29±1.91	302.25±7.54	3.38±0.31	29.14±2.87	+	0	108.70±5.99	142.60±8.88	36	15.72±1.50	2.71±0.20	+	+
Vernonia sp.	106±1.97	32±2.41	261.10±4.29	10.39±1.48	29.89±1.17	+	0	88.49±3.2	100.02±8.7	34	24.69±1.17	7.80±0.15	0	+
Smilax aspera	46±3.00	36±3.01	300.27±7.98	8.70±5.56	19.17±1.23	+	0	99.34±8.90	151.28±7.56	33	15.68±1.53	6.10±0.06	0	+
Smilax canariensis	46±2.99	40±3.89	297.86±7.90	7.12±0.67	14.23±1.32	+	257.00±9.21	0	0	0	13.21±1.23	6.30±0.56	0	+
Smilax china	46±2.25	44±4.01	199.80±18.4	3.60±0.70	26.40±1.85	+	140.40±4.21	0	0	0	26.4±1.71	3.00±0.26	0	+
Caryota mitis	69±3.15	44±3.71	127.39±4.05	3.90±0.61	27.30±1.56	+	72.79±4.83	0	0	0	19.50±3.04	3.90±1.21	+	+
Photos repens	104±0.28	7±1.30	100.09±1.71	3.90±0.68	11.70±1.56	+	74.10±3.04	0	0	0	6.49±0.70	3.90±0.41	0	+
Rhaphydophora angustifolia	110±8.21	27±1.18	389.83±18.6	16.89±1.88	75.39±6.63	+	0	36.39±2.81	196.26±4.44	9	42.90±4.44	22.00±2.18	0	+

SPECIES	LOWER STOMATAL DENSITY	LOWER STOMATAL LENGTH	LOWER STOMATAL WIDTH	LOWER STOMATAL SURFACE	LOWER TRASPIRING SURFACE	TR.SURF / LEAF AREA %	UPPER STOMATAL DENSITY	UPPER STOMATAL LENGTH	UPPER STOMATAL WIDTH	UPPER STOMATAL SURFACE	UPPER TRANSPIR. SURFACE	TR. SURF / LEAF SURFACE %
Hemigramma decurrens	44±3.95	48.51±3.12	35.28±1.71	855.70	37,651	3.8	0	0	0	0	0	0
Microopteris chinensis	355±19.76	36.75±3.58	22.05±1.40	405.10	143,775	14.3	0	0	0	0	0	0
Podocarpus latifolius	111± 0.69	40.00±2.45	30.00±2.84	600.00	66,600	6.6	0	0	0	0	0	0
Castanopsis chinensis	400±19.76	22.05±2.80	17.64±1.40	194.40	77,760	7.7	0	0	0	0	0	0
Castanopsis cuspidata	400±17.35	29.40±0.78	14.70±0.28	216.09	86,436	8.6	0	0	0	0	0	0
Castanopsis fissa	577±19.76	24.99±0.35	14.70±0.28	183.60	105,937	10.6	0	0	0	0	0	0
Quercus agrifolia	222±12.83	17.38±2.00	10.86±2.25	94.37	20,951	2.1	0	0	0	0	0	0
Quercus chrysolepis	400±16.74	17.28±1.20	10.27±0.83	130.33	35,495	3.5	0	0	0	0	0	0
Quercus hui	488±16.45	19.11±0.44	14.70±0.28	140.40	68,515	6.8	0	0	0	0	0	0
Quercus ilex	266±16.45	18.16±0.99	17.30±1.28	157.12	41,762	4.2	0	0	0	0	0	0
Quercus mirsinaefolia	533±19.21	19.11±0.44	11.76±1.56	112.30	59,856	5.9	0	0	0	0	0	0
Quercus serrata	933±18.66	16.17±2.18	13.23±0.38	106.90	99,738	10.0	0	0	0	0	0	0
Quercus suber	222±11.83	18.16± 0.30	34.60±2.33	314.16	69,708	7.0	0	0	0	0	0	0
Gironniera subaequalis	311±18.14	22.05±1.71	11.76±0.38	129.60	40,306	4.0	0	0	0	0	0	0
Ficus nervosa	400±17.63	14.70±0.35	11.76±0.38	86.43	34,572	3.4	0	0	0	0	0	0
Celtis sinensis	488±16.48	14.70±2.65	8.82±1.40	64.82	31,632	3.2	0	0	0	0	0	0
Adenanthos cuneatus	577±15.56	23.04±1.13	13.84±0.96	159.43	91,991	9.2	400±18.30	21.90±1.67	13.84±1.12	151.54	60,616	6.1
Banksia grandis	0	0	0	0	0	0	0	0	0	0	0	0
Banksia littoralis	355±12.66	23.04±1.99	14.98±1.50	172.56	61,237	6.1	0	0	0	0	0	0
Banksia quercifolia	0	0	0	0	0	0	0	0	0	0	0	0
Conospermum caeruleum	311±11.09	27.69±2.66	13.8±0.99	191.54	59,569	5.9	222±20.00	28.68±2.80	13.85±0.96	199.78	35,433	3.5
Conospermum crassinervium	311±11.11	27.29±2.80	9.79±1.14	130.69	40,023	4.0	222±20.05	27.68±3.00	9.45±1.40	130.78	28,860	2.8
Faurea saligna	189±21.28	30.54±1.81	26.46±1.41	404.04	76,356	7.6	189±21.20	30.54±1.81	26.46±1.41	404.04	76,364	7.6
Grevillea pulchella	266±19.05	9.50±1.00	7.12±0.66	33.82	9,044	0.9	0	0	0	0	0	0
Isopogon attenuatus	266±12.83	24.22±2.00	14.87±1.30	180.07	47,899	5.0	222±12.87	36.33±2.55	23.63±2.00	424.33	94,201	9.4
Lambertia multiflora	222±20.56	40.34±2.22	23.04±1.97	464.71	103,166	10.3	0	0	0	0	0	0
Leucadendron gandogeri	178±12.83	36.72±0.69	24.99±0.73	459.19	81,736	8.2	178±12.83	26.79±0.69	23.19±0.73	310.38	55,230	5.5
Leucadendron linoides	200±12.83	20.58±1.56	15.55±1.21	159.70	31.940	3.2	200±12.83	20.58±1.67	15.75±1.21	159.70	31,940	3.1
Leucadendron nervosum	133±12.83	60.58±0.77	48.00±2.74	1440.00	191,520	19.1	133±12.83	45.33±0.77	37.33±0.74	846.07	112,529	11.2
Leucadendron salignum	177±11.11	66.00±1.31	60.00±4.44	1980.00	350,460	35.0	177±11.11	66.00±0.45	60.00±4.47	1980.00	350,460	35.0
Leucospermum calligerum	267±02.83	26.62±1.76	20.09±2.60	263.20	70,243	7.0	222±12.83	26.62±1.41	20.09±1.41	263.38	58,470	5.8
Leucospermum hypophyll.	177±16.45	32.18±4.44	18.95±4.28	304.90	47,259	4.7	155±12.80	32.18±4.45	18.95±4.43	304.90	47,275	4.7
Persoonia longifolia	133±11.11	55.07±3.00	30.84±2.40	857.35	114,087	11.4	89±7.00	58.60±6.00	29.30+3.00	858.49	76,405	7.6
Petrophile ericifolia	200±19.81	29.06±2.79	22.08±2.70	320.35	64,070	6.4	200±11.11	29.07±3.00	22.04±1.80	320.35	64,070	6.4
Petrophile linearis	355+19.00	35.40±1.45	26.80±1.41	475.34	168,745	16.9	222±20.69	31.44±1.45	17.30±1.41	269.36	59,798	6.0
Protea amplexicaulis	44±5.60	69.30±2.64	64.07±1.60	2218.60	97,618	9.8	44±2.69	69.33±1.45	64.00±1.60	2218.6	98,595	9.8
Protea cynaroides	67±1.69	64.00±2.73	52.67±2.00	1685.40	112,922	11.2	44±0.69	64.00±2.73	52.67±2.00	1685.40	74,899	7.4
Protea latifolia	133±11.69	39.00±3.37	31.20±3.63	608.41	80,917	8.1	133±11.83	39.00±4.37	31.20±2.73	608.41	80,917	8.1

SPECIES	LOWER STOMATAL DENSITY	LOWER STOMATAL LENGTH	LOWER STOMATAL WIDTH	LOWER STOMATAL SURFACE	LOWER TRANSPIRING SURFACE	TR.SURF / LEAF AREA %	UPPER STOMATAL DENSITY	UPPER STOMATAL LENGTH	UPPER STOMATAL WIDTH	UPPER STOMATAL SURFACE	UPPER TRANSPIR. SURFACE	TR.SURF. / LEAF SURFACE %
Protea longifolia	89±7.04	64.00±4.00	54.00±3.00	1728.00	153,792	11.4	89±5.08	64.00±4.00	54.00±3.00	1728.03	153,602	15.4
Protea welwitschii	211±21.84	15.07±5.00	12.49±3.10	94.12	19,858	2.0	67±12.00	15.07±6.00	12.49±3.00	94.10	6,305	0.6
Stirlingia-latifolia	311±12.83	24.22±4.00	12.97±1.87	157.00	48,827	4.9	222±18.00	25.08±2.70	14.70±1.90	184.31	40,921	4.1
Synaphaea petiolaris	222+12.57	40.32±2.40	17.30±1.30	348.00	77,465	7.7	133±11.99	36.88±3.60	18.44±1.50	340.01	45,224	4.5
Xylomelum occidentale	222±10.85	42.65±4.30	29.96±3.00	638.83	141,835	14.2	177±16.00	44.98±4.60	29.96±3.00	637.90	119,238	12.0
Peumus boldus	177±7.84	22.80±2.30	24.70±2.50	281.51	49,840	5.0	0	0	0	0	0	0
Cryptocarya alba	355±28.11	16.45±1.00	15.82±1.43	130.10	46,192	4.6	0	0	0	0	0	0
Cryptocarya chinensis	444±23.56	19.11±0.44	14.70±0.28	140.40	62,337	6.2	0	0	0	0	0	0
Cryptocarya concinna	711±28.64	23.52±2.08	17.64±1.76	207.40	147,461	14.7	0	0	0	0	0	0
Laurus azorica	222±21.15	26.00±2.00	26.00±2.50	338.00	75,036	7.6	0	0	0	0	0	0
Laurus nobilis	177±12.45	27.60±1.44	26.00±1.28	358.80	63,508	6.3	0	0	0	0	0	0
Lindera chunii	533±19.87	22.05±1.71	14.70±1.71	162.00	86,381	8.6	0	0	0	0	0	0
Neolitsea sericea	311±18.14	19.11±0.44	17.64±1.40	168.52	52,403	5.2	0	0	0	0	0	0
Hibbertia cuneiformis	355±23.45	27.50±2.00	17.50±1.47	240.63	85,422	8.5	0	0	0	0	0	0
Hibbertia hypericoides	355±23.45	23.70±2.00	12.50±1.00	148.10	52,575	5.2	0	0	0	0	0	0
Eurya japonica	444±23.11	17.64±0.48	11.76±1.28	103.70	46,043	4.6	0	0	0	0	0	0
Ternostroemia japonicua	177±11.12	29.40±2.18	22.05±2.18	320.10	566,578	5.7	0	0	0	0	0	0
Itea chinensis	533±19.45	14.70±0.34	7.35±0.28	54.01	28,792	2.9	0	0	0	0	0	0
Pittosporum viridiflorum	222±11.11	18.56±1.05	11,39±0.67	105.09	23,329	2.3	0	0	0	0	0	0
Adenostoma fasciculatum	311±12.32	26.60±2.46	23.37±1.78	310.82	96,658	9.7	0	0	0	0	0	0
Heteromeles arbutifolia	311±23.44	20.53±1.89	13.53±1.29	138.88	43,191	4.3	0	0	0	0	0	0
Prunus ilicifolia	266±13.65	25.43±2.00	20.54±1.97	261.16	69,468	6.9	0	0	0	0	0	0
Prunus lusitanica	222±11.11	25.20±2.43	24.40±2.34	307.40	68,243	6.8	0	0	0	0	0	0
Quillaja saponaria	488±32.16	25.65±2.00	15.20±1.45	194.94	95,131	9.5	488±35.00	25.65±2.63	15.03+2.00	194.00	95,111	9.5
Acacia podalyriaefolia	311±23.12	26.25±2.57	21.25±2.10	278.90	86,737	8.7	311±30.00	26.25±2.60	21.25±2.10	278.90	57,118	5.7
Acacia rostellifera	311±23.12	29.00±3.00	9.60±0.94	139.20	43,291	4.3	266±25.01	29.00±3.00	9.60±0.94	139.20	37,031	3.7
Brachysema sericeum	133±13.00	16.25±1.60	18.34±0.12	149.03	19,821	1.9	0	0	0	0	0	0
Ceratonia siliqua	318±27.98	14.25±1.42	7.60±0.75	54.15	17,220	1.7	0	0	0	0	0	0
Aporosa yunnanensis	355±30.68	17.64±1.71	14.70±1.71	129.60	46,008	4.6	0	0	0	0	0	0
Antidesma venosum	166±21.28	13.88±0.55	5.88±0.49	40.81	6,773	0.7	0	0	0	0	0	0
Glochidion obovatum	533±28.59	17.64±1.28	13.23±1.18	116.60	62,148	6.2	0	0	0	0	0	0
Boronia crenulata	311±27.80	30.00±2.98	27.50±2.70	412.50	128,287	12.8	311±27.80	30.00±3.00	27.50±2.70	412.50	36,857	3.7
Diplolaena microchephala	222±21.22	20.00±1.98	20.00±1.97	200.00	44,440	4.4	0	0	0	0	0	0
Mischocarpus pentapetalus	355±28.36	20.58±1.71	11.76±0.70	121.01	42,955	4.3	0	0	0	0	0	0
Lithraea caustica	355±39.00	21.85±2.22	13.30±1.30	145.30	51,581	5.1	0	0	0	0	0	0
Pistacia atlantica	222±11.11	26.90±2.60	22.00±2.00	295.90	65,690	6.6	0	0	0	0	0	0
Pistacia lentiscus	222±11.11	26.00±3.00	18.70±1.90	243.10	53,968	5.4	0	0	0	0	0	0
Rhus excisa	533±23.46	24.00±2.40	12.00±1.00	144.00	76,752	7.6	533±9.92	24.00±2.50	12.00±1.00	144.00	76,752	7.6

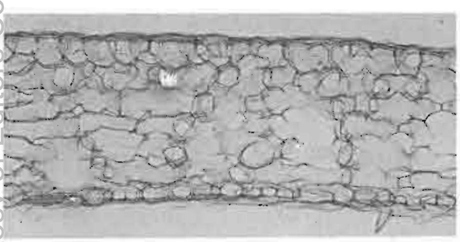
SPECIES	LOWER STOMATAL DENSITY	LOWER STOMATAL LENGTH	LOWER STOMATAL WIDTH	LOWER STOMATAL SURFACE	LOWER TRANSPIRING SURFACE	TR. SURF / LEAF AREA %	UPPER STOMATAL DENSITY	UPPER STOMATAL LENGTH	UPPER STOMATAL WIDTH	UPPER STOMATAL SURFACE	UPPER TRANSPIR. SURFACE	TR. SURF. / LEAF SURFACE %
Ilex aquifolium	266±23.00	22.80±2.20	20.30±1.90	231.40	61,552	6.1	0	0	0	0	0	0
Ilex canariensis	133±0.69	21.70±1.99	15.40±1.45	167.10	22,214	2.2	0	0	0	0	0	0
Ilex rugosa	266±88.89	32.34±2.43	22.05±1.69	356.50	94,842	9.4	0	0	0	0	0	0
Ceanothus megacarpus	0	0	0	0	0	0	0	0	0	0	0	0
Ceanothus oliganthus	177±13.00	17.93±1.00	8.15±0.56	73.00	12,931	1.3	0	0	0	0	0	0
Ceanothus spinosus	355±13.54	17.15±1.70	13.80±0.23	118.00	41,890	4.2	0	0	0	0	0	0
Rhamnus alaternus	266±88.89	25.20±2.13	20.30±2.00	255.80	68,043	6.8	0	0	0	0	0	0
Rhamnus californica	311±18.14	22.82±2.20	15.75±1.50	179.70	55,887	5.6	0	0	0	0	0	0
Rhamnus crenulata	177±11.09	27.60±2.46	23.60±2.30	325.70	57,649	5.8	0	0	0	0	0	0
Rhamnus glandulosa	222±11.11	23.60±2.30	22.00±2.00	259.60	57,631	5.7	0	0	0	0	0	0
Tetrastigma planicaule	311±18.14	22.05±2.80	14.70±2.18	162.06	50,400	5.0	0	0	0	0	0	0
Elaeocarpus sylvestris	577±88.92	24.99±2.80	14.70±1.95	183.60	105,937	10.5	0	0	0	0	0	0
Urena lobata	444±28.72	23.52±2.35	14.70±2.07	172.80	76,723	7.7	0	0	0	0	0	0
Pterospermum lanceaefolium	577±88.92	17.64±1.28	13.23±1.15	116.60	67,278	6.7	0	0	0	0	0	0
Xylosma monospora	311±18.14	21.56±0.60	16.58±1.05	178.73	55,575	5.6	0	0	0	0	0	0
Agonis flexuosa	133±11.11	16.43±1.50	9.08±0.90	74.59	9,921	0.9	177±11.00	15.57±1.45	8.65±0.80	67.34	11,919	1.2
Agonis hypericifolia	266±12.83	16.71±1.13	8.65±0.80	72.27	19,224	2.0	222±16.70	16.71±1.50	9.20±0.90	78.86	17,505	1.7
Beaufortia decussata	222±10.00	19.37±1.87	17.30±1.20	167.55	37,185	3.7	222±10.00	25.26±2.00	18.33±1.45	231.50	51,282	5.1
Calothamnus quadrifidus	222±9.90	16.85±1.59	7.33±0.69	61.75	13,708	1.3	222±12.90	16.85±1.56	7.78±0.70	61.75	13,708	1.3
Calothamnus sanguineum	266±12.83	17.71±1.68	10.79±1.09	95.54	25,413	2.5	266±12.79	17.21±1.56	10.79±0.55	95.54	25,413	2.5
Darwinia lejostyla	222±11.11	26.40±2.20	23.10±2.00	304.90	67,688	6.8	0	0	0	0	0	0
Eucalyptus caesia	349±23.00	31.14±1.23	17.30±0.56	269.36	57,480	5.7	222+15.00	33.42+3.25	17.30+1.20	289.08	64,176	6.4
Eucalyptus calophylla	266±12.83	29.42±3.00	14.70±1.44	216.09	94,006	9.4	0	0	0	0	0	0
Eucalyptus marginata	266±15.00	20.58±1.22	14.70±0.33	151.20	40,219	4.0	0	0	0	0	0	0
Hypocalymma angustifolia	222±15.09	14.86±1.22	6.05±0.60	44.98	9,985	1.0	222±15.08	14.25±1.29	6.47±0.50	46.09	10,212	1.0
Kunzea recurva	133±10.22	31.14±1.89	19.89±3.00	309.68	41,187	4.1	133±10.09	17.30±1.66	8.30±0.80	71.80	9,549	0.9
Melaleuca acerosa	311±11.11	18.58±1.70	9.06±0.90	84.16	26,155	2.6	311±11.11	18.16±1.79	8.65±0.79	78.54	24,425	2.4
Melaleuca huegelii	266±12.83	22.04±2.12	11.66±1.10	128.50	34,181	3.4	266±12.83	31.14±3.00	20.76±2.00	323.23	85,918	8.6
Syzygium jambos	533±19.90	29.40±2.61	17.64±1.48	259.30	138,207	13.8	0	0	0	0	0	0
Blastus cochinchinensis	400±19.75	26.46±0.28	23.52±0.22	311.10	124,440	12.4	0	0	0	0	0	0
Melastoma candidum	311±12.83	17.64±1.36	14.70±1.28	129.60	40,305	4.0	0	0	0	0	0	0
Melastoma dodecandrum	311±11.45	16.17±0.28	13.23±1.46	106.90	33,246	3.3	0	0	0	0	0	0
Melastoma sanguineum	311±11.83	24.90±2.80	19.11±1.86	238.00	73,987	8.7	0	0	0	0	0	0
Schefflera octophylla	177±11.11	17.64±1.32	16.17±0.93	142.60	25,240	2.5	0	0	0	0	0	0
Heteromorpha trifoliata	311±11.11	21.54±1.22	13.23±0.92	142.48	44,311	5.5	0	0	0	0	0	0
Arbutus canariensis	222±10.89	28.50±2.00	21.10±1.79	300.70	66,755	6.6	0	0	0	0	0	0
Arbutus menziesii	311±22.00	20.58±1.50	13.23±0.70	136.02	42,336	4.2	0	0	0	0	0	0
Arbutus unedo	311±16.00	28.50±2.65	23.60±2.01	336.30	104,589	10.4	0	0	0	0	0	0

SPECIES	LOWER STOMATAL DENSITY	LOWER STOMATAL LENGTH	LOWER STOMATAL WIDTH	LOWER STOMATAL SURFACE	LOWER TRANSPIRING SURFACE	TR.SURF / LEAF AREA %	UPPER STOMATAL DENSITY	UPPER STOMATAL LENGTH	UPPER STOMATAL WIDTH	UPPER STOMATAL SURFACE	UPPER TRANSPIR. SURFACE	TR. SURF. / LEAF SURFACE %
Arctostaphylos glandulosa	266±11.34	31.54±3.00	27.17±2.50	428.47	113,937	11.3	177±11.11	31.54±3.09	27.17±1.99	428.47	75,839	7.6
Arctostaphylos glauca	311±12.83	28.25±2.78	22.27±2.00	314.56	97,829	9.8	222±12.83	28.25±2.56	22.27±2.00	314.56	69,832	7.0
Erica multiflora	355±13.98	9.00±0.89	9.15±0.56	41.20	14,626	1.5	0	0	0	0	0	0
Erica plukenetii	355±14.99	9.00±0.88	9.15±0.66	41.20	14,626	1.5	0	0	0	0	0	0
Ardisia sieboldii	311±11.27	22.05±3.15	14.70±1.60	162.06	50,400	5.0	0	0	0	0	0	0
Myrsine africana	266±12.83	20.91±0.87	14.86±0.67	155.36	41,326	4.1	0	0	0	0	0	0
Rapanea melanophloeos	222±11.11	24.01±1.20	18.62±0.98	223.53	49,624	4.9	0	0	0	0	0	0
Sideroxylon inerme	266±88.89	18.95±1.28	16.33±1.19	154.73	41,150	4.1	0	0	0	0	0	0
Diospyros morrisiana	266±11.31	17.64±1.40	13.23±3.58	116.60	31,016	3.1	0	0	0	0	0	0
Euclea divinorum	255±11.11	19.84±1.28	11.76±0.89	116.66	29,748	2.9	0	0	0	0	0	0
Euclea racemosa	39±12.56	90.00±7.00	60.20±1.00	2700.00	105,300	10.3	0	0	0	0	0	0
Euclea undulata	88±12.77	66.00±8.99	36.00±4.99	1188.00	104,544	10.5	0	0	0	0	0	0
Olea europaea	266±11.11	15.40±3.78	10.60±0.20	81.50	21,706	2.1	0	0	0	0	0	0
Olea europaea ssp.africana	266±11.99	19.70±2.30	13.39±1.23	132.30	35,192	3.5	0	0	0	0	0	0
Olea europaea ssp.cerasif.	177±10.99	23.60±2.54	13.60±1.03	153.60	27,152	2.7	0	0	0	0	0	0
Phillyrea angustifolia	177±0.69	26.00±2.43	21.10±2.00	274.30	48,551	4.8	0	0	0	0	0	0
Phillyrea media	177±0.89	26.00±2.15	22.80±2.07	296.40	52,463	5.2	0	0	0	0	0	0
Psychotria capensis	200±12.83	14.37±0.74	9.37±0.70	67.32	13,464	1.3	0	0	0	0	0	0
Psychotria manillensis	400±22.09	29.40±1.89	19.11±0.43	280.90	112,360	11.2	0	0	0	0	0	0
Psychotria zombamontana	222±11.11	14.54±0.82	13.39±0.75	97.34	21,609	2.2	0	0	0	0	0	0
Rosmarinus officinalis	488±33.19	13.84±1.20	8.65±0.77	59.85	29,207	2.9	0	0	0	0	0	0
Viburnum rigidum	177±6.86	35.28±4.75	22.05±2.65	388.90	68,835	6.8	0	0	0	0	0	0
Viburnum rugosa	266±12.78	29.30±2.76	23.60±2.30	345.70	91,956	9.2	0	0	0	0	0	0
Viburnum tinus	266±12.76	34.20±3.00	25.20±2.50	430.40	114,486	11.4	0	0	0	0	0	0
Vernonia sp.	222±11.12	32.34±5.30	20.58±1.70	332.70	73,859	7.4	0	0	0	0	0	0
Smilax aspera	177±1.00	31.70±2.99	26.00±2.00	412.00	72,924	7.3	0	0	0	0	0	0
Smilax canariensis	177±2.09	36.60±3.00	27.60±2.65	505.10	89,403	8.9	0	0	0	0	0	0
Smilax china	133±0.69	24.40±3.75	14.99±1.96	182.87	24,322	2.4	0	0	0	0	0	0
Caryota mitis	444±19.85	33.81±3.12	17.64±1.18	298.00	132,312	13.2	177±3.69	33.81±2.56	10.29±1.15	173.90	30,789	3
Photos repens	177±10.11	17.64±1.56	14.70±1.98	129.60	22,939	2.3	0	0	0	0	0	0
Rhaphydophora angustifolia	177±9.91	33.81±1.56	16.17±1.71	273.30	48,374	4.9	0	0	0	0	0	0

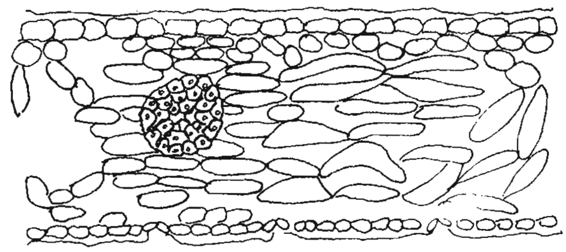
ATLAS OF LEAF ANATOMY

ASPIDIACEAE

Hemigramma decurrens (Hook.) Copel.



145 µm



100 µm

Distribution: *A tall fern which is a typical component of the understorey of dense tropical monsoon forests in southern China.*

Leaf surface attains 25 cm²; lamina (298 µm thick, comparable to the thickest tropical leaves studied) with dorsiventral symmetry.

Upper cuticle uniformly smooth (7.8 µm), glabrous type. Remarkably thick underlying epidermis (up to 27.3 µm wide) consists of compact and quite uniform rectangular cells.

Mesophyll undifferentiated (247.3 µm deep), disposed between the two epidermis as a homogeneous layer of rounded or elongated cells.

Small intercellular spaces present in the mesophyll.

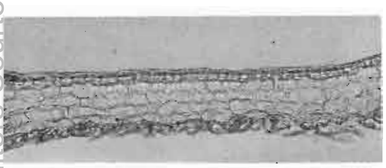
Mechanical tissue almost lacking in leaf section.

Lower epidermis much thinner than the upper and consists of a single layer (average 8.9 µm) of small rectangular cells.

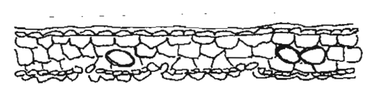
Stomata confined to the lower side, causing asymmetry of the lamina. Stomata (rima 48.5 µm long) are slightly sunken into wide substomatal chambers formed in the mesophyll – the largest among all laurophyll and sclerophyll examples studied – and cover the enormous surface of 855 µm² yet have very low density (does not exceed 44/mm²), so the transpiring surface hardly attains 37,650 µm²/mm² (only 3.8% of the leaf area).

GLEICHENIACEAE

Hicriopteris chinensis (Ros.) Ching



60 µm



70 µm

Distribution: *A small fern which is a common component of the understorey of tropical monsoon forests in southern China.*

Leaf surface (averages 20 cm²) with dorsiventral symmetry in cross section; barely reaches 68.9 µm thick, the thinnest leaf among all the species studied.

Upper cuticle uniformly flat and smooth (attains almost 1.9 µm), glabrous type. Thin epidermis does not exceed 7.8 µm and consists of a single layer of uniform rectangular cells.

Mesophyll fairly compact and undifferentiated (51.9 µm thick), extends between the two epidermis and consists of small rounded cells. Limited intercellular spaces.

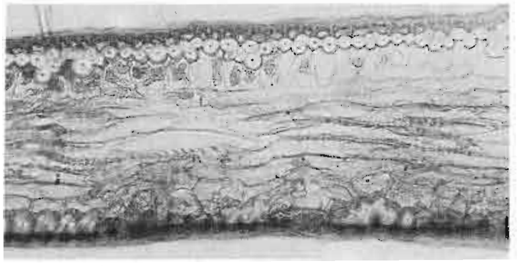
Mechanical tissue absent except for isolated sclerenchymatous fibers that are present in the mesophyll.

Lower epidermis thinner (barely attains 5.8 µm) than the upper and consists of small rectangular cells assembled in a single layer. Lower cuticle markedly undulate (1.9 µm thick), glaucous type.

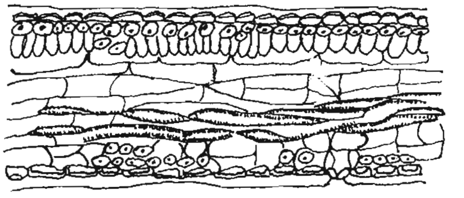
Stomata rather wide (rima 36.7 µm long) in the lower epidermis, slightly sunken in the substomatal chambers; the stomata cover a surface of 405 µm². Density attains 355/mm2, so the transpiring surface covers 143,775 µm²/mm² (14.4% of the leaf area, one of the largest among all of the species studied).

PODOCARPACEAE

Podocarpus latifolius R. Br.



87 μm



100 μm

Distribution: *A tall tree common in subtropical forest; diffused in the Transvaal region of southeastern Africa.*

Leaf surface averages 10 cm². Lamina (236.9 μm thick) with dorsiventral symmetry in cross section.

Cuticle ranges from 12 μm to 16 μm in the lower and upper sides, respectively; glabrous type. Monolayered underlying epidermis (attains 12 μm thick on both leaf surfaces) consists of quite uniform small cells.

Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (barely attains 26 μm, 11% of the total blade thickness) composed of a single layer of slightly elongated cells. The largest portion of the mesophyll is given to the spongy parenchyma (159 μm wide) and consists of weakly diversified cells: larger and more compact in the upper portion, thinner and more widely-spaced in the lower.

Intercellular spaces are extremely reduced in the spongy parenchyma, so that symplast largely prevails over the apoplast.

Vessels markedely lignified are abundant in the spongy portion.

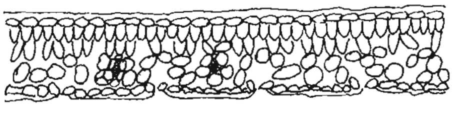
Important mechanical tissue in the leaf section (clustered linearly-aligned sclereids disposed against the epidermis layers) but less frequent on the lower side and extended as a large band at the leaf margins.

Stomata disposed in the epidermis layer on the lower side and protected by wide antechambers formed in the swollen cuticle; the largest stomata (rima 40 μm long, surface 600 μm²) of the examples studied from the Transvaal. Density does not exceed 111/mm², so the transpiring surface only reaches 66,600 μm²/mm² (about 8% of leaf area).

FAGACEAE

Castanopsis chinensis Hance

90 μm



100 μm

Distribution: *A tall tree that is dominant in the mature stages of the tropical monsoon forest in southern China.*

Leaf surface averages 15 cm²; lamina (117 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle flat and uniformly smooth (9 μm thick), glabrous type. Underlying epidermis consists of a single layer (15.6 μm thick) of small cells.

Mesophyll with clearly differentiated palisade and spongy parenchyma; the former (41.5 μm thick) (35.5% of the total leaf) composed of two thin layers of slightly-elongated cells. The upper is longer and more uniform than the inner. The latter layer (35.3 μm thick) consists of rounded or elongated cells.

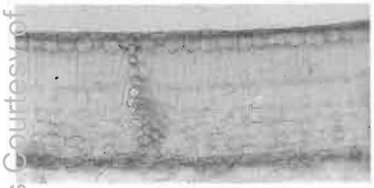
Wide intercellular spaces are present in the spongy portion.

Mechanical tissue poorly represented in the leaf section except for short isolated sclerenchymatous fibers in the mesophyll.

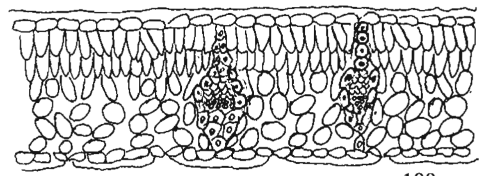
Monolayered lower epidermis (15.6 μm thick). Lower cuticle (not exceeding 7.8 μm) thinner than the upper.

Stomata rather small (rima barely attains 22 μm and surface does not exceed 194 μm²) on the lower side, slightly sunken in the epidermis. Density reaches 400/mm², so the transpiring surface covers 77,760 μm²/mm² (7.7% of the leaf area).

Castanopsis cuspidata Schottky



133 µm



100 µm

Distribution: *A tall tree that is a common component of the hot-temperate laurophyll forest in central Japan.*

Average surface of leaf reaches 13 cm²; lamina (213 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle (13.5 µm thick) overlays the epidermis and consists of a single layer (16.5 µm thick) of uniform rectangular cells; smooth glabrous type.

Two well-differentiated parenchyma in the mesophyll: fairly compact palisade consists of three layers (72 µm deep, 33.8% of the total mesophyll) of narrow elongated cells; spongy portion attains 85.5 µm (13% wider than the palisade) and is composed of rounded or slightly-elongated cells.

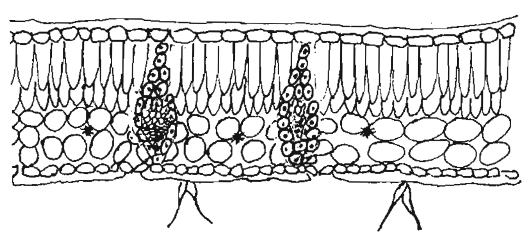
Wide intercellular spaces present in this parenchyma, so apoplast largely prevails over symplast.

Mechanical tissue well-represented in the leaf section: both scattered sclerenchymatous fibers and large bundle sheath-extensions are found in the mesophyll and extend between the two epidermis. The latter, present also in the other *Castanopsis* examples studied, is the true peculiarity of the leaf structure of the all genus.

Stomata (rima 29 µm long and surface 216 µm²) confined to the lower epidermis (16.5 µm thick) and are overlaid by the cuticle layer (13.5 µm thick). Density attains 400/mm², so the transpiring surface covers 86,436 µm²/mm² (8.6% of leaf area).

Castanopsis fissa R. & W.

100 µm



100 µm

Distribution: *A low tree that is common in the small and large gaps of the tropical monsoon forest in southern China.*

Average leaf surface 22 cm². Lamina attains 212 µm thick; dorsiventral symmetry in cross section.

Upper cuticle smooth and slightly undulate (21 µm thick, the thickest cuticle among the tropical examples studied), glabrous type. Thin underlying epidermis (barely attains 16.9 µm) consists of a single layer of small rectangular cells.

Two portions contribute in forming the mesophyll, the assimilatory and the lacunary parenchyma. The former (69.8 µm deep) consists of two layers of narrow and elongated cells, covering almost 50% of the leaf; the latter (62.9 µm thick) composed of a uniform layer of rounded cells.

Intercellular spaces limited in the spongy portion.

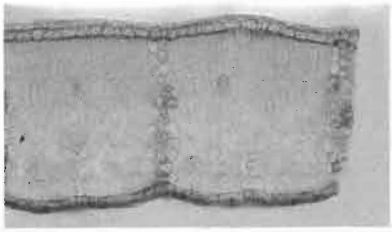
Mechanical tissue well represented in the leaf section: small sclerenchymatous fibers present in the spongy parenchyma.

Monolayered lower epidermis does not exceed 12.8 µm. Lower cuticle very thick (attains 20.7 µm; again, the largest among the tropical examples studied).

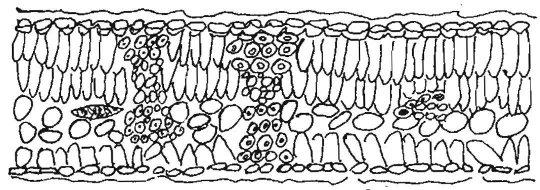
Sparse pluricellular hairs found on the lower side.

Stomata rather large (rima 24 µm long and the surface 183 µm² large) and present in the lower epidermis; very high density (577.7 µm²), so the transpiring surface covers 106,065 µm²/mm² (up to 10% of the leaf area; the largest percentage compared to the other *Castanopsis* examples studied).

Quercus agrifolia Neé.



100 µm



100 µm

Distribution: *A small tree that is a common component of chaparral and woodlands formations in southern California.*

Average leaf surface 8 cm², one of the smallest leaves of the Fagaceae species studied. Lamina (222 µm thick) with dorsiventral symmetry in cross section, one of the thinnest sclerophyll leaves studied.

Upper cuticle weakly undulate and smooth (8 µm thick), glabrous type. Underlying monolayered epidermis (also 8 µm thick) composed of somewhat squared cells with greatly thickened outer walls.

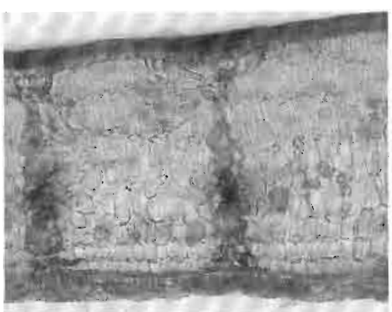
Two parenchyma clearly differentiated in the mesophyll: palisade (104 µm deep) consists of two uniform layers of narrow elongated cells (47% of the total thickness); spongy parenchyma consists of more compactly-assembled rounded cells in the inner portion and of palisade-like cells (only 88 µm) disposed against the lower epidermis.

Important mechanical tissue in the leaf section: large bundle sheath-extensions that extend throughout the mesophyll between the two epidermis, and short isolated sclerenchymatic fibers in the spongy parenchyma.

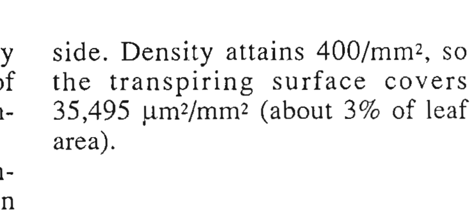
Lower epidermis (7.5 µm) overlaid by the smooth cuticle (does not exceed 5.5 µm).

Stomata rather small on the lower side (rima only 17 µm long and surface 94 µm²). Density does not exceed 222/mm², so the transpiring surface covers 20,950 µm²/mm² (2% of leaf area, the smallest among *Quercus* species studied).

Quercus chrysolepis Liebm.



80 µm



100 µm

Distribution: *A tall tree that is a common component of woodlands formations; widely diffused in the mediterranean region of southern California.*

Leaf surface averages 17 cm². Lamina (263 µm thick) with dorsiventral symmetry in transverse section.

Upper cuticle slightly undulate and smooth (only 6 µm), glabrous type. Underlying epidermis composed of a single layer (11 µm thick) of rather flattened cells.

Mesophyll with clearly differentiated palisade and spongy parenchyma: palisade (105 µm deep) consists of two or three layers of narrow columnar cells and occupies 40% of the entire thickness; spongy portion (124 µm wide) composed of densely-assembled rounded or elongated cells.

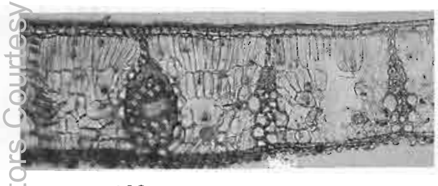
Mechanical tissue well-represented in the leaf section (a common feature of all of *Quercus* leaves tested); large bundle sheath-extensions cross the entire mesophyll and rare, isolated sclerenchymatous fibers are present in the spongy parenchyma.

Several glandular carvities in the mesophyll.

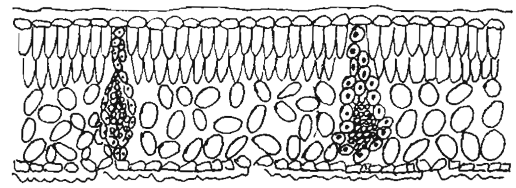
Lower epidermis (10 µm) overlaid by cuticle (also thin, barely reaching 7 µm).

Stomata (rima 18 µm long, surface 130 µm²) confined to the lower side. Density attains 400/mm², so the transpiring surface covers 35,495 µm²/mm² (about 3% of leaf area).

Quercus hui Chun



130 μm



100 μm

Distribution: *A tall tree that is a common component in the mature stages of the tropical monsoon forest in southern China.*

Average leaf surface does not exceed 16 cm². Lamina (220 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle flat and uniformly smooth, barely attains the thickness of 13.8 μm, glabrous type. Underlying epidermis consists of a single layer (16.3 μm thick) of small rectangular cells.

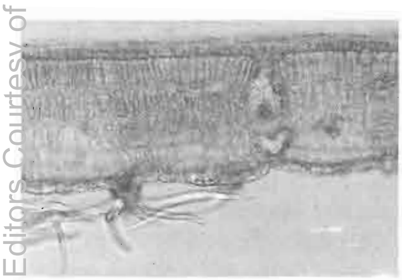
Two portions contribute in forming the mesophyll: the palisade and spongy parenchyma. Chlorenchyma composed of two layers of narrow densely-pressed cylindrical cells and covers 75,5 μm (not more than 34% of the entire leaf). The largest portion of the leaf section is given to the spongy parenchyma (78.7 μm) and consists of elongated uniform cells.

Intercellular spaces, wide and abundant, are present in the spongy parenchyma.

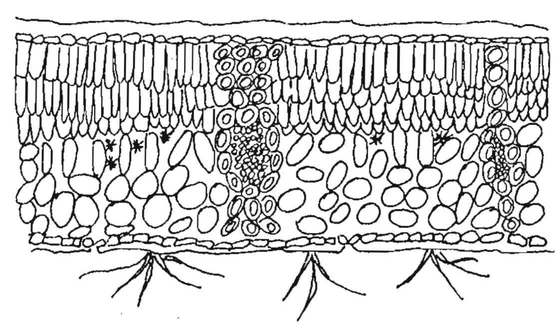
Mechanical tissue found in the mesophyll as large bundle sheath-extensions that extend from the upper to the lower epidermis; composed of collenchymatous elements that largely prevail over sclerenchymatous elements.

Stomata (rima 19 μm long and surface reaches 140 μm²) confined to the lower side and are sunken in the epidermis (thinner than the upper; does not exceed 14.7 μm); overlaid by glaucous, undulate lower cuticle, (21,6 μm thick) glaucous type. Density attains 488/mm², so the transpiring surface attains 68,515 μm²/mm² (6.8% of leaf area).

Quercus ilex L.



180 μm



100 μm

Distribution: *A tall tree that is a characteristic species of the mediterranean belt in the northern coasts of the Mediterranean Basin.*

Leaf surface averages 19 cm². Lamina (312 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle weakly undulate (12 μm thick), glabrous type. Upper epidermis consists of a single layer (13 μm thick) of compact rectangular cells.

Mesophyll clearly differentiated into palisade and spongy parenchyma: palisade (132 μm deep, 42% of the total cross section) forms the largest portion of the mesophyll and consists of three layers of narrow compact cells; spongy parenchyma (108 μm thick) composed of densely-assembled cells.

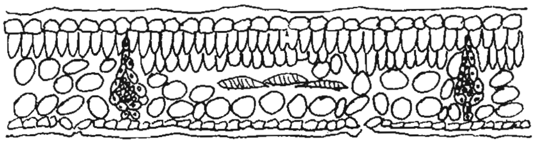
Mechanical tissue well-represented in the blade section; large bundle sheath-extensions (consisting mainly of sclerenchymatous elements) are frequently found in the mesophyll together with some isolated sclerenchymatic fibers.

Lower epidermis (11 μm thick) overlaid by smooth cuticle (10 μm thick) and characterized by pluricellular branched hairs that densely cover the entire surface.

Stomata rather small (rima 18 μm long surface 157 μm²) and confined to the lower epidermis. Density of stomata does not exceed 266/mm² (comparable to the lowest values recorded in the *Quercus* species examined), so the transpiring surface covers 41,792 μm²/mm² (about 4% of leaf area).

Quercus myrsinaefolia Blume

41 μm



100 μm

Distribution: *A tall tree common in the low altitude temperate evergreen forest of southern Hondo Island (Japan).*

Leaf surface averages 30 cm², one of the largest of the evergreen *Quercus* leaves studied. Lamina (165.6 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly flat and smooth, glabrous type. Monolayered upper epidermis (22 μm thick) composed of squared compact cells.

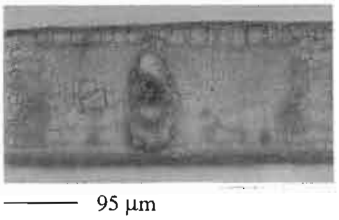
Mesophyll with clear differentiation of palisade and spongy portions; the former (51.9 μm deep) consists of two layers of narrow columnar cells and accounts for 31.3% of the entire thickness; the latter (81.9 μm) accounts for the largest portion of the leaf thickness and is composed of small or weakly-elongated cells. This wide parenchyma lacks intercellular spaces.

Mechanical tissue conspicuously represented in the leaf section: large bundle sheath-extensions (mainly collenchymatous) extend from the upper to the lower epidermis and are present in the mesophyll together with rare isolated sclerenchymatous fibers.

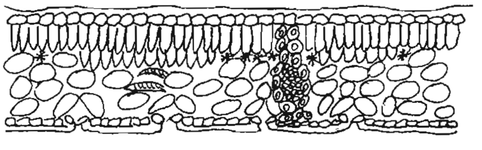
Upper epidermis rather thin (does not exceed 9 μm) and overlaid by thin cuticular layer (averages 9 μm).

Stomata rather small (rima 19 μm long; surface barely attains 112.3 μm²) and located on the lower side. Very high density (attains 533/mm²), so the transpiring surface covers 59,855 μm²/mm² (5.9% of leaf surface).

Quercus serrata Thunb.



95 μm



100 μm

Distribution: *A tall tree that is a common component of the temperate evergreen forest at low altitudes in southern Hondo Island (Japan).*

Leaf surface averages 12 cm² and reaches the thickness of 165.6 μm, one of the thinnest among the *Quercus* examples studied; dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth monolayered (15.6 μm thick), glabrous type, overlays the epidermis and is composed of small rectangular cells (12.4 μm wide).

Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade consists of narrow columnar cells arranged into two layers (averages 60.8 μm, 36.7% of total leaf thickness), the upper twice as deep as the inner (which is composed of discontinuous cells). The largest portion (85.8 μm) of the mesophyll is given to the spongy parenchyma, which is composed of small, uniform and somewhat rounded cells.

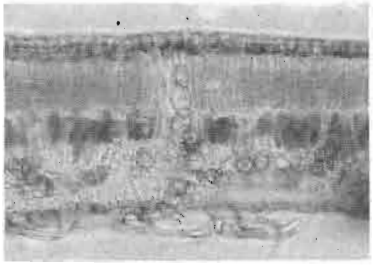
Intercellular spaces rather limited in the mesophyll.

Important mechanical tissue (a constant feature of all of *Quercus* leaf sections); large bundle sheath-extensions, are frequently found in the mesophyll and are disposed between the two epidermis.

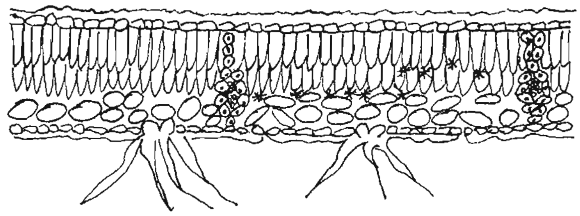
Lower epidermis uniformly smooth and monolayered (only 9.3 μm thick), covered by the glabraus cuticle (does not exceed 7.8 μm; half with respect to the upper).

Stomata very small (rima barely attains 16 μm and surface does not exceed 106.9 μm²; comparable to the smallest tropical and subtropical species studied) confined to the lower epidermis, yet density enormously increased up to 933/mm² (the highest density recorded), so the transpiring surface reaches 99,737 μm²/mm² (10% of leaf area).

Quercus suber L.



75 µm



100 µm

Distribution: *A tall tree that is a common component of the mesophytic mediterranean woodlands in the western part of the Mediterranean Basin.*

Leaf surface averages 8 cm^2. Lamina (162 µm thick) with dorsiventral symmetry in transverse section.

Upper cuticle rough and markedly-undulate (6 µm thick), the, only *Quercus* cuticle belonging to the glaucous type, among the examples studied. Underlying epidermis consists of a single layer (13 µm thick) of small compact cells.

Mesophyll clearly diversified into palisade and spongy parenchyma: palisade attains 78 µm (48% of the leaf thickness) and is composed of two layers of densely-assembled narrow cells; spongy portion (reaching a thickness of 44 µm), consists of rounded and elongated cells.

Mechanical tissue occurring as isolated sclerenchymatous fibers in the spongy portion and large bundle sheath-extensions that cross the entire mesophyll.

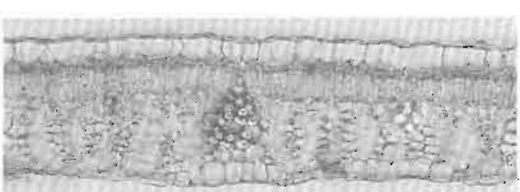
Several brownish masses of tannin are present in the lower mesophyll.

Long-branched pluricellular hairs densely cover the lower epidermis (11 µm thick), which is overlaid by the cuticle (10 µm thick), glabrous type.

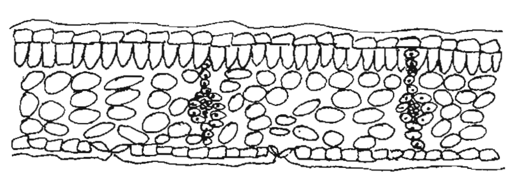
Stomata rather small (rima barely attains 18 µm, surface 314 μm^2 large) confined to the lower side. Density does not exceed 222/mm^2, so the transpiring surface covers 69,708 $\mu m^2/mm^2$ (about 7% of leaf area).

ULMACEAE

Gironniera subaequalis Planch.



100 µm



100 µm

Distribution: *A small tree that is more common in gaps of the canopy of the tropical monsoon forest found in southern Japan.*

Average leaf surface attains 53 cm^2 (one of the largest blades studied); lamina (172.4 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly flat (16.2 µm thick), glabrous type. Underlying epidermis somewhat thin and consists of a single layer of squared cells and barely attains 14 µm.

Mesophyll with clear differentiation of palisade and spongy parenchyma: the latter occupies about two-thirds of the total mesophyll. Palisade (only 28% of the total parenchyma) consists of weakly-elongated cells, and does not exceed a thickness of 48 µm. Spongy portion, composed of rounded and elongated cells, heterogeneous in size, and covers 72.3 µm.

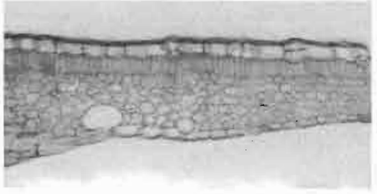
Wide intercellular spaces are frequently found in this parenchyma.

Mechanical tissue present as small clustered sclereids that surround the vascular tissues in the spongy mesophyll and rare bundle sheat-extensions.

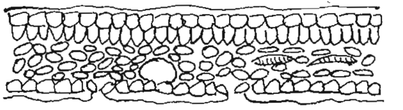
Stomata (rima 22 µm long and surface barely attains 129 μm^2) located in the lower epidermis (11 µm thick) and overlaid by an equally thin cuticular layer that does not exceed 10.3 µm. Density reaches 311/mm^2, so the transpiring surface covers 40,305 $\mu m^2/mm^2$ (only 4% of leaf area).

MORACEAE

Ficus nervosa Heyne



100 µm



100 µm

Distribution: *A tall tree that is a common component of the monsoon tropical forest diffused in southern China.*

Average leaf surface does not exceed 22 cm², rather small in comparison to the broader tropical leaves examined. Rather thin blade (barely attains 119.6 µm) with dorsiventral symmetry in cross section.

Upper cuticle smooth and flat (8.3 µm thick), glabrous type. Remarkably thick underlying epidermis consists of a single layer of somewhat heterogeneous squared cells (18 µm thick), with outer walls somewhat-thickened by the cuticle proper, that also penetrates between the tangential walls of the cells.

Mesophyll consists of small palisade and wide spongy parenchyma: palisade composed of compact and slightly-elongated cells (18% of the total); does not exceed the thickness of 21 µm; wide spongy parenchyma (averages 58.1 µm, about three times larger than palisade) consists of small fairly compact rounded cells; therefore, intercellular spaces quite limited. Wide glandular cavities present.

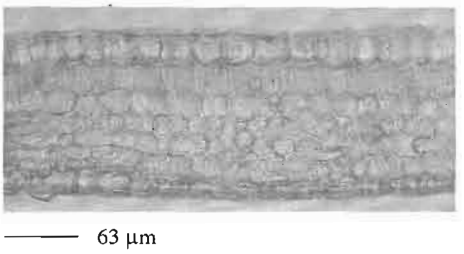
Mechanical tissue poorly represented in the leaf section, limited to small clustered sclereids that surround the vessels, and rare sclerenchymatous fibers in the spongy mesophyll.

Lower epidermis (11 µm thick) overlaid by smooth cuticle (6.2 µm thick).

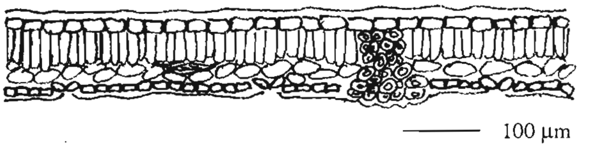
Stomata very small (rima 14 µm long and surface only 86.3 µm²) and confined to the lower side. Density reaches 400/mm², so the transpiring surface covers 34,572 µm²/mm² (3.4% of leaf area).

URTICACEAE

Celtis sinensis Willd.



63 µm



100 µm

Distribution: *A tall tree that is a common component of the temperate mountain evergreen forest in China and Japan.*

Leaf surface averages 32 cm². Lamina (126 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle smooth and thin (does not exceed 8 µm), glabrous type like most of the tropical and subtropical species studied. Underlying epidermis consists of a single layer (14 µm thick) of squared cells, with outer walls markedly thickened.

Mesophyll with clear differentiation of palisade and spongy parenchyma: the former (49.8 µm deep) composed of extremely elongated narrow cells that occupy 43.9% of the total thickness; the latter consists of quite uniform rounded cells that cover 39 µm.

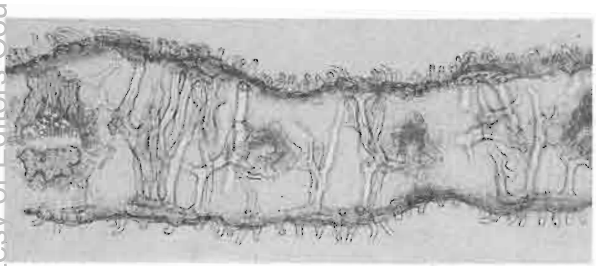
Mechanical tissue well-represented in the leaf section: large bundle sheath-extensions extend between the two epidermis, a common feature of most *Fagaceae* and *Lauraceae* samples studied.

Lower epidermis (7.8 µm thick) overlaid by the smooth cuticle (also 7.8 µm thick).

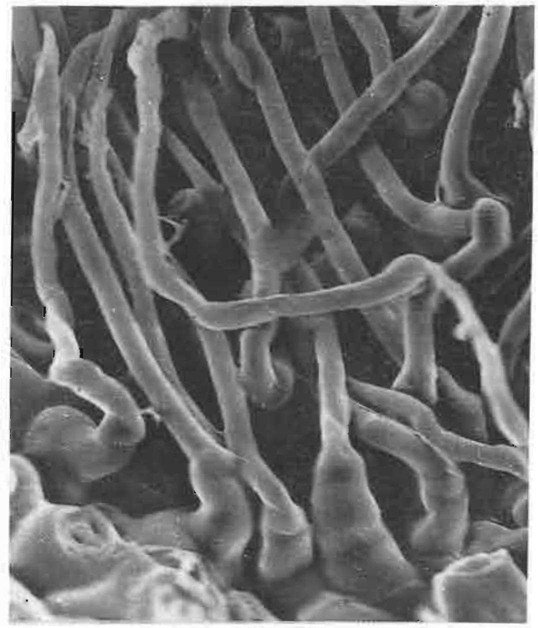
Stomata extremely small (rima 14.7 µm long and surface only 64.8 µm² large) and confined to the lower side, slightly sunken in the epidermis, but density attains 488/mm², so the transpiring surface reaches 31,632 µm²/mm² (3.1% of leaf area).

PROTEACEAE

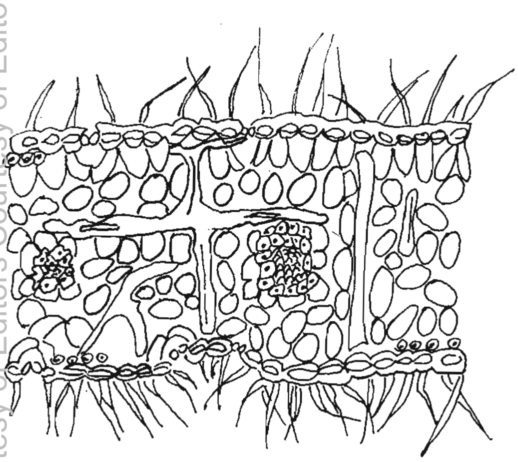
Adenanthos cuneatus Labill.



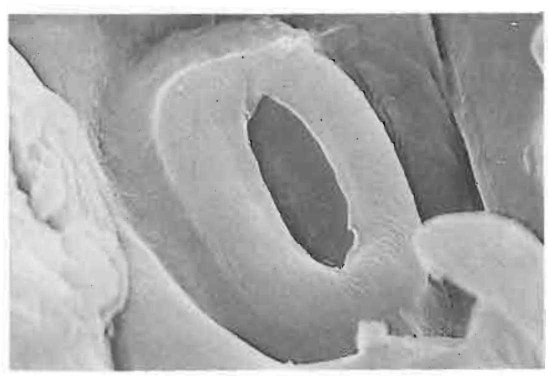
133 μm



20 μm



100 μm



2 μm

Distribution: *A low shrub common in the kwongan in southwestern Australia.*

Average leaf surface very small; does not exceed 2 cm², among the smallest exhibited by *Proteaceae* examples. Lamina (332.4 μm thick) with isolateral symmetry in cross section.

Upper cuticle rough and somewhat undulate (8.3 μm thick), glaucous type, overlays the epidermis that consists of squared cells with markedly thickened outer walls (19.7 μm wide). Lower cuticle (8.3 μm) similar to the upper one and overlays the monolayered epidermis (16.2 μm).

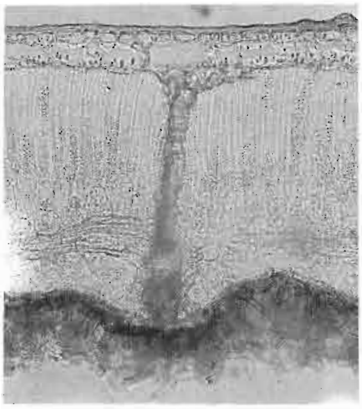
Mesophyll (279.9 μm thick) lacking any differentiation of palisade and spongy parenchyma: weakly-elongated cells occupy the entire mesophyll and are disposed between the two epidermis.

Intercellular spaces very small, yet wide substomatal chambers formed in the mesophyll are disposed against the upper and lower epidermis.

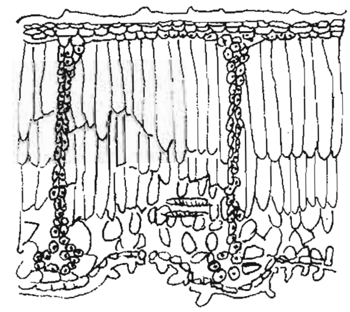
Important mechanical tissue: highly developed and diversified slerenchyma; small sclereids, laid out linearly, are present just under both epidermis, interposed with large T-shaped sclereids that extend from the outer to the inner mesophyll; in addition, macrosclereids cross the section from the upper to lower epidermis; irregularly branched sclereids also occur; finally, clustered sclereids in a wide ring surround the main veins.

Stomata on both sides (rima 23 μm and 21.9 μm long and the surfaces are 159 μm² and 151 μm² large, in the upper and lower side respectively) sunken in the epidermis or occur in wide shallow crypts formed in the lower portion of the mesophyll, and are protected by long unicellular hairs; similar in size in both the lower and upper epidermis, yet very different densities (577/mm² and 400/mm² in lower and upper sides, respectively), so the transpiring surfaces occupy 91,991 μm²/mm² and 60,000 μm²/mm² (ranging from 9.2% to 6% of the leaf area).

Banksia grandis Willd.



98 µm



100 µm

Distribution: *A small tree that is a common component of the open woodlands on sand plains in the dry-mediterranean area of southwestern Australia.*

Leaf surface extremely large (averages up to 100 cm²), the biggest leaf among all of the examples studied. Lamina with dorsiventral symmetry, 395.5 µm in cross section.

Upper cuticle (9.2 µm thick) markedly undulate and rough, glaucous type. Underlying epidermis (8 µm thick) consists of two or (rarely) three layers of small quite flattened cells, a common feature of the *Banksia* species examined but nonetheless very unusual in most of the other sclerophylls studied.

Mesophyll consists of two diversified parenchyma; palisade (294 µm deep, 69% of the total — the largest portion of the leaf section) composed of two layers of narrow cells, the upper extremely elongated; spongy parenchyma (70 µm thick) consists of rounded and elongated cells.

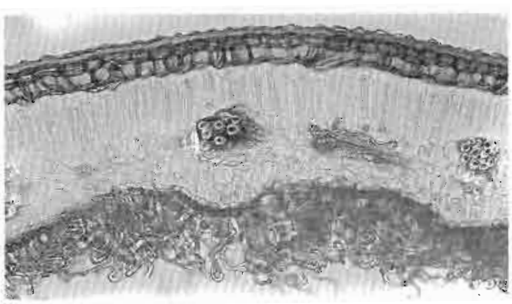
Intercellular spaces somewhat limited in this parenchyma.

Important mechanical tissue in the leaf section: small in-line clustered sclereids are present just under the upper epidermis and big very peculiar sclerenchymatic bundle sheat-extensions cross the mesophyll from the upper to the lower epidermis.

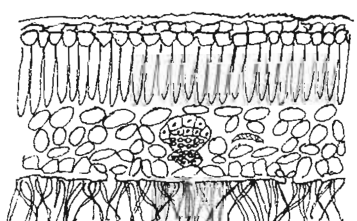
Stomata in the lower side sunken in shallow, wide crypts and protected by abundant short unicellular hairs – a very particular feature of the species.

Lower epidermis (7.4 µm thick) monolayered and overlaid by the smooth cuticle (6.9 µm thick).

Banksia littoralis R. Br.



100 µm



100 µm

Distribution: *A shrub that is a common component of the kwongan in the dry-mediterranean region of southwestern Australia.*

Leaf surface averages 4 cm². Dorsiventral symmetry in cross section. Lamina (215 µm thick) the thinnestn of the *Banksia* samples studied.

Upper cuticle (14.5 µm thick) rough with many protrusions, glaucous type. Underlying bilayered epidermis composed of wide cells with thickened walls that reach the remarkable thickness of 34.9 µm.

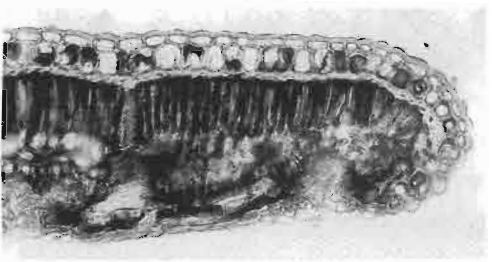
Mesophyll consists of two clearly diversified parenchyma: palisade and spongy parenchyma of almost the same thickness; palisade (70 µm deep) composed of a single layer of extremely elongated cells (33% of the total section); spongy parenchyma (68.8 µm wide) consists of densely-assembled and rather elongated cells, so intercellular spaces are somewhat limited.

Mechanical tissue poorly represented in the mesophyll except for small clustered sclereids that protect the vessels.

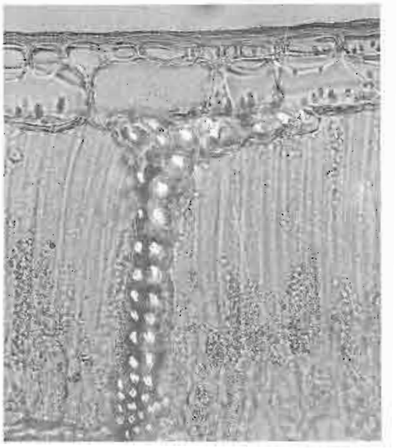
Lower epidermis (14 µm thick) monolayered and overlaid by thin flat cuticle (11 µm).

Stomata rather small (rima does not exceed 23 µm and surface 172 µm²) confined to the lower side; densely covered by long, tangled unicellular hairs. Density reaches 355/mm², so the transpiring surface attains 61,237 µm²/mm² (about 6% of leaf area).

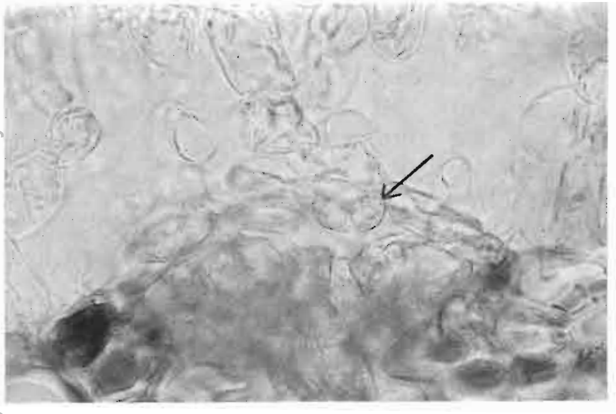
Banksia quercifolia R. Br.



170 µm



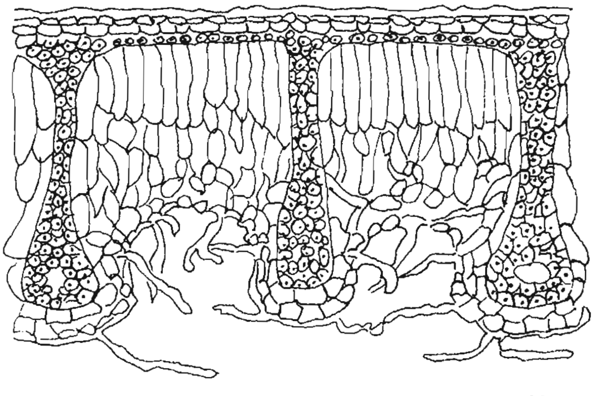
35 µm



13 µm

11 µm

6 µm



100 µm

Distribution: *A widespread shrub in the kwongan of the dry-mediterranean region of southwestern Australia.*

Leaf surface averages 3 cm². Lamina (418 µm thick; the thickest *Banksia* studied) with dorsiventral symmetry in cross section.

Upper cuticle smooth and undulate (13 µm thick), glabrous type.

Upper epidermis very thick (among the largest recorded in the leaf examples studied) and consists of two layers (up to 77 µm thick) of irregularly squared cells with thickened walls, the inner much larger than the outer.

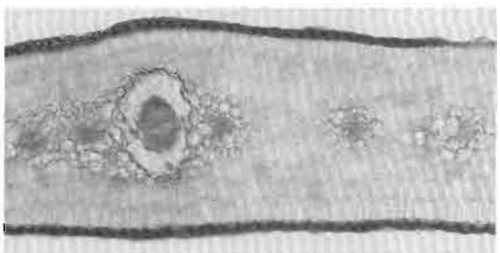
Mesophyll consists of two weakly differentiated portions: palisade composed of two or (rarely) three layers of compact elongated cells 144 µm deep (34% of the total thickness); spongy parenchyma (150 µm wide) consists of palisade-like cells and large intercellular lacunae.

Mechanical tissue remarkably well-represented in the mesophyll: a compact layer of small sclereids lies under the upper epidermis and large sclerenchymatic bundle sheat-estensions cross the mesophyll, closely resembling those occurring in *Banksia grandis*.

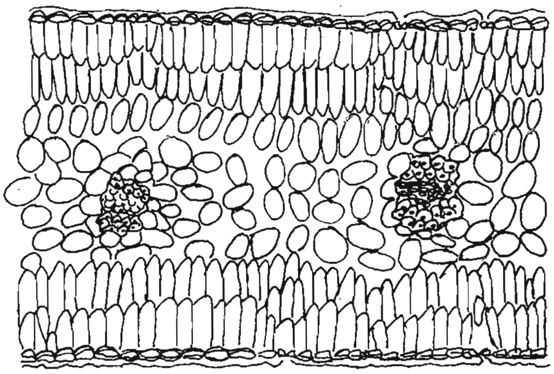
Lower epidermis (20.7 µm thick) monolayered and overlaid by the markedly papillose cuticle (12.4 µm thick), glaucous type.

Stomata on the lower side are deeply sunken in wide narrow crypts formed in the spongy parenchyma and protected by long unicellular hairs that densely cover these cavities.

Conospermum caeruleum R. Br.



183 μm



100 μm

Distribution: *A low shrub that is a common component of kwongan formations in the dry-mediterranean region of southwestern Australia.*

Small leaf surface (averages 7 cm^2). Lamina somewhat thickened (attains 475.7 μm) with isolateral symmetry in cross section.

Upper cuticle (9.6 μm thick) uniformly rough and weakly undulate, glaucous type. Underlying epidermis consists of a single layer (12.1 μm thick) of small cells.

Mesophyll weakly differentiated into palisade and spongy portion, the latter located between the upper and lower layers of the former. The largest portion of the mesophyll belongs to the palisade and consists of two layers (231 μm deep, 48% of the mesophyll thickness) of narrow compact cells disposed against both epidermis. Spongy parenchyma (200 μm thick) composed of palisade-like, rather elongated cells that cover the inner portion of the leaf section.

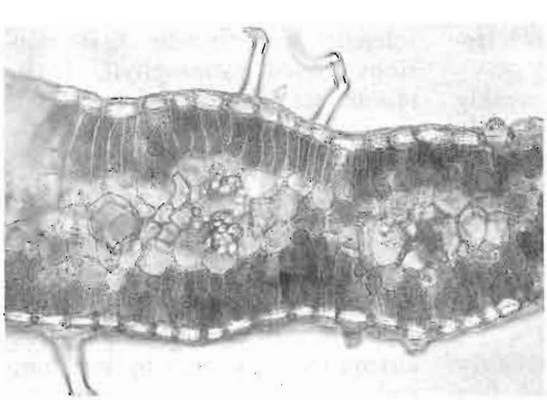
Intercellular spaces very limited in the mesophyll.

Lower epidermis (11 μm thick) overlaid by the cuticle (11 μm thick) and closely resembles the upper one.

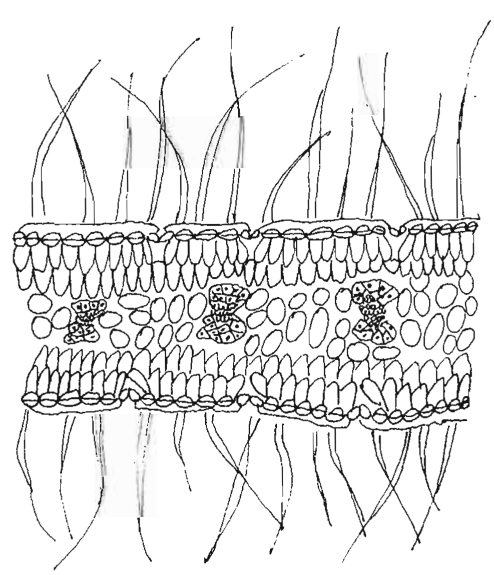
Mechanical tissue is present at leaf margins as clustered sclereids and as a wide ring that surrounds the main vessels in the spongy portion.

Stomata rather large (rima 28 μm long, surface ranges from 191.5 μm^2 to 199.4 μm^2 in the lower and upper sides, respectively) sunken in the epidermis on both sides, the upper similar to the lower. Density averages 311/mm^2 on both surfaces, so the transpiring surfaces attain the same value of 59,568 $\mu m^2/mm^2$ (about 6% of leaf area).

Conospermum crassinervium Meissner



100 μm



100 μm

Distribution: *A low shrub that is common in the kwongan; found in the mediterranean region of southwestern Australia.*

Average leaf surface attains 7 cm2; lamina (260 µm thick, much larger and thinner than the congeneric example studied) isolateral in cross section.

Upper cuticle smooth and flat (barely attains 6.2 µm thick), glabrous type; the epidermis consists of a single layer (17 µm thick) of quite uniform small cells.

Mesophyll with clear differentiation of palisade and spongy parenchyma. Palisade composed of two layers of narrow and fairly compact elongated cells that are disposed against the upper and lower epidermis; both cover 89 µm (40% of the mesophyll thickness). Spongy parenchyma (110 µm wide) disposed as a band between the two epidermis and consists of small rounded cells.

Intercellular spaces somewhat limited in this parenchyma.

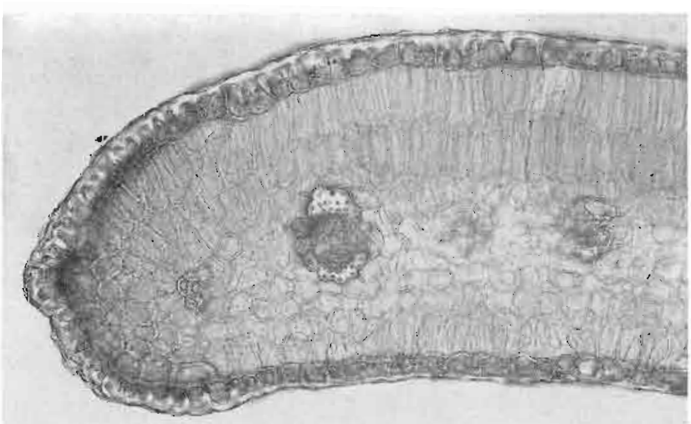
Mechanical tissue poorly represented in the leaf section: only small clustered sclereids are present in the spongy tissue and surround the vessels.

Lower cuticle (11 µm thick) smooth and slightly wider than the upper and overlays the epidermis (15 µm thick).

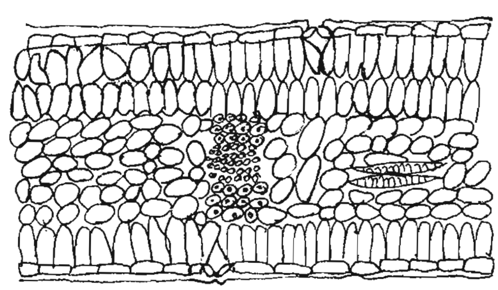
Stomata located on both sides (rima 27 µm long and surface only 130 μm^2 on the upper as well as the lower side), slightly sunken in the epidermis and rather small if compared to congeneric species studied. Density ranges from 222/mm^2 to 311/mm^2, therefore the transpiring surface covers 28,860 $\mu m^2/mm^2$ and 40,022 $\mu m^2/mm^2$ in the upper and lower epidermis, respectively (from 2.8% to 4% of leaf area).

Very long abundant unicellular hairs are present on both sides.

Faurea saligna Harv.



76 µm



100 µm

Distribution: *A small tree common in warm subtropical evergreen forests in the Transvaal region in southwestern Africa.*

Leaf surface averages 15 cm^2. Lamina (345 µm thick) with isolateral symmetry in cross section.

Smooth upper and lower cuticle (5 µm and 6 µm thick respectively, one of the thinnest among sclerophyll species studied), glabrous type.

Monolayered epidermis ranges from 24 µm to 26 µm thick.

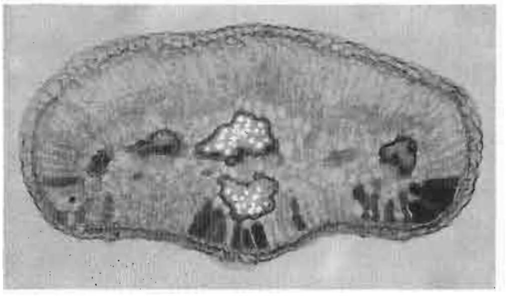
Two parenchyma in the mesophyll: palisade (140 µm deep, 43% of total thickness) consists of two double layers of narrow compact cells; spongy tissue (134 µm thick) is a band between the two palisades and composed of compact rounded cells.

Intercellular spaces less developed in this parenchyma.

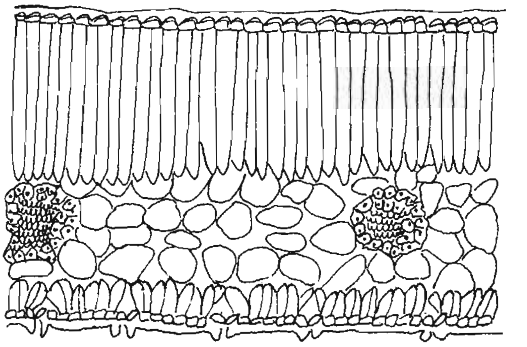
Mechanical tissue consists of small clustered sclereids that surround the veins.

Stomata rather large (rima 30 µm long, surface 404 µm2) on both sides with the same size and density in both the upper and lower surface. Density does not exceed 189/mm^2, so the transpiring surface attains 76,364 $\mu m^2/mm^2$ (about 8% of leaf area on both sides).

Grevillea pulchella (R. Br.) Meissner



142 μm



100 μm

Distribution: *A low shrub diffused in the kwongan and woodlands formation in sand plains in southwestern Australia.*

Small leaf surface (averages 1.5 cm²), among the smallest sclerophyll species studied. Dorsiventral symmetry in cross section (397.5 μm thick).

Upper cuticle uniformly smooth and flat (18 μm thick), glabrous type; markedly undulate and thinner lower cuticle (15 μm thick) with prominent papillae, glaucous type.

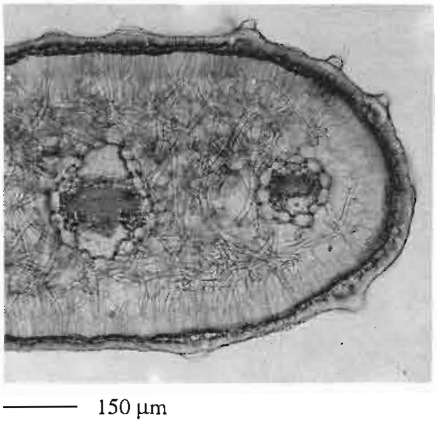
Epidermis monolayered and composed of small rectangular cells, the upper one 18 μm, the lower 10 μm thick.

Mesophyll clearly differentiated into two portions: palisade (148 μm deep) consists of two single layers – the upper extremely elongated – of narrow columnar cells that occupy about 60% of the total; spongy parenchyma (90 μm thick) is a band between the two palisades and consists of round cells.

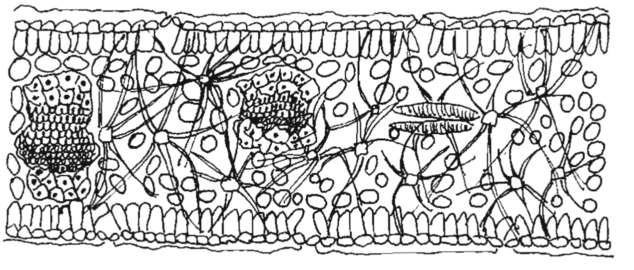
Mechanical tissue is present in the spongy parenchyma as large rings that totally surround vessels.

Stomata confined to the lower side and protected by wide antechambers shaped by a cuticular layer (rima 10 μm long and surface only 40 μm² large, among the smallest of sclerophyll examples studied). Density also low and does not exceed 266/mm², so the transpiring surface limited to 6764 μm²/mm² (less than 1% of leaf area).

Isopogon attenuatus R. Br.



150 μm



200 μm

Distribution: *A low shrub that is a common component of the kwongan on the sand plains of the dry-mediterranean region of southwestern Australia.*

Small leaf area (averages 3 cm²). Lamina rather thick (attains 598 µm) with isolateral symmetry in transverse section.

Upper cuticle rough undulate (14 µm thick), glaucous type; lower cuticle 13 µm thick.

The epidermis consists of a single layer of squared cells and ranges from 21 µm to 20 µm thick in the upper and lower sides.

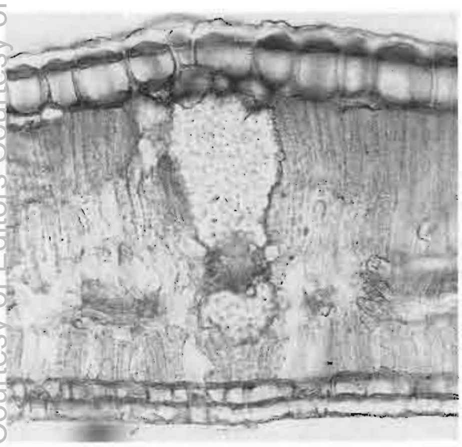
Mesophyll consists of two parenchyma: palisade (142 µm thick; occupying 24% of the total section) composed of two layers of narrow cylindrical cells; spongy parenchyma (388 µm thick) composed of small compact cells, and occupies the largest portion of the mesophyll between the two palisades.

Very limited intercellular space in this parenchyma.

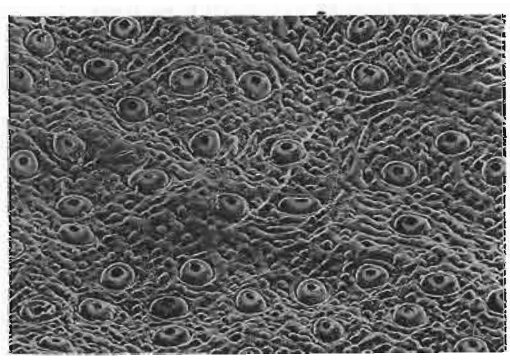
Mechanical tissue important and of very peculiar aspect: consists of astroslereids (the only example of astrosclereids found among the sclerophyll species studied) mostly present as a dense network in the spongy portion, together with clustered sclereids that surround the vascular tissue.

Stomata (rima range between 24 µm and 36 µm, and surface between 180 µm² and 424 µm² from the upper to lower epidermis) on both sides protected by wide antechambers formed by the cuticle; lower density 266/mm² and the upper 222/mm², so the transpiring surfaces attain 47,899 µm²/mm² and 94,201 µm²/mm², respectively (5% and 9% of leaf area, respectively).

Lambertia multiflora Lindley

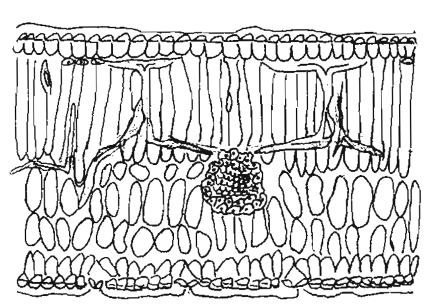


70 µm



100 µm

12 µm



100 µm

Distribution: *A low shrub common in the kwongan on the sand plain of the dry-mediterranean region of southwestern Australia.*

Average leaf surface barely reaches 1.5 cm². Lamina (359 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle (11 µm thick) rough and undulate, glabrous type. Very thick upper epidermis consists of a single layer (attains 56 µm) of squared cells with strongly thickened outer and tangential walls.

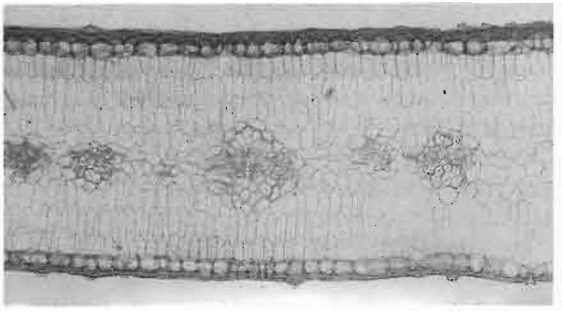
Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (15'4 µm deep, 43% of the total leaf thickness) composed of extremely elongated cells; spongy parenchyma (101 µm thick) consists of palisade-like elongated cells in the lower portion against the epidermis.

Important mechanical tissue is present in the mesophyll as large clusters of sclereids that surround vessels and branched macrosclereids that extend from the upper epidermis to the inner mesophyll portion.

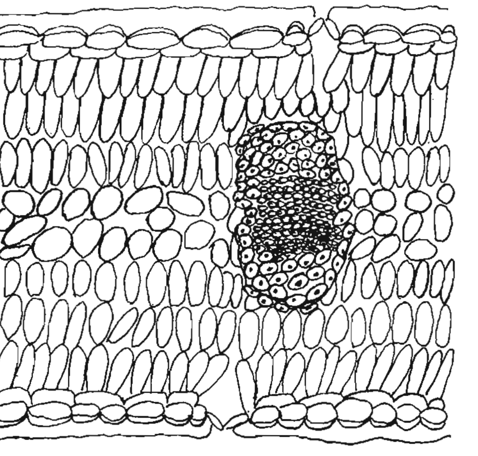
Lower epidermis (21 µm thick) overlaid by glaucous cuticle (14 µm thick).

Stomata rather large (rima 40 µm long, surface 465 µm²) confined to the lower side. Density does not exceed 222/mm², so the transpiring surface covers 103,166 µm²/mm² (10% of leaf area).

Leucadendron gandogeri Bourke



197 μm



100 μm

Distribution: *A small tree that is a common component of the mediterranean vegetation of southwestern Africa.*

Leaf surface averages 16 cm^2. Rather thick lamina (up to 592 μm) with isolateral symmetry in transverse section.

Upper cuticle somewhat thick (30 μm thick), glabrous type, lacks any protrusions. Monolayered epidermis (ranges from 29 μm to 31 μm from the upper to the lower side) composed of squared cells with thickened walls.

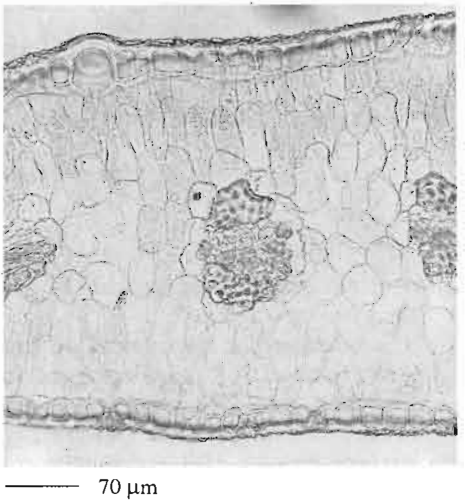
Mesophyll consists of palisade and spongy parenchyma: the largest portion of the multilayered mesophyll is composed of the palisade (369 μm thick, 62% of the total section); spongy parenchyma (107 μm thick) present as a band in the inner portion of the leaf section and consists of compact rounded cells.

Mechanical tissue is present in the mesophyll as clustered sclereids that surround the vessels.

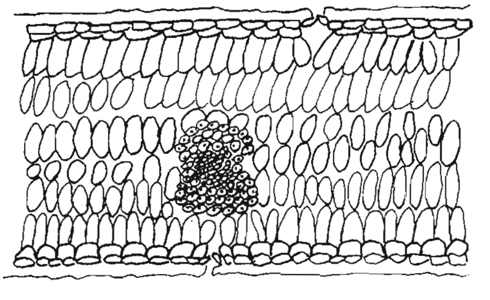
Lower cuticle (27 μm thick) closely resembles the upper.

Stomata rather wide (rima range from 28 μm to 37 μm, and surface from 310 μm^2 to 459 μm^2 in the upper and lower sides, respectively) on both sides. Density does not exceeds 178/mm^2 on both epidermis, so the transpiring surface covers 81,644 $\mu m^2/mm^2$ and 55,230 $\mu m^2/mm^2$ (about 8% and 5% of the lower and upper leaf area, respectively).

Leucadendron linoides Knight



70 μm



100 μm

Distribution: *A small tree common in the subtropical evergreen forest in the Transvaal region of south-eastern Africa.*

Small average leaf surface (0.3 cm^2 or less). Lamina (355 µm thick) isolateral in cross section.

Upper cuticle uniformly flat and smooth (14 µm thick), glabrous type. Underlying epidermis (25 µm thick) consists of two layers of compact rather rectangular cells.

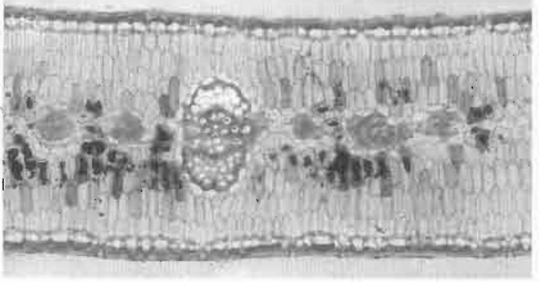
Undifferentiated mesophyll (266 µm thick) consists of compact and elongated cells.

Mechanical tissue is present in the mesophyll as wide rings of clustered sclereids that surround the vessels.

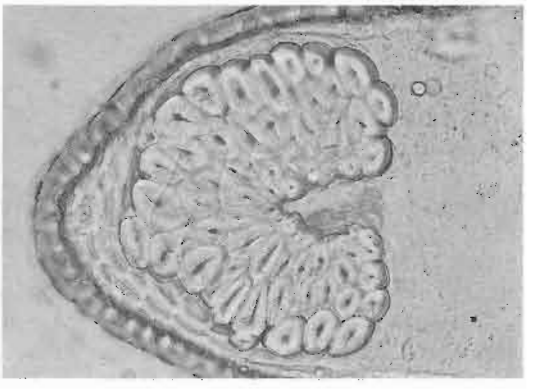
Lower epidermis (35 µm thick), the thickest among all the examples studied). Lower cuticle (15 µm thick) closely resembles the upper.

Stomata rather small (rima 21 µm long, surface 160 μm^2) on both surfaces are similar in size and density. Density attains 200/mm^2; so the transpiring surface covers 31,940 $\mu m^2/mm^2$ (6.4% of leaf area).

Leucadendron nervosum Phill. & Hutch.

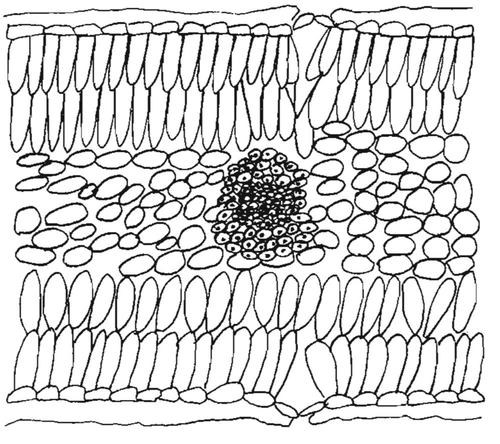


187 µm



115 µm

20 µm



100 µm

Distribution: *A small tree that is a common component of the mediterranean vegetation of southwestern Africa.*

Leaf surface averages 7 cm^2, quite small in comparison to other examples of Capensic *Leucadendron* studied. Lamina (561 µm thick, one of the largest species studied) with isolateral symmetry.

Upper cuticle markedly undulate (43 µm thick, the thickest recorded of all the examples tested), glaucous type. Epidermis reaches the same thickness of 19 µm on both sides and consists of two layers of big rounded cells.

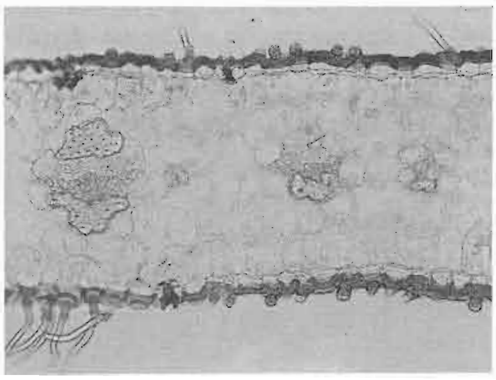
Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (302 µm deep) occupies 54% of the total leaf section with two layers of narrow elongated cells; spongy parenchyma (134 µm thick) composed of rather heterogeneous cells.

Mechanical tissue poorly represented in the spongy portion: only small clustered sclereids surround the vessels but remarkably present at leaf margins.

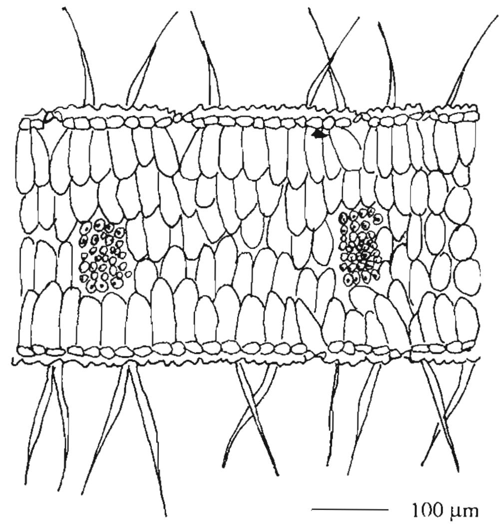
Lower cuticle (45 µm thick) also very thick, glaucous type, and is similar to the upper.

Stomata on both sides (rima ranging from 60 µm to 45 µm, surface from 1440 μm^2 to 846 μm^2) among the largest observed; stomata larger in the lower than in the upper surface; yet density does not exceed 133/mm^2 on both epidermis, so upper transpiring surface covers 112,529 $\mu m^2/mm^2$ and the lower 191,520 $\mu m^2/mm^2$ (11% and 19% of leaf area, respectively, among the widest values recorded).

Leucadendron salignum R. Br.



100 μm



100 μm

Distribution: *A small tree common in the mediterranean vegetation of southwestern Africa.*

Average leaf surface attains 12 cm². Lamina (319.8 μm thick in cross section) with isolateral symmetry.

Cuticle markedly papillose (15.6 μm thick), glaucous type, similar on both sides. Epidermis (also 15.6 μm thick on the upper and lower surfaces) consists of a single layer of rather squared cells.

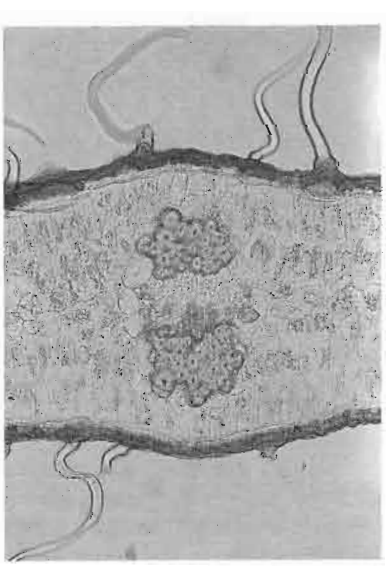
Undifferentiated mesophyll (257.4 μm wide) composed of compact palisade-like and rather elongated cells that are more compactly-assembled against the upper and lower epidermis.

Intercellular spaces very limited in the mesophyll.

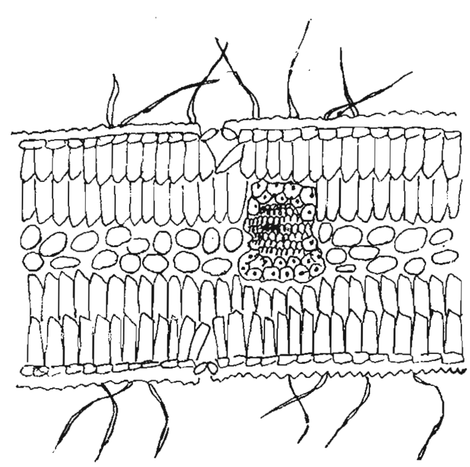
Mechanical tissue present as clustered sclereids that surround the vessels.

Stomata extremely wide (rima 66 μm long, the longest of the examples recorded; surface 1980 μm² large, one of the largest observed) and protected by long unicellular hairs on both sides. Density attains 177/mm², so the transpiring surface covers 350,460 μm²/mm² (35% of leaf area), the largest surface covered by stomata among all the species studied.

Leucospermum calligerum Knight



100 μm



100 μm

Distribution: *A low shrub that is a common component of the mediterranean vegetation of southwestern Africa.*

Small leaf surface (barely averages 0.7 cm²). Lamina (338.5 µm thick) with isolateral symmetry in cross section.

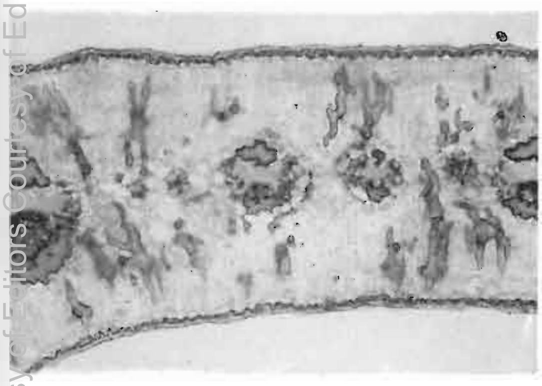
Cuticle heavily undulate (ranges from 18 µm to 16 µm thick) in the upper and lower sides, respectively) with many protrusions, glaucous type on both surfaces. Upper epidermis (12.8 µm thick, like the lower one) consists of a single layer of rather flattened cells.

Mesophyll consists of two parenchyma: palisade (222.8 µm deep, 66% of the total section) is composed of two layers of compact elongated cells confined against the upper and lower epidermis; spongy parenchyma is a thin band (55.7 µm wide) between the two palisades and is covered by compact rounded cells.

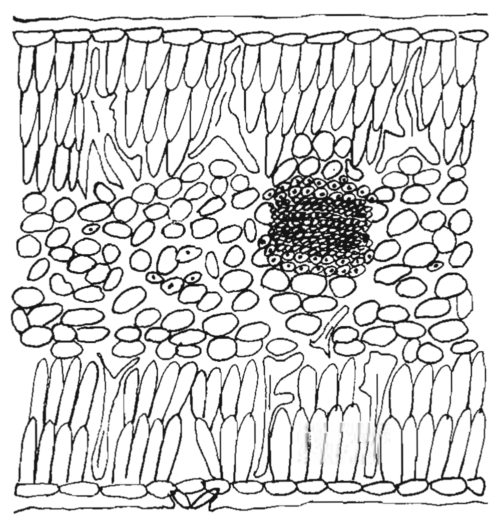
Mechanical tissue present as small clustered sclereids that surround the vessels.

Stomata on both sides are similar in size (rima 26.6 µm and surface 263.3 µm² on both epidermis) and protected by unicellular hairs; upper density (222/mm²) slightly smaller than the lower (266/mm²), so the transpiring surfaces are quite similar and attain 58,470 µm²/mm² and 70,243 µm²/mm², respectively (between 6% and 7% of the leaf area).

Leucospermum hypophyllocarpodendron (L.) Druce



189 µm



100 µm

Distribution: *A low shrub that is frequently found in the warm humid temperate forest of the Transvaal region of southeastern Africa.*

Leaf surface averages 3.5 cm². Lamina (662.8 µm thick), with isolateral symmetry in cross section.

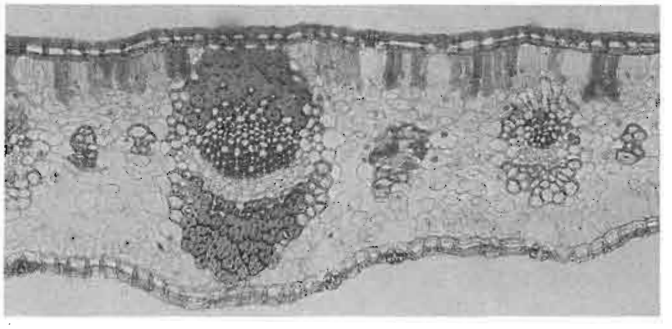
Cuticle rather rough (30 µm thick on both sides), glaucous type. Epidermis monostratified (upper 12.9 µm thick and lower 10.2 µm thick) and consists of rectangular cells.

Mesophyll consists of palisade and spongy parenchyma: the largest portion of the mesophyll is given to the palisade, composed of narrow columnar cells assembled in two layers disposed against the upper and lower epidermis; together they attain the remarkable thickness of 397.2 µm and occupy about 60% of the total section; spongy parenchyma (186 µm thick) is disposed between the two palisade layers and consists of compact rounded cells.

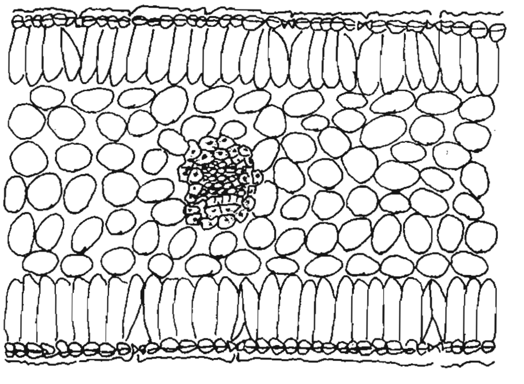
Mechanical tissue present in the spongy as wide sclerenchymatic rings that surround the vessels or as isolated schereids; big macrosclereids in the palisade layer are also present.

Stomata on both sides (rima 32 µm long, surface 304 µm²) attain the same size and density. Density does not exceed 155/mm², so the transpiring surface covers 47,259 µm²/mm² (about 5% of the leaf area on each side).

Persoonia longifolia R. Br.



144 μm



100 μm

Distribution: *A small tree that is frequently found in the understorey of the* Eucalyptus *diversicolor forest in the very humid area of southern Australia.*

Leaf average surface attains 45 cm^2. Lamina (432 μm thick) isolateral in cross section.

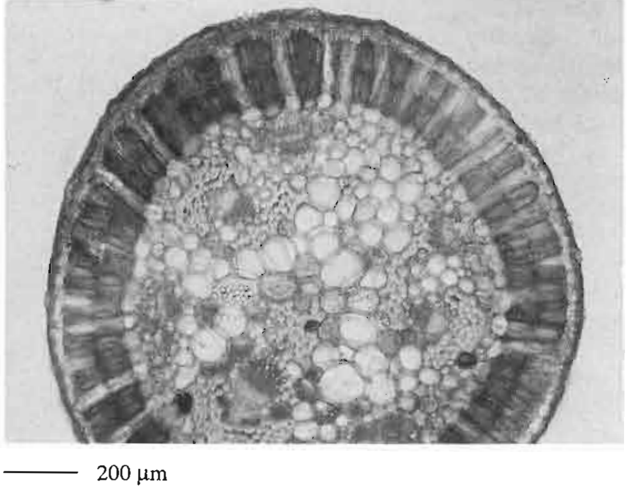
Upper cuticle markedly papillose (15.9 μm thin, like the lower), glaucous type. Epidermis (24.2 μm thick on both sides) monolayered and consists of squared cells with markedly thickened outer walls.

Two parenchyma in the mesophyll: two palisades (138 μm thick, occupy 32% of the total section) confined against each epidermis and consist of a single layer of narrow elongated cells; spongy parenchyma (214 μm thick, the largest portion of the mesophyll) consists of compact rounded cells.

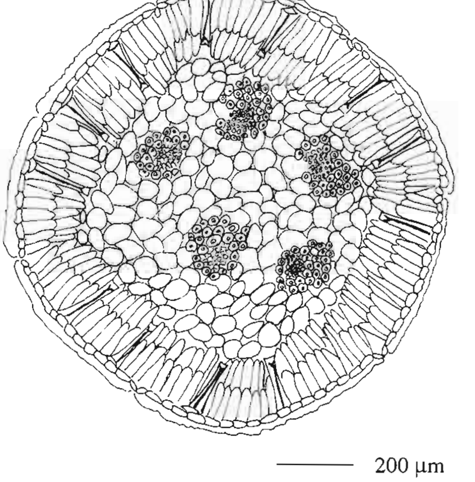
Mechanical tissue present as small sclereids that surround the vessels in the mesophyll.

Stomata wide (both sides similar in size: rima 40 μm long, surface 348 μm^2 large in the lower side; rima 36 μm long, surface 340 μm^2 large in the upper). Density does not exceed 133 mm^2 on the upper surface, almost double the lower (222 mm^2), so the transpiring surfaces attain 77,464 $\mu m^2/mm^2$ and 45,220 $\mu m^2/mm^2$, respectively (about 8% to 4% of each leaf surface).

Petrophile ericifolia R. Br.



200 μm



200 μm

Distribution: *A low shrub that is a common component of the kwongan in the dry-mediterranean region of southwestern Australia.*

Ericoid leaf; average surface barely attains 1 cm2. Lamina extremely thick (attains 1115.8 µm, among the thickest cross sections of all examples studied) with radial symmetry in cross section.

Cuticle rather rough (12 µm thick), glaucous type. Underlying epidermis consists of a single layer (20.7 µm thick) of rather uniform rectangular cells.

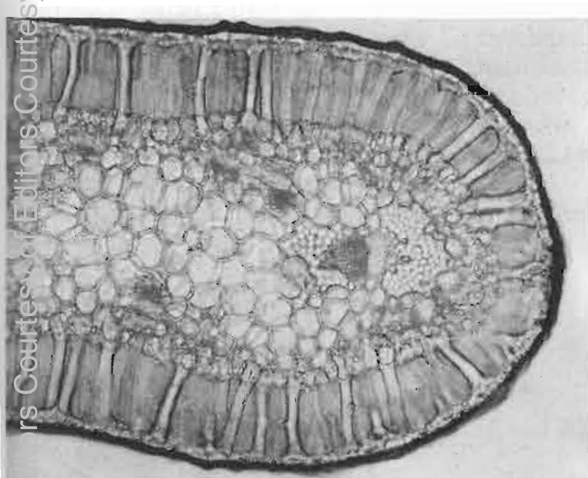
Mesophyll with clear differentiation of palisade and spongy parenchyma: the latter averages 749.7 µm (about one half of the leaf thickness); the former (298.3 µm deep, 27% of the mesophyll) consists of two layers of compact, narrow elongated cells.

Intercellular spaces fairly limited in the spongy portion.

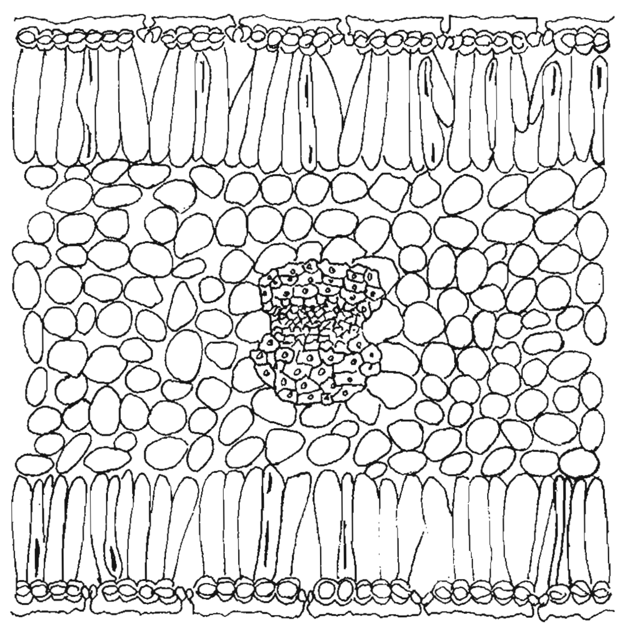
Mechanical tissue well-represented in the leaf section: both sclerenchymatic fibers and macrosclereids are present in the parenchyma, the former surround the vascular tissue, the latter frequently inserted among palisade cells and extends from the epidermis to the first layer of lacunary parenchyma.

Stomata disposed against the epidermis and are protected by a swollen cuticle that forms a wide antechamber above the guard cells; rima barely attains the length of 29.2 µm and surface 320 µm2 (quite small in comparison to other *Proteaceae* examples studied, which can attain a size up to five times larger). Density accounts for 200/mm², so the transpiring surface is rather limited, covering 64,070 µm/mm² (about 6% of leaf area).

Petrophile linearis R. Br.



160 µm



110 µm

Distribution: *A low shrub that is common in the kwongan and in the understorey of open woodlands in the dry-mediterranean region of southwestern Australia.*

Small leaf surface barely averages 2.5 cm². Lamina with isolateral symmetry in transverse section attains the remarkable thickness of 846.5 µm, among the thickest of the leaves studied.

Cuticle rough undulate (16 µm thick), glaucous type, similar on both sides. Epidermis (21 µm on the upper side and 18 µm on the lower) consists of a single layer of squared cells with thickened walls.

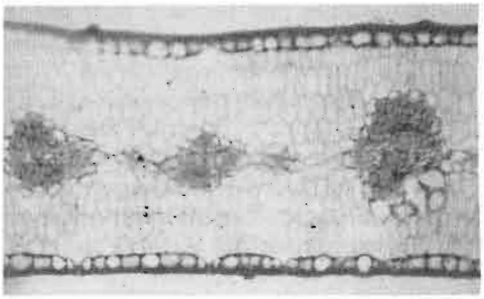
Two parenchyma occur in the mesophyll: palisade (305 µm deep) consists of two layers of compact narrow cells disposed against each epidermis; palisade accounts for 36% of the total thickness. Spongy parenchyma (469 µm thick) is disposed between the two palisades and is composed of rounded cells.

Intercellular spaces very limited in this parenchyma.

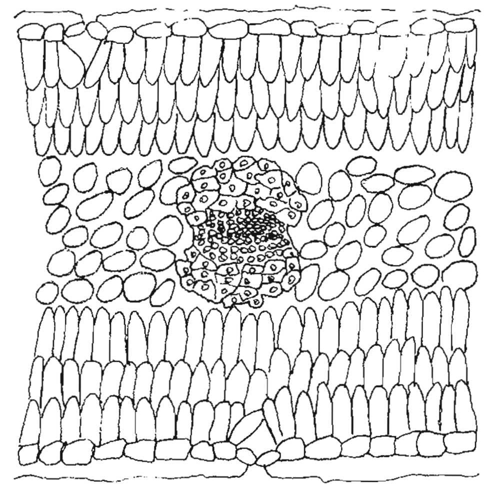
Important mechanical tissue is present in the leaf section: abundant macrosclereids inserted among the palisade cells lengthening from the epidermis to the inner mesophyll portion; clustered sclereids surround the vessels.

Stomata on both sides rather large (rima ranges from 31 µm to 35 µm, surface from 269 µm² to 475 µm² in the upper and lower side, respectively) protected by the swollen cuticle. Density 355/mm² (lower) and 222/mm² (upper), so the transpiring surfaces attain 168,746 µm²/mm² and 59,838 µm²/mm², respectively (about 17% and 6% of lower and upper leaf area).

Protea amplexicaulis R. Br.



200 μm



100 μm

Distribution: *A shrub that is a common component of the mediterranean vegetation of southwestern Africa.*

Leaf surface averages 10 cm^2. Lamina (618 μm thick) with isolateral symmetry in cross section.

Cuticle smooth and weakly-undulate (the upper 30 μm thick, the lower only 15 μm thick), glabrous type. Monolayered epidermis (from 28 μm in the upper to 24 μm in the lower side) consists of squared cells.

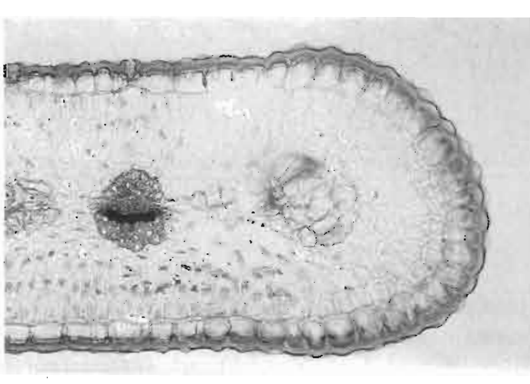
Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (340 μm thick, 55% of the entire section) consists of two double layers of compact cylindrical cells; spongy parenchyma (180 μm) is a band of rounded cells disposed between the two palisades.

Small intercellular spaces are present in this parenchyma.

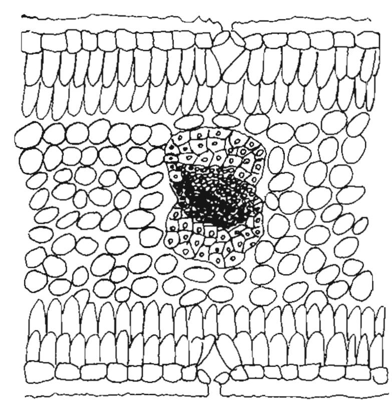
Mechanical tissue as clustered sclereids that surround the veins.

Stomata remarkably big (the largest, along with *Euclea racemosa* among the examples studied: rima 69 μm long, surface 2218 μm^2 large) and attain the same size and density on both sides. Density does not exceed 44/mm^2, so the transpiring surface covers 97,618 $\mu m^2/mm^2$ (about 10% of each leaf surface).

Protea cynaroides L.



170 μm



120 μm

Distribution: *A shrub commonly found in the mediterranean vegetation of southwestern Africa.*

Leaf area averages 25 cm^2. Lamina (640 μm thick) with isolateral symmetry in transverse section.

Cuticle rather smooth (28 μm thick on both sides), glabrous type. Monolayered epidermis consists of large squared cells and attains the remarkable thickness of 39 μm and 34 μm in the lower and upper sides, respectively.

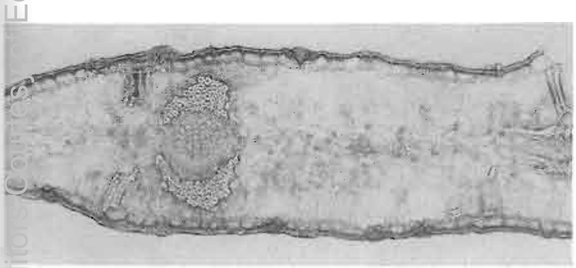
Two parenchyma in the mesophyll: palisade (108 μm deep, 17% of total section) consists of two double layers of narrow elongated cells; spongy parenchyma (314 μm wide) occupies the largest portion of the mesophyll with rather compact rounded cells.

Mechanical tissue as clustered sclereids surrounds the vascular tissue.

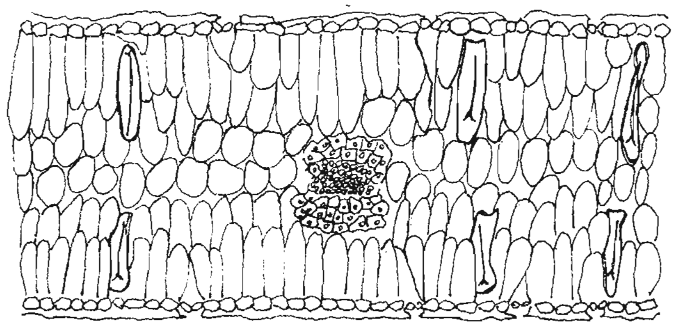
Wide glandular cavities in the spongy parenchyma.

Stomata remarkably large and same-sized (rima 64 μm long, surface 1685 μm^2 wide) on both of the two surfaces. Upper density does not exceed 44/mm^2; the lower one attains to 67/mm^2, so the transpiring surfaces range from 74,899 $\mu m^2/mm^2$ to 112,348 $\mu m^2/mm^2$, respectively (about 7% and 11% of each surface).

Protea latifolia R. Br.



175 µm



100 µm

Distribution: *A shrub common in the mediterranean vegetation of southwestern Africa.*

Average leaf surface attains 13 cm^2. Lamina (421 µm thick) with isolateral symmetry in cross section.

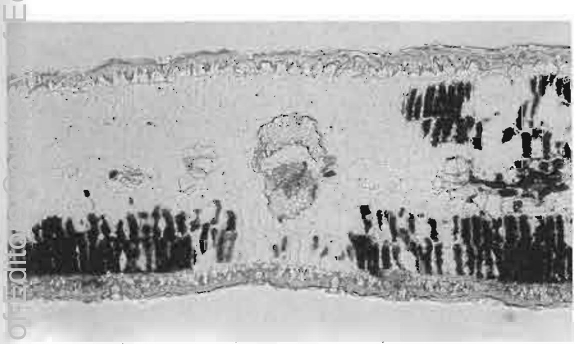
Cuticle smooth (12 µm thick on both sides), glabrous type. Upper epidermis monolayered (23 µm thick, the same as the lower).

Two slightly-differentiated parenchyma in the mesophyll: palisade (300 µm thick, 70% of the total thickness) occupies the largest portion of the mesophyll with compact elongated cells; spongy parenchyma (does not exceed 51 µm) disposed as a thin band of palisade-like cells between the two clorenchyma.

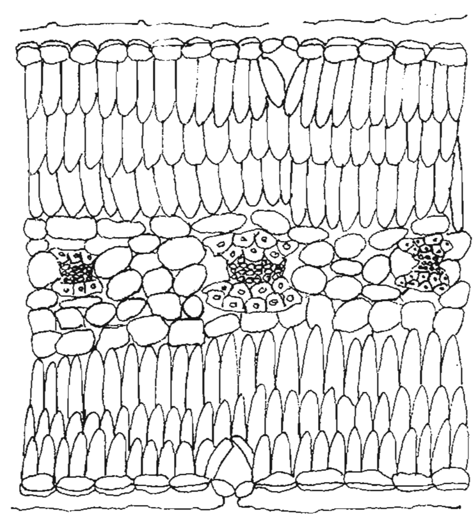
Important mechanical tissue is present in the leaf section: abundant stick-shaped macrosclereids extend through the palisade, and clustered sclereids surround the veins.

Stomata rather large and attain the same size and density on both sides (rima 39 µm long, surface 608 μm^2). Density does not exceed 133/mm^2, so the transpiring surface covers 80,917 $\mu m^2/mm^2$ (8% of each leaf surface.)

Protea longifolia R. Br.



190 µm



100 µm

Distribution: *A tall shrub that is a frequent component of the mediterranean vegetation of southwestern Africa.*

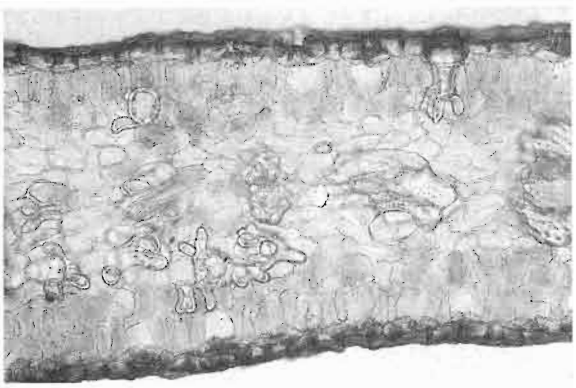
Leaf surface averages 63 cm^2. Lamina (644.57 µm thick) with isolateral symmetry in transverse section. Lower and upper cuticle rather flat (36 µm thick), glabrous type.

Epidermis monolayered and composed of quite-broad squared cells that range from 33 µm on the upper side to 27 µm on the lower. Clearly differentiated mesophyll with two parenchyma: palisade (343 µm thick, 53% of the entire thickness) consists of two double layers of compact cylindrical cells; spongy parenchyma (168 µm thick) occupies the central portion of the mesophyll between the two palisades with rather compact rounded cells assembled as a band.

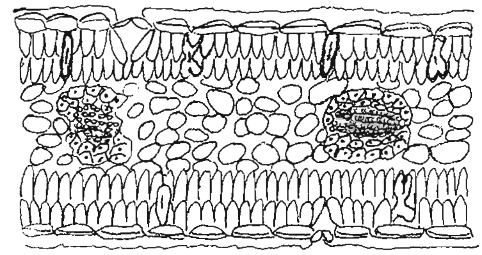
Mechanical tissue present as clustered sclereids that surround the vessels.

Stomata simular on both sides, extremely large (rime 64 µm long, surface 1728 μm^2 large, among the largest of all the examples studied), yet density does not exceed 89/mm^2, so that transpiring surface covers 153,602 $\mu m^2/mm^2$ (about 15% of each leaf surface).

Protea welwitschii R. Br.



74 µm



100 µm

Distribution: *A common shrub in the warm humid temperate forest in the Transvaal region of southeastern Africa.*

Leaf surface averages 13.02 cm^2. Lamina (316 µm thick) with isolateral symmetry in transverse section. Upper and lower cuticle (attains 8 µm thick) rough, belonging to glaucous type. Epidermis monolayered (ranges from 19 µm thick on the upper side to 21 µm on the lower) and composed of rectangular cells.

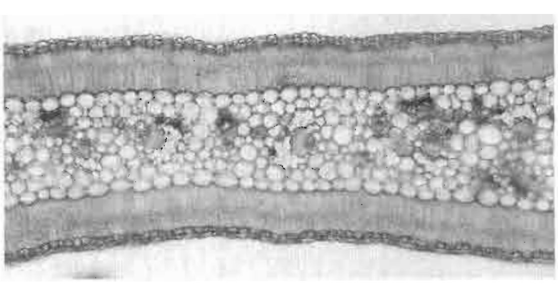
Two clearly differentiated parenchyma in the mesophyll: palisade (141 µm thick, 45% of the entire section) consists of two double layers of narrow weakly-elongated cells; spongy parenchyma (119 µm thick) composed of slightly compact rounded cells disposed between the two palisades.

Intercellular spaces rather limited.

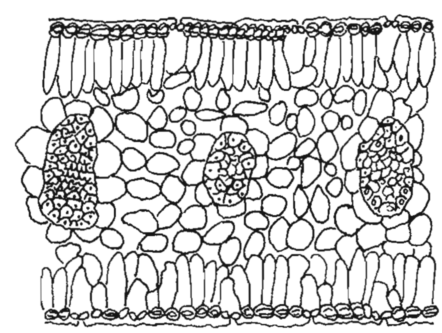
Important mechanical tissue present in the spongy tissue as clustered sclereids that surround veins, and as abundant macrosclereids and osteosclereids, that are also inserted between the palisade cells.

Stomata rather small (rima 15 µm long, surface 94 µm^2) on both sides (similar on each leaf surface); density ranges from 67/mm^2 on the upper side to 211/mm^2 on the lower, so that the upper transpiring surface is 6,305 µm^2/mm^2 (covers less than 1% of leaf area) and the lower is 19,858 µm^2/mm^2 (covers about 2% of leaf area).

Stirlingia latifolia R. Br.



145 µm



100 µm

Distribution: *A low shrub common in southwestern Australia in the kwongan and woodlands stages after fires.*

Average leaf surface attains 25 cm^2. Lamina (394.2 µm thick) with isolateral symmetry in cross section.

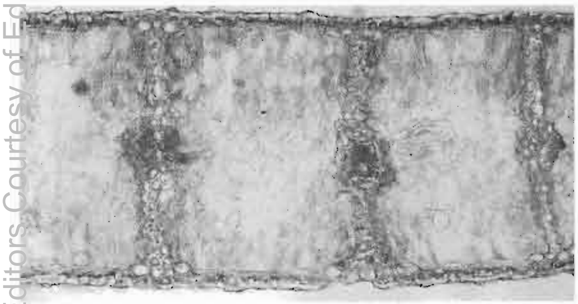
Upper cuticle smooth (13.8 µm thick; the lower 14.7 µm thick, both glaucous type). Upper and lower epidermis (12.8 µm and 22.4 µm, respectively) consist of markedly squared cells with thickned walls.

Mesophyll with clear differentiation of palisade and spongy parenchyma; palisade composed of two layers of narrow columnar cells disposed against the upper and lower epidermis; both attain 131.4 µm (33% of the mesophyll thickness). Spongy parenchyma (98 µm thick) disposed as a band between the two palisade layers and consists of rounded and rather compact cells.

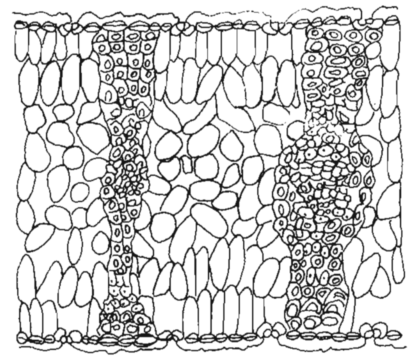
Mechanical tissue poorly represented in the leaf section: only isolated sclerenchymatous fibers are present in the spongy portion.

Stomata on both epidermis very similar in size (rima 24.2 µm and 25 µm long, surface 157 µm^2 and 184 µm^2 large in the upper and lower sides, respectively). Density ranges from 222/mm^2 to 311/mm^2 and transpiring surface from 40,921 µm/mm^2 to 48.827 µm/mm^2 in the upper and lower epidermis (about 5% of the leaf area on both sides).

Synaphea petiolaris R. Br.



156 μm



121 μm

Distribution: *A low shrub that is common in the kwongan in the mediterranean region of southwestern Australia.*

Leaf surface averaging 2 cm^2. Lamina (547 μm thick) with isolateral symmetry in transverse section.

Cuticle rough (ranges from 21 μm to 20 μm on upper and lower leaf surfaces, respectively), glaucous type.

Epidermis (ranges from 14 μm thick on upper side to 16 μm on lower) composed of a single layer of rectangular cells with thick walls.

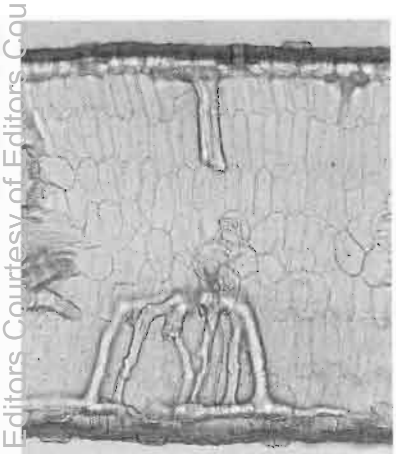
Two clearly differentiated parenchyma in the mesophyll: palisade (234 μm thick, 43% of total section) composed of two double layers of compact cylindrical cells; spongy parenchyma (242 μm thick) disposed as a band between the two parenchyma and consists of rounded cells.

Intercellular spaces are common in the inner portion of mesophyll.

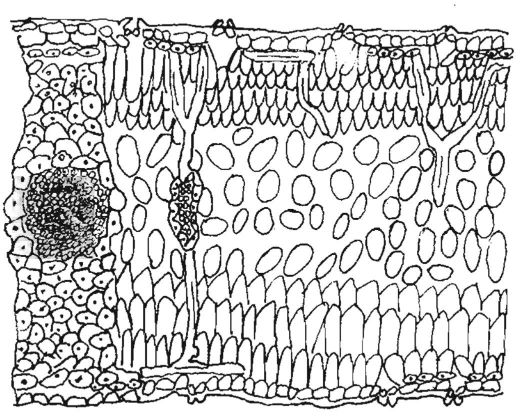
Important mechanical tissue present in the mesophyll as large sclerenchimatic boundle sheat-extensions.

Stomata rather large (rima from 40 μm to 37 μm and surface from 349 μm^2 to 340 μm^2 on lower and upper leaf surfaces, respectively) on both sides; lower density does not exceed 222/mm^2, the upper less (133/mm^2), so that lower transpiring surface covers 77,465 $\mu m^2/mm^2$ and the upper 45,224 $\mu m^2/mm^2$ (about 8% and 4% of leaf surfaces, respectively).

Xylomelum occidentale R. Br.



100 μm



100 μm

Distribution: *A small tree frequently found in the kwongan and woodlands on shallow soils in the dry-mediterranean area of southwestern Australia.*

Average leaf surface attains 25 cm^2. Lamina (527 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle smooth and undulate (13 μm thick), glabrous type. Upper epidermis (23.1 μm thick) composed of a compact layer of uniform, flattened cells.

Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (223.5 μm deep, 42% of the total thickness) consists of extremely elongated cells confined against each epidermis; spongy parenchyma (233.5 μm) present as a broad band disposed between the two palisades and is composed of rounded cells.

Substomatal cavities in the palisade layers very limited.

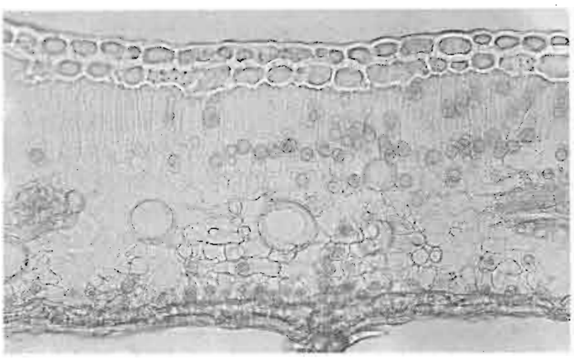
Important mechanical tissue present as extremely large bundle sheath-extensions, mostly sclerenchymatous, that cross the mesophyll from the upper to the lower epidermis, together with clustered or isolated T-shaped macrosclereids confined against each epidermis and compact linearly-aligned sclereids below the upper epidermis.

Lower epidermis monolayered (19 μm thick) and overlaid by smooth cuticle (13.8 μm thick).

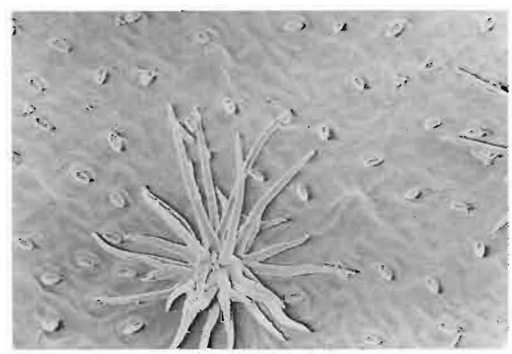
Stomata on both sides are quite similar in size and density (rima range from 43 µm to 45 µm, surface from 639 µm² to 673 µm² in the lower and upper sides, respectively). Density does not exceed 222/mm² and 177/mm², so lower transpiring surface covers 141,835 µm²/mm² and the upper 119,283 µm²/mm² (about 14% and 12% of leaf area on each side, one of the largest transpiring surfaces of the species studied).

MONIMIACEAE

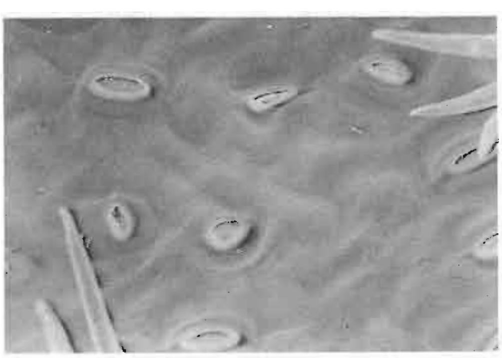
Peumus boldus Molina



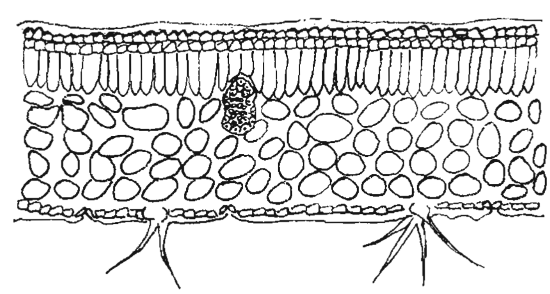
65 µm



35 µm



10 µm



100 µm

Distribution: *A small tree that is a frequent component of the mesic mathorral in the mediterranean area of Chile.*

Leaf surface attains 22 cm². Lamina (238 µm thick) with dorsiventral symmetry in transverse section.

Cuticle smooth (ranges from 7 µm thick on upper side to 2 µm thick on lower), glabrous type.

Upper epidermis (28 µm thick) consists of two layers of small rectangular cells, but the lower epidermis is monolayered and thickness decreases to 17 µm.

Two differentiated parenchyma in the mesophyll: palisade (62 µm thick, 26% of total thickness) composed of a single layer of narrow cylindrical cells; spongy parenchyma (thickness increases to 121 µm) consists of compact rounded cells.

Intercellular spaces small.

Several brunish masses and glandular cavities are present in the mesophyll.

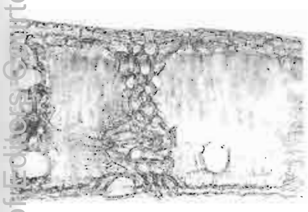
Mechanical tissue barely present in the leaf section.

Stomata rather small (rima 22 µm, surface 282 µm²) confined to the lower side; density does not exceed 177/mm², so that transpiring surface covers 138,233 µm²/mm² (about 14% of leaf surface).

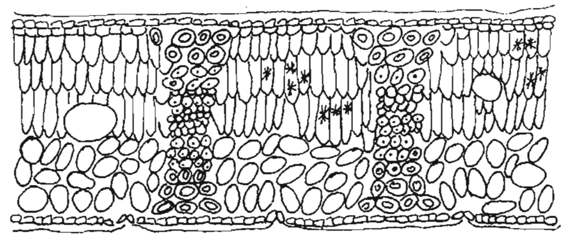
Short pluricellular hairs present on the lower epidermis.

LAURACEAE

Cryptocarya alba R. Br.



125 µm



100 µm

Distribution: *A small tree that is frequently found in the matorrall in the mediterranean region of central Chile.*

Average leaf surface attains 8 cm². Lamina (277.2 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle smooth (4.8 µm thick), glabrous type; the rather papillose lower cuticle attains 3.2 µm, glaucous type. Peculiar upper epidermis consists of two layers of compact rectangular cells and attains the remarkable thickness of 33.3 µm; monolayered lower epidermis (9 µm thick) .

Mesophyll with clear differentiation of palisade and spongy parenchyma: the former (123.6 µm deep) is composed of two layers of columnar cells that cover 45% of the total leaf thickness; spongy parenchyma (103.2 µm thick) consists of rounded cells.

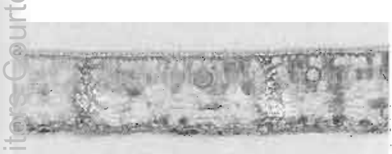
Intercellular spaces somewhat limited in this parenchyma.

Important mechanical tissue is present in the mesophyll as large bundle sheath-extensions, and mainly consists of sclerenchymatous elements that extend between the two epidermis.

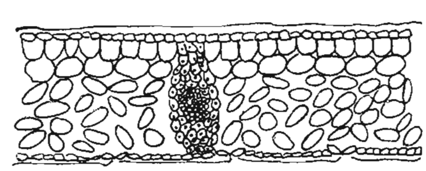
Wide glandular cavities and several oxalate crystals are also present in the mesophyll.

Stomata rather small (rima barely reaching 16.4 µm, surface only 130 µm² wide) confined to the lower side. Density attains 355/mm², so the transpiring surface covers 46,192 µm²/mm² (about 5% of leaf area).

Cryptocarya chinensis (Hance) Hemsl.



95 µm



50 µm

Distribution: *A tall tree that is a characteristic species of the tropical monsoon forest in southern China.*

Average leaf surface attains 22 cm². Lamina (194 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle flat (15.6 µm thick), as uniformly smooth the lower (12.8 µm thick). Underlying epidermis consists of a single layer of squared cells and does not exceed 9 µm – thinner than the lower one, which attains 15.6 µm.

Mesophyll (141 µm thick) undifferentiated consists of small slightly-elongated cells. Intercellular spaces limited. Two parenchyma occur in the mesophyll.

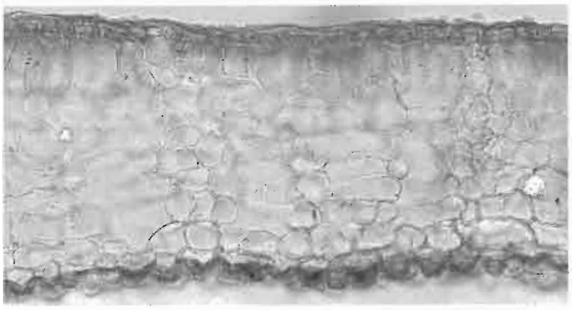
Palisade (51 µm thick, 39% of the total thickness) consists of two layers of weakly elongated cells; spongy portion (91 µm thick) composed by compact cells.

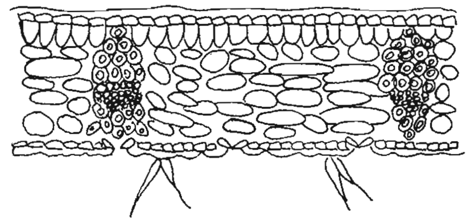
Important mechanical tissue, closely resembling that of the South American *Cryptocarya* species studied, is present in the mesophyll as large sclerenchymatic bundle sheath-extensions that extend from the upper to the lower epidermis.

Several glandular cavities in the parenchyma.

Stomata rather small (rima 19 µm long and surface 140 µm²) located in the lower side. Density attains 444/mm², so the transpiring surface covers 62,363 µm²/mm² (about 6% of leaf area).

Cryptocarya concinna Hance





60 μm 100 μm

Distribution: *A tall tree that is important in the mature stages of the tropical monsoon forest in southern China.*

Leaf surface averages 28 cm^2. Lamina (193 μm thick in cross section) with dorsiventral symmetry.

Upper cuticle uniformly smooth (12 μm thick), glabrous type; lower cuticle (12 μm thick) markedly papillose, glaucous type.

Underlying epidermis (14.2 μm thick) consists of compact rectangular cells.

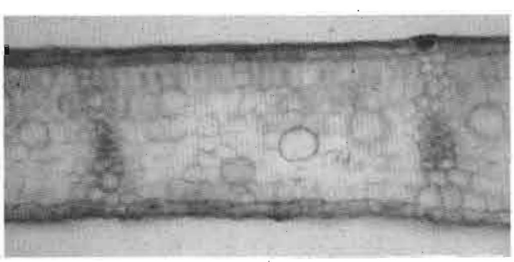
Two weakly differentiated parenchyma occur in the mesophyll. Palisade (44.30 μm thick, 29% of the total thickness) consists of slightly elongated cells; the spongy portion (100 μm thick) is composed by rounded and compact cells.

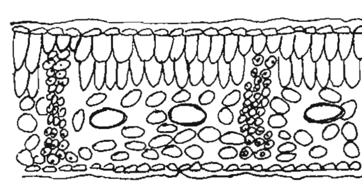
Mechanical tissue as bundle sheath-extensions that cross the mesophyll; less developed than in *Cryptocarya chinensis*.

Wide glandular cavities are also present in the mesophyll.

Stomata (rima 23 μm long and surface 207 μm^2) in the lower side are found in the epidermis (9 μm thick); extremely high density (attains 711/mm^2), so the transpiring surface covers 147,177 $\mu m^2/mm^2$ (about 14% of leaf area, the largest of the *Cryptocarya* examples studied).

Laurus azorica (Seub.) Franco





100 μm 100 μm

Distribution: *A small tree that is dominant in the closed canopy of the laurophyll forest of the subcoastal ranges of the Canary Islands.*

Average leaf surface attains 11 cm2. Lamina (204 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth (5.6 μm thick), glabrous type, but the rather papillose lower cuticle (4.3 μm thick) is glaucous. Monolayered epidermis consists of rectangular cells that range from 16 μm to 13 μm thick in the upper and lower sides.

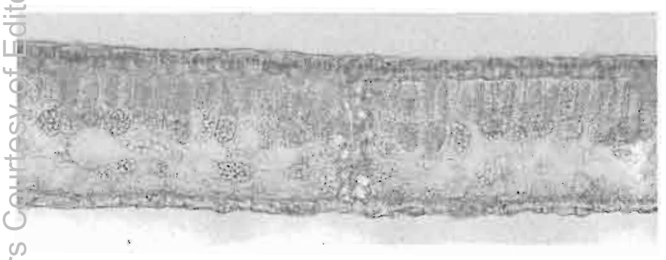
Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (71.4 μm deep) consists of two layers of columnar cells and occupies 34% of the total section; spongy parenchyma (93.2 μm thick) composed of rather elongated cells.

Wide substomatal chambers are present in the spongy portion.

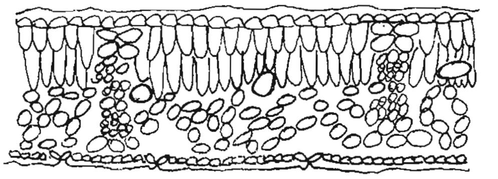
Several large glandular cavities in the mesophyll.

Stomata large (rima 26 μm long, surface 338 $\mu m^2/mm^2$) confined to the lower epidermis. Density attains 338/mm^2, so the transpiring surface attains 75,036 $\mu m^2/mm^2$ (about 7% of leaf area).

Laurus nobilis L.



100 µm



100 µm

Distribution: *A tall tree that is frequently found in the hygrophilous woodlands of the mediterranean belt of the Mediterranean Basin.*

Average leaf surface 14 cm^2. Lamina (248 µm thick) with dorsiventral symmetry in transverse section.

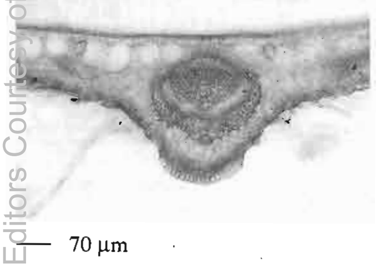
Cuticle rough and undulate (ranges from 7.7 µm to 8.2 µm in the upper and lower sides, respectively), glaucous type. Epidermis (the upper 12.6 µm thick and the lower 8.5 µm) consists of a single layer of flattened rectangular cells.

Two parenchyma are present in the mesophyll: palisade (102 µm deep) consists of two layers of cylindrical cells and occupies 45% of the leaf thickness; spongy parenchyma (87.8 µm thick) composed of rounded cells forming wide lacunae above the stomata.

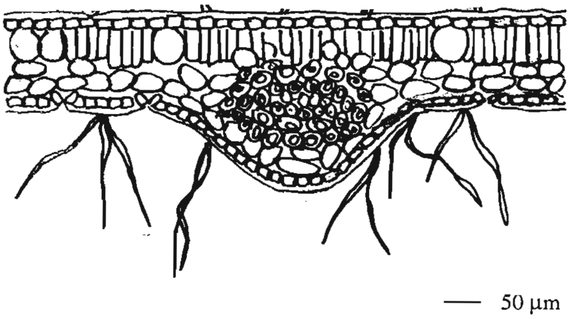
Mechanical tissue is present in the mesophyll as bundle sheath-extensions and is composed of sclerenchymatous and collenchymatous elements, the latter mostly near the two epidermis.

Stomata in the lower side; rather comparable to canariensis species both in size and density (rima 27.6 µm long, surface 358.8 $µm^2$ large). Density attains 177/mm^2, so the transpiring surface covers 63,366 $µm^2/mm^2$ (about 6% of the leaf area).

Lindera chunii Merr.



70 µm



50 µm

Distribution: *A tall tree that is an important component of the mature stages of the tropical monsoon forest in southern China.*

Average leaf surface 30 cm^2, dorsiventral symmetry in cross section (142 µm thick).

Upper cuticle smooth (10.3 µm thick), glabrous type. Underlying epidermis like the lower and is composed of a single layer (16 µm thick) of uniform rectangular cells.

Mechanical tissue poorly represented in the leaf section.

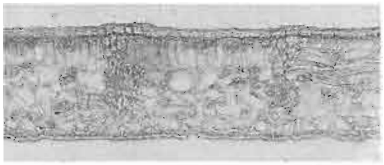
Mesophyll with clear differentiation of palisade and spongy portions; the former occupies 50% of the mesophyll with a single layer (45.4 µm thick) of somewhat-heterogeneous cells; the latter (44 µm thick) consists of small elongated cells.

Intercellular spaces limited in this parenchyma.

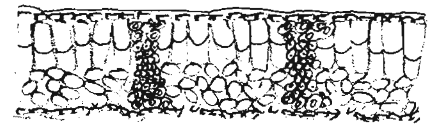
Sparse long hairs present on the lower leaf side.

Stomata small (rima 22 µm long, surface 162 $µm^2$) in the lower side. Density attains 533/mm^2, so the transpiring surface covers 86,381 $µm^2/mm^2$ (about 9% of leaf area).

Neolitsea sericea Koidz.



100 μm



100 μm

Distribution: *A tree frequently found in the evergreen subtropical forest in Hondo Island (Japan).*

Average leaf surface attains 56 cm2. Lamina (147 μm thick) with dorsiventral symmetry in cross section.

Cuticle extremely thin and smooth (does not exceed 1.9 μm and 1.4 μm in upper and lower side, respectively), glabrous type. The epidermis consists of a single layer of small uniform cells that ranges from 8.8 μm to 7.3 μm between upper and lower lamina surfaces.

Mesophyll with clearly differentiated palisade and spongy parenchyma, like most of the subtropical Japanese examples studied: palisade (60% of the total mesophyll, two times larger than the spongy portion, which barely attains 39.1 μm and that is composed of small rounded cells) consists of a single layer (88.6 μm deep) of large and elongated cells.

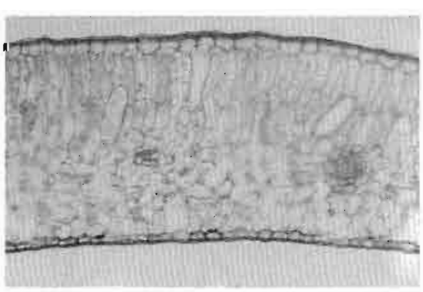
Intercellular spaces rather limited in the spongy parenchyma.

Mechanical tissue well-represented in the leaf section: large bundle sheath-extensions cross the mesophyll from the upper to the lower epidermis and surround the vascular tissue.

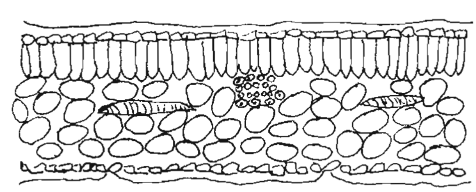
Stomata small (rima 19 μm long, surface 168 μm^2) in the lower side. Density does not exceed 311/mm^2, so the transpiring surface covers 52,403 μm^2/mm^2 (about 5% of leaf area).

DILLENIACEAE

Hibbertia cuneiformis (Labill.) Smith



150 μm



200 μm

Distribution: *A small shrub common in the kwongan and open woodlands in the dry-mediterranean region of southwestern Australia.*

Average leaf surface attains 2 cm^2. Lamina (413 μm thick) with dorsiventral symmetry in transverse section.

Cuticle smooth and weakly undulate (the upper 15.6 μm, the lower 7.8 μm thick), glabrous type. Monolayered epidermis (23.4 μm thick on both sides) consists of a single layer of uniform rectangular cells.

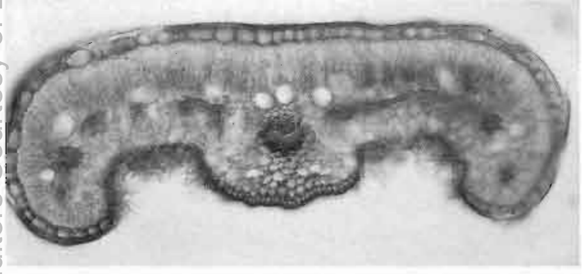
Mesophyll consists of two parenchyma: palisade (109 μm thick) composed of a single layer of narrow compact cells and occupies 26% of the leaf section; spongy parenchyma (234 μm thick) interspersed with intercellular spaces and occupies the largest portion of the mesophyll with rounded cells.

Mechanical tissue poorly represented in the blade thickness.

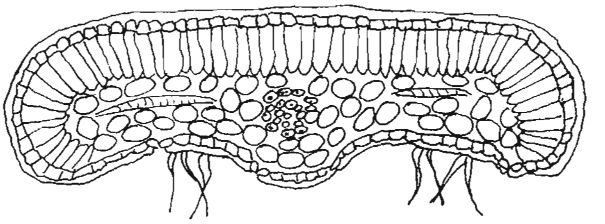
Glandular cavities are also present in the mesophyll.

Stomata large (rima 27.5 μm long, surface 240.6 μm^2/mm^2) confined to the lower epidermis. Density attains 355/mm^2, so the transpiring surface covers 85,422 μm^2/μm^2 (about 8% of leaf area).

Hibbertia hypericoides (D.C.) Benth.



175 μm



175 μm

Distribution: *A small shrub that is a common component of kwongan and open woodlands in the dry-mediterranean area of southwestern Australia.*

Average leaf surface extremely small (barely attains O.9 cm^2).

Lamina (280 μm thick, half compared to Hibbertia cuneiformis) with revolute margins, dorsiventral symmetry in cross section.

Uniformly smooth cuticle (16 μm thick in the upper side, almost twice the lower one, which does not exceed 7.8 μm), glabrous type. Underlying epidermis remarkably thick consists of a single layer (attains 31.2 μm) of squared cells with thickened walls; the lower epidermis is much thinner and does not exceed 15.6 μm.

Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (124.8 μm deep, 44% of the total section) slightly thinner at leaf margin and consists of one layer of compact narrow cells; fairly compact spongy parenchyma (86 μm thick) with small rounded cells.

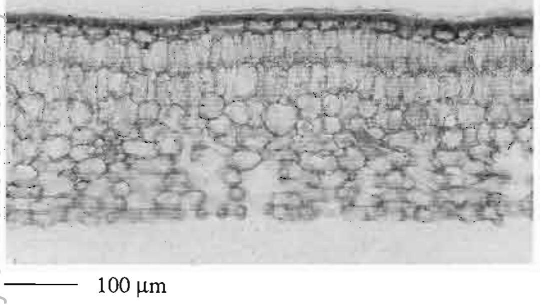
Mechanical tissue poorly represented in the leaf section except for some isolated sclerenchymatous fibers that are present in the mesophyll, and small clustered sclereids that surround the main veins.

Several glandular cavities also present.

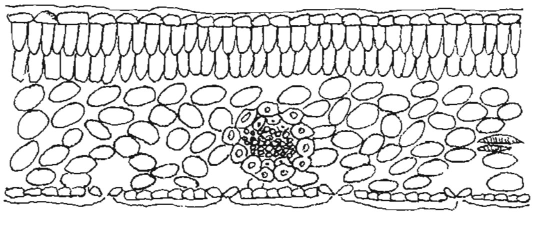
Stomata small (rima 24 μm long, surface 148 μm^2) confined to the lower side and held in wide crypts between the midrib and the leaf margin; densely covered by short pluricellular hairs. Density attains 355/mm^2, so the transpiring surface covers 52,575 $\mu m^2/mm^2$ (about 5% of leaf area).

TEACEAE

Eurya japonica Thunb.



100 μm



100 μm

Distribution: *A shrub or small tree that is a common component of the mountain-temperate forest in Japan.*

Average leaf surface attains 11 cm^2. Lamina (252 μm thick) with dorsiventral symmetry in cross section.

Cuticle very thin, smooth and undulate (does not exceed 3.7 μm on both sides), glabrous type. Monolayered upper epidermis (12.7 μm thick; like the lower) consists of uniform rectangular cells.

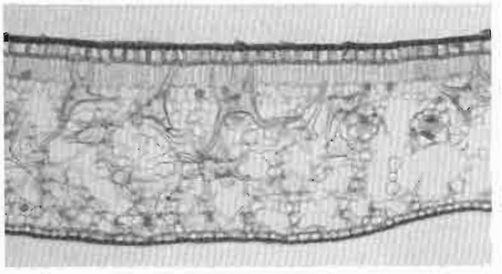
Two parenchyma in the mesophyll; palisade (70.5 μm thick) consists of two layers of compact elongated cells and occupies 27% of the entire thickness; the largest portion of the mesophyll given to the spongy parenchyma (148 μm thick) and is composed of rather elongated cells.

Wide intercellular spaces in this parenchyma, so apoplast prevails over symplast.

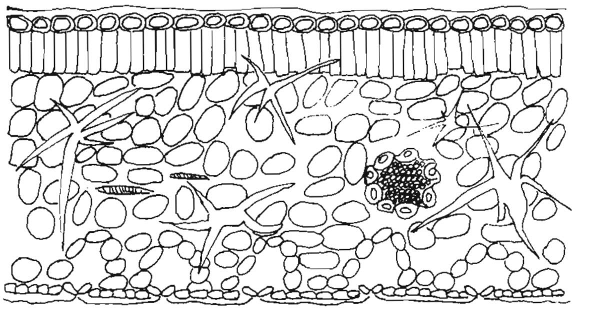
Mechanical tissue is present in the spongy parenchyma as isolated sclerenchymatous fibers and small clustered sclereids that surround the vessels.

Stomata somewhat small (rima 17.6 μm long, surface only 103.7 μm^2 wide) only on the lower side. Density attains 444/mm^2, so the transpiring surface covers 46,042 $\mu m^2/mm^2$ (about 5% of leaf area).

Ternstroemia japonica Thunb.



200 μm



125 μm

Distribution: *A tree that is common in the temperate mountain-forest in southern Japan.*

Average leaf surface attains 12 cm². Lamina (499 μm thick, the largest among tropical and subtropical species studied) with dorsiventral in transverse section.

Upper cuticle flat and smooth (15.6 μm thick; similar to the lower), glabrous type.

Underlying epidermis remarkably thick (34 μm thick, the lower much thinner and does not exceed 18.7 μm) consists of a single layer of uniform cells.

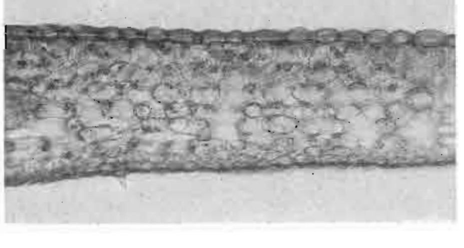
Mesophyll with clearly differentiated palisade and spongy parenchyma: thin palisade (57.7 μm, 11.5% of the total); spongy parenchyma largely prevails over palisade (357.2 μm total thickness, the largest observed among tropical and subtropical species studied).

Mechanical tissue of very peculiar aspect: several astrosclereids abundant in the mesophyll; this configuration is extremely rare in leaves of evergreen species and has been observed elsewhere only in *Isopogon attenuatus* from Australia. Isolated sclerenchymatous fibers are also present.

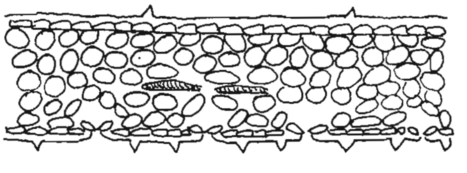
Stomata very large (rima 29 μm long, surface 320 μm²) located in the lower side. Density does not exceed 177/mm², so the transpiring surface covers 56,658 μm²/mm² (about 6% of leaf area).

SAXIFRAGACEAE

Itea chinensis Hook. et Arn.



100 μm



100 μm

Distribution: *A tree common in the tropical monsoon forest in southern China.*

Average leaf surface attains 12 cm2. Lamina (177 μm thick) with dorsiventral symmetry in cross section .

Cuticle flat, glabrous type, sparsely covered by short spine-like hairs; upper and lower cuticle barely attain 7.8 μm. Monolayered epidermis consists of rectangular cells, the upper 9 μm thick like the lower.

Undifferentiated mesophyll (142.9 μm wide) composed of uniform, round cells.

Scarce intercellular spaces present in the mesophyll.

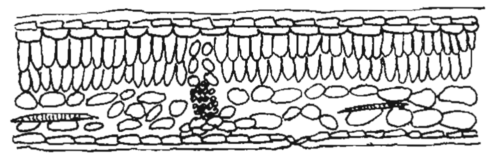
Mechanical tissue rare; present in the leaf section as isolated sclerenchymatous fibers.

Stomata extremely small (rima does not exceed 14.7 μm and surface barely attains 54 μm ²) confined to the lower side and disposed in the epidermis layer. Density attains 533/mm², so the transpiring surface is among the smallest of the tropical species studied and occupies 28,792 μm²/mm² (about 3% of leaf area).

PITTOSPORACEAE

Pittosporum viridiflorum Sims.

100 µm



100 µm

Distribution: *A small tree that is a common component of the warm temperate humid forest in the Transvaal region of southeastern Africa.*

Leaf surface averages 15.6 cm^2. Lamina thin (does not exceed 179.3 µm) with dorsiventral symmetry in cross section.

Cuticle uniformly smooth, glabrous type (the upper 9.7 µm thick, the lower 7.3 µm thick). Upper epidermis (25 µm thick) peculiar and consists of two layers of uniform rectangular cells.

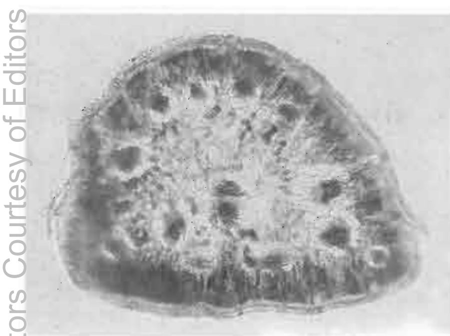
Mesophyll with clear differentiation of palisade and spongy portion palisade (50.5 µm deep) composed of two layers of cylindrical cells and occupies 28% of the leaf section; spongy mesophyll (64 µm wide) consists of rounded and elongated cells widely separated by intercellular spaces.

Mechanical tissue is present in the mesophyll both as isolated sclerenchymatic fibers in the spongy parenchyma and large bundle sheath-extensions that extend between the two epidermis.

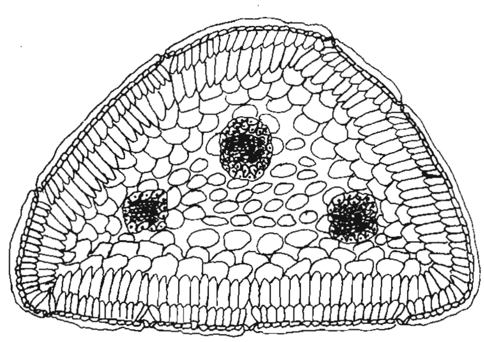
Stomata small (rima barely attains 18.5 µm, surface does not exceed 105.6 µm^2) in the lower surface. Density quite low and attains 222/mm^2, so the transpiring surface covers 23,329 µm^2/mm^2 (about 2% of leaf area, among the smallest of the species studied).

ROSACEAE

Adenostoma fasciculatum Hook. & Arn.



160 µm



145 µm

Distribution: *A tall shrub that is a frequent component of the xeric chaparral in southern California.*

Ericoid leaf with an extremely small surface (does not exceed 0.7 cm^2). Lamina with radiate symmetry in transverse section (581 µm thick) rather thick compared to other sclerophyll examples studied.

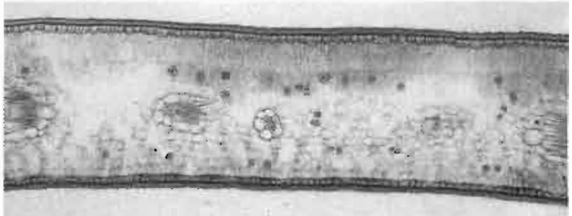
Cuticle markedly papillose (9 µm thick), glaucous type; sparsely covered by very short hairs. Monolayered epidermis (10 µm thick) consists of small flattened cells.

Mesophyll with clear differentiation of palisade and spongy portions; palisade (17% of the total section) radiates from the epidermis to the inner mesophyll and is composed of two layers (100.7 µm deep) of narrow cells, the upper more elongated than the lower; the largest portion of the mesophyll is given to the spongy tissue and occupies 441.9 µm with compact rounded cells.

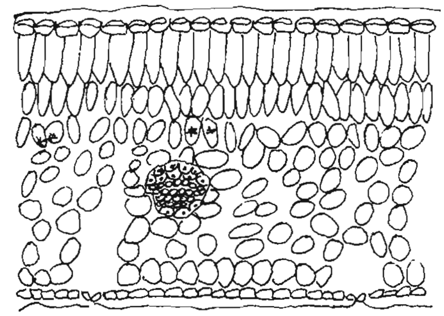
Mechanical elements are present as small clustered sclereids that surround vascular tissue in the spongy tissue.

Stomata large (rima 26.6 µm long, surface 310.8 µm^2) and disposed all around the leaf surface, somewhat sunken in the epidermis and protected by a swollen cuticle. Density attains 311/mm^2, so the transpiring surface covers 96,658 µm^2/mm^2 (10% of leaf area, among the largest of the ericoid leaves studied).

Heteromeles arbutifolia H. Roem. L.C.



200 µm



100 µm

Distribution: *A small tree frequently found in the high chaparral and evergreen woodlands diffused in southern California.*

Average leaf surface attains 19 cm^2. Lamina (408 µm thick) with dorsiventral symmetry in transverse section.

Cuticle markedly undulate, glaucous type, ranges between 8.8 µm thick and 7.9 µm in the upper to the lower sides.

Epidermis consists of a single layer of rather uniform rectangular cells, the upper epidermis (26.2 µm thick, the lower 21.2 µm) with heavily thickened outer walls .

Two parenchyma in the mesophyll: palisade (150.7 µm thick, 37% of the total section) consists of two or sometimes three layers of narrow cylindrical cells; spongy parenchyma (192.77 µm thick), about one third larger than the palisade, is composed of rounded cells.

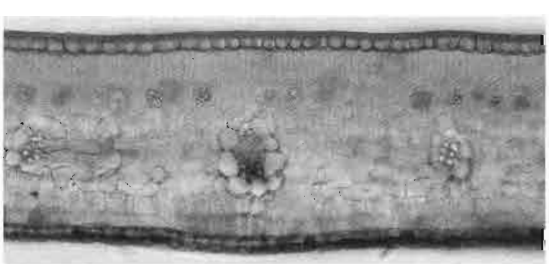
Small intercellular spaces present in this parenchyma.

Mechanical tissue poorly represented in the leaf section: only isolated sclerenchymatous fibers are present in the spongy tissue.

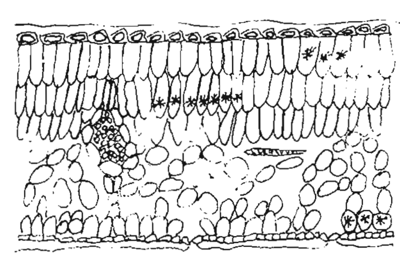
Several oxalate crystals in the assimilatory tissue.

Stomata rather small (rima attains 20.5 µm, surface does not exceed 138.8 μm^2) and confined to the lower side. Density attains 311/mm^2, so the transpiring surface covers 43,191 $\mu m^2/mm^2$ (about 4% of leaf area).

Prunus ilicifolia Walp.



110 µm



100 µm

Distribution: *A small tree common in the evergreen woodlands in the mediterranean region of southern California.*

Average leaf surface attains 13 cm^2. Lamina (296.2 µm thick) with dorsiventral symmetry in cross section.

Cuticle rather undulate (ranges between 10.3 µm and 8.6 µm from the upper to the lower side), glaucous type. Monolayered upper epidermis (16.4 µm thick; normally larger than the lower, which attains 11.6 µm) consists of a single layer of uniform rectangular cells.

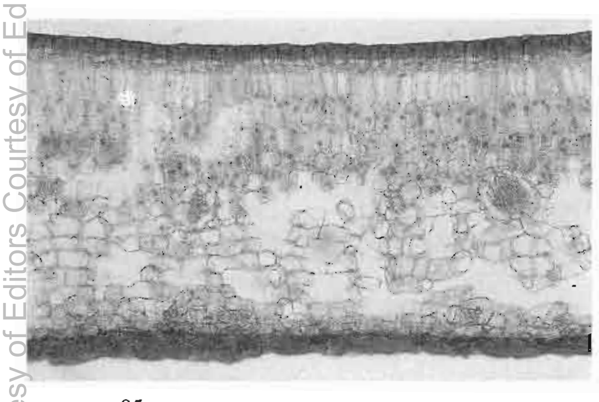
Mesophyll with clear differentiation of palisade and spongy tissue: palisade (132.3 µm deep) consists of three layers of fairly compact narrow cells and occupies 45% of the entire section; spongy parenchyma (116.7 µm thick) composed of small rounded and elongated cells forming wide lacunae disposed against the stomata in the lower portion.

Mechanical tissue well-represented in the leaf thickness: bundle sheath-extensions, mainly collenchymatous, are common in the mesophyll together with scattered sclerenchymatous fibers.

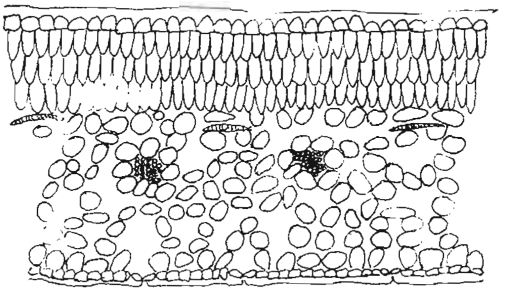
Several oxalate crystals are present in the mesophyll.

Stomata large (rima 25.4 µm long, surface 261.1 μm^2) and disposed in the lower epidermis. Density attains 266/mm^2, so the transpiring surface covers 69,468 $\mu m^2/mm^2$ (about 7% of leaf area).

Prunus lusitanica L.



85 μm



100 μm

Distribution: *A small tree that is a frequent component of open laurophyll forest canopy in the Canary Islands.*

Small leaf surface averages 4 cm2. Lamina (346 μm thick) with dorsiventral simmetry in transverse section

Upper cuticle uniformly smooth, glabrous type, barely attains 7.6 μm and similar to the lower (73 μm thick). Underlying epidermis consists of a single layer (attains 20 μm) of compact squared cells.

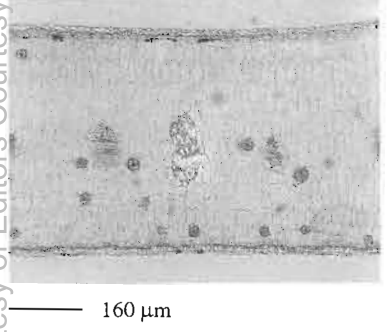
Mesophyll consists of two clearly diversified portions, palisade and spongy parenchyma. The palisade (108 μm deep, 31% of the total thickness) consists of three layers of columnar cells; the latter (188.5 μm thick), about two times larger than assimilatory portion, consists of uniform rounded cells.

Wide lacunae in the lower mesophyll in correspondence with the stomata.

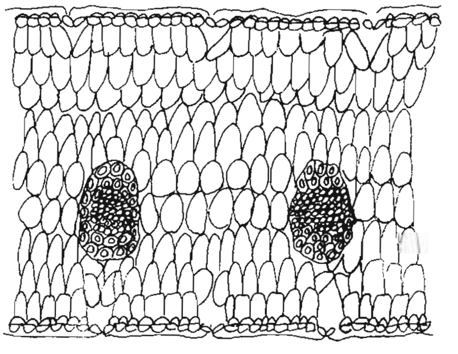
Mechanical tissue poorly represented in the leaf section.

Stomata (rima 25 μm long, surface 307 μm^2) in the lower side, confined to the epidermis (14.2 μm thick). Density does not exceed $222/mm^2$, so the transpiring surface covers 68,242.8 $\mu m^2/mm^2$ (about 7% of leaf area).

Quillaja saponaria Molina



160 μm



110 μm

Distribution: *A small tree that is a frequent component of matorral and woodlands in central Chile.*

Leaf surface averages 6 cm^2. Lamina thick (attains 503 μm) with isolateral symmetry in transverse section.

Upper cuticle weakly undulate and smooth (12 μm thick), glabrous type. Underlying epidermis consists of a single layer (23 μm thick) of rather compact squared cells with heavily thickened outer walls.

Mesophyll undifferentiated (452 μm thick) and composed of densely-assembled and palisade-like elongated cells. Small substomatal chambers are present in the mesophyll.

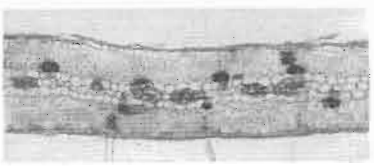
Mechanical tissue represented by rare scattered sclerenchymatous fibers and small clustered sclereids that surround vessels.

Lower cuticle (5 μm thick) overlays the epidermis (10 μm thick).

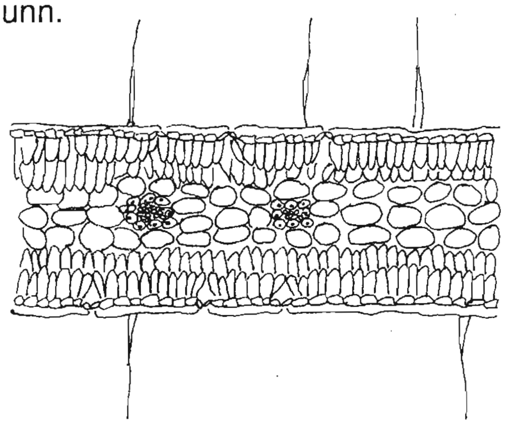
Stomata small (rima 25 μm long, surface 195 μm^2), similar on both sides, and protected by swollen cuticle. Density attains $488/mm^2$, on both epidermis, so transpiring surface covers 95,131 $\mu m^2/mm^2$ on the upper and lower sider (about 10% of leaf area, the largest among broad-leaved *Rosaceae* studied).

LEGUMINOSAE

Acacia podalyriaefolia A. Cunn.



180 µm



100 µm

Distribution: *A tall shrub that is common in kwongan and thicket formations in the dry-mediterranean area of southwestern Australia.*

Phylloid surface averages 5 cm^2. Lamina (234 µm thick) with isolateral symmetry in cross section.

Upper cuticle weakly undulate and rough (8 µm thick, like the lower one), glaucous type. Both epidermis consist of a single layer (16 µm thick) of small squared cells.

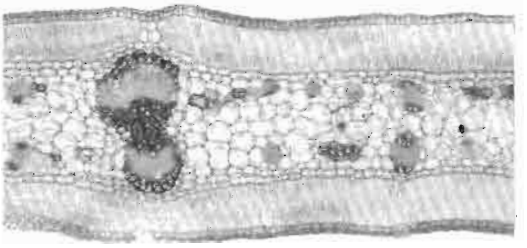
Palisade and spongy parenchyma clearly differentiated in the mesophyll: palisade (125 µm deep, 57% of total thickness) consists of two double layers of densely-assembled columnar cells; spongy parenchyma (62 µm thick) disposed as a band of compact rounded cells between the two palisades.

Mechanical tissue poorly represented: only limited sclerenchyma that surround the vessels.

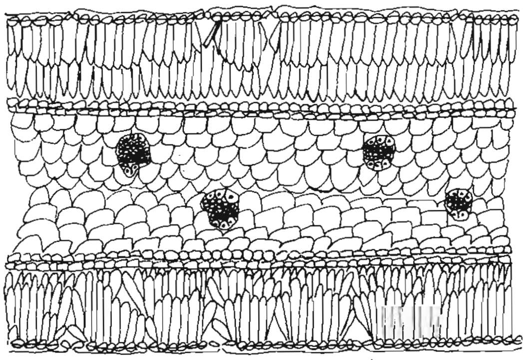
Long sparse unicellular hairs are present on the upper and lower epidermis.

Stomata wide (rima 26 µm long, surface 279 μm^2) present on both sides with the same size and density. Density attains 311/mm^2, so the transpiring surface covers 86,737 $\mu m^2/mm^2$ (about 9% of leaf area on each surface).

Acacia rostellifera Benth.



200 µm



120 µm

Distribution: *A low shrub that is common in kwongan and thicket formations diffused in the dry-mediterranean area of southwestern Australia.*

Phylloid surface averages 4 cm^2. Lamina (554 µm thick) isolateral in cross section, two times thicker than the congeneric species studied.

Cuticle smooth (8 µm thick on both surfaces), glabrous type.

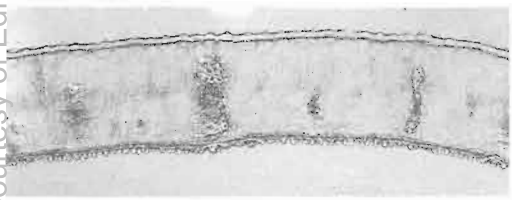
Upper epidermis monolayered (19 µm thick) thinner than the lower (23.4 µm thick) and consists of small rounded and uniformly thickened cells.

Two parenchyma in the mesophyll: palisade (242 µm deep, 44% of entire leaf section) composed of two double layers of extremely compact narrow cells confined against the upper and lower epidermis; spongy parenchyma (257 µm thick) with rounded cells that occupy the inner mesophyll portion and disposed between two layers of small, compact and epidermis-like cells.

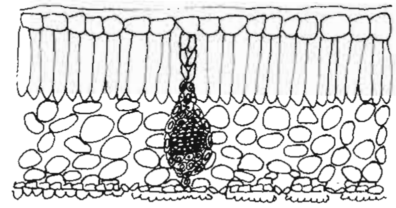
Mechanical tissue represented by limited sclerenchyma that surround the veins.

Stomata small (rima 29 µm long, surface 139 μm^2) and present on both sides. Upper density attains 266/mm^2, the lower 311/mm^2, so the transpiring surfaces range from 37,031 $\mu m^2/mm^2$ to 53,738 $\mu m^2/mm^2$, respectively (about 4% and 5% of each leaf area).

Brachysema sericeum (Smith) Domin



210 µm



125 µm

Distribution: *A creeping shrub that is a common component of the kwongan formation in the dry-mediterranean area of southwestern Australia.*

Leaf surface small (averages 2 cm^2). Lamina (304 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle markedly papillose and uniformly smooth, glaucous type, barely attains 16 µm thick, much thinner than the lower (23 µm thick, glaucous type).

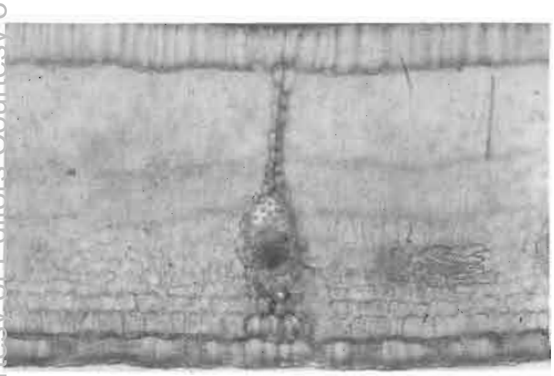
Upper epidermis remarkably thick and monolayered (attains 31 µm; the lower 16 µm), consists of compact squared cells.

Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (101 µm deep, 33% of entire section) composed of one layer of extremely elongated compact cells; spongy parenchyma (117 µm thick) consists of rather heterogeneous and somewhat widely-spaced cells.

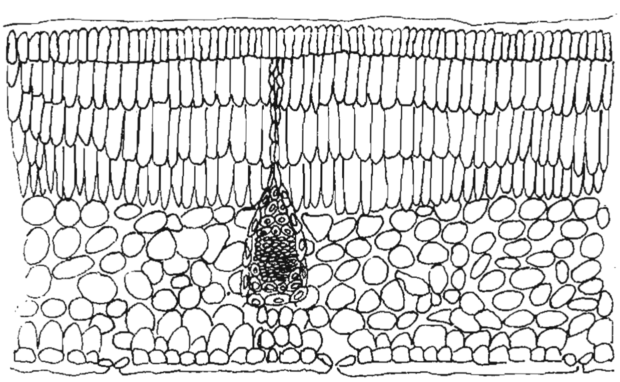
Mechanical tissue well represented as large boundle sheat-extensions lenghtening between the two epidermis.

Stomata rather small (rima 16 µm long, surface 149 μm^2) confined to the lower side. Density does not exceed 133/mm^2, so that transpiring surface covers 19,821 $\mu m^2/mm^2$ (about 2% of leaf surface, one of the smallest transpiring surfaces of the examples studied).

Ceratonia siliqua L.



100 µm



100 µm

Distribution: *A small tree diffused in the xeric maquis of the dry-mediterranean area of the Mediterranean Basin.*

Leaflet surface averages 12 cm^2. Lamina (451 µm thick) with dorsiventral symmetry in cross section.

Cuticle markedly rough and undulate, glaucous type, ranging between 19 µm on the upper side and 17 µm on the lower. Monolayered upper epidermis consists of compact squared cells and attains the considerable thickness of 40 µm, among the thickest of the species studied. Lower epidermis 21 µm thick.

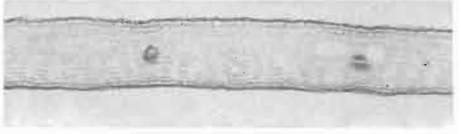
Mesophyll with clear differentiation of two parenchyma: palisade (194 µm deep, 42% of the total section) composed of three layers of extremely compact narrow cells; spongy parenchyma (159 µm), consists of quite widely-spaced rounded cells.

Mechanical tissue well-represented in the mesophyll: clustered sclereids present as large rings that surround vessels, and scattered isolated sclerenchymatous fibers.

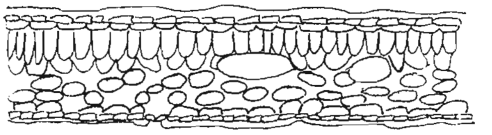
Stomata extremely small (rima 14 µm, surface 54 μm^2) confined to the lower epidermis and protected by the swollen cuticle. Density does not exceed 318/mm^2, so the transpiring surface covers 17,220 $\mu m^2/mm^2$ (about 2% of leaf surface, among the smallest of the species studied).

EUPHORBIACEAE

Antidesma venosum E. Mey.



80 µm



50 µm

Distribution: *A small tree common in the warm temperate humid forest of the Transvaal region of south-eastern Africa.*

Leaf surface averages 12 cm^2. Lamina (147 µm thick) with dorsiventral in transverse section.

Upper cuticle smooth (8 µm thick; twice as thick as the lower, 4 µm thick), glabrous type.

Upper epidermis peculiar (16 µm thick) and composed of two layers of flattened rectangular cells; monolayered lower epidermis (attains 13 µm thick).

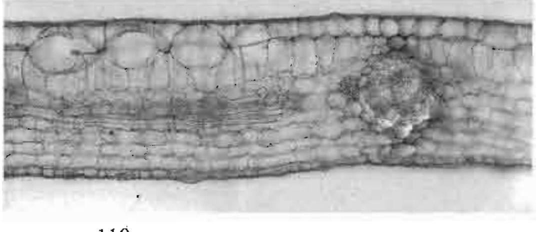
Two parenchyma in the mesophyll: palisade (58 µm thick, 49% of total thickness) consists of one layer of narrow compact cells; spongy parenchyma (49 µm thick) composed of widely-spaced rounded cells.

Mechanical tissue poorly represented.

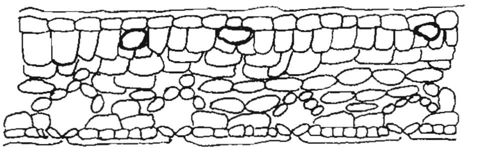
Large glandular cavities occur in the spongy parenchyma.

Stomata small (rima 14 µm, surface 41 µm2) and confined to the lower side. Density does not exceed 166/mm^2, so the transpiring surface covers 6,774 $\mu m^2/mm^2$ (less than 1% of leaf surface, one of the smallest values recorded; cfr. *Grevillea pulchella*).

Aporosa yunnanensis Metc.



110 µm



100 µm

Distribution: *A tall tree common in the tropical monsoon forest in southern China.*

Leaf surface averages 15 cm^2. Lamina (188 µm thick) with dorsiventral in transverse section.

Upper cuticle uniformly smooth (11 µm thick, like the lower), glabrous type. Monolayered upper epidermis (29 µm thick; lower epidermis 16 µm thick) consists of squared cells.

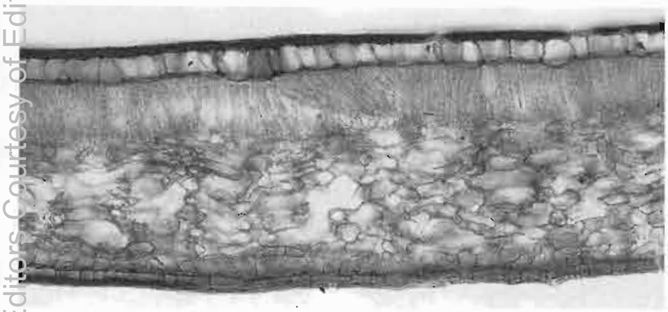
Undifferentiated mesophyll (135 µm) consists of somewhat widely-spaced heterogeneous cells.

Mechanical tissue present as isolated sclerenchymatous fibers and small clustered sclereids that surround the veins.

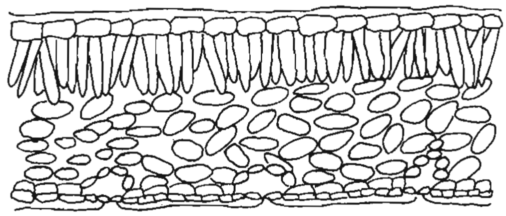
Conspicuous glandular cavities characterize the leaf section.

Stomata small (rima 18 µm long, surface 130 μm^2) and confined to the lower side. Density attains 355/mm^2, so the transpiring surface covers 46,008 $\mu m^2/mm^2$ (about 5% of leaf area).

Glochidion obovatum Sieb. et Zucc.



78 µm



100 µm

Distribution: *A tall tree that is a common component of the subtropical evergreen forest of Hondo Island (Japan).*

Leaf surface averages 6 cm^2. Lamina (265 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle slightly undulate and smooth (15 µm thick; the lower 9 µm thick), glabrous type.

Epidermis monolayered (ranges from 19 µm on the upper side to 16 µm on the lower) and consists of squared cells.

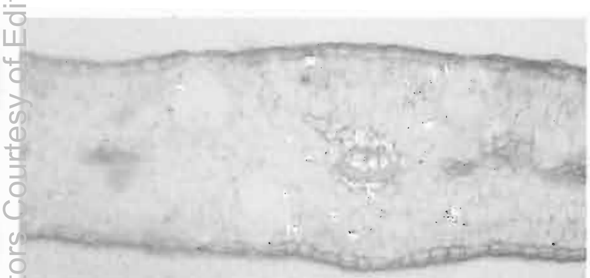
Two parenchyma in the mesophyll: palisade (64 µm thick, 24% of total section) consists of one layer of elongated cells; spongy parenchyma (141 µm thick) composed of somewhat widely-spaced heterogeneous cells.

Mechanical tissue poorly represented.

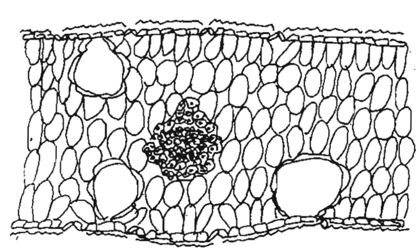
Stomata small (rima 18 µm, surface 117 μm^2) on the lower side. Density attains 533/mm^2, so the transpiring surface covers 62,148 $\mu m^2/mm^2$ (about 6% of leaf area).

RUTACEAE

Boronia crenulata Smith



100 µm



100 µm

Distribution: *A small shrub that is a common component of the kwongan in the dry-mediterranean area of southwestern Australia.*

Extremely small average leaf surface (does not exceed 1 cm^2). Lamina (296 µm thick) with isolateral symmetry in transverse section.

Upper cuticle weakly undulate and uniformly smooth (8 µm thick; the lower attains 11 µm), glabrous type.

Epidermis monolayered and ranges from 16 µm to 12 µm in the upper and lower sides, respectively.

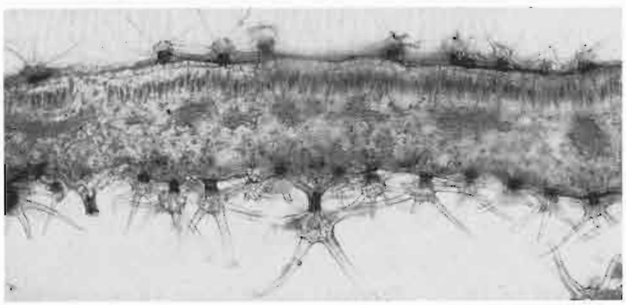
Undifferentiated mesophyll (250 µm thick) consists of compact palisade-like cells that form very small substomatal chambers.

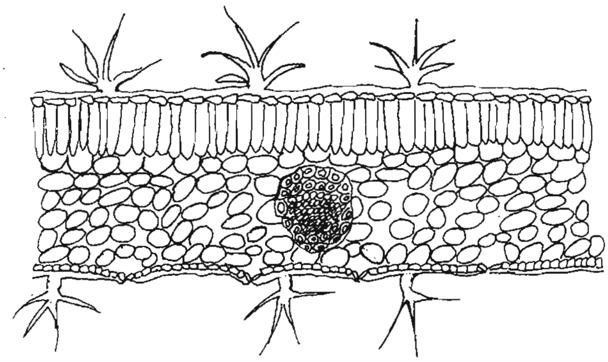
Mechanical tissue poorly represented in the leaf section.

Wide glandular cavities in the mesophyll.

Stomata wide of the same size and density (rima 30 µm long, surface 412 μm^2) and present on both sides. Density attains 311/mm^2, so the transpiring surface covers 128,287 $\mu m^2/mm^2$ (about 13% of leaf area, among the largest transpiring surfaces in the species examined).

Diplolaena microcephala Bartl





148 μm

100 μm

Distribution: *small shrub that is common in the kwongan in southwestern Australia.*

Extremely small average leaf surface does not exceed 1 cm^2.

Lamina (265 μm thick) with dorsiventral symmetry in cross section.

Weakly undulate upper and lower cuticle (8 μm thick), glabrous type. Candelabra-like branched hairs of peculiar aspect densely cover upper and lower surfaces.

Upper and lower epidermis monolayered (16 μm thick).

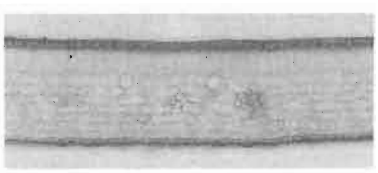
Two parenchyma in the mesophyll: palisade (78 μm deep, 29% of entire section) consists of a single layer of narrow, elongated cells; spongy parenchyma (140 μm) composed of widely-spaced rounded cells.

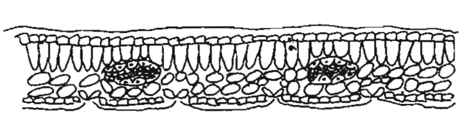
Mechanical tissue scarcely represented in the leaf section.

Stomata (rima attains 20 μm and surface 200 μm^2) in the lower side uniformly protected by hairs. Density attains 222/mm^2, so transpiring surface covers 44,440 $\mu m^2/mm^2$ (about 4% of leaf area).

SAPINDACEAE

Mischocarpus pentapetalus (Roxb.) Radlk.





35 μm

50 μm

Distribution: *A tall tree frequently found in the tropical monsoon forest of southern China.*

Average leaf surface attains 65 cm^2, one of the largest tropical leaves studied. Lamina very thin (does not exceed 95.8 μm) with dorsiventral symmetry in cross section.

Cuticle uniformly smooth (the upper 7.8 μm thick, the lower barely attains 5 μm), glabrous type. Epidermis monolayered (7.8 μm thick on both sides).

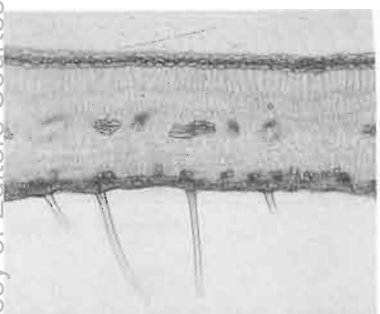
Mesophyll with clear differentiation of palisade and spongy portions: palisade (35.8 μm deep) occupies about 36% of the total section with narrow elongated cells; spongy parenchyma (31.2 μm thick) consists of rather compact and weakly-elongated cells.

Mechanical tissue poorly represented.

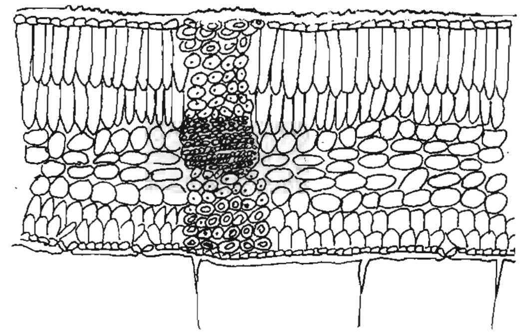
Stomata in the lower side rather small and slightly sunken (rima 20 μm long, surface 121 μm^2). Density attains 355/mm^2, so the transpiring surface covers 42,958 $\mu m^2/mm^2$ (about 4% of leaf area).

ANACARDIACEAE

Lithraea caustica Hook. & Horn.



187 μm



100 μm

Distribution: *A tall shrub or a small tree, dominant in the matorral and mesic woodlands in the mediterranean area of central Chile.*

Average leaf surface attains 7 cm^2. Lamina (317 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle smooth and slightly undulate (10.5 μm thick), glabrous type; the lower (attains 7.3 μm) is markedly rough and papillose, glaucous type.

Unicellular hairs are present on both sides, rare and shorter on the upper but relatively abundant and longer on the lower.

Epidermis monolayered and ranges from 14.6 μm and 13.8 μm between upper and lower surfaces, respectively.

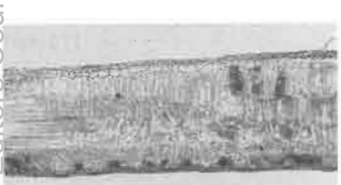
Mesophyll with clear differentiation of two parenchyma: palisade (135 μm thick, 42% of the total section) with two layers of densely-compacted cylindrical cells; spongy parenchyma (135 μm wide) occupies half of the leaf thickness with rather rounded cells.

Wide intercellular spaces absent in this parenchyma.

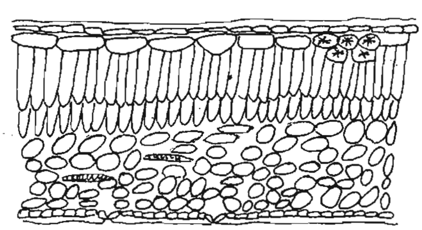
Large boundle sheat-extensions occur in the mesophyll.

Stomata small (rima 21.8 μm long, surface 145.3 μm^2) and confined to the lower side and covered by a swollen cuticle. Density attains 355/mm^2, so the transpiring surface covers 54,925 $\mu m^2/mm^2$ (about 6% of leaf area).

Pistacia atlantica Desf.



170 μm



100 μm

Distribution: *A small tree common in the open canopy of the laurophyll forest in the Canary Islands.*

Leaf surface averages 9 cm^2. Lamina (254 μm thick) with dorsiventral symmetry in cross section.

Cuticle uniformly smooth and slightly undulate (4.9 μm thick on both sides), glabrous type. Upper epidermis (30 μm thick), of peculiar aspect, consists of two heterogeneous layers of thin compact cells on the outer portion and of thick, somewhat heterogeneous collenchymatic-like squared cells on the inner portion. Clustered oxalate crystals are present in this layer.

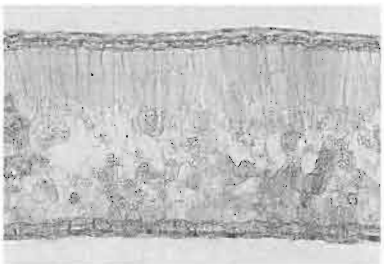
Two clearly differentiated parenchyma in the mesophyll: palisade (115 μm deep, 45% of the total section) consists of narrow columnar cells, the upper ones extremely elongated and three times longer than the lower; spongy parenchyma (91 μm wide) composed of widely-spaced rounded cells.

Mechanical tissue weakly represented in the mesophyll.

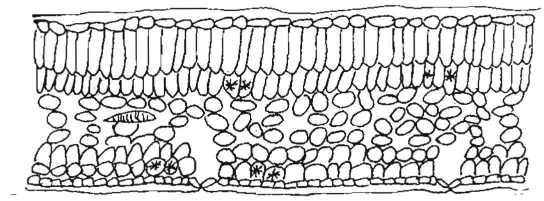
Lower epidermis consists of a single layer (7.3 μm thick) of rectangular cells.

Stomata wide (rima 26.9 μm long, surface 295 μm^2) and present on the lower side. Density 222/mm^2, so the transpiring surface covers 65,690 $\mu m^2/mm^2$ (about 7% of leaf area).

Pistacia lentiscus L.



100 µm



100 µm

Distribution: *A tall shrub that is a common component of the xeric maquis diffused in the central-southern mediterranean area of the Mediterranean Basin.*

Leaflet average surface attains 5 cm². Lamina (246.5 µm thick) with dorsiventral symmetry in cross section; its anatomy closely resembles the laurophyll *Pistacia* example studied.

Cuticle rough and markedly undulate (5.7 µm and 4.2 µm thick on the upper and lower surfaces, respectively), glaucous type. Monolayered epidermis ranges from 11.5 µm to 9.4 µm in the upper and lower side.

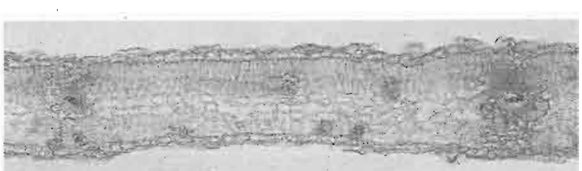
Two parenchyma in the mesophyll: palisade (98.2 µm deep) consists of two layers of elongated cells (the outer two times longer than the inner) and occupies 40% of the total leaf section; spongy parenchyma (117 µm thick) composed of small widely-spaced rounded cells in the inner portion and more compact and palisade-like cells in the lower.

Clustered oxalate crystals in the mesophyll.

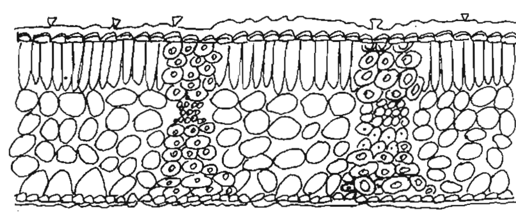
Mechanical tissue poorly represented.

Stomata large (rima 26 µm long, surface 243 µm²) and present in the lower side. Density quite low, does not exceed 222/mm², so the transpiring surface covers 53,968 µm²/mm² (about 5% of leaf area).

Rhus excisa Thunb.



190 µm



110 µm

Distribution: *A tree common in the mediterranean vegetation of southwestern Africa.*

Small average leaf surface does not exceed 1.7 cm². Lamina (250 µm thick) with dorsiventral symmetry in cross section.

Cuticle remarkably undulate and papillose (7.8 µm thick on both sides), glaucous type, with short glandular tricomes on the upper surface. Upper and lower epidermis consist of a single layer (15.6 µm thick) of small uniform cells.

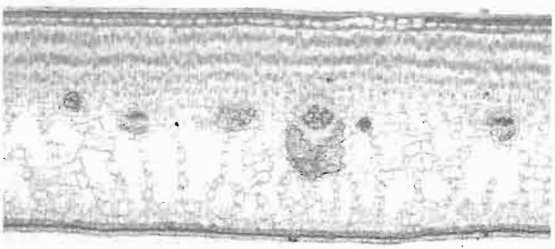
Two parenchyma in the mesophyll: palisade (70.20 µm thick) occupies 28% of the total; the spongy portion (132,6 µm thick) consists of compact and rounded cells.

Mechanical tissue well-represented in the mesophyll: large bundle sheath-extensions, mainly sclerenchymatous, cross the leaf section from the upper to lower epidermis.

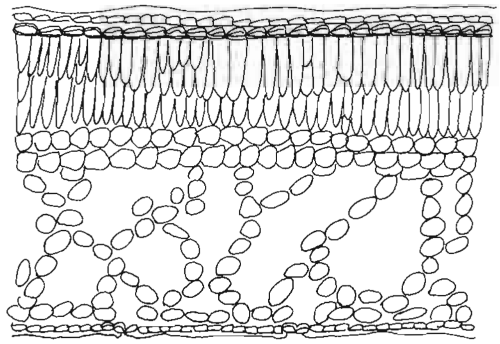
Stomata small (rima 24 µm long, surface does not exceed 144 µm²) and present in the lower surface; protected by the swollen cuticle. Yet density attains 533/mm², so the transpiring surface covers 76,752 µm²/mm² (about 8% of leaf area).

AQUIFOLIACEAE

Ilex aquifolium L.



200 µm



125 µm

Distribution: *A tall tree that is a component of relics woodlands and the mesic facies of the mediterranean belt in the Mediterranean Basin.*

Average leaf surface attains 29 cm^2. Lamina (556.6 µm thick, the thickest of the *Aquifolium* species examined), dorsiventral in cross section. Smooth cuticle (10.9 µm thick in the upper side, 12.9 µm in the lower), glabrous type.

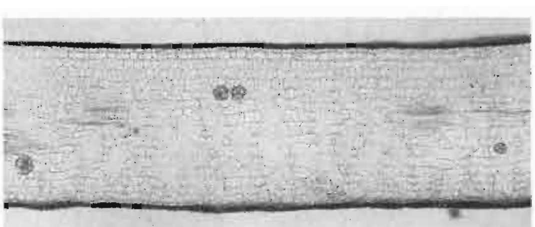
Upper epidermis (35.8 µm, the thickest epidermis among the congeneric species studied) of peculiar aspect and consists of two layers of small flattened cells, the first thinner than the second; the lower epidermis (does not exceed 13.7 µm) almost half compared to the upper.

Two parenchyma in the mesophyll: palisade (162.2 µm deep) consists of two or even three layers of compact narrow cells and occupies 29% of the total section; spongy parenchyma (320.8 µm thick) comprises the largest portion of the mesophyll and is composed of widely-spaced and rounded cells.

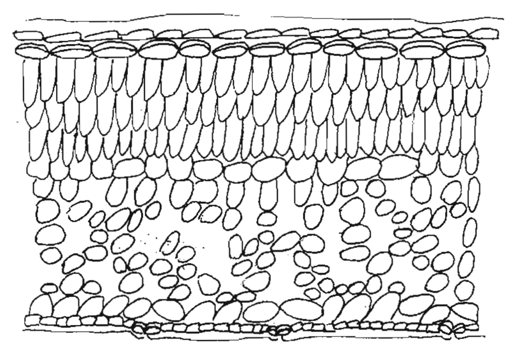
Mechanical tissue poorly represented.

Stomata wide (rima 22.8 µm long, surface 237.4 $µm^2$) and confined to the lower side. Density does not exceed 266/mm^2, so the transpiring surface covers 61,552 $µm^2/mm^2$ (about 6% of leaf area).

Ilex canariensis Poiret



200 µm



120 µm

Distribution: *A tall tree that is frequently found in the closed canopy of laurophyll forest in the Canary Islands.*

Average leaf surface attains 20 cm^2. Lamina (424 µm thick, the thickest of the canariensis species studied) with dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth and flat (9.5 µm thick), glabrous type. Underlying epidermis (34.5 µm thick) closely resembles that of other mediterranean species studied and consists of two layers of rectangular cells.

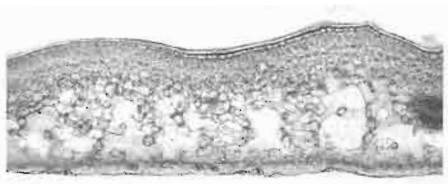
Two parenchyma within the mesophyll: palisade (137 µm deep) consists of a double layer of compact elongated cells and occupies 33% of the total section; spongy parenchyma (219.9 µm thick) occupies the largest portion of the mesophyll with widely-spaced rounded cells.

Mechanical tissue poorly represented.

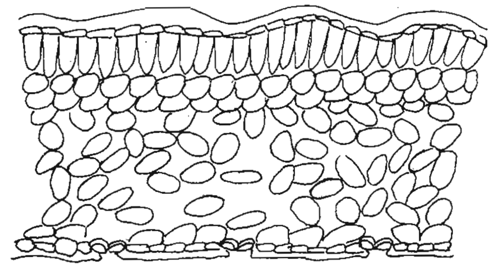
Lower epidermis monolayered (13.9 µm thick) and overlaid by cuticle (8.7 µm thick), glabrous type.

Stomata small (rima 21 µm long, surface 167 $µm^2$) and protected by swollen cuticle in the lower side. Density only attains 133/mm^2, so the transpiring surface does not exceed 22,214 $µm^2/mm^2$ (about 2% of leaf area, only one third compared to other mediterranean species examined).

Ilex rugosa F. Schmidt



150 μm



100 μm

Distribution: *A tall tree that is a common component of the evergreen subtropical mountain forest in southern Japan.*

Leaf surface very small: averages 2 cm², the smallest of Ilex examples studied. Lamina (313 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle undulate (12 μm thick), glabrous type.

Underlying epidermis consists of a single layer (23 μm thick) of squared cells.

Mesophyll with clear differentiation of palisade and spongy portions: the former (74.4 μm deep) occupies about 24% of the mesophyll and consists of a single layer of cylindrical cells; the latter (159 μm wide) composed of widely-spaced elongated cells.

Lower epidermis monolayered (20.4 μm thick) and overlaid by smooth cuticle (12 μm thick), glabrous type.

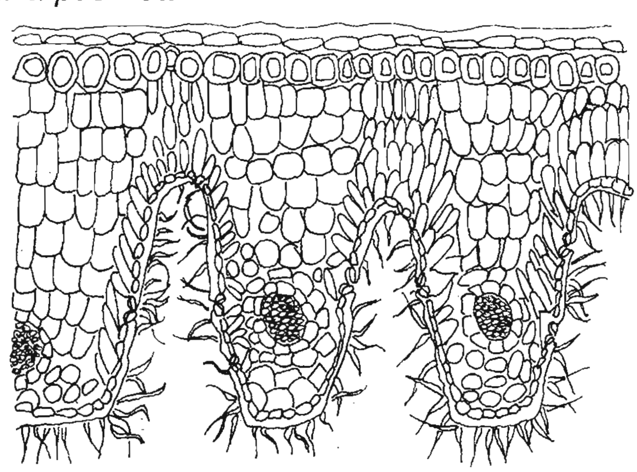
Mechanical tissue poorly represented.

Stomata small (rima 32 μm long, surface 356 μm²) and confined to the lower side. Density also low and does not exceed 266/mm², so transpiring surface covers 94,842 μm²/mm² (about 2% of leaf area, the largest transpiring surface of the *Ilex* species studied).

RHAMNACEAE

Ceanothus megacarpus Nutt.

170 μm



100 μm

Distribution: *A tall shrub that is common in the xeric chaparral in the mediterranean area of southern California.*

Leaf surface very small: averages 1 cm². Dorsiventral symmetry in cross section (582.2 μm thick, the thickest of the *Ceanothus* species studied).

Upper cuticle rough and undulate (12.6 μm thick), glaucous type. Underlying epidermis extremely thick (attains 55 μm) and consists of thin cells in the first layer and of thicker squared cells with heavily-thickened walls in the second layer.

Mesophyll very peculiar and undifferentiated (484 μm thick, characterized by deep wide crypts sunken in the lower side); mostly composed of densely-assembled squared cells; a smaller portion is composed of palisade-like elongated cells.

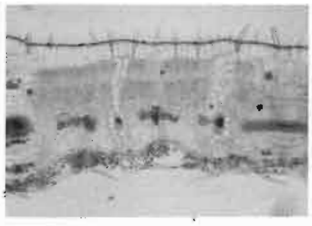
Vascular tissue confined to the lower mesophyll portion between crypt cavities.

Mechanical tissue poorly represented.

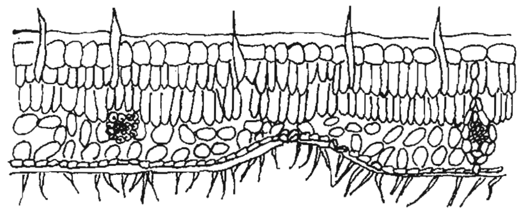
Lower epidermis monolayered (13.5 μm thick) and overlaid by cuticle (16 μm thick).

Stomata confined to the lower side and held in crypts (one of the very few species exhibiting wide crypts among all of the examples studied), and is densely covered by long unicellular hairs.

Ceanothus oliganthus Nutt.



110 μm



100 μm

Distribution: *A tall shrub that is common in the xeric chaparral in the mediterranean area of southern California.*

Leaf surface very small (barely averages 0.5 cm²). Lamina (179 μm thick, the thinnest among *Ceanothus* species sectioned) with dorsiventral symmetry in cross section.

Upper cuticle markedly undulate (8 μm thick), glaucous type, densely covered by short spine-like unicellular hairs. Underlying epidermis very thick (a common feature of all of the *Ceanothus* examples studied) and consists of a single layer (40 μm thick) of squared cells.

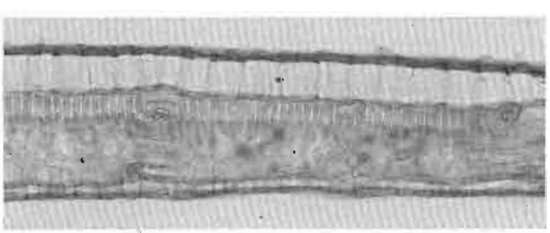
Two parenchyma within the mesophyll: palisade (61 μm thick) occupies 34% of the total section with a double layer of narrow elongated cells; spongy parenchyma (50.3 μm thick) consists of small somewhat compactly-assembled, rounded cells.

Mechanical tissue well-represented: both isolated sclerenchymatous fibers and large bundle sheath-extensions (mostly sclerenchymatous) that extend from the upper to the lower epidermis, are present in the mesophyll.

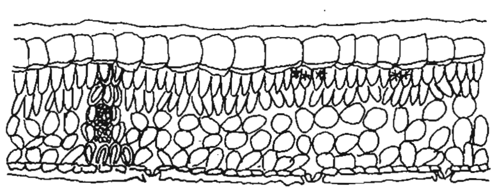
Lower epidermis (13.2 μm thick) overlaid by cuticle (6.4 μm thick).

Stomata very small (rima barely attains 17.9 μm, surface 73 μm²/mm²) present in the lower surface and confined to wide shallow crypts and protected by long, dense unicellular hairs. Density does not exceed 177/mm², so the transpiring surface covers 12,921 μm²/mm² (about 1% of leaf area, one of the lowest transpiring surfaces of all the species studied).

Ceanothus spinosus Nutt.



170 μm



170 μm

Distribution: *A small shrub that is common in the xeric chaparral in the mediterranean area of southern California.*

Leaf surface averages 2 cm². Lamina (342.5 μm thick) with dorsiventral symmetry in cross section.

Cuticle smooth and weakly undulate (8.6 μm thick), glabrous type; overlays the wide epidermis (attains the considerable thickness of 52.7 μm.) and consists of a single layer of squared cells with uniformly thickened walls.

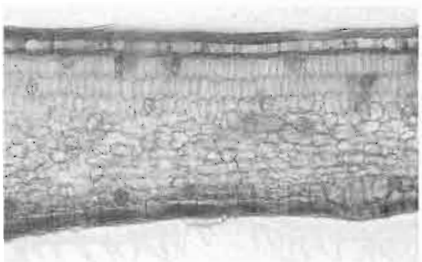
Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (66 μm deep) consists of a double layer of compact elongated cells, and occupies 19% of the total cleaf section; spongy parenchyma (197 μm wide) with irregularly-spaced rounded cells.

Mechanical tissue well-represented: large bundle sheath-extensions, mostly sclerenchymatous, extend between the two epidermis.

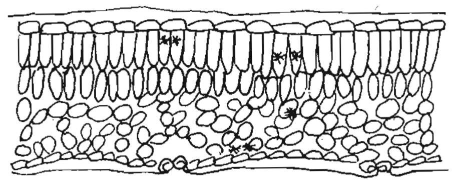
Lower epidermis (13.8 μm thick) also monolayered and is covered by the smooth lower cuticle (barely attains 3.4 μm).

Stomata rather small (rima 17 μm long, surface 117 μm² large in the lower side). Density attains 355/mm², so the transpiring surface covers 41,890 μm²/mm² (about 4% of leaf area).

Rhamnus alaternus L.



100 μm



110 μm

Distribution: *A small tree that is common in the high maquis and woodlands in the northern mediterranean area of the Mediterranean Basin.*

Average leaf surface attains 4 cm^2. Lamina (254 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle flat and uniformly smooth (8.7 μm thick), glabrous type. Underlying epidermis consists of a single layer (17.7 μm thick) of rectangular cells.

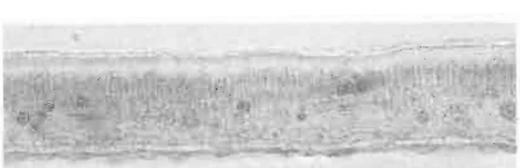
Two parenchyma in the mesophyll: palisade (88.8 μm deep, 35% of the total thickness) with a double layer of elongated cells, spongy parenchyma (116 μm thick) composed of widely-spaced rounded cells.

Mechanical tissue poorly represented.

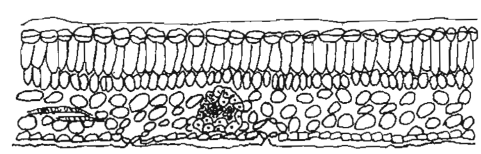
Lower epidermis monolayered (11.8 μm thick) and overlaid by smooth cuticle (10 μm thick).

Stomata small (rima 17 μm long, surface 258 μm^2) and present in the lower side. Density does not exceed 266/mm^2, so the transpiring surface covers 68,042 μm^2/mm^2 (about 7% of leaf area).

Rhamnus californica Esch.



140 μm



130 μm

Distribution: *A small tree that is a common component of mesic woodlands in the mediterranean area of southern California.*

Average leaf surface attains 5 cm^2. Lamina (172 μm thick, the thinnest *Rhamnus* specimen studied) with dorsiventral symmetry in cross section.

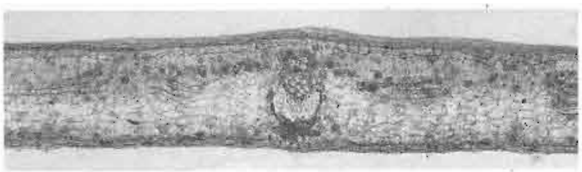
Upper cuticle smooth and undulate (8.1 μm thick), glabrous type; lower cuticle (5.4 μm thick) also smooth. Monolayered epidermis; the thick upper epidermis (attains 29.3 μm) consists of squared cells with thickened outer walls; the lower is much thinner and does not exceed 8.6 μm.

Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (57 μm deep) occupies 33% of the leaf section with a double layer of compact elongated cells, the upper two times longer than the inner; spongy parenchyma (63 μm thick) composed of small fairly-compact rounded cells.

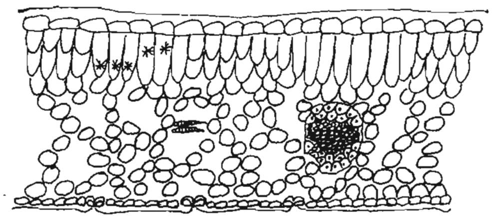
Mechanical tissue represented as rare isolated sclerenchymatous fibers and clustered sclereids that surround the vessels.

Stomata (rima 22.8 μm long and surface 179.7 μm^2) confined to the lower side. Density attains 311/mm^2, so the transpiring surface covers 55,887 μm^2/mm^2 (about 6% of leaf area).

Rhamnus crenulata Ait.



180 µm



100 µm

Distribution: *A small tree that is common in the closed canopy of laurophyll forest in the Canary Islands.*

Average leaf surface attains 5 cm². Lamina (253 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth (4.8 µm thick), glabrous type. Underlying epidermis consists of a single layer (19 µm thick) of rather compact rectangular cells.

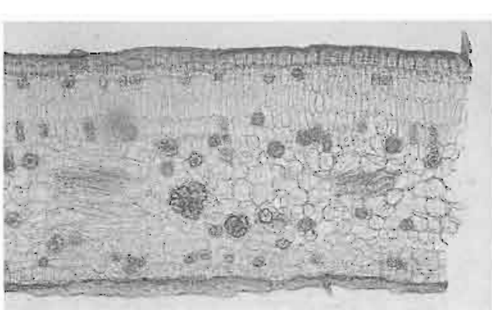
Two parenchyma within the mesophyll: palisade (66.6 µm deep, 26% of the total section) consists of a single or even double layer of uniform columnar cells; spongy parenchyma more than twice as thick as the palisade (144 µm thick) and consists of widely-spaced rounded cells.

Lower epidermis (16 µm thick) overlaid by smooth cuticle (2.9 µm thick).

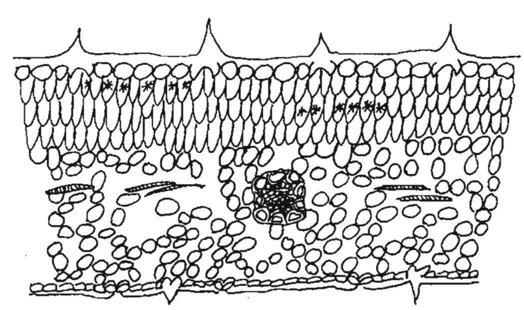
Mechanical tissue poorly represented.

Stomata large (rima 27 µm long, surface 325 µm²) and present in the lower side, the largest of *Rhamnus* examples considered). Yet density does not exceed 177/mm², so the transpiring surface covers 57,648 µm²/mm² (about 6% of leaf area, comparable to laurophyll and sclerophyll *Rhamnus* examples studied).

Rhamnus glandulosa Ait.



100 µm



100 µm

Distribution: *A small tree that is common in the laurophyll forest in the Canary Islands.*

Average leaf surface attains 5 cm². Lamina (285.8 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle flat and thin (does not exceed 6.6 µm), glabrous type, provided with peculiar short spine-like hairs. Upper epidermis consists of a single layer (18 µm thick) of compact rectangular cells.

Two parenchyma in the mesophyll: palisade (81.5 µm deep, 34% of the total section) composed of three layers of compact elongated cells; spongy parenchyma (158.2 µm wide, about two times larger than the palisade) consists of rounded cells widely-spaced in the inner portion.

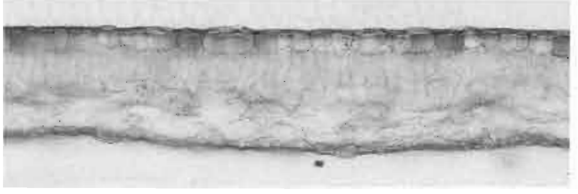
Mechanical tissue present as isolated sclerenchymatous fibers in the spongy portion.

Lower epidermis (16 µm thick) overlaid by the uniformly smooth cuticle and sparsely covered by short spine-like unicellular hairs.

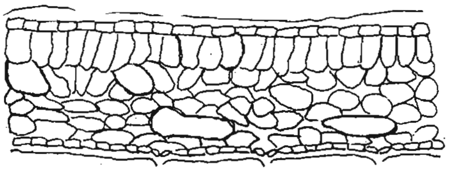
Stomata rather wide (rima 23 µm long, surface 259 µm²/mm²) present in the lower side. Density attains 222/mm², so the transpiring surface covers 57,631 µm²/mm² (about 6% of leaf area).

VITACEAE

Tetrastigma planicaule Gagnep.



100 μm



80 μm

Distribution: *A woody climber that is common in the closed canopy of the tropical monsoon forest in southern China.*

Leaf surface averages 6 cm². Lamina (135 μm thick) with dorsiventral simmetry in transverse section.

Upper cuticle uniformly smooth and flat (3.9 μm thick), glabrous type, overlays the epidermis that consists of a single layer of quite uniform rectangular cells that barely attain 5.6 μm.

Differentiated mesophyll: palisade (17 μm thick) not exceeding 14% of the total; spongy parenchyma (100 μm thick) consists of rounded cells.

Intercellular spaces remarkable: resemble wide lacunae and are present in the mesophyll, mostly in the inner portion.

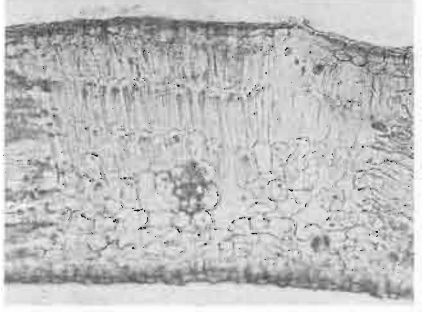
Mechanical tissue present as small clustered sclereids that surround the veins.

Lower epidermis (5.4 μm thick) overlaid by smooth cuticular layer (3.9 Êm thick).

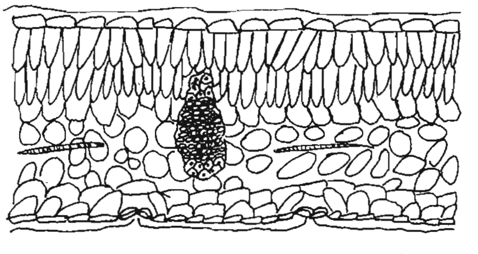
Stomata quite small (rima 22 μm long, surface 162 μm²) present in the lower side. Density attains 311/mm², so the transpiring surface covers 50,400 μm²/mm² (about 5% of leaf area).

TILIACEAE

Elaeocarpus sylvestris Poiret



85 μm



100 μm

Distribution: *A tall tree frequently found in the humid evergreen subtropical forest in southern Japan.*

Average leaf surface attains 6 cm². Lamina (295 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle slightly undulate and uniformly smooth (8.2 μm thick), glabrous type. Underlying epidermis consists of a single layer (19.5 μm thick) of fairly-compact squared cells.

Two parenchyma within the mesophyll: palisade (144 μm deep, 38.5% of the entire section) composed of two or even three layers of narrow, somewhat irregularly-assembled elongated cells; spongy parenchyma (133 μm wide) consists of uniform rounded cells.

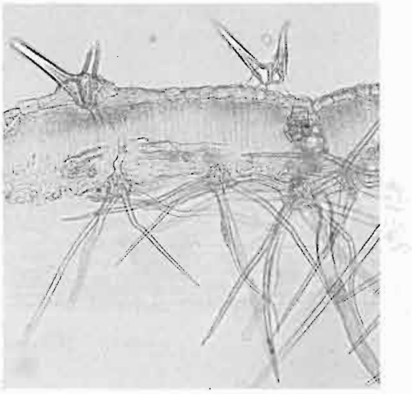
Wide intercellular spaces are not present in this parenchyma.

Mechanical tissue present as short clustered sclerenchymatous fibers. Lower epidermis (16.5 μm thick) also monolayered and is overlaid by smooth cuticle (75 μm thick).

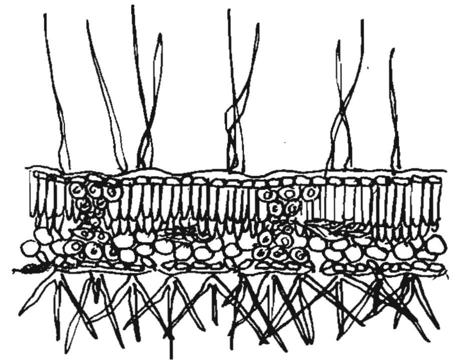
Stomata small (rima 24.9 μm long, surface 183 μm²) and present in the lower side. Density attains 577/mm², so the transpiring surface covers 105,937 μm²/mm² (about 10% of leaf area, among the largest transpiring surfaces of tropical and subtropical species studied).

MALVACEAE

Urena lobata L.



100 µm



100 µm

Distribution: *A tall tree that is frequently found in the closed canopy of the tropical monsoon forest in southern China.*

Average leaf surface attains 12 cm². Lamina (129 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle smooth flat (11 µm thick), glabrous type, covered by long sparse (though much denser on the lower cuticle) pluricellular hairs; lower cuticle (7.8 µm thick) also smooth .

Underlying epidermis monolayered (7.8 µm thick) composed of compact uniform cells.

Mesophyll with clearly differentiated palisade and spongy parenchyma: palisade (60.8 µm deep) occupies 47% of the total section with narrow cylindrical cells; spongy parenchyma (34 µm thick, half compared to palisade portion) consists of small, fairly-compact rounded cells.

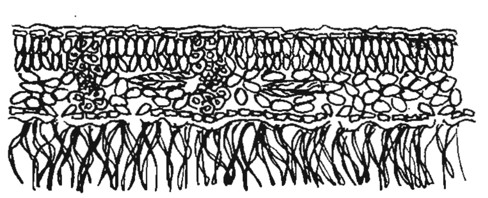
Mechanical tissue well-represented in the leaf section: large bundle sheath-extensions, mostly sclerenchymatous, extend between upper and lower epidermis and are present in the mesophyll together with short, clustered sclerenchymatous fibers.

Stomata quite small (rima 23.5 µm long, surface 172 µm²) and present in the lower side, disposed in the epidermis (7.8 µm thick). Density attains 444/mm², so transpiring surface covers 76,723 µm²/mm² (about 7% of leaf area).

STERCULIACEAE

Pterospermum lanceaefolium Roxb.

60 µm



100 µm

Distribution: *A tall tree that is frequently found in the monsoon tropical forest in southern China.*

Average leaf surface attains 23 cm². Lamina (119 µm thick, among the thinnest examples studied) with dorsiventral symmetry in cross section.

Upper cuticle (5.4 µm thick) smooth, glabrous type. Underlying epidermis extremely thin (does not exceed 4.6 µm) and monolayered.

Two parenchyma in the mesophyll: palisade (49.4 µm thick, 41% of the total) consists of a double layer of elongated cells; spongy parenchyma (46.8 µm wide) composed of fairly compact rounded cells.

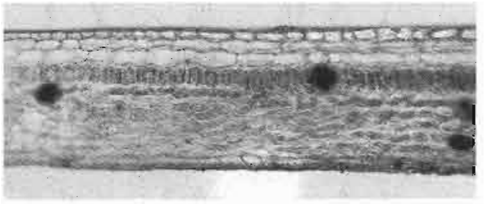
Mechanical tissue well-represented in the leaf section: large bundle sheath-extensions, mostly sclerenchymatous, extend between the two epidermis and are present together with short clustered sclerenchymatous sclereids.

Lower epidermis (5.4 µm thick) also monolayered and is overlaid by the rather undulate cuticle (7.4 µm thick), densely covered by long, pluricellular hairs.

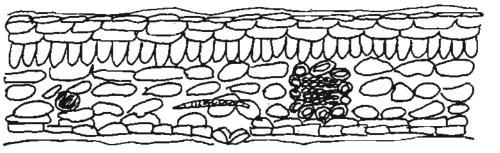
Stomata very small (rima 17.6 µm long, surface 116 µm²) and present in the lower side. Density attains 577/mm², so the transpiring surface covers 67,278 µm²/mm² (about 7% of leaf area).

BIXACEAE

Xylosma monospora Harv.



100 µm



100 µm

Distribution: *A tall tree that is frequently found in the subtropical forest in the Transvaal region of southeastern Africa.*

Leaf surface averages 32 cm². Lamina (163.8 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth (6.6 µm thick), glabrous type, sparsely covered by short unicellular and pluricellular hairs.

Upper epidermis rather peculiar and attains the considerable thickness of 32.4 µm and is composed of two layers of compact rectangular cells, the inner two times thicker than the upper.

Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (27 µm thick, 16% of leaf section) consists of a single layer of narrow weakly-elongated cells; spongy parenchyma (64.8 µm wide, composed of rounded and elongated cells.

Mechanical tissue present as small sclereids that surround vessels and short isolated sclerenchymatous fibers in the spongy tissue.

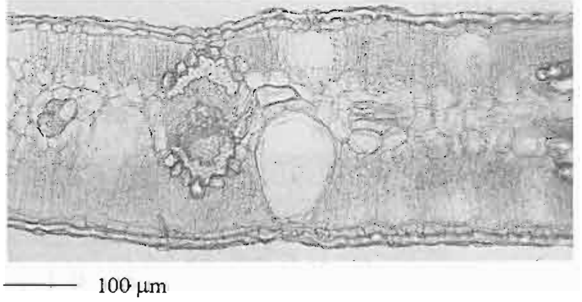
Lower epidermis (19.8 µm thick) monolayered and provided with a cuticular layer (13.2 µm thick).

Several brounish masses occur in the mesophyll.

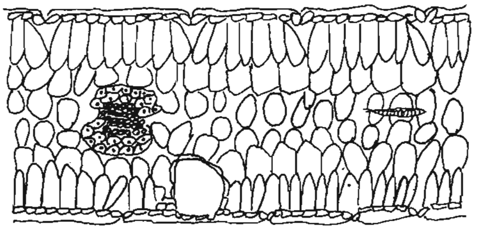
Stomata rather small (rima 21.5 µm long, surface 179 µm²) and present in the lower side. Density attains 311/mm², so the transpiring surface covers 55,575 µm²/mm² (about 5% of leaf area).

MYRTACEAE

Agonis flexuosa (Spreng.) Schauer



100 µm



100 µm

Distribution: *A tall tree that is frequently found in mesic woodlands of the mediterranean area in southwestern Australia.*

Average leaf surface attains 6 cm². Lamina (302 µm thick in cross section) with isolateral symmetry.

Cuticle smooth and weakly undulate (12 µm thick on both sides), glabrous type. Epidermis (11.4 µm thick on upper and lower surface) consists of a single layer of small rectangular cells.

Two diversified parenchyma in the mesophyll: palisade (107 µm thick, 36% of the total) consists of two layers of elongated cells confined against each epidermis; spongy parenchyma disposed between the two palisades as a band (134.9 µm wide) composed of somewhat widely-spaced and weakly-elongated cells.

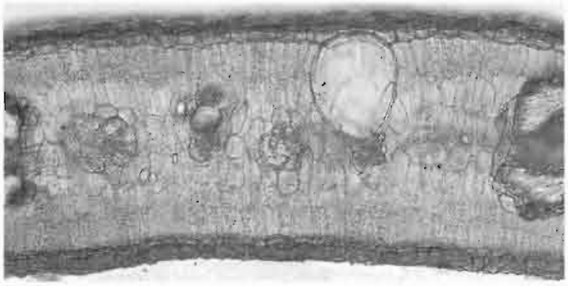
Limited substomatal chambers in the palisade layers.

Wide glandular cavities are present in the mesophyll.

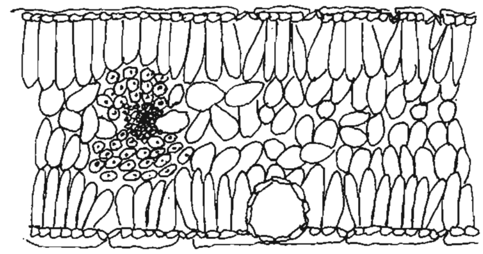
Mechanical tissue as a ring of clustered sclereids that surround the vessels, and isolated sclerenchymatous fibers in the spongy tissue.

Stomata very small (rima ranging from 15 µm to 16 µm, surface increasing from 67 µm² to 74 µm² in the upper and lower sides, respectively). Density attains 177/mm² and 133/mm², so the transpiring surface ranges from 11,859 µm²/mm² to 9842 µm²/mm² in the upper and lower surfaces, respectively (about 1% of leaf area on both epidermis).

Agonis hypericifolia Schauer



95 μm



100 μm

Distribution: *A tall tree that is frequently found in mesic woodlands of the mediterranean area of southwestern Australia.*

Average leaf surface extremely small (does not exceed 0.4 cm^2). Lamina (306.8 μm thick) with isolateral symmetry in cross section; closely resembles *Agonis flexuosa* in its anatomy.

Cuticle markedly undulate and rough (11 μm thick on both sides), glaucous type. Epidermis monolayered (the upper 17.3 μm, the lower 14.8 μm thick).

Two weakly-differentiated parenchyma in the mesophyll: palisade (116 μm deep, 38% of the total section) consists of two single layers of compact elongated cells confined against each epidermis; spongy parenchyma (135.2 μm thick) consists of densely-assembled, palisade-like elongated cells.

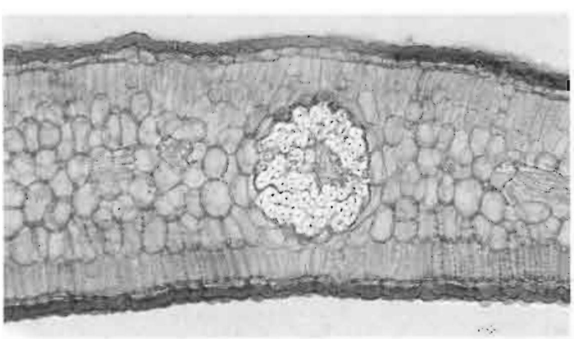
Wide glandular cavities are present in the mesophyll.

Very limited substomatal chambers in the palisade layers.

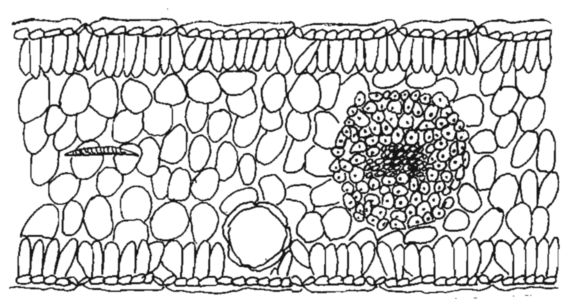
Mechanical tissue as large clusters of sclereids that surround the vessels.

Stomata on both sides similar in size and density (rima 16 μm long, surface barely ranges from 78.8 μm^2 to 72.2 μm^2 in the upper and lower sides). Density ranges from 222/mm^2 to 266/mm^2, so transpiring surface covers 17,505 $\mu m^2/mm^2$ and 19,224 $\mu m^2/mm^2$ in the upper and lower epidermis, respectively (about 2% of leaf area on each side).

Beaufortia decussata R. Br.



100 μm



100 μm

Distribution: *A low shrub frequently found in the kwongan in southwestern Australia.*

Average leaf surface extremely small and barely attains 0.5 cm^2.

Lamina (346 μm thick) with dorsiventral symmetry in cross section.

Cuticle (13.8 μm upper, 11.7 μm lower) markedly papillose, glaucous type. Monolayered epidermis (ranges from 8.6 μm to 15.2 μm upper and lower surfaces).

Mesophyll with clearly differentiated palisade and spongy parenchyma: palisade (86.4 μm deep, 25% of the total section) consists of two single layers of compact narrow cells confined against each epidermis; spongy tissue occupies the largest portion of the mesophyll as a band (210 μm thick) disposed between the two palisades and consists of compact, rounded cells.

Wide glandular cavities in the mesophyll.

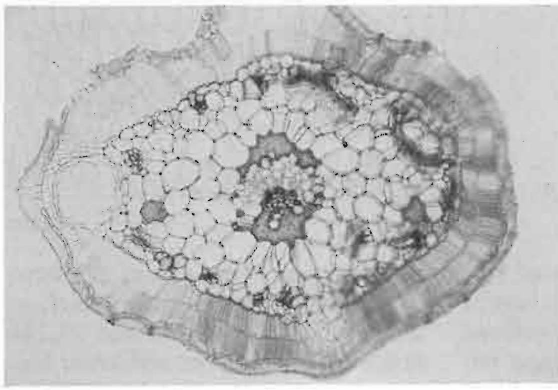
Very limited substomatal chambers in the palisade layers.

Mechanical tissue present as large ring of clustered sclereids that surround the veins.

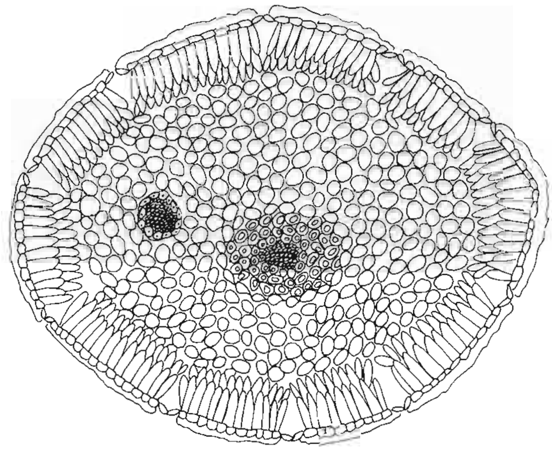
Stomata on both sides (rima ranging from 19 μm to 25 μm and surface from 167 μm^2 to 231 μm^2 in the lower and upper sides respectively) with same density.

So transpiring surface covers 51,282 $\mu m^2/mm^2$ and 37,185 $\mu m^2/mm^2$ in the upper and lower surfaces, respectively (about 5% to 4% of each leaf side).

Calothamnus quadrifidus R. Br.



220 µm



200 µm

Distribution: *A low shrub spread throughout the kwongan in the dry-mediterranean area of southwestern Australia.*

Ericoid leaf with a very small surface (barely attains 17 mm²). Radial symmetry in cross section (attains 1,126 µm, which is the largest among all cut leaves).

Cuticle rough, markedly undulate and extensive (28.8 µm thick), related to the glabrous type.

The underlying epidermis (23.8 µm thick) is composed of a single compact layer of uniform rectangular cells.

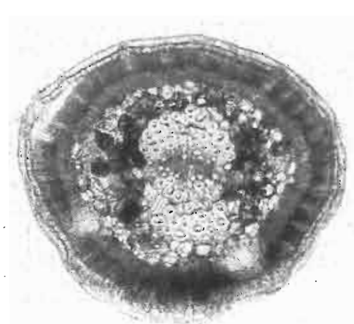
Mesophyll with clearly-differentiated palisade and the spongy portion: assimilatory parenchyma (253.8 µm thick) consists of two layers of narrow, elongated cylindrical cells and occupies 22% of total leaf thickness; spongy parenchyma, about three times thicker than palisade (766.8 µm thick), consists of small, rounded cells that are densely-assembled as a ring that surrounds the large midvein.

Wide intercellular spaces lacking in this parenchyma.

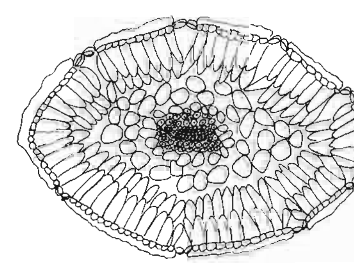
Mechanical tissue represented only by clustered sclerenchymatous fibers, which protect the vessels.

Stomata disposed in the epidermis layer and distributed all around the leaf surface and protected by wide antechambers formed by the swollen cuticle; rather small in size (the rima just 16.8 µm and the surface does not exceed 61.7 µm²). Density 222/mm², so the transpiring surface covers 13,708 µm²/mm² (1.3% of leaf area, only half compared to *C. sanguineus.*

Calothamnus sanguineus Labill.



190 µm



220 µm

Distribution: *A low shrub that is common in the kwongan in the dry-mediterranean area of southwestern Australia.*

Ericoid leaf with extremely small surface (18 mm²).

Lamina (667 µm in cross section, half in comparison to *C. quadrifidus*) with radial symmetry.

Cuticle rather rough and markedly undulate (14.1 µm thick), glaucous type, slightly swelling over the stomatal guard cells. Underlying epidermis composed of a single layer (17.3 µm thick) of homogeneous rectangular cells.

Two parenchyma clearly differentiated in the mesophyll: palisade consists of two layers (211 µm deep) of narrow elongated cells, the upper often longer than the lower. They represent 32% of the total section; the spongy parenchyma (393 µm thick) occupies the inner portion of the mesophyll and is composed of irregularly-assembled rounded or elongated cells.

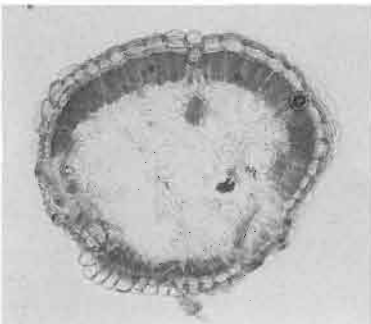
Wide intercellular spaces lacking in this parenchyma.

Mechanical tissue absent except for the clustered sclereids that surround the midvein.

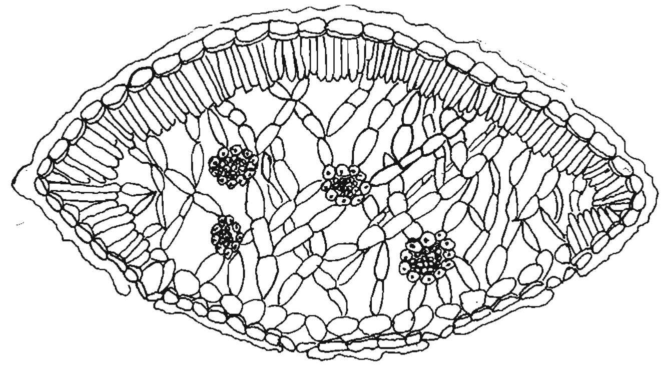
Stomata (rima does not exceed 17.7 µm in length and surface barely attains 95.5 µm²) surround the epidermis layer and are protected by wide antechamber formed by the cuticle layer; rather limited substomatal chambers (formed in the compact palisade layer).

Rather low density (attains 266/mm²), so the transpiring surface is 25,413 µm²/mm² (2.5% of the leaf area, which is two times larger than C. quadrifidus).

Darwinia lejostyla (Turcz.) Domin



130 µm



100 µm

Distribution: *A low shrub found in the mountain thicket of Stirling Range in southwestern Australia.*

Surface barely averages 8 mm²; ericoid leaf with dorsiventral symmetry in cross section (449 µm thick).

Cuticle rather smooth and undulate (14.5 µm thick), glaucous type. Epidermis made up by a single layer (22.14 µm thick) of densely-packed squared cells with greatly thickened outer walls.

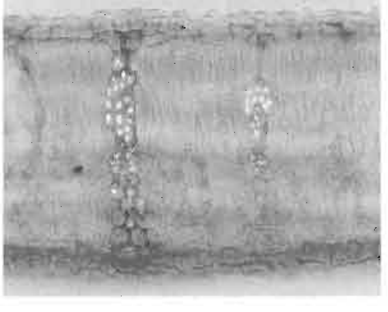
Mesophyll with clearly differentiated palisade and spongy parenchyma: the former very compact, composed of a single layer of elongated cells that barely attain 60.5 µm and occupy the upper portion of the mesophyll (13% of the total, progressively lower at leaf margins and almost disappears on the lower side).

Spongy parenchyma (317 µm hrick) very peculiar and consists of thin widely spaced and elongated cells.

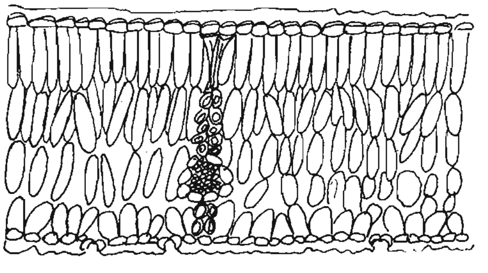
Mechanical tissue occur in the spongy as small clustered selereids that ring the vessels.

Stomata rather large (rima is 26 µm long and the surface is 304.9 µm²) present only on the lower side and slightly sunken into the epidermis. Density attains 222/mm², so the transpiring surface covers 67,687 µm²/mm² (6.7% of the leaf area, a rather high value compared to the other ericoid leaves studied).

Eucalyptus calophylla Lindley



110 µm



100 µm

Distribution: *A tall tree common in the mixed woodlands of the dry-mediterranean region in southwestern Australia.*

Average leaf surface 21 cm², with dorsiventral symmetry in cross section. Lamina attains a thickness of 311.7 µm.

Upper cuticle undulate (8.6 µm thick), glaucous type. Epidermis composed of a single layer (17.6 µm thick) of quite uniform rectangular cells with somewhat-thickened inner walls.

Two portions contribute in forming the mesophyll: the palisade and spongy parenchyma. The former is composed of a double layer (104.8 µm deep) of densely-pressed and extremely-elongated cells and occupies 33% of the total leaf section. The latter (146.7 µm thick) represents the larger portion of the mesophyll, where palisade-like, rather elongated cells are regularly assembled.

Intercellular spaces limited, particularly in the lower portion.

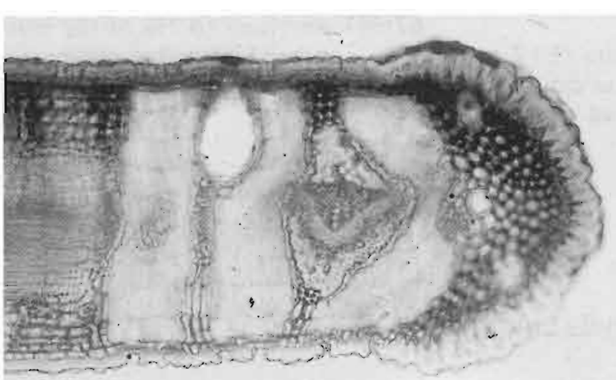
Important mechanical tissue is present: frequent, extremely-large bundle sheath-extensions (that consist of lignified palisade cells in the upper portion) cross the mesophyll from the upper to the lower epidermis and surround the vascular tissue; sclerenchymatous elements prevail over collenchymatous. Small sclerenchymatous fibers are also present in the spongy portion.

Stomata confined against the compact mesophyll layer and are sunken in the lower epidermis (17.3 μm thick, with thin walls) and protected by wide antechambers above the guard cells.

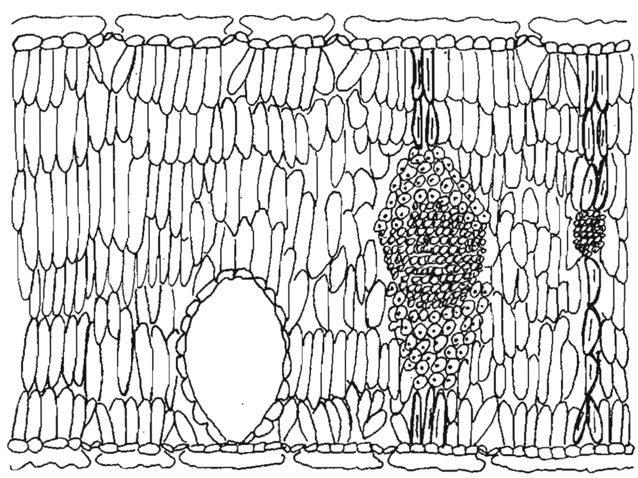
Cuticle (16.6 μm thick), glaucous type.

Stomatal rima 29.4 μm long and surface 216 μm^2 large; density does not exceed 266/mm^2, so the transpiring surface covers 57,479 μm (5.7% of the leaf area, barely larger than that of *E. marginata*).

Eucalyptus caesia Benth.



150 μm



100 μm

Distribution: *A tall tree that is common in the woodlands of the dry-mediterranean region in southwestern Australia.*

Leaf surface does not exceed 24 cm^2 (616 μm in cross section, twice as large as the other *Eucalyptus* specimens studied and also distinguished by isolateral symmetry of the leaf section).

Upper and lower cuticle rather thick, rough and weakly undulate (29.2 μm thick), both sides glaucous type. Cuticular protrusions form a wide antechamber above the guard cells.

Underlying epidermis made up of a single layer (18 μm thick) of rectangular cells and closely resembles the lower epidermis (17.3 μm thick).

Undifferentiated mesophyll: rather elongated cells densely-assembled into a single palisade-like portion (522.9 μm) are present throughout the mesophyll; intercellular spaces very limited among these cells, but large glandular cavities are also present.

Mechanical tissue very well-represented: consists of important bundle sheath-extensions that extend between the upper and lower epidermis; sclerenchymatous elements prevail over collenchymatous, especially those that surround the vascular tissue.

Stomata (lower rima is 33.4 μm and the surface 289 μm^2, while the upper rima is 31.1 and the surface 269.3 μm^2) protected by wide antechambers above the guard cells and are present on both leaf sides (the lower slightly larger than the upper). Remarkably divergent densities (222/mm^2 on the upper side, so the transpiring surface covers 64,158 $\mu m^2/mm^2$ – 6.4% of leaf surface – and 349/mm^2 on the lower, so the transpiring surface attains 93,881 $\mu m^2/mm^2$ – 9.3% of the leaf area).

thick) of quite uniform rectangular cells.

Mesophyll with clearly differentiated palisade and spongy parenchyma: the former radiates from the epidermis to the inner portion of the mesophyll and is composed of two layers (274 µm deep, 41% of the total section) of narrow, densely-pressed columnar cells; the upper is generally longer than the lower. Large glandular cavities are also present in the palisade.

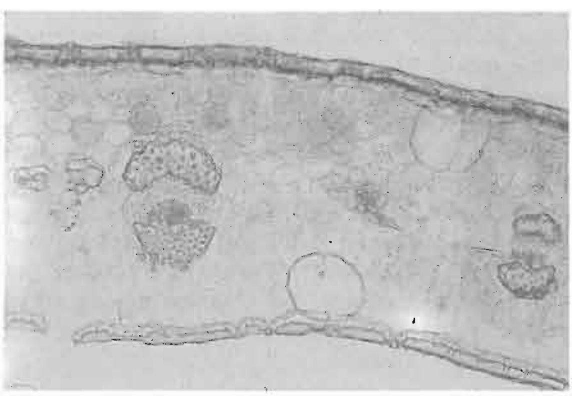
Spongy portion (339.7 µm thick, constituting most of the leaf thickness) consists of small, rounded or markedly-elongated cells and occupies the middle portion of the section.

Intercellular spaces rather limited in the spongy parenchyma.

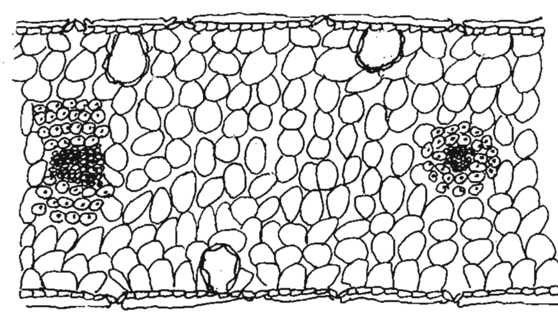
Mechanical tissue lacking except for some sclerenchymatous fibers, either isolated or clustered as a ring that protect vessels in the spongy tissue.

Stomata at the epidermic level disposed all around the blade margin and protected by the swollen cuticle, which forms a wide antechamber above the guard cells; rima barely attains 14.3 µm and surface does not exceed 44.9 μm^2 large (rather small in comparison to other ericoid leaves studied). Density up to 222/mm^2, so the transpiring surface 9,985 $\mu m^2/mm^2$ (1% of the leaf area, one of the smallest among all of the species studied).

Kunzea recurva Schauer



100 µm



100 µm

Distribution: *A low shrub that is common in the kwongan in the drymediterranean region of southwestern Australia.*

Average leaf surface (5 cm^2); lamina (347 µm thick) with isolateral symmetry in cross section.

Upper cuticle rather rough and undulate (12.4 µm thick), glaucous type, overlays the upper epidermis is composed of a single layer (which does not exceed 17.6 µm) of rather uniform squared or weakly-elongated cells.

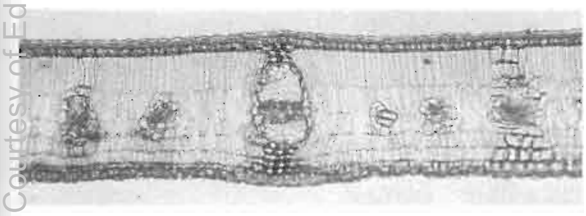
Undifferentiated mesophyll (286.82 µm thick, uniformly covered by closely-spaced and round cells. Wide glandular cavities are present among the palisade cells. Spongy parenchyma (does not exceed 106.5 µm) disposed between the two palisades and is composed of densely-assembled rounded cells; wide intercellular spaces therefore lacking.

Mechanical tissue present in the leaf mesophyll as isolated sclerenchymatous fibers scattered in the spongy parenchyma, and as clustered sclereids that surround the vascular tissue.

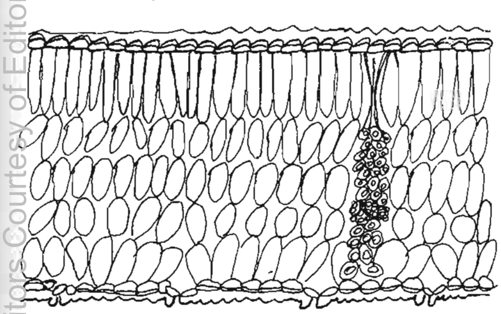
Lower cuticle and epidermis (14.8 µm and 15.8 µm thick, respectively) closely resemble the upper.

Stomata on both sides at the epidermis level protected by a marked protrusion of the cuticular layer; rather different in size (rima 31.8 µm and 17 µm long, and the surface is 309 μm^2 and 71.8 μm^2 large in the lower and upper sides, respectively). Density up to 133/mm^2 high on both surfaces, so lower transpiring surface 41,187 $\mu m^2/mm^2$, about two times as large as the upper, which is only 9,549 $\mu m^2/mm^2$ (ranges from 1% to 4% of the leaf area).

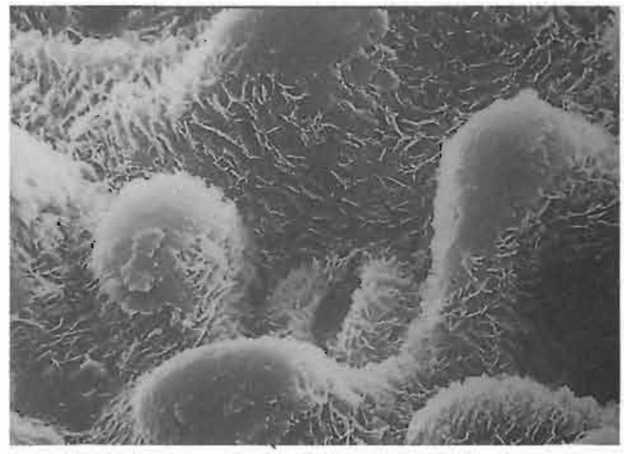
Eucalyptus marginata Donn.



210 µm



100 µm



10 µm

Distribution: *A tall tree or mallee that is common in the mixed woodlands of the Jarrah forest in the dry-mediterranean and meso-mediterranean region in southwestern Australia.*

Leaf surface averages 45 cm², with dorsiventral symmetry in cross section (356 µm thick) and anatomically similar to *E. calophylla* specimens.

Upper cuticle (16 µm thick) with marked protrusions on its surface, glaucous type. Underlying epidermis consists of a single layer (20 µm thick) of quite uniform rectangular cells provided with somewhat thickened outer walls.

Mesophyll with clearly differentiated palisade and spongy parenchyma: the former (averages 93.7 µm, only 26% of the leaf thickness) consists of a single layer of elongated cells; the latter (attains 189.6 µm, which is twice the palisade) accounts for most of the mesophyll thickness. Wide intercellular spaces are present among the slightly-elongated cells of this parenchyma.

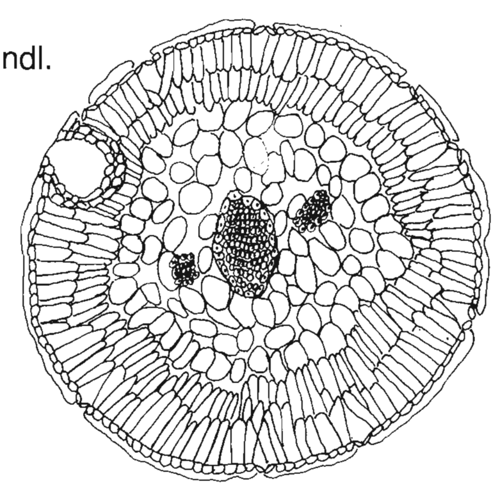
Mechanical tissue very well-represented in the leaf section: frequent macroscleryds and sclerenchymatous fibers are present in the mesophyll, arranged together to form large bundle sheat-extensions that extend from the upper to the lower epidermis.

Lower epidermis (19.3 µm thick) very similar to the upper and is provided with thickened outer cells walls.

Stomata disposed in the epidermis layer, very well protected by the swollen cuticle (also glaucous, 16.9 µm thick), which forms a wide antechamber above the guard cells; rima barely attains 20.5 µm and surface 151.2 µm² large. Density does not exceed 266/mm², so transpiring surface 40,219 µm²/mm² (4% of the leaf area, the smallest among all of the three Eucalyptus leaves studied).

Hypocalimma angustifolia Endl.

200 µm



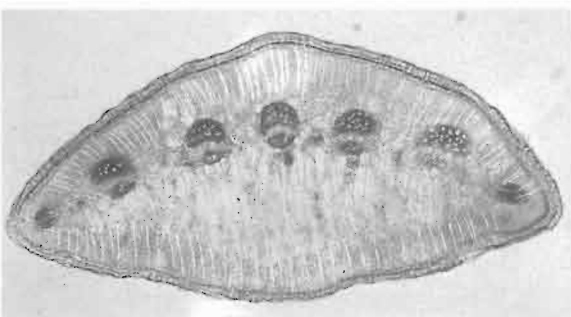
110 µm

Distribution: *A low shrub that is common in the kwongan and woodlands in the dry-mediterranean area of southwestern Australia.*

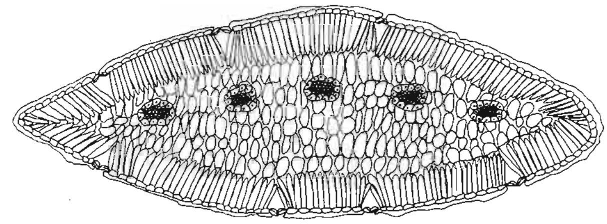
Ericoid leaf with very small surface (barely attains 10 mm²). Rather thick lamina (attains 667.4 µm) with radial symmetry in cross section. Cuticle rather rough and slightly undulate (11.4 µm thick), glaucous type.

The underlying epidermis consists of a single layer (15.5 µm

Melaleuca acerosa Schauer



150 µm



195 µm

Distribution: *A small shrub that is common in the thicket formation spread over the degraded stages of stabilized dunes in the dry-mediterranean region of southwestern Australia.*

Ericoid leaf hardly attains 18 mm^2, rather flattened in cross section with isolateral symmetry (528.6 µm thick).

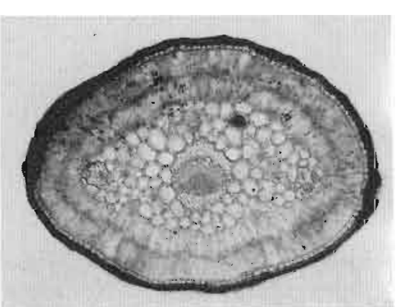
Cuticle layer weakly undulate (13 µm thick), glaucous type. Underlying epidermis rather thin (does not exceed 12.4 µm) and composed of a single layer of uniform rectangular cells.

Clearly differentiated palisade and spongy parenchyma within the mesophyll: 39% of the total thickness occupied by the former, which consists of two layers (206 µm thick) of densely-assembled elongated cells that ring the spongy tissue; the latter (267.8 µm thick) is composed of densely-pressed and rather squared cells, occupies most of the leaf section.

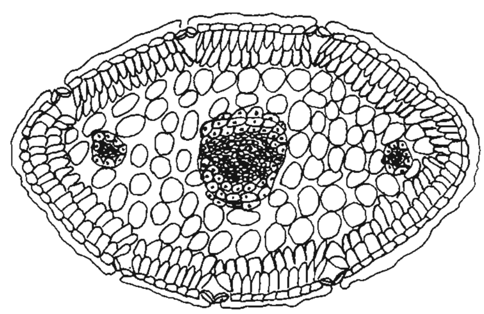
Mechanical tissue poorly represented except for small rare sclerenchymatous fibers that occur in the spongy portion, and some clustered sclereids that surround the vessels.

Stomata located all around the epidermis, protected by a large antechamber above the guard cells; small substomatal chambers formed in the palisade portion; stomata rather small (rima 18.5 µm and 18.1 µm and surfaces 84.1 μm^2 and 78.5 μm^2 in the lower and upper sides, respectively). Density 311/mm^2 on both sides, so the transpiring surface barely attains 26,155 $\mu m^2/mm^2$ on lower side and 24,258 $\mu m^2/mm^2$ on the upper (2.6% to 2.4% of the leaf area, respectively).

Melaleuca huegelii Endl.



135 µm



120 µm

Distribution: *A low shrub that is common in the thicket on stabilized dunes in the dry-mediterranean region of southwestern Australia.*

Gently flattened ericoid leaf surface barely attains 12 mm^2; isolateral symmetry in cross section (461 µm thick). Extensive undulate cuticle (11.2 µm thick), glaucous type. Underlying epidermis composed of a single layer (attains 21.6 µm in thickness) of quite uniform rectangular cells.

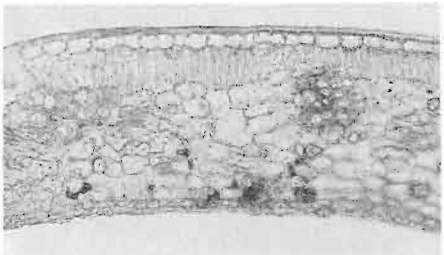
Mesophyll with clearly differentiated palisade and spongy portions: the former radiates from the epidermis to the inner mesophyll and consists of two layers (96 µm deep, 21% of the total thickness) of similar densely-pressed elongated cells. The latter (298 µm) composed of rather small rounded cells confined to the middle portion of the leaf section, and extends between the two palisades.

Wide intercellular spaces are frequently found in this parenchyma.

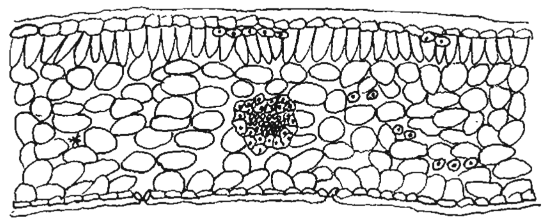
Mechanical tissue poorly represented in the leaf section: only a small ring of clustered sclereids that surrounds the vascular tissue.

Stomata (rima 22 µm in lenght and 128,5 μm^2 wide) located all over the epidermis layer and protected by wide antechambers formed by the swollen cuticle; limited substomatal chambers formed in the palisade portion. High density on both sides (266/mm^2), so the transpiring surface covers 34,181 $\mu m^2/mm^2$ (3.4% of lower and upper leaf area).

Syzygium yambos (L.) Alston



110 µm



100 µm

Distribution: *A tall tree that is common in the subtropical forest in southern Japan.*

Leaf surface averages 60 cm^2, with dorsiventral symmetry in cross section. Lamina remarkably thick (attains 272 µm, one of the thickest subtropical species studied).

Upper cuticle smooth and thin (attains 8.4 µm), glabrous type. Underlying epidermis rather thick (attains 24 µm) composed of fairly compact squared cells.

Palisade and spongy parenchyma clearly differentiated in the mesophyll: assimilatory parenchyma composed of one layer (69.6 µm deep) of irregularly-arranged and barely-elongated cells that occupy 25% of the leaf thickness; spongy parenchyma (averages 144 µm thick) accounts for most of the mesophyll and is disposed between the palisade and the lower epidermis.

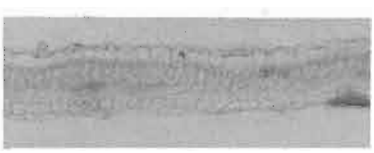
Intercellular spaces rather limited in the spongy parenchyma.

Mechanical tissue occur in the mesophyll both as isolated and small sclereids, located under the epidermic and palisade layers or as clustered sclereids surrounding the vascular tissue.

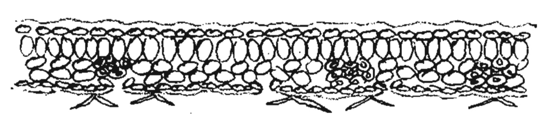
Stomata rather large (rima 29.4 long and surface 259.3 µm^2) and located in the lower epidermis (only 7 µm in thick). Remarkable density (up to 533/mm^2), so the transpiring surface covers 138,207 µm^2/mm^2 (14% of the leaf area, the highest percentage registered in the tropical and subtropical species examined).

MELASTOMACEAE

Blastus cochinchinensis Loureiro



50 µm



60 µm

Distribution: *A shrub that is common in the understorey of the tropical monsoon forest in southern China.*

Average leaf surface attains 16 cm^2. Lamina very thin (only 85.4 µm) with dorsiventral symmetry in cross section.

Upper cuticle (7 µm weakly) undulate, glabrous type. Thin underlying epidermis (barely attains 10 µm thick) composed of a single layer of uniform and rather rounded cells.

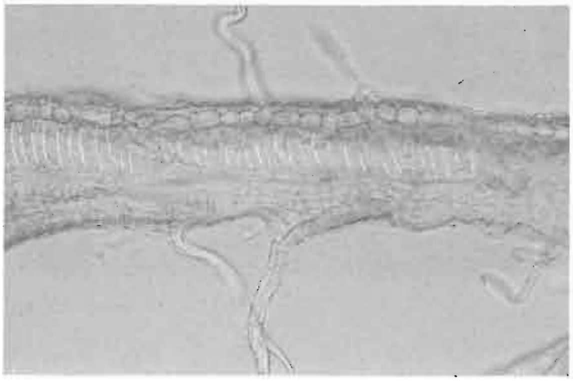
Mesophyll with clearly differentiated palisade and spongy parenchyma: palisade (24 µm thick, 28% of total mesophyll thickness) consists of elongated cells; spongy mesophyll (attains 29 µm thick) almost the same as the assimilatory portion and is covered by rounded or elongated cells.

Mechanical tissue present as small clustered sclereids that surround the vascular tissue.

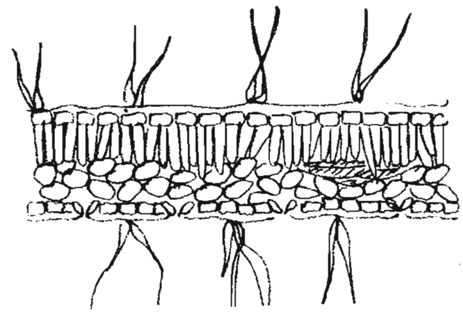
Lower epidermis (6.9 µm thick) overlaid by the flat cuticle (8.3 µm thick) and covered by pluricellular hairs.

Stomata rather large (rima 26 µm long, surface 311 µm^2) and located in the lower epidermis. Density attains 400/mm^2, so the transpiring surface, covers 1324,440 µm^2/mm^2 (about 12% of leaf area, among the largest of tropical examples studied).

Melastoma candidum D. Don



100 µm



100 µm

Distribution: *A shrub that is common in the understorey of the closed canopy of the tropical monsoon forest in southern China.*

Leaf surface averages 10 cm², the smallest among the Melastomaceae examined. Lamina (151.4 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle smooth (7.8 µm thick), glabrous type. Underlying epidermis (20 µm thick) consists of rather uniform rectangular cells.

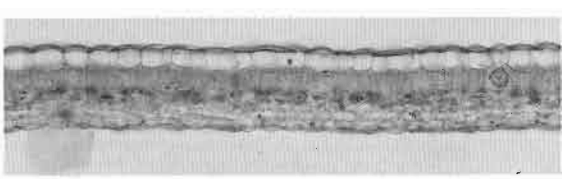
Two parenchyma in the mesophyll: palisade (49 µm thick, 34% of the leaf thickness) composed of narrow columnar cells, usually regularly-assembled; spongy parenchyma (44.5 µm thick) occupies the remaining portion of the mesophyll with rounded cells.

Intercellular spaces very limited in this parenchyma.

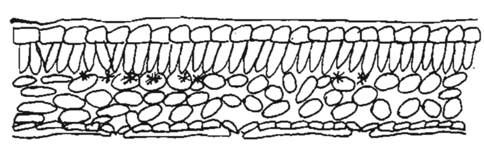
Mechanical tissue present as rare, isolated sclerenchymatous fibers in the spongy tissue.

Stomata rather large (rima 17.6 µm long, surface 129.6 µm²) and slightly sunken in the lower epidermis (14.4 µm thick). Density attains 311/mm², so the transpiring surface covers 80,642 µm²/mm² (8% of leaf area). Sparse, long pluricellular hairs are present on both leaf sides.

Melastoma dodecandrum Loureiro



140 µm



100 µm

Distribution: *A low tree that is common in the understorey of the closed canopy of the tropical monsoon forest in southern China.*

Leaf surface averages 40 cm², one of the largest tropical species studied. Lamina (156 µm thick, comparable to the thinnest tropical specimens) with dorsiventral symmetry in cross section.

Upper cuticle flat or weakly undulate (7.8 µm thick, like the lower), glabrous type.

Mesophyll with clearly differentiated palisade and spongy portion: rather limited palisade occupies only 28% of the total thickness (44 µm deep) and consists of slightly elongated cells; spongy parenchyma (51.9 µm thick, slightly thicker than the photosynthetic portion) composed of rounded cells.

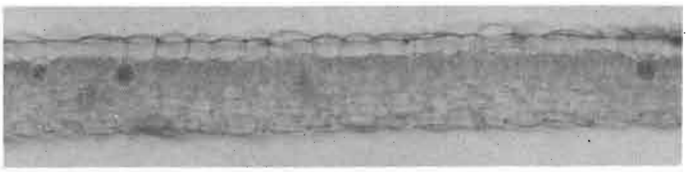
Limited intercellular spaces in this parenchyma.

Mechanical tissue not present except for small clustered sclereids in the spongy mesophyll.

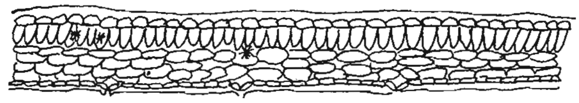
Several oxalate crystals occur in the mesophyll.

Stomata rather small (rima 16 µm long and surface only 106.9 µm²) and confined to the lower epidermis and composed of a single layer (22 µm thick) of cells. Density attains 311/mm², so transpiring surface barely attains 33.246 µm²/mm² (3% of the leaf area, among the smallest of the tropical species studied).

Melastoma sanguineum Sims



— 50 μm



— 50 μm

Distribution: *A low tree that is common in the understorey of the tropical monsoon forest in southern China.*

Average leaf surface attains 36 cm². Blade with dorsiventral symmetry attains the thickness of 97.4 μm in cross section (comparable to the *Melastoma* examples studied).

Upper cuticle smooth (uniformly 7.8 μm thick), glabrous type. Underlying epidermis monolayered and consists of somewhat-flattened rectangular cells (15.6 μm thick); with, the outer walls slightly thickened.

Two parenchyma in the mesophyll: palisade (32.4 μm thick, the largest portion of the leaf thickness, about 29.7% of the total) composed of rather-compact and uniform, narrow elongated cells; spongy parenchyma (24 μm thick) consists of fairly compact rounded cells.

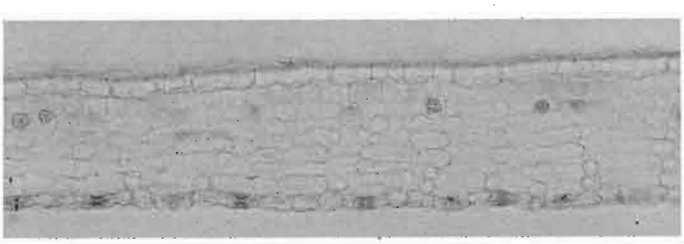
Intercellular spaces quite limited in the spongy tissue, but wide substomatal chambers that surround stomata are present.

Mechanical tissue poorly represented in the leaf except for rare, isolated sclerenchymatous fibers.

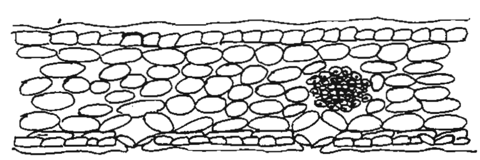
Stomata in the lower epidermis (9 μm thick) remarkable in size (rima 25 μm long and surface 238.9 μm²). Density attains 311/mm², so the transpiring surface is correspondingly high (attains 73,987 μm²/mm², about 9% of leaf area).

ARALIACEAE

Schefflera octophylla (Lour.) Harms



—— 90 μm



—— 100 μm

Distribution: *A low tree that is common in the small and large canopy gaps of the tropical monsoon forest in southern China.*

Average leaf surface attains 20 cm² Lamina (177 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle flat and uniformly smooth (3.9 μm thick), glabrous type. Underlying epidermis consists of a single layer (20.7 μm thick) of squared cells.

Undifferentiated mesophyll (128 μm thick) completely covered by uniform elongated cells.

Wide intercellular spaces are present in the mesophyll.

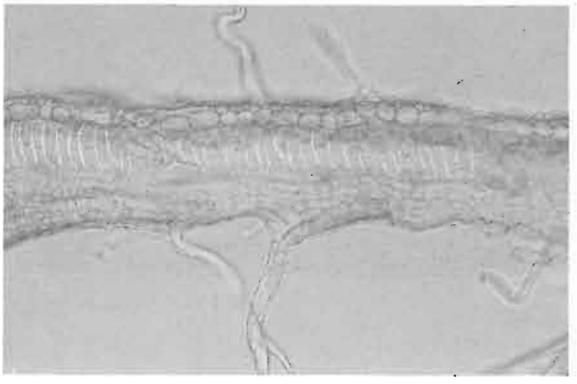
Mechanical tissue present as isolated sclerenchymatous fibers and small clustered sclereids that surround the vessels.

Several oxalate, crystals occur in the mesophyll.

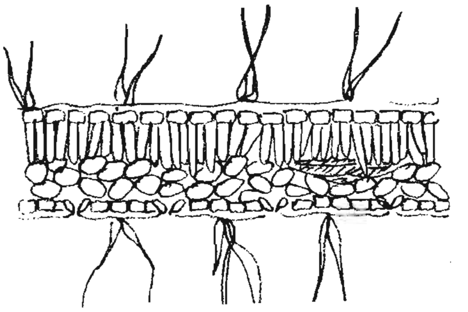
Lower epidermis (19 μm thick) also monolayered and overlaid by smooth cuticle (3.9 μm thick).

Stomata small (rima 17.6 μm long, surface 142 μm²) on the lower side. Density does not exceed 177/mm², so the transpiring surface covers 25.134 μm²/mm² (about 2% of leaf area).

Melastoma candidum D. Don



100 μm



100 μm

Distribution: *A shrub that is common in the understorey of the closed canopy of the tropical monsoon forest in southern China.*

Leaf surface averages 10 cm^2, the smallest among the Melastomaceae examined. Lamina (151.4 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle smooth (7.8 μm thick), glabrous type. Underlying epidermis (20 μm thick) consists of rather uniform rectangular cells.

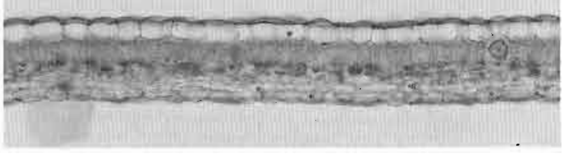
Two parenchyma in the mesophyll: palisade (49 μm thick, 34% of the leaf thickness) composed of narrow columnar cells, usually regularly-assembled; spongy parenchyma (44.5 μm thick) occupies the remaining portion of the mesophyll with rounded cells.

Intercellular spaces very limited in this parenchyma.

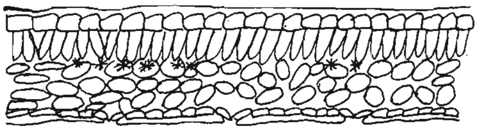
Mechanical tissue present as rare, isolated sclerenchymatous fibers in the spongy tissue.

Stomata rather large (rima 17.6 μm long, surface 129.6 μm^2) and slightly sunken in the lower epidermis (14.4 μm thick). Density attains 311/mm^2, so the transpiring surface covers 80,642 $\mu m^2/mm^2$ (8% of leaf area). Sparse, long pluricellular hairs are present on both leaf sides.

Melastoma dodecandrum Loureiro



140 μm



100 μm

Distribution: *A low tree that is common in the understorey of the closed canopy of the tropical monsoon forest in southern China.*

Leaf surface averages 40 cm^2, one of the largest tropical species studied. Lamina (156 μm thick, comparable to the thinnest tropical specimens) with dorsiventral symmetry in cross section.

Upper cuticle flat or weakly undulate (7.8 μm thick, like the lower), glabrous type.

Mesophyll with clearly differentiated palisade and spongy portion: rather limited palisade occupies only 28% of the total thickness (44 μm deep) and consists of slightly elongated cells; spongy parenchyma (51.9 μm thick, slightly thicker than the photosynthetic portion) composed of rounded cells.

Limited intercellular spaces in this parenchyma.

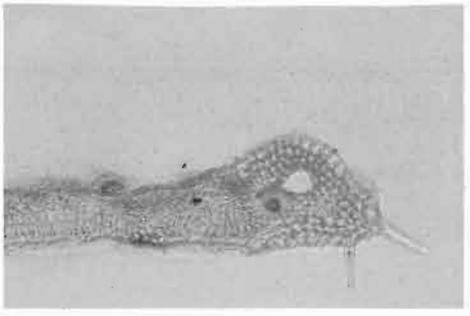
Mechanical tissue not present except for small clustered sclereids in the spongy mesophyll.

Several oxalate crystals occur in the mesophyll.

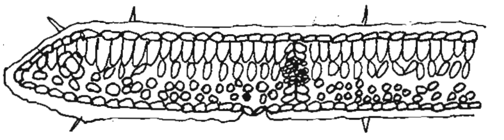
Stomata rather small (rima 16 μm long and surface only 106.9 μm^2) and confined to the lower epidermis and composed of a single layer (22 μm thick) of cells. Density attains 311/mm^2, so transpiring surface barely attains 33.246 $\mu m^2/mm^2$ (3% of the leaf area, among the smallest of the tropical species studied).

UMBELLIFERAE

Heteromorpha trifoliata Eckl. & Zeyh.



— 50 μm



— 50 μm

Distribution: *A tree that is frequently found in the humid subtropical forest in the Transvaal region of southeastern Africa.*

Average leaf surface attains 7 cm^2. Lamina rather thin (barely attains 113.6 μm thick) with dorsiventral symmetry in transverse section.

Upper cuticle uniformly smooth (9.6 μm thick), glabrous type, sparsely covered by short unicellular hairs. Epidermis rather peculiar (17.1 μm thick); consists of a compact layer of small flattened cells.

Mesophyll with clear differentiation of palisade and spongy parenchyma: palisade (34.5 μm thick, 30% of the total leaf thickness) composed of a double layer of small weakly-elongated cells; spongy parenchyma (39.7 μm) consists of small, widely-spaced rounded cells.

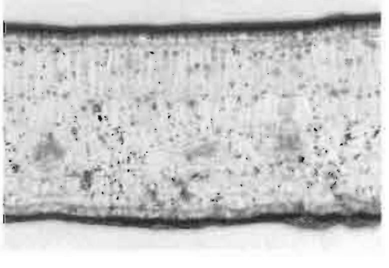
Lower epidermis monolayered (5.2 μm thick) and is overlaid by smooth cuticle (17.4 μm thick) sparsely covered by short pluricellular hairs.

Mechanical tissue well-represented in the leaf section: frequent bundle sheath-extensions cross the mesophyll, from the upper to the lower epidermis.

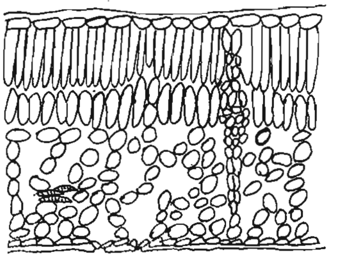
Stomata rather small (rima 21.5 μm long, surface 142 μm^2) confined to the lower side. Density attains 311/mm^2, so the transpiring surface covers 44,311 $\mu m^2/mm^2$ (4% of leaf area).

ERICACEAE

Arbutus canariensis Duham.



—— 93 μm



— 80 μm

Distribution: *A tall tree that is common in the laurophyll forest in the Canary Islands.*

Average leaf surface attains 7 cm^2. Lamina (243 μm thick) with dorsiventral symmetry in cross section, anatomically very similar to *Arbutus* specimens studied from the mediterranean region.

Upper cuticle uniformly smooth (9.7 μm thick), glabrous type. Underlying epidermis consists of a single layer (12.2 μm thick) of quite uniform rectangular cells.

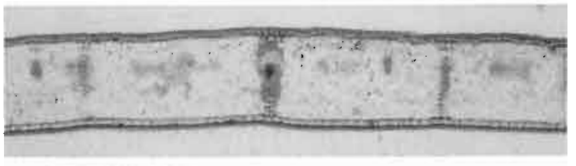
Two parenchyma in the mesophyll: palisade (101 μm deep, 41% of the total thickness) consists of a double layer of cylindrical cells, the upper layer two times thicker than the lower; spongy parenchyma (102 μm wide) composed of small widely-spaced rounded cells.

Mechanical tissue well-represented in the leaf section: large bundle sheath-extensions (the upper portion mostly collenchymatous) are present in the mesophyll together with isolated sclerenchymatous fibers.

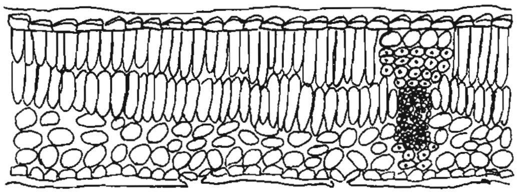
Lower epidermis (11.5 μm thick) also monolayered and overlaid by smooth cuticle (6.2 μm thick).

Stomata rather large (rima 28.5 μm long, surface 300 μm^2) and confined to the lower side. Density attains 222/mm^2, so the transpiring surface covers 66,755 $\mu m^2/mm^2$ (about 7% of leaf area).

Arbutus menziesii Pursh



200 μm



100 μm

Distribution: *A tall tree that is common component of open woodlands in the mediterranean area of southern California.*

Average leaf surface attains 9 cm². Lamina (237.4 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle (6.9 μm thick) smooth, glabrous type; lower cuticle markedly rough and much thicker (attains 11 μm), glaucous type. Upper epidermis consists of a single layer (18.5 μm thick) of rather uniform rectangular cells with heavily thickened outer walls; the lower epidermis (barely attains 6.9 μm) also monolayered and thinner than the upper.

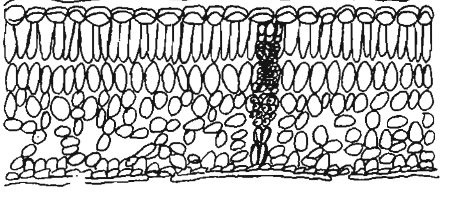
Two parenchyma in the mesophyll: palisade (102 μm deep, 43% of the total thickness) consisting of a double layer of compact elongated cells; spongy tissue (91.6 μm thick) covered by closely-spaced rounded cells.

Mechanical tissue well-represented in the leaf section: large bundle sheath-extensions, mostly sclerenchymatous, extend between the two epidermis.

Stomata small (rima 20 μm long, surface 136 μm²) and located in the lower side. Density attains 311/mm², so the transpiring surface covers 42,336 μm²/mm² (about 4% of leaf area).

Arbutus unedo L.

100 μm



155 μm

Distribution: *A small tree that is a common component of open woodlands in the northern area of Mediterranean Basin.*

Average leaf surface attains 12 cm². Lamina 374 μm thick in cross section.

Upper cuticle uniformly smooth and flat (5 μm thick), glabrous type. Upper epidermis attains the remarkable thickness of 24 μm and consists of a single layer of uniform compact cells with heavily thickened outer walls.

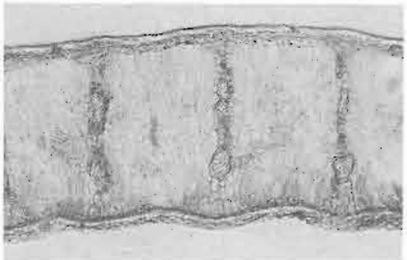
Mesophyll with clearly differentiated parenchyma: palisade (157 μm deep, 42% of leaf thickness) consists of a double layer of cylindrical cells; spongy parenchyma (164 μm wide) composed of heterogeneous cells that simulate a rough palisade in the upper portion.

Mechanical tissue present as large bundle sheath-extensions that cross the mesophyll.

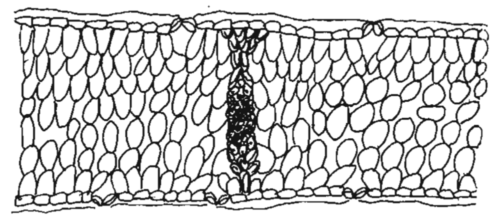
Lower epidermis (15 μm thick) also monolayered and overlaid by smooth cuticle (4 μm thick).

Stomata rather large (rima 28.5 μm long, surface 336.3 μm²) and present in the lower side. Density attains 311/mm², so the transpiring surface covers 104,589 μm²/mm² (about 10% of leaf area, the largest transpiring surface of *Arbutus* examples studied).

Arctostaphylos glandulosa Lindl.



150 µm



150 µm

Distribution: *A tall shrub that is common component of mesic chaparral in the mediterranean area of southern California.*

Average leaf surface attains 10 cm^2. Lamina (360.9 µm thick) with isolateral symmetry, anatomically very similar to the "*glauca*" species examined.

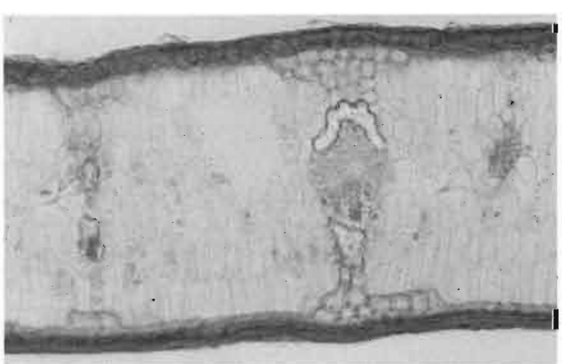
Cuticle rough and markedly undulate (13.5 µm thick on both sides), glaucous type. Both epidermis consist of a single layer of compact uniform cells and attain the thickness of 13.5 µm.

Undifferentiated mesophyll (308 µm thick) compsed of closely-spaced elongated cells, palisade-like assembled against the epidermis.

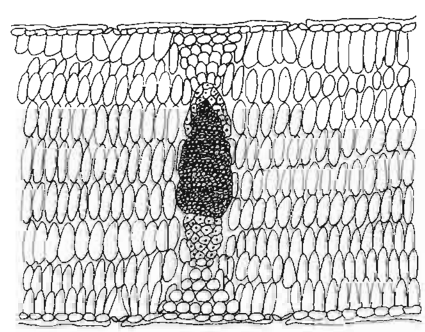
Mechanical tissue well-represented in the leaf section: abundant bundle sheath-extensions, mainly collenchymatous in the upper and lower portion, cross the mesophyll from the upper to the lower epidermis.

Stomata on both sides (rima 31.5 µm long, surface 428 µm^2 on both surfaces) among the largest of species studied. Density ranges from 177/mm^2 to 266/mm^2 in the upper and lower sides, respectively, so the transpiring surfaces cover 75,829 µm^2/mm^2 and 113,954 µm^2/mm^2, respectively (about 8% to 11% of the upper and lower sides).

Arctostaphylos glauca Lindl.



160 µm



160 µm

Distribution: *A tall shrub that is common component of mesic chaparral in the mediterranean area of southern California.*

Average leaf surface attains 7 cm^2. Lamina (635 µm thick) with isolateral symmetry in cross section.

Upper cuticle rough and markedly undulate (19.6 µm thick), glaucous type. Underlying epidermis (11.5 µm thick) monolayered and consists of compact rectangular cells.

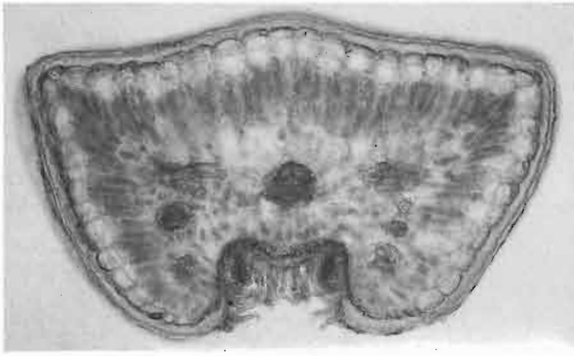
Undifferentiated mesophyll (580 µm wide) uniformly covered by poorly-spaced and rather elongated cells, assembled palisade-like.

Lower epidermis (13.8 µm thick) also monolayered and is overlaid by the markedly rough glaucous cuticle (10.3 µm thick).

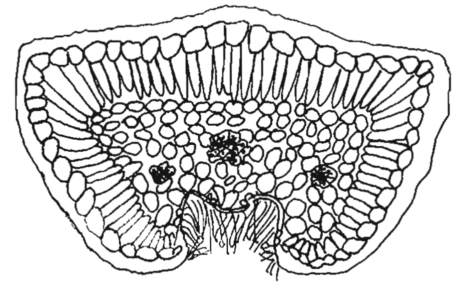
Mechanical tissue well-represented in the mesophyll: abundant bundle sheath-extensions (mainly collenchymatous in the upper and lower portion) that extend from the upper to lower epidermis.

Stomata wide (rima 28.2 µm long, surface 314.5 µm^2) present on both sides. Density ranging from 222/mm^2 to 311/mm^2, so the transpiring surface attains from 69,832 µm^2/mm^2 to 97,828 µm^2/mm^2 in the upper and lower sides, respectively (about 7% to 10% of each leaf surface).

Erica multiflora L.



140 μm



160 μm

Distribution: *A small shrub that is common in the low maquis and garrigue in the coastal ranges of the Mediterranean Basin.*

Ericoid leaf with extremely small surface (does not exceed 0.3 cm²). Lamina (526 μm thick) with dorsiventral symmetry in cross section, anatomically very similar to the capensic species studied.

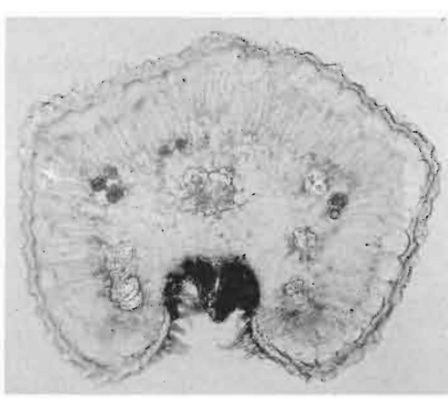
Cuticle slightly undulate and uniformly smooth (21 μm thick all around the margin section), glabrous type. Underlying epidermis consists of a single layer of uniform cells and attains the remarkable thickness of 70.5 μm.

Mesophyll with two clearly differentiated parenchyma: palisade (216 μm deep, 41% of the total thickness) composed of a single layer of compact elongated cells that are slightly shorter along leaf margins; spongy parenchyma (174 μm thick) consists of small fairly compact rounded cells.

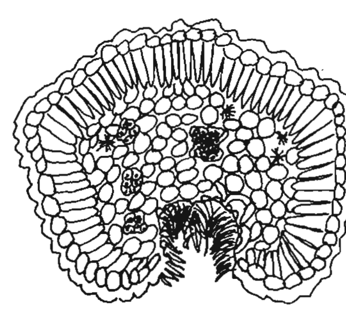
Mechanical tissue poorly represented in the leaf section: small isolated sclerenchymatous fibers are present in the spongy mesophyll together with small clusters of sclereids that surround the veins.

Stomata extremely small (rima barely attains 9 μm, surface does not exceed 41 μm²) and present in the lower side; confined to wide, shallow crypts formed in the spongy portion and protected by dense unicellular hairs. Density attains 355/mm², so the transpiring surface covers 14,626 μm²/mm² (about 1% of leaf area, one of the smallest transpiring surfaces among species studied).

Erica plukenetii L.



100 μm



130 μm

Distribution: *A small shrub that is a common component of the heathlands in the mediterranean area of southwestern Africa.*

Ericoid leaf with extremely small average surface (does not exceed 0.4 cm²). Lamina (396 μm thick) with dorsiventral symmetry in cross section.

Cuticle uniformly smooth and slightly undulate, glabrous type; ranges from 11.5 μm on the upper side to 9.9 μm on the lower.

Epidermis monolayered (40 μm thick).

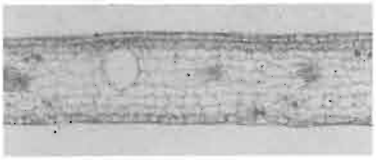
Mesophyll with clearly differentiated palisade and spongy parenchyma: the former (85.8 μm thick, barely occupies 22% of the total section) consists of closely-spaced cylindrical cells; the latter (208 μm thick) occupies the largest portion of the mesophyll and is covered by elongated, fairly-compact rounded cells.

Mechanical tissue poorly represented in the mesophyll: rare isolated sclerenchymatous fibers are present in the spongy tissue together with small clustered sclereids that surround the veins.

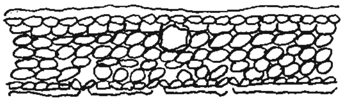
Stomata extremely small (rima 9 μm long, surface 41 μm²) present in the lower side confined to a small portion that slightly resembles a wide shallow crypt. Density attains 355/mm², so the transpiring surface covers 14,555 μm²/mm² (about 1% of leaf area, similar to that recorded in *Erica multiflora*).

MYRSINACEAE

Ardisia sieboldii Miq.



— 110 μm



— 110 μm

Distribution: *A tall tree that is frequently found in the evergreen subtropical forest in southern Japan.*

Average leaf surface attains 35 cm^2. Lamina (212 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth and extremely thin (does not exceed 2.7 μm), glabrous type. Underlying epidermis (21 μm thick) monolayered and composed of rather compact squared cells.

Undifferentiated mesophyll (164 μm thick) covered by uniform quite-elongated cells.

Wide intercellular spaces lack in the mesophyll.

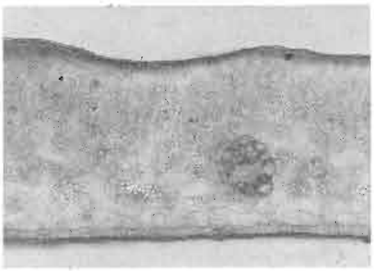
Mechanical tissue poorly represented in the leaf section: small sclerenchymatous fibers sparsely scattered throughout the mesophyll.

Lower epidermis (20 μm thick), also monolayered, closely resembles the upper and is overlaid by a smooth and very thin cuticle (does not exceed 2.6 μm).

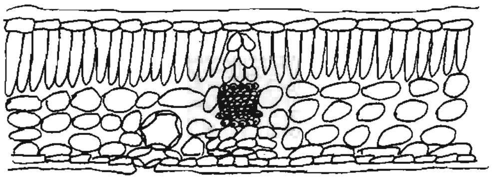
Large glaudular cavities occur in the mesophyll.

Stomata rather small (rima 22 μm long, surface 162 μm^2) and confined to the lower side. Density attains 311/mm^2, so the transpiring surface covers 50,400 $\mu m^2/mm^2$ (about 5% of leaf area).

Myrsine africana L.



— 90 μm



— 100 μm

Distribution: *A small tree that is a common component of the warm humid temperate forest in the Transvaal region of southeastern Africa.*

Average leaf surface small (does not exceed 1 cm^2). Lamina (213.2 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth (10.7 μm thick), glabrous type; the lower even thinner (does not exceed 9 μm).

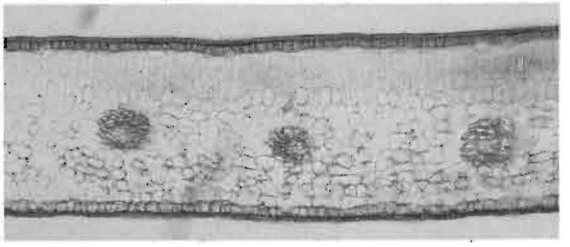
Upper epidermis consists of a single layer (15.9 μm thick) of quite uniform flattened cells.

Two parenchyma clearly differentiated in the mesophyll: palisade consists of a single layer (85 μm deep, 40% of the entire thickness) of cylindrical cells; spongy parenchyma (80.7 μm thick) composed of heterogeneous widely-spaced cells.

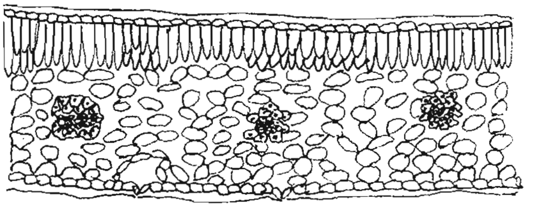
Mechanical tissue well-represented in the leaf section: bundle sheath-extensions cross the mesophyll from the upper to lower epidermis.

Stomata rather small (rima 20.9 μm long, surface 155 μm^2) and located on the lower side. Density attains 266/mm^2, so the transpiring surface covers 41,326 $\mu m^2/mm^2$ (about 4% of leaf area).

Rapanea melanophloeos Mez



200 µm



200 µm

Distribution: *A small tree that is a common component of the warm temperate humid forest in the Transvaal region of southeastern Africa.*

Average leaf surface attains 15 cm². Lamina (448.7 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth (attains 24 µm), glabrous type.

Underlying epidermis (22.2 µm thick) consists of compact squared cells.

Two parenchyma in the mesophyll: palisade (118.2 µm deep, 26% of the total section) consists of a single or even double layer of similar, cylindrical elongated cells; spongy tissue (attains 240.8 µm) accounts for the largest portion of the mesophyll and is composed of small, widely-spaced rounded and elongated cells.

Lower epidermis (25.2 µm thick) also monolayered and is overlaid by flat smooth cuticle (18 µm thick).

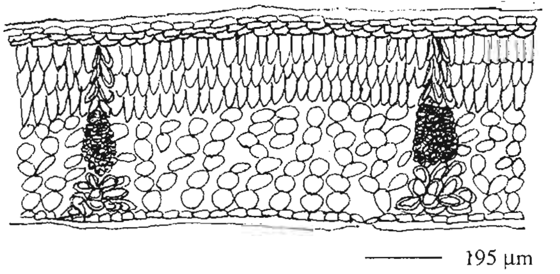
Mechanical tissue poorly represented in the leaf section.

Stomata rather wide (rima 24 µm long, surface 223.5 µm²) on the upper side. Density attains 222/mm², so the transpiring surface covers 49,624 µm²/mm² (about 5% of leaf area).

SAPOTACEAE

Sideroxylon inerme L.

100 µm



195 µm

Distribution: *A tall shrub frequently found in the fynbos in the mediterranean vegetation of southwestern Africa.*

Average leaf surface attains 16.5 cm². Lamina 556.5 µm thick in cross section with dorsiventral symmetry.

Upper cuticle smooth (19.5 µm thick), glabrous type; the lower (18 µm thick) also flat and smooth.

Underlying epidermis, of peculiar aspect, consists of three layers of uniform compact cells and attains the remarkable thickness of 52.5 µm; the lower epidermis (attains 31.4 µm) also rather thick and consists of a single layer of rectangular cells.

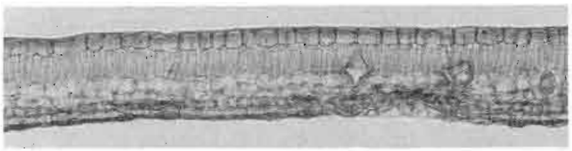
Mesophyll with clearly differentiated palisade and spongy portion: palisade (271 µm deep, 49% of the entire leaf section) accounts for the largest portion of the mesophyll and consists of three layers of densely-assembled cylindrical cells; spongy parenchyma (barely attains 163.5 µm) composed of closely-spaced rounded cells.

Mechanical tissue well-represented in the leaf section: abundant bundle sheath-extensions cross the mesophyll from the upper to the lower epidermis.

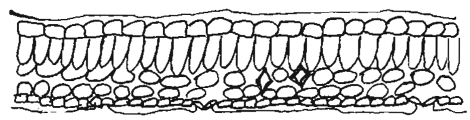
Stomata rather small (rima 18.9 µm long, surface 154.7 µm²) located in the lower side. Density does not exceed 266/mm², so transpiring surface covers 41,158 µm²/mm² (about 4% of leaf area).

EBENACEAE

Diospyros morrisiana Hanae



— 50 µm



— 50 µm

Distribution: *A small tree common in the tropical monsoon forest in southern China.*

Leaf surface averages 16 cm^2; dorsiventral symmetry in cross section (120.3 µm, comparable to the thinnest specimens studied).

Upper cuticle flat (7.8 µm thick), glabrous type, like the lower cuticle.

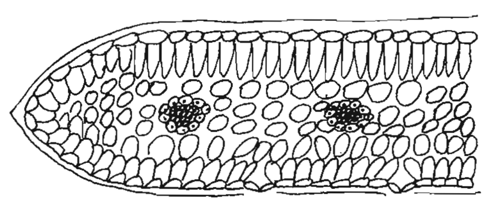
Mesophyll with clearly differentiated palisade and spongy portion: palisade (occupies 50% of the mesophyll) with rather uniform densely-assembled elongated cells (32 µm deep); spongy parenchyma (37 µm thick) composed of small fairly-compact, weakly-elongated cells.

Mechanical tissue present as isolated sclerenchymatous fibers scattered in the spongy tissue.

Stomata located in the lower side, slightly sunken in the epidermis, and amongst the smallest of the species examined (rima barely attains 17 µm, surface 116 μm^2); density does not exceed 266/mm^2, so the transpiring surface covers 31,016 $\mu m^2/mm^2$ (3.1% of leaf area).

Euclea divinorum Hiern

— 170 µm



— 100 µm

Distribution: *A tall shrub that is common in the warm, humid temperate forest in the Transvaal region of southeastern Africa.*

Average leaf surface attains 9 cm^2. Lamina (221 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle rather flat and uniformly smooth (7 µm thick, like the lower), glabrous type.

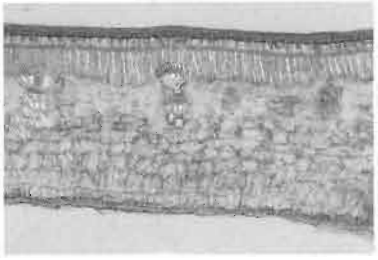
Epidermis (21 µm thick) consists of rather compact squared cells, the lower also monolayered and slightly thinner than the upper (does not exceed 19.1 µm).

Mesophyll with clearly differentiated palisade and spongy portion: palisade (55.8 µm thick, 25% of the total thickness) consists of compact elongated cells; spongy parenchyma (110.2 µm thick) composed of widely-spaced rounded cells.

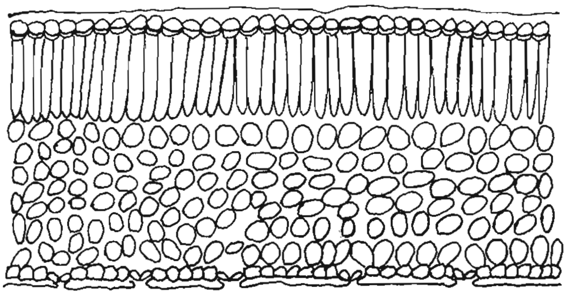
Mechanical tissue present as isolated sclerenchymatous fibers and clustered sclereids that surround vessels.

Stomata rather small (rima 19.8 µm long, surface 116.6 μm^2) confined to the lower side. Density attains 255/mm^2, so the transpiring surface covers 29,748 $\mu m^2/mm^2$ (about 3% of leaf area).

Euclea racemosa Murr.



210 μm



130 μm

Distribution: *A tall shrub that is common in the fynbos in the mediterranean vegetation of southwestern Africa.*

Average leaf surface rather small (does not exceed 2 cm²). Lamina (462 μm thick) dorsiventral in transverse section.

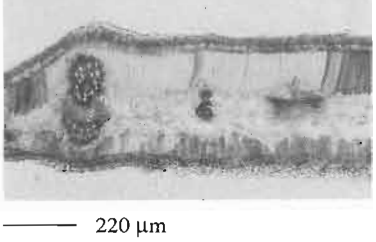
Upper cuticle rather rough and weakly undulate (attains the thickness of 18 μm), glaucous type. Underlying epidermis (attains 30 μm) consists of remarkably-thick uniform squared cells.

Two parenchyma in the mesophyll: palisade composed of a single layer (72 μm thick, barely 16% of the total section) of elongated compact cells; spongy parenchyma (300 μm thick) accounts for the largest mesophyll portion (about four times the palisade) and consists of fairly widely-spaced rounded cells in the inner portion and of rather elongated cells in the lower, disposed against the epidermis and assembled palisade-like.

Mechanical tissue present as clustered sclereids that surround vessels.

Stomata extremely large (rima attains 90 μm, the longest among studied examples) in the lower side protected by the swollen cuticle; surface up to 2,700 μm² large. Density attains 39/mm², so transpiring surface covers 105,300 μm²/mm² (about 10% of leaf area).

Euclea undulata Thunb.



220 μm

90 μm

Distribution: *A small shrub frequently found in the mediterranean vegetation of southwestern Africa.*

Leaf surface rather small (averages 2.5 cm²). Lamina (358.8 μm thick) with dorsiventral symmetry, anatomically similar to the congeneric species examined.

Upper cuticle markedly undulate, papillose and rather thick (attains 23.4 μm), glaucous type. Underlying epidermis consists of a single layer (attains 23.4 μm thick) of compact squared cells with thickened outer walls.

Two parenchyma in the mesophyll: palisade (93.6 μm deep, 26% of the leaf section) consists of a single layer of extremely-elongated cells; spongy parenchyma (attains 179.4 μm) about twice as large as the palisade and is composed of small, fairly-compact rounded cells.

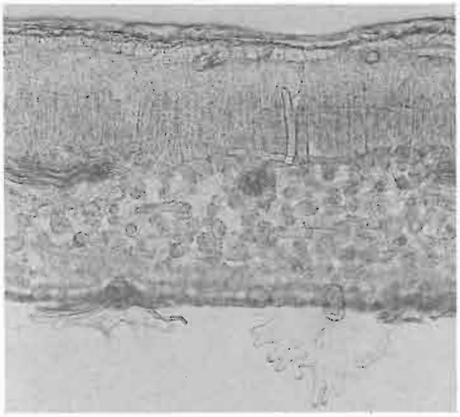
Lower epidermis (15.6 μm thick) monolayered and overlaid by rough, markedly papillose cuticle (also 23 μm thick).

Mechanical tissue present as clustered sclereids that surround vessels in the spongy tissue.

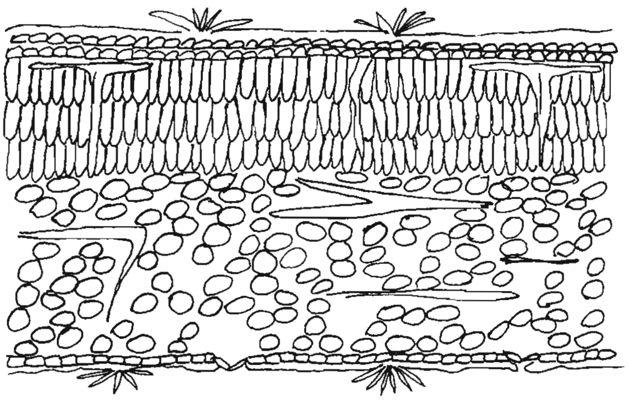
Stomata extremely large (rima 66 μm long and surface up to 1,188 μm²) and present on the lower epidermis; protected by swollen cuticle. Density attains 88/mm², so the transpiring surface covers 104,544 μm²/mm² (about 10% of leaf area).

OLEACEAE

Olea europaea L.



130 μm



100 μm

Distribution: *A small characteristic tree of the hot mediterranean belt in the southern Mediterranean Basin.*

Leaf surface averages 10 cm². Lamina (451 μm thick, the thickest of the *Olea* species studied) with dorsiventral symmetry in cross section.

Upper cuticle rather smooth (12.1 μm thick), glabrous type, covered by pluricellular stellate hairs. Upper epidermis rather peculiar and consists of a double layer (15 μm thick, the upper much thinner than the inner) of compact uniform cells.

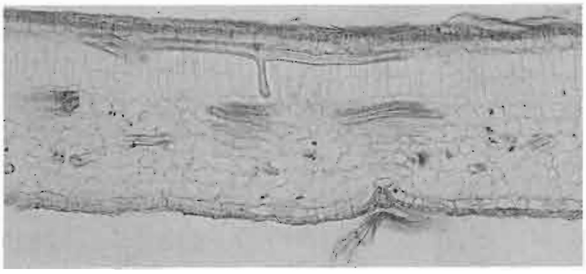
Two parenchyma clearly differentiated in the mesophyll: palisade (136.9 μm thick) occupies 30% of total thickness with two or three layers of narrow elongated cells; spongy parenchyma (268 μm thick) composed of widely-spaced small cells.

Lower epidermis (11.8 μm thick) monolayered and covered by smooth cuticle (6.1 μm thick) and densely covered by pluricellular stellate hairs.

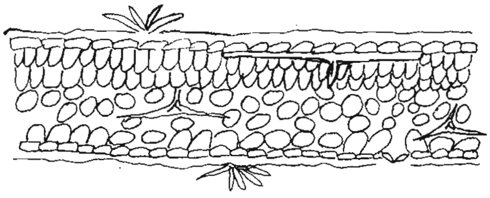
Mechanical tissue well-represented: abundant T-shaped macrosclereids are present in the palisade layer, both confined against the epidermis and facing the lacunary mesophyll, whereas branched stick-shaped sclereids are scattered throughout the spongy tissue.

Stomata very small (rima 15 μm long, surface 81.6 μm²) in the lower side. Density attains 266/mm², so the transpiring surface covers 21,706 μm²/mm² (about 2% of leaf area).

Olea europaea L. ssp. africana P.S. Green



75 μm



100 μm

Distribution: *A small tree that is common in the humid warm temperate forest in the Transvaal region of southeastern Africa.*

Average leaf surface attains 9 cm². Lamina with dorsiventral symmetry in cross section (188 μm thick, the thinnest among *Olea* species studied).

Upper cuticle uniformly smooth (barely attains 7.3 μm), glabrous type, covered with sparse pluricellular hairs. Underlying epidermis consists of a single layer (13.2 μm thick) of rather uniform flattened cells.

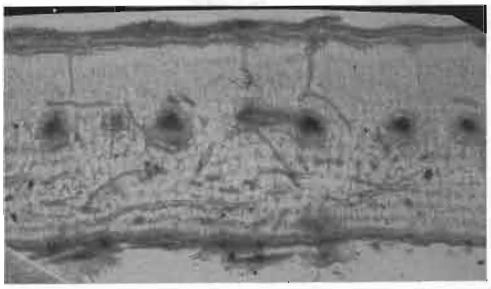
Mesophyll with two clearly differentiated parenchyma: palisade (51 μm deep) occupies 27% of total thickness with a double layer of weakly-elongated cells; spongy parenchyma (98 μm thick), consists of small, widely-spaced rounded cells.

Mechanical tissue very peculiar (a common feature of all *Olea* species studied): abundant T-shaped macrosclereids are present in the palisade layer disposed against the upper epidermis but are also sparse in the spongy mesophyll; rare, isolated sclerenchymatous fibers are also present in the spongy tissue.

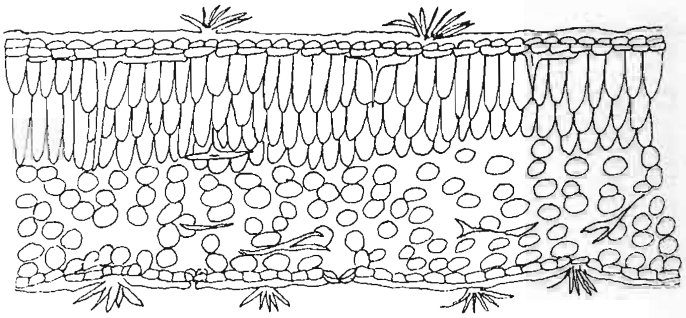
Lower epidermis (12.2 μm thick) also monolayered and is overlaid by a smooth cuticle (5.6 μm thick) covered by long unicellular hairs.

Stomata rather small (rima 19 μm long, surface 132 μm²) present on the lower side. Density does not exceed 266/mm², so the transpiring surface covers 39,192 μm²/mm² (about 4% of leaf area).

Olea europaea L. ssp. cerasiformis Kuntk. et Sund.



130 µm



105 µm

Distribution: *A small tree that is common in the warm open temperate humid forest in the Canary Islands.*

Leaf surface averages 10 cm². Lamina (366.6 µm thick) with dorsiventral symmetry, among the largest of the canariensis species examined.

Upper cuticle uniformly flat and rather thin (does not exceed 6.9 µm), glabrous type, sparsely covered by pluricellular stellate hairs. Underlying epidermis consists of a single layer (10.2 µm thick) of uniform cells.

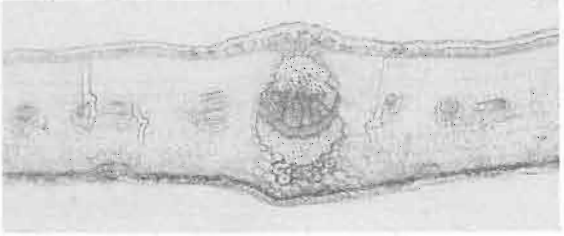
Mesophyll with two clearly differentiated parenchyma: palisade (167 µm deep) occupies 46% of the total section with narrow, densely-assembled elongated cells; spongy parenchyma (averages 163 µm) consists of small, widely-spaced rounded cells.

Lower epidermis (12.2 µm thick) also monolayered, provided with smooth cuticular layer (5.7 µm thick) densely covered by pluricellular stellate hairs.

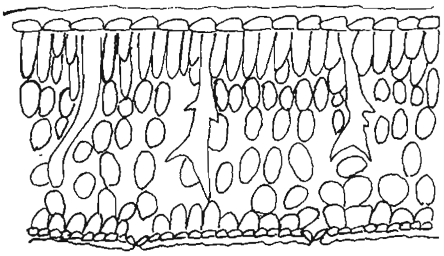
Mechanical tissue well-represented: abundant T-shaped macrosclereids in the palisade portion mainly confined against the upper epidermis, and branched stick-shaped sclereids are present in the spongy mesophyll.

Stomata rather small (rima 23 µm long, surface 153 µm²) present on the lower side. Density also low (does not exceed 177/mm²) so transpiring surface covers 27,151 µm²/mm² (about 3% of leaf area).

Phillyrea angustifolia L.



170 µm



100 µm

Distribution: *A small tree frequently found in the humid, warm temperate forest in the Canary Islands.*

Average leaf surface rather small (attains 2 cm²). Lamina (307 µm thick) with dorsiventral symmetry in cross section.

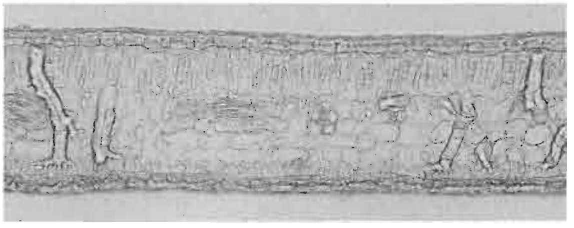
Upper cuticle uniformly flat (12 µm thick), glabrous type; the lower also smooth (14 µm thick). Monolayered upper epidermis composed of a single layer (7.8 µm thick) of compact cells, like the lower epidermis (6 µm thick).

Two slightly-diversified parenchyma in the mesophyll: palisade (112 µm thick) occupies 35% of total thickness with two or three layers of columnar cells; spongy parenchyma (155 µm thick) consists of closely-spaced and rather elongated cells that are assembled palisade-like in the lower portion.

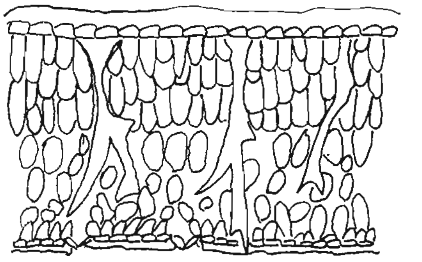
Important mechanical tissue present: abundant extremely-elongated and irregularly-branched macrosclereids cross the mesophyll from the upper epidermis to the lower spongy parenchyma.

Stomata rather large (rima 26 µm long, surface 274 µm²) confined to lower side. Density reaches 177/mm², so the transpiring surface averages 48,551 µm²/mm² (about 5% of leaf area).

Phillyrea media L.



150 µm



100 µm

Distribution: *A tall shrub that is common in open to closed maquis in the northern Mediterranean Basin.*

Leaf surface averages 8 cm². Lamina (306 µm thick) with dorsiventral in transverse section, anatomically similar to the canariensis species examined.

Upper cuticle uniformly flat and smooth (11.5 µm thick, the lower attains 10.9 µm), glabrous type. Underlying epidermis also thin, (barely attains 10 µm) and consists of a compact layer of markedly flattened cells: slightly thinner in the lower side (attains 9 µm).

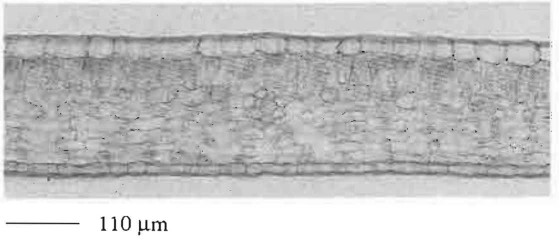
Two weakly diversified parenchyma in the mesophyll: palisade consists of one or two layers (108 µm thick, 35% of the total section) of densely-assembled columnar cells; spongy parenchyma (155 µm thick) consists of closely-spaced and rather elongated cells in the inner mesophyll portion, assembled palisade-like in the lower.

Important mechanical tissue: abundant extremely-elongated branched macrosclereids cross the mesophyll from the upper epidermis to the inner spongy portion.

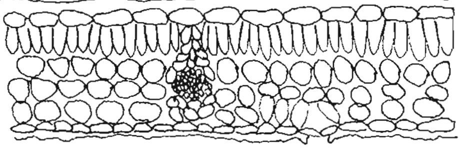
Stomata rather large (rima 26 µm long, surface 294 µm²) present in the lower side. Density does not exceed 177/mm², so the transpiring surface covers 52,463 µm²/mm² (about 5% of leaf area, the same as the canariensis species studied).

RUBIACEAE

Psychotria capensis Vatke



110 µm



100 µm

Distribution: *A tall tree frequently found in the humid, warm temperate forest in the Transvaal region of southeastern Africa.*

Average leaf surface attains 20 cm². Lamina (186.6 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth (6.9 µm thick), glabrous type. Underlying epidermis consists of a single layer (24.3 µm thick) of uniform rectangular cells.

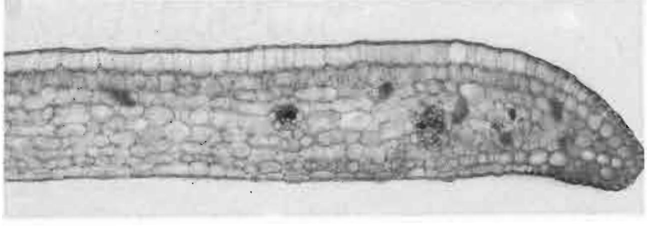
Mesophyll with two clearly differentiated parenchyma: palisade (50.5 µm thick) occupies 27% of the total section with fairly-compact elongated cells; spongy parenchyma (85.6 µm wide) consists of widely-spaced rounded cells.

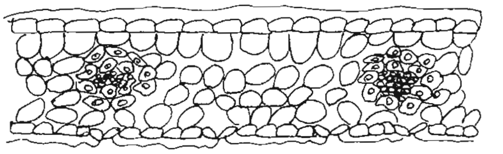
Lower epidermis, also monolayered (11.6 µm thick), covered by smooth cuticular layer (7.5 µm thick).

Mechanical tissue poorly represented in the mesophyll by rare bundle sheath-estensions.

Stomata very small (rima 14.3 µm long, surface 67.3 µm²) located in the lower side. Density attains 200/mm², so the transpiring surface covers 13,464 µm²/mm² (about 1% of leaf area).

Psychotria manillensis Bartl.





100 μm

100 μm

Distribution: *A tall tree that is a common component of the humid subtropical forest in southern Japan.*

Average leaf surface attains 113 cm^2, the largest lamina of all examples studied. Dorsiventral symmetry in cross section (191 μm thick).

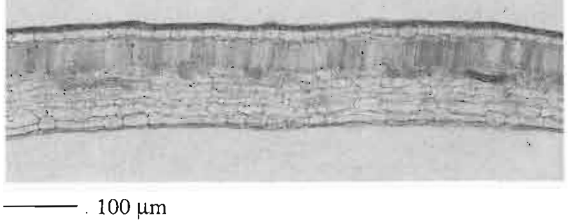
Upper and lower cuticle flat and smooth (7.3 μm thick), glabrous type. Underlying epidermis composed of compact uniform cells and attains the thickness of 22 μm, like the lower.

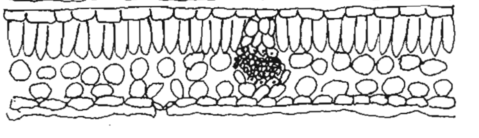
Mesophyll weakly differentiated (132.3 μm wide), the only one among the *Psychotria* species studied, composed of rather small weakly-elongated cells palisade-like arranged in the upper portion.

Mechanical tissue poorly represented: small clustered sclereids surround the vascular tissue.

Stomata very wide (rima 29 μm long, surface 280 μm^2) confined to the lower side. Density attains 400/mm^2, so the transpiring surface covers 112,000 $\mu m^2/mm^2$ (about 11% of leaf area, the largest among *Psychotria* examples studied).

Psychotria zombamontana (Kuntze) E. Petit





100 μm

100 μm

Distribution: *A tall tree frequently found in the humid, warm temperate forest in the Transvaal region of southeastern Africa.*

Leaf surface averages 14.4 cm^2. Lamina (137 μm thick) with dorsiventral symmetry in cross section.

Cuticle rather smooth (ranges from 7.8 μm to 6.7 μm in the upper and lower sides, respectively), glabrous type. Upper epidermis (14.4 μm thick) composed of uniform rectangular cells, about two times as thick than the lower one (attains 8.9 μm).

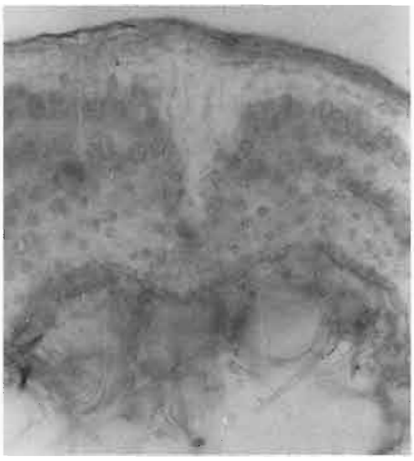
Two parenchyma in the mesophyll: palisade consists of a single layer (40.7 μm thick) of elongated cells and occupies 30% of total thickness; spongy parenchyma (58.3 μm wide) composed of rather compact and elongated cells.

Mechanical tissue poorly represented in the mesophyll: small clustered sclereids that surround vessels and rare boundle sheath-extensions.

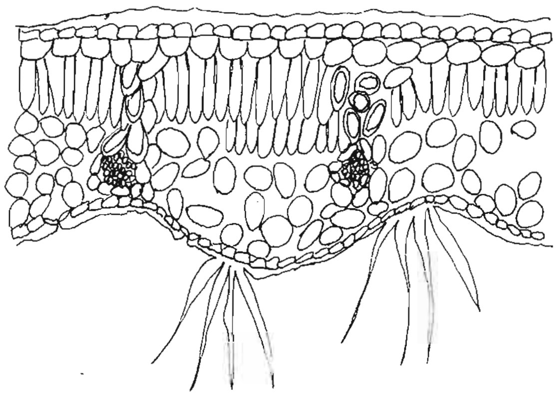
Stomata very small (rima 14.5 μm long, surface 97.3 μm^2) in the lower side. Density attains 222/mm^2, so the transpiring surface covers 21,609 $\mu m^2/mm^2$ (about 2% of leaf area).

LABIATAE

Rosmarinus officinalis L.



95 µm



100 µm

Distribution: *A small shrub that is a common component of the garigue in the xeric areas of Mediterranean Basin.*

Extremely small leaf surface (does not exceed 0.8 cm²). Lamina (286 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle smooth and undulate (12.8 µm thick), glabrous type. Underlying epidermis peculiar (22 µm thick) consists of a double layer of compact rectangular cells.

Mesophyll with clearly differentiated palisade and spongy parenchyma: palisade (113.8 µm deep) occupies 40% of total thickness with narrow, elongated cells; spongy parenchyma (111.4 µm thick) consists of closely-spaced rounded cells.

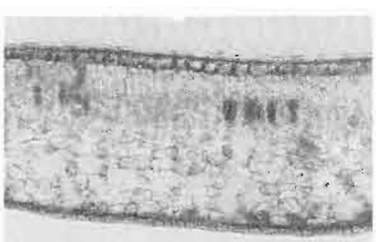
Mechanical tissue occurs as collenchimatic extensions that extend from the upper epidermis surrounding vessels.

Lower epidermis (14.5 µm thick) overlaid by cuticular layer (also thin – does not exceed 11 µm) and densely covered by branched pluricellular hairs.

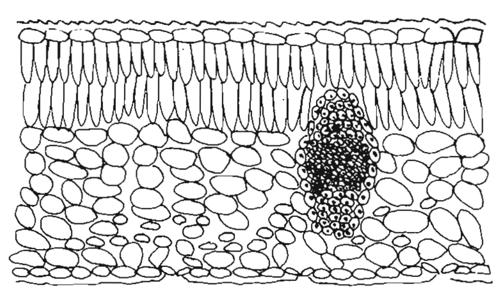
Stomata very small (rima 13.8 µm long, surface 59.8 µm²/mm²) in the lower side. Density attains 488/mm², so the transpiring surface covers 29,280 µm²/mm² (about 3% of leaf area).

CAPRIFOLIACEAE

Viburnum rigidum Vent.



200 µm



110 µm

Distribution: *A tall tree that is a common component of the temperate mountain forest in southern Japan.*

Average leaf surface attains 15 cm². Lamina (405 µm thick, the thickest of *Viburnum* examined species) with dorsiventral symmetry in cross section.

Upper cuticle flat, uniformly smooth (7.8 µm thick, like the lower), glabrous type. Underlying epidermis monolayered and rather compact (23.4 µm thick).

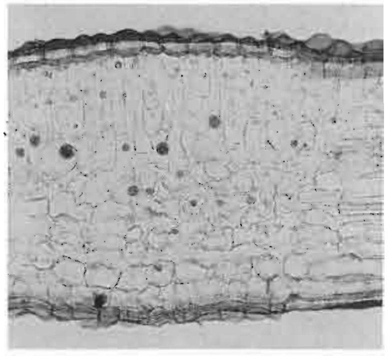
Two well diversified parenchyma in the mesophyll: palisade (152 µm deep) occupies 37% of the total section with a double layer of narrow columnar cells; spongy parenchyma (197 µm wide) consists of widely-spaced heterogeneous cells.

Lower epidermis (16.8 µm thick) also monolayered.

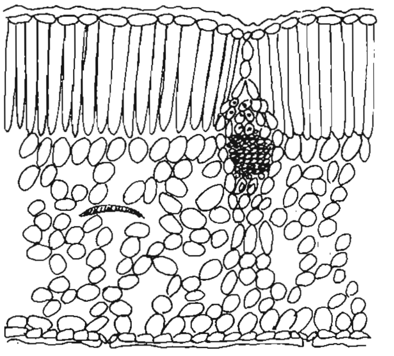
Mechanical tissue poorly represented.

Stomata very large (rima 35 µm long, surface 388.9 µm²) in the lower side. Density does not exceed 177/mm², so the transpiring surface covers 69,107 µm²/mm² (about 7% of leaf area).

Viburnum rugosa Pers.



115 µm



90 µm

Distribution: *A tall shrub that is a common component of the humid, warm temperate forest in Canary Islands.*

Average leaf surface attains 15 cm². Lamina (405 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle markedly undulate (7.8 µm thick), glaucous type.

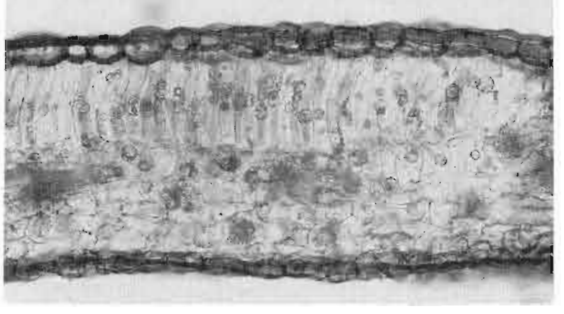
Underlying epidermis monolayered composed of a single layer (23.4 µm thick) of compact rectangular cells.

Mesophyll with two clearly differentiated parenchyma: palisade (attains 119.5 µm thick) occupies 31% of total section with narrow, extremely-elongated cells; spongy parenchyma (about two times as thick as palisade) occupies 219.6 µm with small, widely-spaced rounded cells.

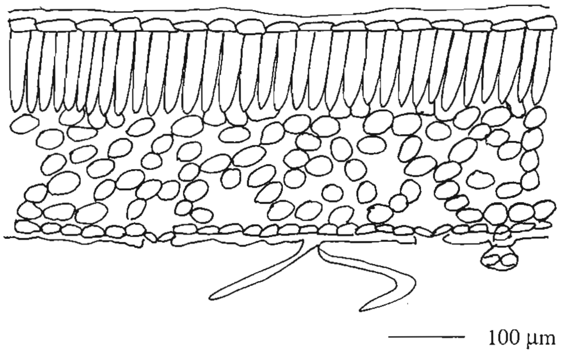
Lower epidermis (13 µm thick) overlaid by smooth cuticle (does not exceed 5 µm).

Mechanical tissue present as bundle sheath-extensions and as isolated sclerenchymatous fibers in the spongy tissue. Stomata very wide (rima 29 µm long, surface 389 µm²) and present in the lower side. Density attains 266/mm², so the transpiring surface covers 91,956 µm²/mm² (about 9% of leaf area).

Viburnum tinus L.



100 µm



100 µm

Distribution: *A tall shrub that is frequently found in the understorey of closed woodlands in the Mediterranean Basin.*

Average leaf surface attains 15 cm². Lamina (302 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle flat and smooth (barely attains 3.3 µm), glabrous type; the lower one even thinner (does not exceed 2.7 µm). Upper epidermis (29 µm thick) monolayered, about two times as thick as the lower (which barely attains 15 µm).

Two parenchyma in the mesophyll: palisade (108.7 µm thick) occupies 36% of the total thickness with compact cylindrical cells; spongy parenchyma (142 µm thick) consists of small, mostly widely-spaced and rather rounded cells.

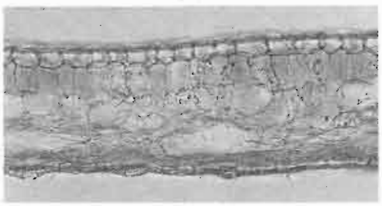
Long pluricellular and short glandular hairs sparsely cover the lower surface.

Mechanical tissue poorly represented.

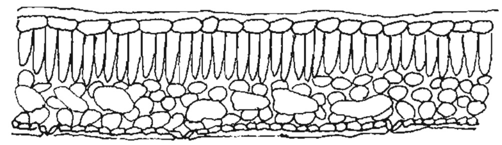
Stomata extremely wide (rima 34 µm long, surface 430 µm²) in the lower side. Density attains 266/mm², so the transpiring surface covers 114,646 µm²/mm² (about 11% of leaf area).

COMPOSITAE

Vernonia sp. Schreb.



150 µm



150 µm

Distribution: *A tall shrub that is common in the understorey of the tropical monsoon forest in southern China.*

Average leaf surface attains 18 cm^2. Leaf with dorsiventral symmetry in cross section (261 µm thick).

Upper cuticle smooth (10 µm thick), glabrous type. Monolayered underlying epidermis (29.8 µm thick) consists of fairly-compact squared cells.

Two parenchyma in the mesophyll: palisade (88 µm thick) occupies 34% of the total; spongy parenchyma (100 µm wide) consist of widely-spaced and rounded cells.

Wide intercellular space in the spongy portion.

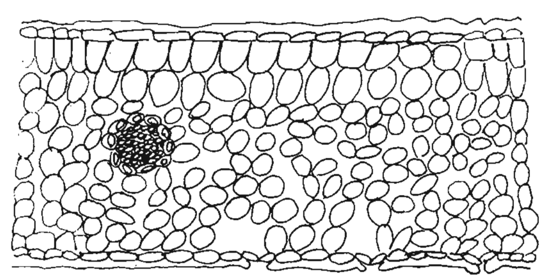
Mechanical tissue poorly represented: rare, isolated sclerenchymatous fibers scattered in the mesophyll.

Stomata rather large (rima 32 µm long, surface 332 µm^2) in the lower side. Density attains 222/mm^2, so the transpiring surface covers 73,925 µm^2/mm^2 (about 7% of leaf area).

LILIACEAE

Smilax aspera L.

250 µm



100 µm

Distribution: *A climber that is frequently found in both the open maquis and closed woodlands of the mediterranean belt in the Mediterranean Basin.*

Average leaf surface attains 10 cm^2. Lamina (300 µm thick in cross section) with dorsiventral symmetry; anatomically similar to the canariensis species studied.

Upper cuticle smooth (8.7 µm thick), glabrous type; the lower does not exceed 6 µm.

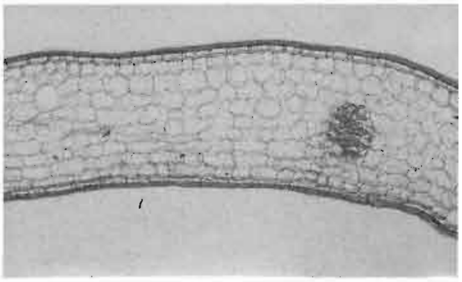
Epidermis consists of flattened cells that range from 19.1 µm to 15.6 µm in the upper and lower sides, respectively.

Two poorly differentiated parenchyma within the mesophyll: rather rough palisade consists of three layers (99.3 µm thick, 33% of the total section) of well-spaced, slightly elongated cells; spongy parenchyma (151 µm thick) consists of widely-spaced rounded cells.

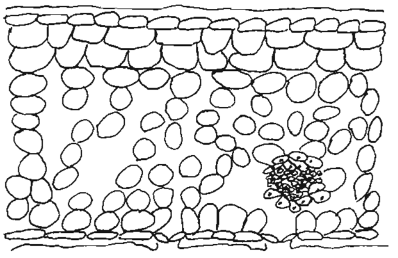
Mechanical tissue scarcely represented.

Stomata rather wide (rima 31 µm long, surface 412 µm^2) in the lower side. Density attains 177/mm^2, so the transpiring surface covers 72,924 µm^2/mm^2 (about 7% of leaf area).

Smilax canariensis Willd.



170 μm



100 μm

Distribution: A *climber that is frequently found in the understorey of the humid, warm temperate forest in the Canary Islands.*

Average leaf surface attains 9 cm^2. Lamina (298 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly smooth (7.2 μm thick), glabrous type.

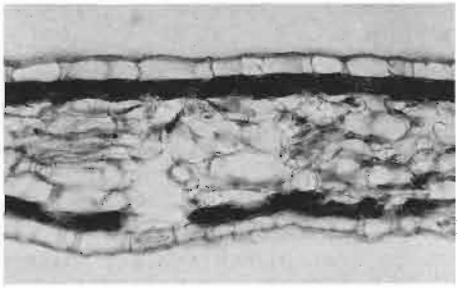
Underlying epidermis monolayered and consists of a single layer (14.2 μm thick) of rather flattened cells.

Undifferentiated mesophyll (257 μm thick) composed of heterogeneous widely-spaced cells in the inner and lower portion, more compact in the upper.

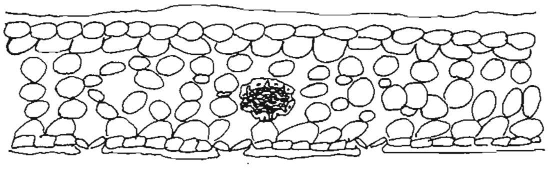
Lower epidermis (13.2 μm thick) monolayered and covered by smooth cuticle (does not exceed 6.3 μm).

Stomata very wide (rima 36 μm long, surface 505 μm^2) in the lower side. Density attains 177/mm^2, so the transpiring surface covers 89,402 $\mu m^2/mm^2$ (about 9% of leaf area).

Smilax china L.



90 μm



100 μm

Distribution: *A climber that is a common component of the understorey of the warm, humid temperate forest in southern Japan.*

Average leaf surface attains 10 cm^2. Lamina (199.8 μm thick) with dorsiventral symmetry in cross section.

Upper cuticle very thin and uniformly smooth (does not exceed 3.6 μm), glabrous type like the lower (3 μm thick). Upper epidermis consists of a single layer (26 μm thick) of squared cells, like the lower epidermis.

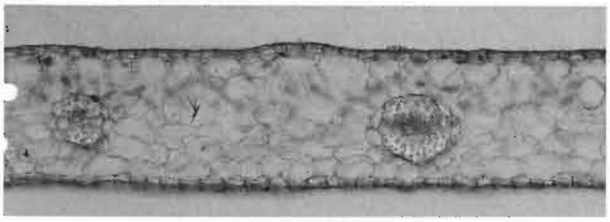
Undifferentiated mesophyll (140.4 μm wide) uniformly composed of widely-spaced and rather elongated cells.

Mechanical tissue poorly represented.

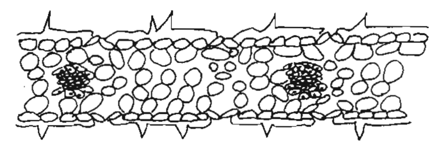
Stomata rather small (rima 24 μm long, surface 182 μm large) confined to the lower side. Density does not exceed 133/mm^2, so transpiring surface covers 24,376 $\mu m^2/mm^2$ (about 2% of leaf area, the smallest transpiring surface of the *Smilax* species studied).

PALMAE

Caryota mitis Loureiro



65 µm



100 µm

Distribution: *A small tree that is common in the low layer of the tropical monsoon forest in southern China.*

Average leaf surface attains 15 cm^2. Blade (127.3 µm thick) with isolateral symmetry, the only one among tropical species studied.

Upper cuticle smooth and slightly undulate (3.9 µm thick, like the lower); both glaubrous type.

Epidermis monolayered (the upper 27 µm thick, the lower only 19 µm).

Undifferentiated mesophyll (72.7 µm thick) consists of small rather-compact cells.

Stomata rather wide (rima 33.8 µm long, surfaces range from 173 µm^2 to 298 µm^2 from the upper to lower side) on both sides. Density rather low on the upper surface (barely attains 177/mm^2, but about twice that figure — 444/mm^2 — on the lower), so the transpiring surface varies widely from 30,780 µm^2/mm^2 to 132,312 µm^2/mm^2 (about 3% and 13% of the leaf surface).

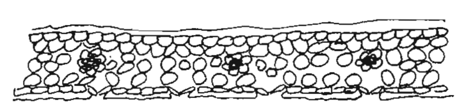
Ordinary mechanical tissue poorly represented in the leaf section.

Short spine-like hairs scattered on both epidermis layers.

ARACEAE

Pothos repens (Lour.) Druce

90 µm



50 µm

Distribution: *A small shrub that is common in the understorey of the tropical monsoon forest in southern China.*

Average leaf surface attains 5 cm^2 (rather small in comparison to the tropical examples studied). Lamina (100 µm thick) with dorsiventral symmetry in cross section.

Upper cuticle uniformly flat and smooth (3.9 µm thick), glabrous type. Underlying epidermis consists of a single layer (barely attains 11.7 µm) of uniform rectangular cells.

Undifferentiated mesophyll: (74 µm wide): small rounded cells uniformly cover the thickness between the two epidermis.

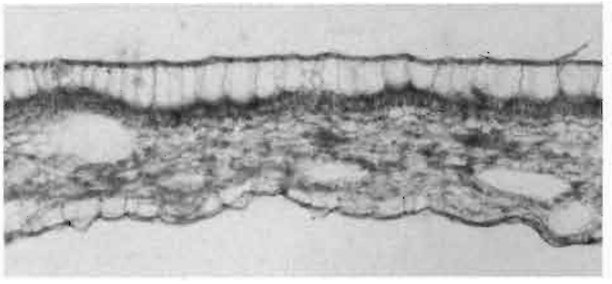
Intercellular space rather limited in the mesophyll.

Mechanical tissue poorly represented in the leaf section: only scattered sclerenchymatous fibers are present in the mesophyll.

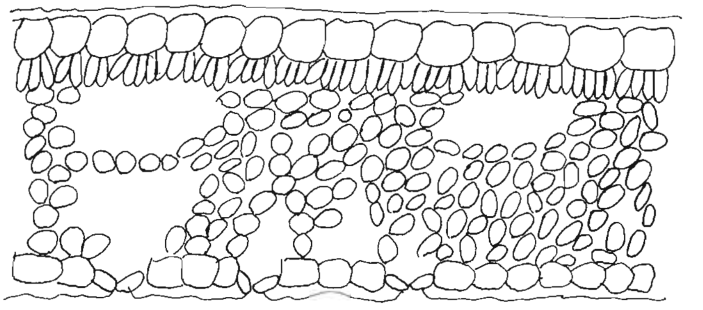
Lower epidermis (6.4 µm thick) overlaid by the smooth cuticle (3.9 µm thick).

Stomata located in the lower side, very small in comparison to the other tropical leaves studied (rima 17.6 µm long, surface 129 µm^2 large). Density also rather low (does not exceed 177/mm^2) so transpiring surface covers 22,939 µm^2/mm^2 (about 2% of leaf area).

Rhaphydophora angustifolia Schott



190 μm



100 μm

Distribution: *A tall tree that is common in the closed canopy of the tropical monsoon forest in southern China.*

Leaf surface averages about 18 cm^2. Lamina (381 μm thick, one of the thickest tropical species studied) with dorsiventral symmetry in cross section. Upper cuticular layer (17 mm thick uniformly flat and smooth, glabrous type. Underlying epidermis extremely thick and composed of a single layer of uniform squared cells, and attains the exceptional thickness of 75.39 μm (the largest epidermis among tropical and sclerophyll species studied).

Mesophyll weakly differentiated into palisade and spongy parenchyma: rather rough and thin palisade that consists of a single layer (36 μm thick) of small elongated cells and occupies only 9.3% of the total leaf thickness. The largest portion of the mesophyll is given to the spongy parenchyma (196 μm thick, six times thicker than the palisade).

Mechanical tissue poorly represented in the mesophyll: only infrequent, clustered sclerenchymatous fibers present in the spongy tissue. Wide glandular cavities are also present in the mesophyll. Lower epidermis (43 μm thick) half in comparison to the upper.

Stomata somewhat large (rima 34 μm long, surface 273.3 μm^2) on the lower side, slightly sunken in the epidermis; but density does not exceed 177/mm^2, so the transpiring surface barely covers 48,375 $\mu m^2/mm^2$ (about 5% of leaf area).

RESULTS

Automatic elaboration of numerical data (Tab. II), pertaining to the micrometrical measurements, allowed us to examine the species studied according to their distribution in the factorial plane.

Principal Component Analysis of 23 characteristics of all species (Fig. 1) resulted in the identification of three main clusters, each of which is composed of species from a similar habitat: species from humid environments were clustered along the positive portion of the 'Y' axis; *Tetrastigma planicaule, Hicriopteris chinensis, Cryptocarya chinensis* and *Lindera chunii*, true monsoon tropical forest species from China, were mainly confined to the upper and medium portion of the graph; *Neolitsea sericea, Glochydion obovatum* and *Elaeocarpus sylvestris*, subtropical species from Japan, were clustered in the lower side, close to species that are common to tropical forest canopy gaps (like *Schefflera octophylla*) and to canariensis species like *Laurus azorica* and *Arbutus canariensis*, clustered in the extreme lower edge of this first cluster.

Mediterranean species, mainly from the northern hemisphere and scattered along the negative half of the 'Y' axis, were placed in the second cluster, where most of the species from the warm-temperate humid forest of Transvaal were also located: *Quercus ilex, Quercus suber, Pistacia lentiscus* (from the Mediterranean Basin), *Quercus agrifolia* and *Ceanothus megacarpus* (from California) were distributed near the edge of the tropical-species cluster and were surrounded by representatives of *Lauraceae* like *Cryptocarya alba* (from Chile) and by a few *Myrtaceae* like *Eucalyptus calophylla* and *Eucalyptus marginata* (from Australia); furthermore, the three *Olea* species (*O. europaea, O. europaea* ssp. *africana* and ssp. *cerasiformis*), respectively coming from winter rain and from the warm-temperate regions, converged.

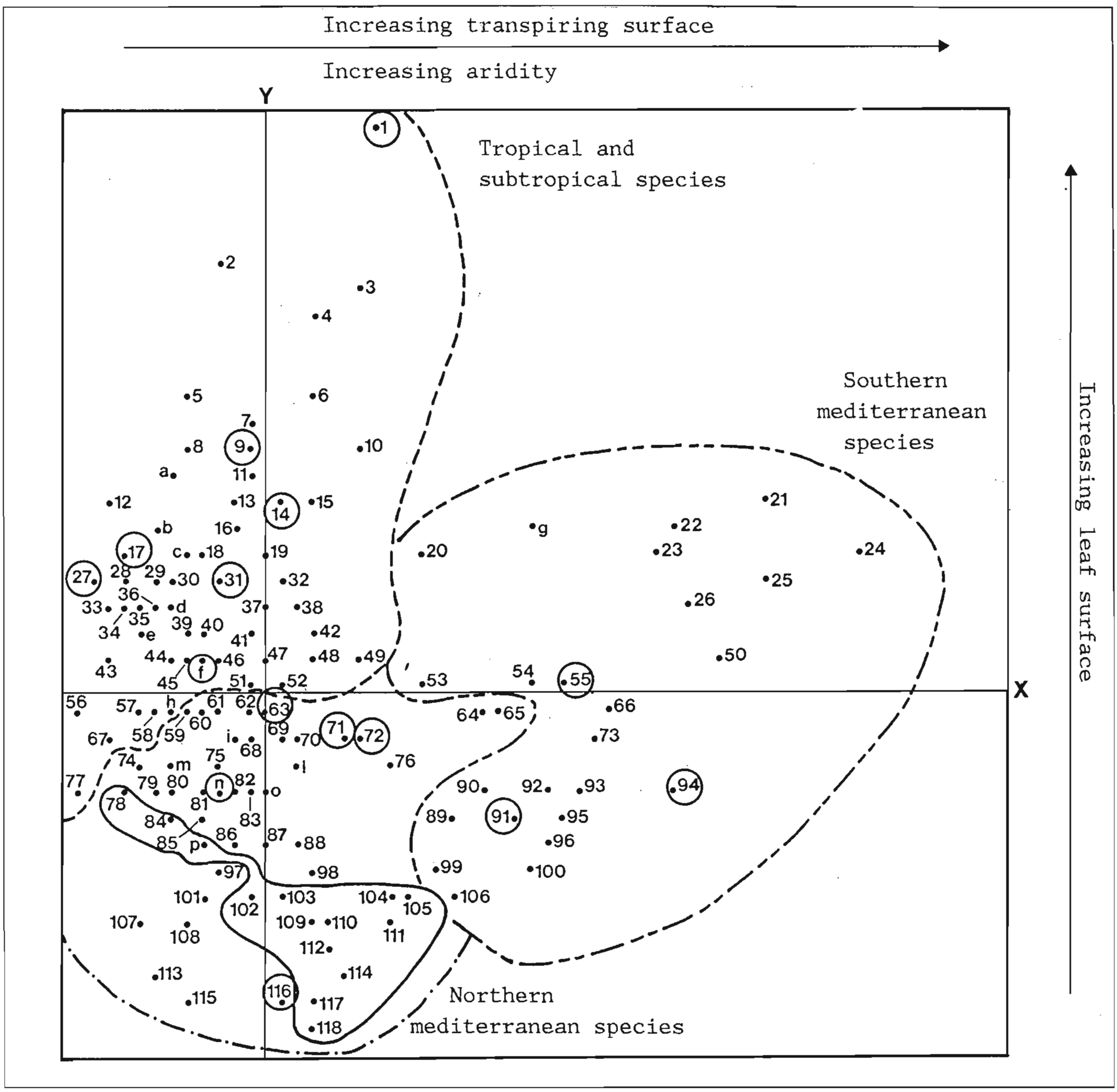


Fig. 1 - P C A of the total species correlated to all characters (matrix 146x23). See pag. 106 for species names.

LEGEND Fig. 1

1 - *Psychotria manillensis*
2 - *Tetrastigma planicaule*
3 - *Mischocarpus pentapetalus*
4 - *Sygyzium yambos*
5 - *Hicriopteris chinensis*
6 - *Hemigramma decurrens*
7 - *Cryptocarya chinensis*
8 - *Ardisia sieboldii*
9 - *Vernonia sp.*
10 - *Gironniera subaequalis*
11 - *Melastoma sanguineum*
a - *Lindera chunii, Cryptocarya concinna*
12 - *Quercus serrata*
13 - *Blastus cochinchinensis*
14 - *Castanopsis fissa*
15 - *Laurus nobilis*
b - *Quercus mirsinaefolia, Castanopsis chinensis*
16 - *Neolitsea sericea*
17 - *Ficus nervosum*
c - *Castanopsis cuspidata, Arbutus unedo*
18 - *Smilax aspera*
19 - *Xylosma monospora*
20 - *Caryota mitis*
g - *Arctostaphylos glandulosa Arctostaphylos glauca*
21 - *Protea cynaroides*
22 - *Protea latifolia*
23 - *Leucadendron salignum*
24 - *Protea longifolia*
25 - *Protea amplexicaulis*
26 - *Leucadendron nervosum*
27 - *Celtis sinensis*
28 - *Aporosa yunnanensis*
29 - *Smilax china*
30 - *Quercus hui*
31 - *Smilax canariensis*
32 - *Rhaphydophora angustifolia*
33 - *Rhamnus alaternus*
34 - *Itea chinensis*
35 - *Elaeocarpus sylvestris*
36 - *Pterospermum lanceaefolium*
d - *Rhamnus crenulata, Schefflera octophylla*
37 - *Peumus boldus*
38 - *Euclea undulata*
e - *Diospyros morrisiana, Melastoma dodecandrum*
39 - *Ilex rugosa*
40 - *Urena lobata*
41 - *Viburnum tinus*
42 - *Podocarpus latifolius*
43 - *Glochidion obovatum*
44 - *Boronia crenulata*
45 - *Rhus excisa*
f - *Arbutus canariensis, Rhamnus glandulosa*
46 - *Prunus ilicifolia*
47 - *Ternostroemia japonica*
48 - *Rapanea melanophloeos*
49 - *Laurus azorica*
50 - *Xylomelum occidentale*
51 - *Viburnum rugosa*
52 - *Eucalyptus calophylla*
53 - *Adenanthos cuneatus*
54 - *Eucalyptus caesia*
55 - *Quillaja saponairia*
56 - *Rhamnus californica*
57 - *Eurya yaponica*
58 - *Prunus lusitanica*
h - *Quercus chrysolepis*
59 - *Cryptocarya alba*
60 - *Quercus agrifolia*
61 - *Phillyrea media*
62 - *Lambertia multiflora*
63 - *Quercus ilex*
64 - *Banksia grandis*
65 - *Conospermum caeruleum*
66 - *Leucadendron gandogeri*
67 - *Pothos repens*
i - *Euclea racemosa, Euclea divinorum*
68 - *Banksia quercifolia*
69 - *Hibbertia cuneiformis*
70 - *Viburnum rigidum*
71 - *Banksia littoralis*
72 - *Leucadendron linoides*
73 - *Faurea saligna*
74 - *Pistacia lentiscus*
m - *Rosmarinus officinalis, Ceanothus spinosus*
n - *Heteromeles arbutifolia Psychotria capensis*
75 - *Pistacia atlantica*
l - *Heteromorpha trifoliata , Ceratonia siliqua*
76 - *Eucalyptus marginata*
77 - *Hibbertia hypericoides*
78 - *Arbutus menziesii*
79 - *Psychotria zombamontana*
80 - *Phillyrea media*
81 - *Ilex canariensis*
82 - *Lithraea caustica*
o - *Pittosporum viridiflorum, Diplolaena microcephala, Antidesma venosum*
83 - *Sideroxylon inerme*
84 - *Darwinia lejostyla*
85 - *Myrsine africana*
86 - *Olea europaea ssp. africana*
p - *Erica plukenetii, Adenostoma fasciculatum*
87 - *Ilex aquifolim*
88 - *Olea europaea*
89 - *Acacia podalyriaefolia*
90 - *Leucospermum calligerum*
91 - *Petrophile linearis*
92 - *Stirlingia latifolia*
93 - *Conospermum crassinervium*
94 - *Persoonia longifolia*
95 - *Synaphaea petiolaris*
96 - *Leucospermum hypophyllocarpodendron*
97 - *Ceanothus megacarpus*
98 - *Olea europaea ssp. cerasiformis*
99 - *Isopogon attenuatus*
100 - *Agonis flexuosa*
101 - *Ceanothus oliganthus*
102 - *Erica multiflora*
103 - *Agonis hypericifolia*
104 - *Melaleuca huegelii*
105 - *Protea welvitschii*
106 - *Acacia rostellifera*
107 - *Brachysema sericeum*
108 - *Melaleuca acerosa*
109 - *Kunzea recurva*
110 - *Beaufortia decussata*
111 - *Petrophile ericifolia*
112 - *Melastoma candidum*
113 - *Calothamnus quadrifidus*
114 - *Grevillea pulchella*
115 - *Banksia quercifolia*
116 - *Calothamnus sanguineum*
117 - *Hypocalymma angustifolium*

The boundary between these two is not so sharp, however, because of the gradual and continual variation of anatomical features along the axis. Even the position of the stomata contributed to underlining this similarity, all the species being hypostomatic. Consequently, the two clusters could be better regarded as one main group characterized by the presence of hypostomatic leaves.

A divergent position, marked by positive values on the axis, was occupied by mostly mediterranean species from the southern hemisphere like *Proteaceae*, such as *Protea longifolia, Leucadendron nervosum* (from the Cape Province), *Xylomelum occidentale, Persoonia longifolia* and *Adenanthos cuneatus* (from southwestern Australia). Some representatives of the *Ericaceae* family, like *Arctostaphylos glauca* and *Arctostaphylos glandulosa* (from the californian mediterranean region) — uniformly characterized by stomata on both sides of the leaf — were also placed in this cluster. Stomata position could therefore be regarded as the main diagnostic feature that discriminates between the two main groups.

Finally, a small group was composed of species with extremely-reduced ericoid leaves: *Hypocalymma angustifolium, Petrophile linearis and Melaleuca acerosa* (characterized by stomata all around the lamina, closer to the amphystomatic group of *Proteaceae*), and *Erica multiflora, Erica plukenetii* and *Darwinia lejostyla* (with stomata confined to the lower side, closer to hypostomatic boreal species); this latter grouping could be considered a subcluster with a significant relation to the main clusters.

Along the 'X' axis, the distribution of species along the factorial plane was mainly associated with increasing values for leaf surface (these were extremely small in ericoid species and very large in tropical species) and, along the 'Y' axis, with increasing values for transpiring surface (ranging from small values for tropical species to higher values for species from the northern and southern mediterranean zones).

It is interesting to note that the characteristics measured were highly redundant and that about 99% of the total information came from only 16 species that are circled in the graph. It is quite significant that *Quercus ilex* and *Arbutus canariensis* represented the mediterranean species from the northern hemisphere, and *Persoonia longifolia, Leucadendron linoides* and *Quillaja saponaria* the southern. The PCA, based on the anatomical characteristics of the specimens (Fig. 2), confirmed the expected strong correlations between various traits: palisade and spongy parenchyma, upper and lower cuticle, and hairiness and lower transpiring surface. On the other hand, no correlation emerged between palisade and mechanical structures, leaf thickness and stomata location and so on.

In order to lower the redundancy due to using many anatomical leaf features, only those characters that describe the main characteristics which synthetically define xeromorphism (i.e., transpiring surface, mechanical structures, mesophyll thickness, and leaf width and length) were processed. The PCA of this reduced matrix (Fig. 3) again confirmed the triple clustering noted above: the clusters were distributed along the 'Y' axis according to increasing transpiring surface (from tropical and subtropical species) in the upper portion of the plane, to mediterranean amphistomatic types (from the southern hemisphere) in the lower portion; species from mediterranean zones in the northern hemisphere and warm-temperate species from the laurophyll forest of the Transvaal and the Canary Islands were located in the middle of the graph. Ericoid species describe a subcluster that is situated in both the amphistomatic mediterranean species group and in the hypostomatic mediterranean and warm-temperate species group.

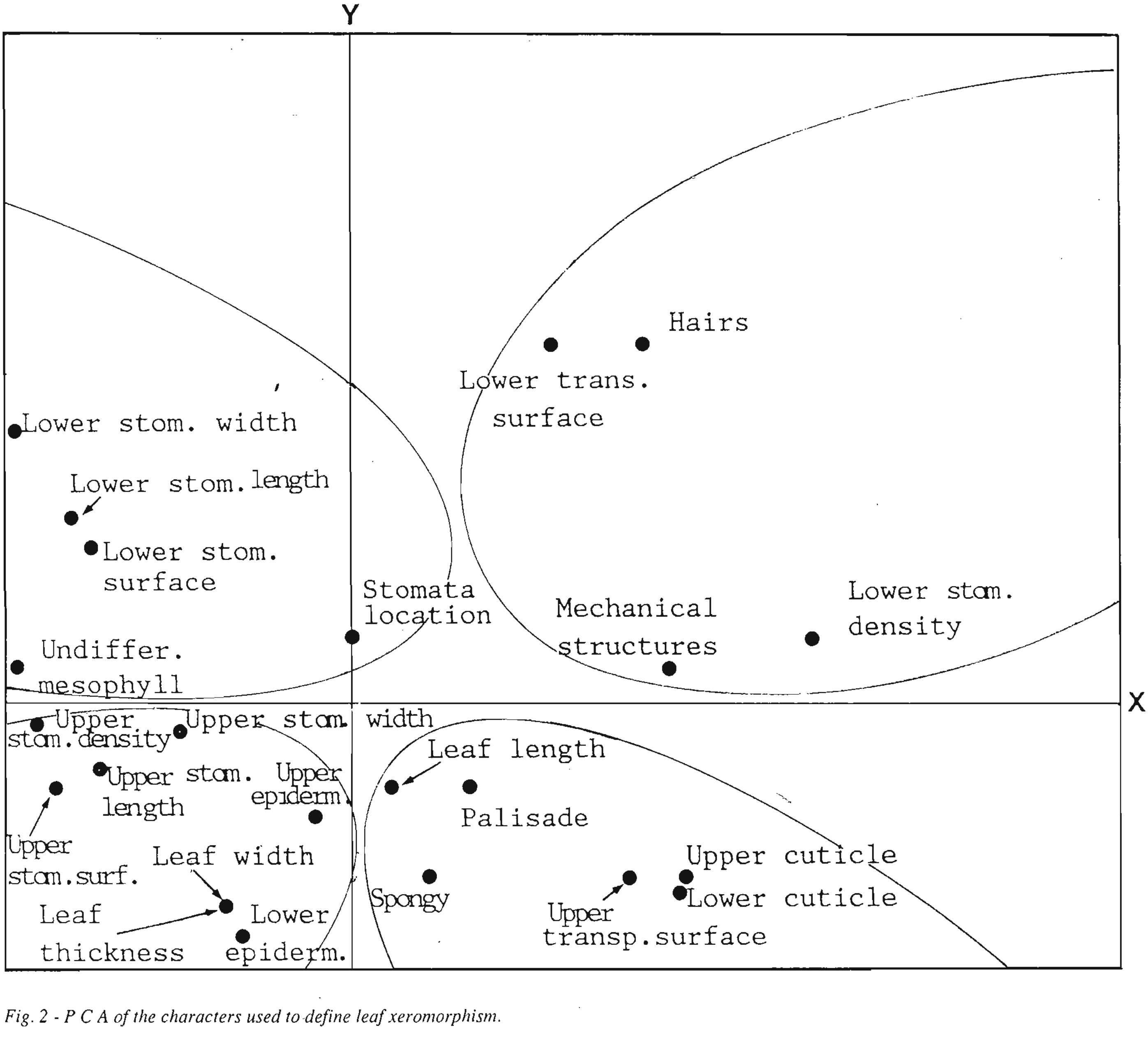


Fig. 2 - P C A of the characters used to define leaf xeromorphism.

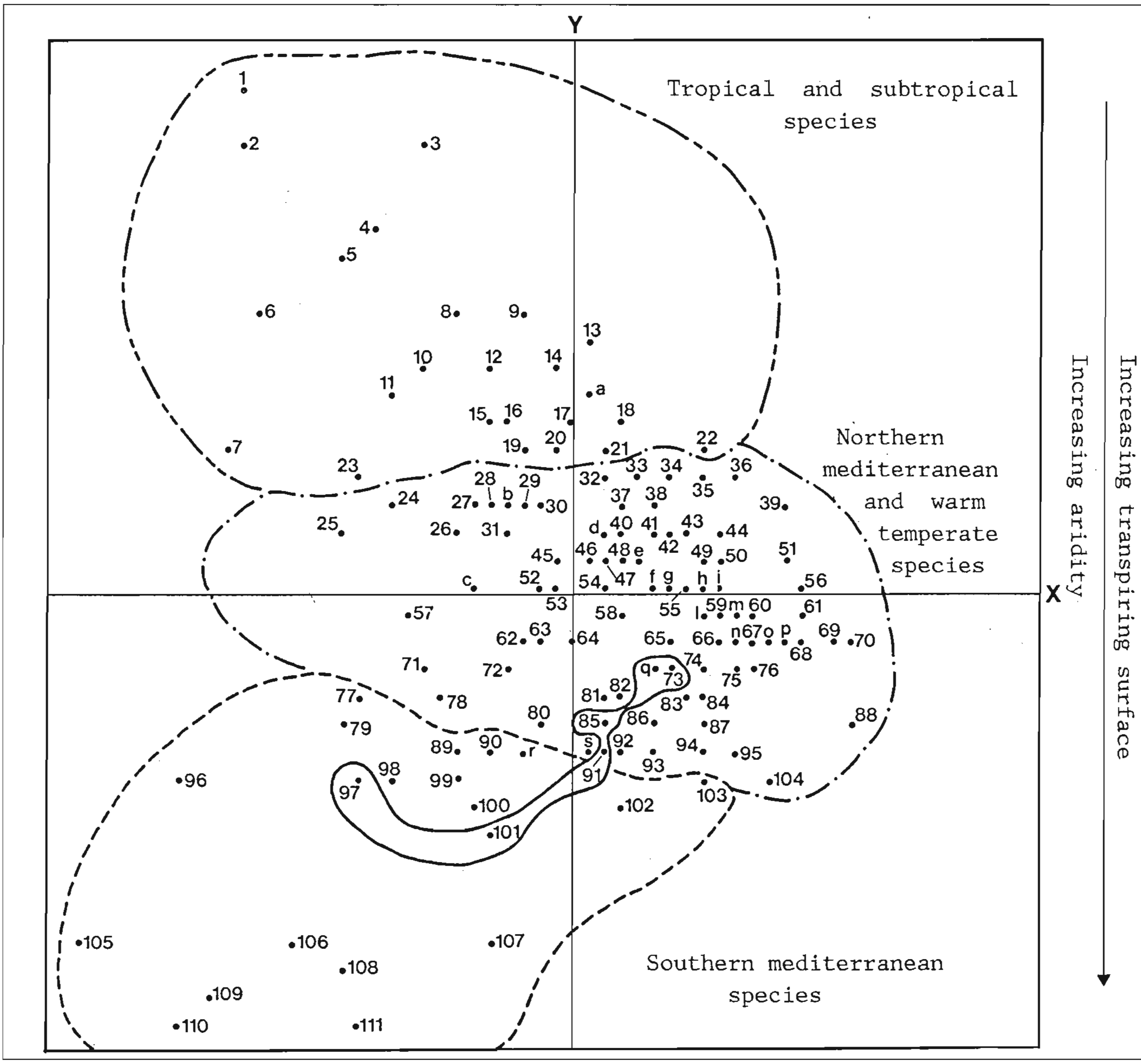


Fig. 3 - P C A of the total species correlated to the characters which may resume leaf xeromorphism (Matrix 146x6).

LEGEND Fig. 3

1 - *Syzygium yambos*
2 - *Psychotria manillensis*
3 - *Hicriopteris chinensis*
4 - *Cryptocarya concinna*
5 - *Blastus cochinchinensis*
6 - *Tetrastigma planicaule*
7 - *Gironniera subaequalis*
8 - *Castanopsis chinensis*
9 - *Melastoma sanguineum*
10 - *Peumus boldus*
11 - *Lindera chunii*
a - *Neolitsea sericea*
12 - *Smilax aspera*
13 - *Mischocarpus pentapetalus*
14 - *Castanopsis fissa*
15 - *Arbutus unedo*
16 - *Elaeocarpus sylvestris*
17 - *Laurus nobilis*
18 - *Quercus serrata*
19 - *Vernonia sp.*
20 - *Castanopsis cuspidata*
21 - *Xylosma monospora*
22 - *Pothos repens*
23 - *Hemigramma decurrens*
24 - *Rhaphydophora angustifolia*
25 - *Conospermum caeruleum*
26 - *Prunus lusitanica*
27 - *Pistacia atlantica*
28 - *Conospermum crassinervium*
b - *Euclea racemosa*
29 - *Hibbertia cuneiformis*
30 - *Prunus ilicifolia*
31 - *Adenostoma fasciculatum*
32 - *Quercus mirsinaefolia*
33 - *Laurus azorica*
34 - *Quercus hui*
35 - *Pterospermum lanceaefolium*
36 - *Banksia littoralis*
37 - *Euclea undulata*
38 - *Ilex rugosa*
39 - *Diplolaena microcephala*
d - *Podocarpus latifolius, Rhamnus alaternus, Cryptocarya chinensis*
40 - *Hibbertia hypericoides*
41 - *Boronia crenulata*
42 - *Cryptocarya alba*
43 - *Urena lobata*
44 - *Lambertia multiflora*
45 - *Viburnum tinus*
46 - *Arbutus canariensis*
47 - *Ardisia sieboldii*
48 - *Glochydion obovatum*
e - *Pistacia lentiscus, Eurya japonica*
49 - *Schefflera octophylla*
50 - *Phillyrea angustifolia*
51 - *Olea europaea*
52 - *Olea europaea ssp. africana*
c - *Stirlingia latifolia, Rhamnus crenulata*
53 - *Rhamnus glandulosa*
54 - *Viburnum rigidum*
f - *Synaphea petiolaris*
g - *Rosmarinus officinalis, Ceanothus spinosus*
55 - *Banksia grandis*
h - *Myrsine africana, Rhamnus californica, Quercus ilex*

i - *Melastoma dodecandrum, Ficus nervosum*
56 - *Heteromorpha trifoliata*
57 - *Melaleuca acerosa*
58 - *Antidesma venosum*
l - *Leucadendron hypophyllocarpodendron, Itea chinensis*
59 - *Phillyrea media*
m - *Lithraea caustica, Psychotria zombamontana*
60 - *Eucalyptus marginata*
61 - *Quercus agrifolia*
62 - *Quillaja saponaria*
63 - *Ternostroemia japonica*
64 - *Rapanea melanophloeos*
65 - *Viburnum rugosa*
66 - *Arbutus menziesii*
m - *Diospyros morrisiana, Eucalyptus calophylla*
67 - *Psychotria capensis*
o - *Quercus chrysolepis, Quercus suber, Ceanothus oliganthus*
p - *Olea europaea ssp. cerasiformis Olea europaea, Melastoma candidum*
69 - *Pittosporum viridiflorum*
69 - *Quercus suber*
70 - *Euclea divinorum*
71 - *Petrophile linearis*
72 - *Smilax aspera*
q - *Erica multiflora, Darwinia lejostyla*
73 - *Erica plukenetii*
74 - *Brachysema sericeum*
76 - *Celtis sinensis*
77 - *Arctostaphylos glandulosa*
78 - *Acacia rostellifera*
79 - *Arctostaphylos glauca*
80 - *Caryota mitis*
81 - *Heteromorpha trifoliata*
82 - *Agonis hypericifolia*
83 - *Grevillea pulchella*
84 - *Kunzea recurva*
85 - *Calothamnus sanguineum*
86 - *Smilax aspera*
87 - *Ceanothus megacarpus*
88 - *Banksia quercifolia*
89 - *Leucospermum calligerum*
90 - *Ilex canariensis*
r - *Ilex aquifolium*
s - *Hypocalymma angustifolium, Agonis flexuosa*
91 - *Faurea saligna*
92 - *Adenanthos cuneatus*
93 - *Petrophile ericifolia*
94 - *Sideroxylon inerme*
95 - *Smilax china*
96 - *Leucadendron nervosum*
97 - *Persoonia longifolia*
98 - *Melaleuca huegelii*
99 - *Leucadendron gandogeri*
100 - *Acacia podalyriaefolia*
101 - *Calothamnus quadrifidus*
102 - *Isopogon attenuatus*
103 - *Beaufortia decussata*
104 - *Ceratonia siliqua*
105 - *Protea longifolia*
106 - *Leucospermum salignum*
107 - *Eucalyptus caesia*
108 - *Xylomelum occidentale*
109 - *Protea cynaroides*
110 - *Protea amplexicaulis*
111 - *Protea latifolia*

A further analysis of the main groups of species was also performed, separately processing the data that pertain to mediterranean species and those that pertain to tropical and warm-temperate species. Tropical and warm-temperate species (Fig. 4) were distributed along the axis according to increasing values for palisade parenchyma, ranging from *Smilax china, Schefflera octophylla* and *Tetrastigma planicaule* (true tropical species with undifferentiated or weakly differentiated mesophyll from the Chinese monsoon forest), to *Neolitsea sericea* and *Quercus serrata* (from the Japanese subtropical and temperate forests, respectively), up to the highest value, registered in Olea europaea ssp. cerasiformis. Two main clusters could be identified: the first one, on the left portion of the graph and marked by negative values, (the canariensis species) and the second one, on the right portion, related to positive 'values, composed of monsoon tropical species located in the middle as a subcluster, (from which mixed temperate and subtropical elements radiated into the upper and lower portions-temperate species being prevalent in the former). The species showed high redundance: in fact, only 14 of the total accounted for about 90% of the information. More than 50% of these few species, like *Itea chinensis, Melastoma dodecendrum, Lindera chunii*, etc., were representives of the monsoon tropical forest. *Ilex canariensis* was the only representative of species from the Canary Islands.

Finally, species from the mediterranean and warm-temperate humid zones were compared (Fig. 5). The results were distributed according to the increase in the percentage of transpiring surface (and of lignified tissue) along the axis, ranging from *Psychotria capensis* and *zombamontana* from the Transvaal region to *Protea longifolia* and *Adenanthos cuneatus* (from the southern hemisphere), with *Quercus ilex* and *Ceanothus spinosus* (from the northern mediterranean region) in the middle of the range.

Two main clusters can be recognized in the factorial plane: the first, on the left, contains amphistomatic species (mostly *Proteaceae*) both from the mediterranean regions of southwestern Australia and the Cape Province but also from the Transvaal; the second, which stretches along the axis, is composed of hypostomatic species that are further subdivided into two smaller groups: the upper one (which includes *Banksia quercifolia* and *littoralis* from southwestern Australia, *Ceanothus oliganthus* and *megacarpus* from California, etc.) is characterized by leaves with abundant hairs on the leaf surface; the lower is composed of species with completely glabrous leaves, like *Laurus nobilis, Arbutus unedo, Eucalyptus marginata* and *calophylla* from the northern and southern hemispheres. Once again, the warm-temperate species were clustered together along with mediterranean hypostomatic species mostly from northern mediterranean regions, except for two *Banksia* from Australia and *Peumus boldus* and *Cryptocarya alba* from the neotropic flora of Chile. Species with ericoid leaves occurred in a small sub-cluster contained in the *Proteaceae* cluster.

In terms of information related to anatomical structure, the number of representative species did not exceed 18 (circled in the graph); these were widely scattered along the factorial plane and represent 98% of the variability. *Protea latifolia* and *longifolia*, and *Adenanthos cuneatus* represented the amphistomatic *Proteaceae* cluster, whereas *Laurus nobilis* and *Arbutus unedo* represented the hypostomatic species along with *Heteromorpha trifoliata, Podocarpus latifolius* and *Olea europaea ssp africana;* once again, mediterranean and warm-temperate species were clustered together.

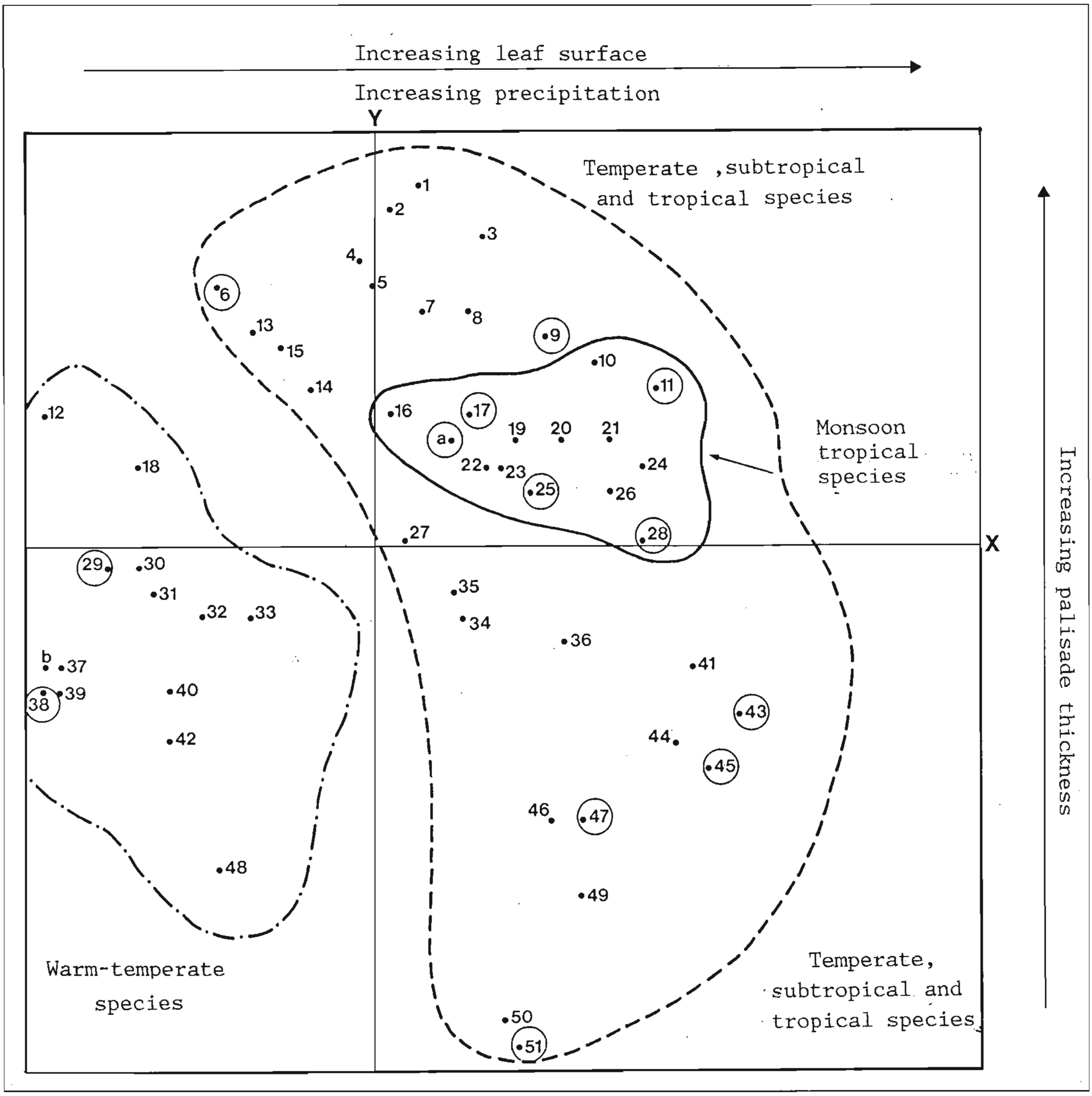


Fig. 4 - P C A of the species from tropical, subtropical and waerm temperate climates (matrix 51x23).

LEGEND Fig. 4

1 - *Quercus serrata*
2 - *Castanopsis fissa*
3 - *Pterospermum lanceaefolium*
4 - *Urena lobata*
5 - *Ficus nervosum*
6 - *Glochydion obovatum*
7 - *Quercus hui*
8 - *Quercus mirsinaefolia*
9 - *Celtis sinensis*
10 - *Cryptocarya concinna*
11 - *Itea chinensis*
12 - *Olea europaea ssp. cerasiformis*
13 - *Eurya japonica*
14 - *Castanopsis cuspidata*
15 - *Elaeocarpus sylvestris*
16 - *Melastoma candidum*
17 - *Lindera chunii*
18 - *Phillyrea angustifolia*
a - *Castanopsis chinensis*
19 - *Gironniera subaequalis*
20 - *Cryptocarya chinensis*
21 - *Blastus cochinchinensis*
22 - *Melastoma sanguineum*
23 - *Diospyros morrisiana*
24 - *Mischocarpus pentapetalus*
25 - *Melastoma dodecandrum*
26 - *Aporosa yunnanensis*
27 - *Sygyzium yambos*
28 - *Pothos repens*
29 - *Ilex canariensis*
30 - *Ilex rugosa*
31 - *Ternstroemia japonica*
32 - *Arbutus canariensis*
33 - *Laurus azorica*
34 - *Rhaphydophora angustifolia*
35 - *Neolitsea sericea*
36 - *Hicriopteris chinensis*
37 - *Viburnum rigidum*
38 - *Viburnum rugosa*
39 - *Prunus ilicifolia*
40 - *Rhamnus glandulosa*
41 - *Psychotria manillensis*
42 - *Pistacia atlantica*
43 - *Tetrastigma planicaule*
44 - *Schefflera octophylla*
45 - *Ardisia sieboldii*
46 - *Caryota mitis*
47 - *Vernonia sp.*
48 - *Rhamnus crenulata*
49 - *Smilax china*
50 - *Hemigramma decurrens*
51 - *Smilax canariensis*

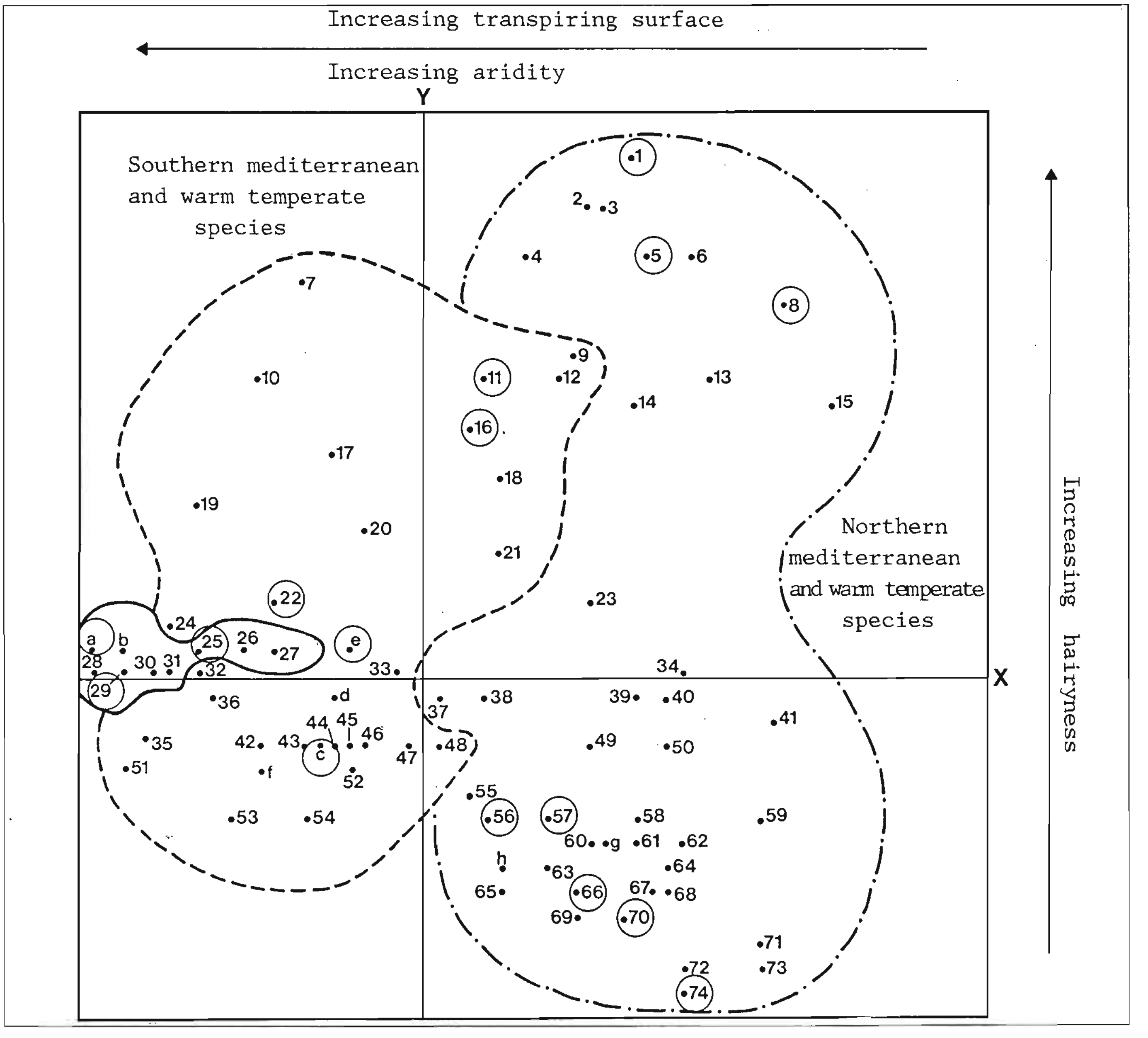


Fig. 5 - P C A of mediterranean species from the five mediterranean ecosystems of the world and warm temperate region of Transvaal (matrix 95x23).

LEGEND Fig. 5

1 - *Myrsine africana*
2 - *Diplolaena microcephala*
3 - *Rosmarinus officinalis*
4 - *Ceanothus megacarpus*
5 - *Ceanothus oliganthus*
6 - *Banksia littoralis*
7 - *Leucospermum calligerum*
8 - *Heteromorpha trifoliata*
9 - *Banksia quercifolia*
10 - *Leucospermum hipophyllicarpo-dendron*
11 - *Adenanthos cuneatus*
12 - *Conospermum crassinervium*
13 - *Euclea divinorum*
14 - *Olea europaea*
15 - *Antidesma venosum*
16 - *Protea latifolia*
17 - *Leucadendron gandogeri*
18 - *Rhus excisa*
19 - *Leucadendron nervosum*
20 - *Leucadendron salignum*
21 - *Protea welwitschii*
22 - *Protea longifolia*
23 - *Lithraea caustica*
24 - *Agonis hypericifolia*
a - *Calothamnus quadrifidus, Melaleuca huegelii, Melaleuca acerosa*
b - *Kunzea recurva, Darwinia lejostyla*
25 - *Adenostoma fasciculatum*
26 - *Erica multiflora*
27 - *Erica plukenetii*
c - *Grevillea pulchella*
28 - *Hibbertia hypericoides*
29 - *Calothamnus sanguineum*
30 - *Hypocalymma angustifolium*
31 - *Petrophile linearis*
32 - *Beaufortia decussata*
33 - *Brachysema sericeum*
34 - *Quercus suber*
35 - *Persoonia longifolia*
36 - *Isopogon attenuatus*
d - *Boronia crenulata, Euclea racemosa, Euclea undulata*
37 - *Lambertia multiflora*
38 - *Ceanothus spinosus*
39 - *Viburnum tinus*
40 - *Quercus ilex*
41 - *Xylosma monospora*
42 - *Agonis flexuosa*
43 - *Arctostaphylos glauca*
44 - *Stirlingia latifolia*
45 - *Synaphaea petiolaris*
46 - *Eucalyptus caesia*
e - *Petrophile ericifolia, Conospermum caeruleum*
47 - *Hibbertia cuneiformis*
48 - *Sideroxylon inerme*
49 - *Olea europaea ssp. africana*
50 - *Peumus boldus*
51 - *Protea amplexicaulis*
52 - *Arctostaphylos glandulosa*
f - *Quillaja saponaria, Faurea saligna Leucadendron linoides*
53 - *Protea cynaroides*
54 - *Xylomelum occidentale*
55 - *Pistacia lentiscus*
56 - *Podocarpus latifolius*
57 - *Heteromeles arbutifolia*
58 - *Rhamnus californica*

59 - *Banksia grandis*
60 - *Ceratonia siliqua*
61 - *Cryptocarya alba*
g - *Eucalyptus calophylla, Eucalyptus marginata*
62 - *Pittosporum viridiflorum*
63 - *Rhamnus alaternus*
h - *Phillyrea angustifolia, Phillyrea media*
64 - *Quercus chrysolepis*
65 - *Rapanea melanophloeos*
66 - *Prunus ilicifolia*
67 - *Quercus agrifolia*
68 - *Arbutus menziesii*
69 - *Ilex aquifolium*
70 - *Arbutus unedo*
71 - *Psychotria capensis*
72 - *Smilax aspera*
73 - *Psychotria zombamontana*
74 - *Laurus nobilis*

DISCUSSION

ADAPTIVE SIGNIFICANCE OF THE EVERGREEN LEAF

The results based on the analysis of leaf anatomy and the numerical analysis can now be discussed, and the more significant data can be noted.

The average value for leaf surface is generally larger in tropical species, reaching 100 cm² in *Psychotria manillensis*; this is still comparable to the surface area of *Banksia grandis*, which also exceeds 100 cm². Lower surface values were noted in *Quercus mirsinaefolia* (50 cm2). These values progressively decreased in *Quercus serrata* and *Quercus hui* leaves, which were quite similar to *Quercus* examples from the mediterranean habitat, like *Quercus ilex* and *Quercus suber*, which averaged 15 to 20 cm². Though this convergence occurs, surface reduction as an adaptation to drier habitat and its significance as a hydroecological factor – discussed in earlier studies (Orshan, 1954, 1964, 1986) – seems to be a general trend manifested by the different groups of species.

The cuticle was generally thin and of the "glabrous" type in species from tropical, subtropical and warm-temperate environments (like *Lindera chunii, Ardisia sieboldii* and *Xylosma monospora*, respectively), but species from winter rain zones (like *Quercus ilex, Arbutus unedo, Peumus boldus*) could also exhibit this feature; the opposite situation, with a markedly papillose cuticle of the glaucous type, appears to be related to the ability to reduce light absorption, which in turn limits leaf temperature (Cutler et al. 1982; Kozlowski, 1976); this latter feature could be found in species from very dry habitats (like *Eucalyptus marginata* and *Arctostaphylos glauca*) and from laurophyll forests too (like *Protea welvitschii*), indicating that the correlation between cuticle type and habitat cannot be considered as fully supported. A multilayered or heavily thickened epidermis that has some role in support (Pjjkko, 1966) is certainly a more common feature among mediterranean species than in the entire group of species from other habitats: *Ceanothus oliganthus* and *Banksia quercifolia* exhibit the largest epidermic layer (ranging from 40 µm to 77 µm), yet *Rhaphydophora angustifolia*, which is representative of the *Araceae* family in tropical forests, averages 75 µm.

An increase in mesophyll thickness and leaf resistance as a result of a changing ratio between leaf surface and increased volume (Orchan, 1986) has also been observed in the mediterranean specimens sampled; mesophyll thickness reaches the extreme value of 1200 µm in *Petrophile ericifolia* and *Calothamnus quadrifidus* (with ericoid leaves), whereas most species (like *Rhaphydophora angustifolia, Ternstroemia yaponica* and *Viburnum rugosa*, from tropical and temperate regions of eastern Asia) average 400 µm. Although undifferentiated mesophyll, a quite primitive and inefficient feature in functional terms (Parkhurst, 1986), is more frequent in tropical than in mediterranean species (up to 20% of tropical species, including *Vernonia* sp., *Smilax china* and *Shefflera octophylla*), it can be noted that the occurrence of two parenchyma within the mesophyll (like in *Castanopsis chinensis, Lindera chunii* and *Melastoma candidum*, and in *Laurus azorica, Rapanea melanophloeos* and *Hetemorpha trifoliata*) is also a common trait in laurophyll forests.

Palisade thickness, possibly related to increased resistance to the diffusion of water vapour (Nobel, 1977; Nobel et al., 1985; Margaris and Vokou, 1982), is highest (ranging from 200 µm to 400 µm) in representatives of the *Proteaceae* family like *Isopogon* attenuatus and *Leucadendron hypophyllocarpodendron*, from mediterranean and warm-temperate regions, respectively. In *Proteaceae* leaves, the palisade is generally composed of two layers that hold the spongy parenchyma as a band between them; consequently, substomatal chambers are confined against the compact cells of the palisade and appear very reduced, notably lessening water loss. Yet the presence of sunken stomata, like those of all the mediterranean *Proteaceae* studied, favours increased resistance to water vapour rather than to CO_2 diffusion (Grieve and Hellmuth, 1970). This results in a greater reduction of transpiration than of photosynthesis. However, palisade thickness (never exceeding 200 µm, and even lower in *Quercus agrifolia, Quercus ilex* and *Viburnum rugosa*, etc.) in most mediterranean species from northern regions is comparable to (and even converging with) the values found in tropical and subtropical species.

Mechanical tissue and transpiring surface appear as the two significant features that account for a clear divergence between mediterranean species and tropical and subtropical species. Extremely well-developed and uniquely-shaped sclerenchyma in *Proteaceae* and *Myrtaceae* represent a unique example of support structures that confer a noticeable rigidity to leaf mesophyll; in comparison, mechanical structures in tropical, subtropical and northern mediterranean species are of lesser significance. It is noteworthy that even if there is a certain degree of divergence between species from wet and dry mediterranean climates, support structures like bundle sheath extensions (Esau, 1965; Mauseth, 1987) are found in both *Quercus ilex* and *Castanopsis cuspidata*, in *Quercus agrifolia* and *Cryptocarya chinensis*, and in *Laurus nobilis* and *Laurus azorica*, indicating that this feature is not highly correlated to drought conditions.

Laurophyll and sclerophyll species should also diverge because of larger transpiring surfaces in mediterranean elements (Walter, 1983); this could be related to larger stomata and a higher density per unit of leaf area. This divergence is confirmed when the tropical specimens are compared to the *Proteaceae* group, which is characterized by stomata on both sides of the lamina; these attain an enormous size in *Leucadendron nervosum* and *Protea cynaroides*, averaging 1500 µm², and above all, in *Protea amplexicaulis*, which reaches 2000 µm² (a transpiring surface of 10% to 20% of leaf area). On the other hand, a much smaller transpiring surface characterizes *Olea europaea ssp. africana* and *Olea europaea ssp. cerasiformis* (averaging about 4% of leaf area), with protected stomata in the lower side of the leaf. These general features appear to be confirmed by numerical analysis of the anatomical data (Figs. 1, 3, 4, 5).

It can therefore be assumed that stomata size and position, combined with mechanical structures, are the main causes of divergence observed among the species studied (Figs. 1, 3). In any case, this is not simply a divergence between laurophylls and sclerophylls. Rather, the two main groups identified correspond to hypostomatic species – both tropical and mediterranean – from the northern hemisphere and to mediterranean amphistomatic species from the southern hemisphere.

Hypostomatic species (always confining stomata to the lower surface of the lamina) from tropical monsoon-environments (Fig. 4) could be regarded as an ancestral group from which species radiate to warm-temperate, to subtropical and to temperate mountain climates. The hypostomatic leaf therefore appears to be a distinctive characteristic of tropical-type species (Buckley et al., 1980; Sobrado and Medina, 1980; Peace, 1981; Tanner, 1982; Bongers and Pompa, 1988). In spite of this evidence, warm-temperate and tropical species (Fig. 5) are clustered with species from mediterranean climates that are also hypostomatic. Therefore, morphological features that characterize hydrophilous plants can also occur in drier habitats; this morphological similarity, according to Stocker (1970), is due to the fact that morphology and anatomy are primarily based on the genotype of the species rather than on the plant's adaptation to prevailing conditions. In this light, the functional significance of anatomical adaptations geared to hydric stress should also be revised.

Recent studies (Salleo and Lo Gullo, 1985, 1989; De Lillis, 1989, 1990) centred on the water relation and gas exchange responses to summer drought by sclerophyllous and deciduous species indicate that evergreen species are not better adapted to water stress than deciduous species, in terms of both maintenance of adequate water supply by means of rigid parenchyma cell walls, and in terms of photosynthetic rates related to the cost of leaf maintenance. This in turn suggests that leaf xeromorphism does not improve the efficiency of water use of mediterranean scleropyll plants with respect to deciduous species. It can be argued that the relation between sclerophylly and water deficit has been overly stressed in ecophysiological studies on mediterranean plants.

Schulze (1982) defined sclerophylly as a leaf feature that should be regarded as an "epiphenomenon" of the water-stress adaptation; i.e., only an exterior effect rather than the direct result of water stress. Sclerophylly may be useful in conferring rigidity to the leaf blade, which would have as a result a heightened ability to regulate leaf angle and orientation under different intensities of light. Sclerophylly, therefore, if considered as due to the increase in the amount of lignified tissue promoted in the dry season, holds no importance as far as water relations are concerned. In this case, a significant role can be attributed (Salleo and Lo Gullo, 1985) to these tissues only in cases when they store water, a useful feature in short-term water deficit associated with nictemeral rhythms.

In our study, a large proportion of sclerenchyma is associated with the amphistomatic species (representatives of *Proteaceae* and *Myrtaceae*) that are endemic in the mediterranean flora of southwestern Australia and southern Africa. Their support structures, which do not show any similarity to other sclerophyllous mediterranean species, have an evolutionary significance, and their presence could be interpreted in a wider ecological sense. In fact, they could be considered (Pignatti, 1989) as the outcome of the relationships involved in the process of coevolution between plants and pollinator fauna, mostly represented by small mammals and marsupials that need to be supported by rigid leaves or coriaceous flowers while collecting pollen.

A correlation between the presence of stomata on both leaf surfaces and factors such as habitat, growth forms and physiology has yet to emerge in the literature (Gindel, 1968; Walter, 1983). Amphystomaty is not directly linked to plant life form – whether annual or perennial, tree or herb – because lower stomata are present in representatives of each type (Mott et al., 1982); nor is the presence of stomata on both leaf surfaces directly correlated to water availability (Parkhurst, 1978). Descriptions of succulent CAM plants show that stomata occur on all surfaces, which is expected because leaves are extremely thick and the CO_2 assimilating tissues are evenly distributed just under the epidermis. Amphistomaty is also the rule for leaves that demonstrate Kranz anatomy, i.e., plants that have C_4 photosynthesis. Thus, species with the highest known photosynthetic rates all have amphistomatic leaves, with the result that they are well adapted to high-light environments (Ehleringer, 1978; Longstreth et al., 1980), whereas hypostomaty is interpreted as an adaptation to conditions of shade (Salisbury, 1927). This is exactly the opposite than would be reasonably expected in terms of protecting stomata from microclimatic stress and controlling transpiration rates.

Many sources of information on ancient vascular flora suggest that amphistomaty should be regarded as a derived condition, since the vascular cryptogams are almost exclusively hypostomatic (Ogura, 1972). Those dicotyledonous taxa described as possessing primitive features, such as vessel-less dicotyledons and other members of the *Annonales* and *Hamamelidales* (among other orders), provide very few instances of amphistomaty (Metcalfe and Chalk, 1950). It has been suggested (Mott et al., 1982) that amphystomaty is correlated with high conductance to CO_2 diffusion, and as such amphistomaty should be advantageous to plants that benefit from high levels of leaf conductance. Both amphystomaty and environmental conditions that favour high maximum-leaf conductance are characteristic of open-area plants: full-sun herbs, low shrubs, early successional deciduous trees.

Not all full-sunlight species will be amphistomatic. Less rapidly growing plants, implying lower photosynthetic rates and lower conductances, tend to be hypostomatic; this condition is typical of all the species of the *Quercus* genus. On the other hand, Parkhurst (1977, 1986) assesses the adaptive value of the hypostomatic leaf; through a detailed mathematical model, he demostrates that the pattern of CO_2 diffusion is enhanced by the presence of an upper layer of densely packed cells and a lower layer of spongy mesophyll with extensive intercellular spaces.

Aside from the consideration of optimum leaf structure, the absence of species with amphistomatic leaves in the woody mediterranean vegetation of the Mediterranean Basin and of southern California (except for *Arctostaphylos* ssp.) is noteworthy.

It could now be asked if a relation exists between leaf anatomy and the resilience of this vegetation type. Resilience in mediterranean species and communities is a feature that enables plants to respond successfully to events that affect plant growth and survival, such as the summer drought that is typical of these regions (Dell et al., 1986. A relation exists between drought adaptation and the reproductive strategies adopted by mediterranean species under recurrent stress situations of this type (i.e., summer aridity) or faced with sporadic stress like fire i.e., woody species that reseed after fire are thought to be much more drought-tolerant than resprouting species (Keeley, 1986; Mooney, 1986). Obligate seeders are frequent among the *Proteaceae* and *Ericaceae* from southern Africa and southwestern Australia, and they are very resilient to fire. However, in California flora this strategy is limited to a few *Rhamnaceae* and *Ericaceae*, and it is even rarer in the Mediterranean Basin (rare *Cistaceae* and *Coniferae*); even fewer species in Chile adopt this strategy.

This evidence suggests that the amphistomatic leaf is the most resilient to environmental drought; among mediterranean species, the amphistomatic *Proteaceae* and *Ericaceae* from southern mediterranean ecosystems and the *Arctostaphylos* genus from California are therefore the most resilient. In this light, the woody vegetation of the Mediterranean Basin – in which the amphistomatic leaf is absent and reseeders are limited to very few like *Cistus* and Pinus – can be regarded as much less resilient to drought than the vegetation of the other mediterranean regions named above. Excluding that amphistomatic reseeders became extinct as a result of the depletion of seed banks in the soil after too-frequent anthropogenic fires no more than 10,000 years ago (Keeley, 1986; Keely and Keeley, 1988; Naveh, 1975), the marked diversity in morphological traits and functional patterns among the different mediterranean flora examined should be investigated in terms of phylogenetic constraints.

The mediterranean vegetation of the northern hemisphere originated from tropical and temperate ancestors in the late Cretaceous (Raven, 1973; Axelrod, 1975). The flora was extremely uniform all over the continent of Laurasia, which did not break up till the Paleozoic, so that it was included in the holoartic realm; it is assumed that the eurasiatic flora developed originally from a cool flora that was rich in *Ginkoaceae*, which were widely diffused during the Jurassic (Vakhrameev, 1964; Dietz and Holden, 1970; Nimis, 1990). During the Oligocene, under a warm oceanic climate, the laurophyll forest spread along the continental borders of the Tethys (Meusel 1970); today this flora is possibly preserved in the Canary Islands and in Baja California. After successive climatic crises of drought, mediterranean flora deriving from this laurophyll flora became established in the late Pliocene and early Pleistocene (Axelrod, 1975; Pignatti, 1979).

The history of Gondwana was very different (Schopf 1970a, 1970b): covered by a cool flora (characterized by *Glossopteris*), it was strongly marked by the drift of continental land masses, starting from the early Mesozoic up to the Tertiary (Du Toit 1937; Krommelbein 1966). During the Cretaceous, Africa broke away whereas the Antarctic, with a warmer climate than the northern hemisphere (Fig. 6), was populated by *Proteaceae* and *Nothofagus*.

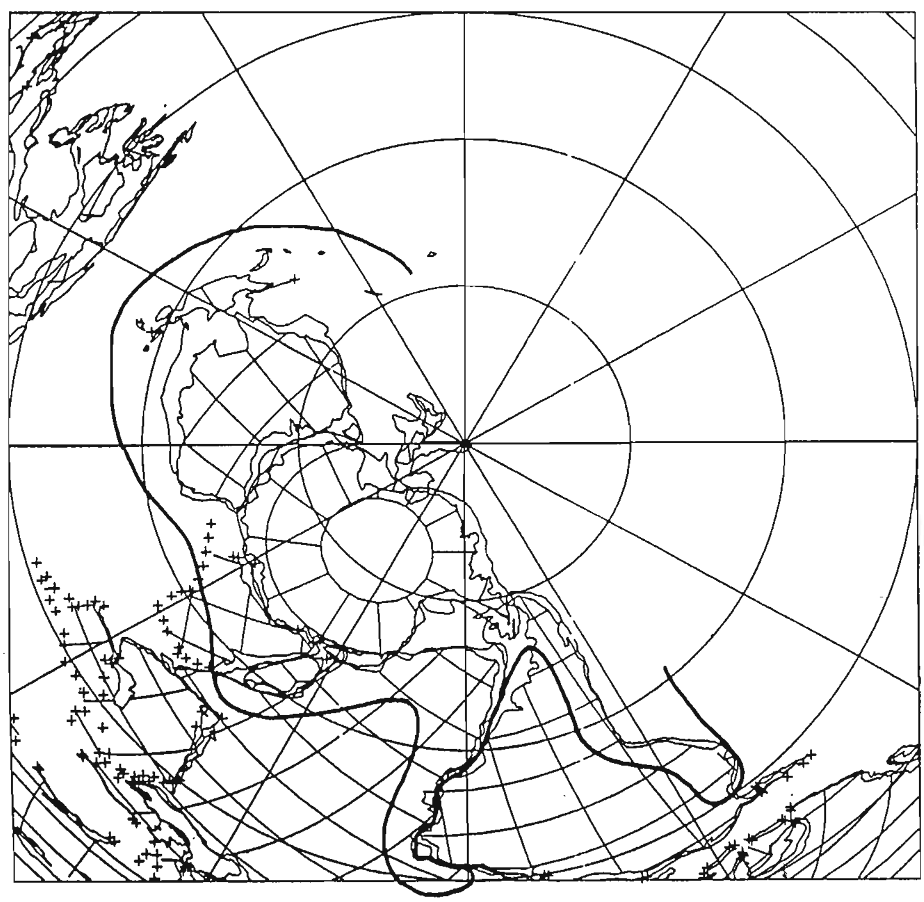


Fig. 6 - Distribution of Proteaceae during Giurassic (from Smith, Hurley and Brinden 1981).

Towards the end of the Tertiary the various land masses that had once been joined together as Gondwana had reached their present positions (Craddock 1982); Australia underwent some significant changes as a result of latitudinal drift and decreases in global temperature (Kremp, 1964). The cooling climate lowered precipitation, and for the first time grasses appeared in the gaps of the tropical rain forest where once only *Nothofagus* and *Myrtaceae* elements had been found.

In the late Miocene, the temperature was progressively decreasing and the ice sheet first appeared on the Antarctic continent. At the boundary of the Miocene and Pliocene the first sclerophyllous formations, dominated by *Proteaceae* and *Myrtaceae*, appeared in Australia. The southern mediterranean flora therefore originated in isolation from ancestors that were adapted to temperate or cool conditions (Singh 1982).

Since anatomical features are genetically determined, they may reflect the long-term history of species evolution. Possibly two different phyla which evolved independently into mediterranean flora should be inferred: i.e., northern mediterranean species originated from hypostomatic tropical elements, while southern mediterranean species originated from amphistomatic elements.

Another important consideration is that the boundary between laurophyll, tropical and sclerophyll species is not always evident. Considering all these arguments together, the term sclerophyll appears somewhat inadequate to describe all mediterranean species as if these were largely uniform. It can be proposed that the two different concepts, sclerophylly and laurophylly, be re-defined.

Finally, these arguments suggest some reservations about regarding the evergreen sclerophyll forest as "the" climax community of mediterranean zones. Functional adaptations of broad-leaved sclerophyll species diffused throughout the northern hemisphere seem to be neither divergent nor better suited than those of deciduous species (De Lillis, 1989, 1990; Salleo and Lo Gullo, 1989), and the ecomorphological similarity between sclerophyll and tropical species is remarkable. Consequently, it can be asked why sclerophyll vegetation has become dominant under mediterranean climatic regimes; similarly, to what extent have man's activities contributed to sclerophyll dominance at the expense of the deciduous Pleistocene forest. The deciduous Pleistocene forest should theoretically represent the 'equilibrium' vegetation type, given the environmental condition of seasonality in the mediterranean regions of the northern hemisphere. Paleo-ecological and bio-geographical evidence provides additional support and suggests a probable higher incidence (Barbero et al. 1974; Barbero and Quezel, 1989) of deciduous elements in the oak forest in the mediterranean belt that is today dominated by sclerophyll species.

THE CLIMAX PROBLEM IN THE MEDITERRANEAN AREA

In the current literature mediterranean vegetation is assigned to two vegetation belts, characterized by the forests of *Quercion ilicis* (under more temperate conditions) and the chaparral of the *Oleo-Ceratonion* or *Pistacio-Rhamnetalia* in more arid areas (Rivas-Martinez, 1974). In Italy (e.g., in Tuscany or Latium) the coastal vegetation can be mostly assigned to *Quercion ilicis* (Marinucci et al., 1980). In the southern coasts of Latium on protected cliffs, small colonies of *Oleo-Ceratonion* can be found; this latter vegetation becomes widespread in Sicily and in southern Sardinia. Both *Quercion ilicis* and *Oleo-Ceratonion* are composed of evergreen sclerophyllous species.

The evergreen forest dominated by *Quercus ilex* in the tree layer was first described by Braun-Blanquet (1936) as *Quercetum ilicis galloprovinciale*. In fact, this vegetation is relatively polymorphic, and in recent years several new associations have been described. In Latium the prevailing climax community is the *Asplenio-Quercetum ilicis*. Along the Adriatic coast (Italy and Yugoslavia) the evergreen oak vegetation is mainly composed by *Orno-Quercetum ilicis*, which is also considered a climax community (Horvatic, 1934).

In the vicinity of Rome, *Asplenio-Quercetum ilicis* is widespread and forms a thin belt along the coast, where it apparently thrives. Mature stands on older dune systems and natural repopulation over remnants of ancient settlements can be regarded as proof that this vegetation represents a climax community. Only 5 to 7 km into the mainland on gently undulate plains 30-60 m above sea level, the mature vegetation is on the contrary dominated by a mixed community of deciduous oaks – *Quercus cerris*, *Q. frainetto*, and others – (Lucchese and Pignatti, 1990). Both vegetation types (*Asplenio-Quercetum ilicis* and *Lathyro-Quercetum cerris*) appear to be climax communities in their respective habitats. In the case of the inland vegetation, increased distance from the shore and altitude are the determining differences in the bioclimate, but it remains unclear if such differences are really so strong as to cause an evergreen climax vegetation to be substituted by a deciduous one. For example, the same differences may hold in southern France (from the *Quercetum ilicis* to *Querco-Carpinetum*) at a distance of several hundred km north (Braun-Blanquet, 1936). It appears unlikely that the narrow coastal landscape near Rome may be deterministic of such a wide bioclimatical gradient, and the hypothesis that soil factors and human impact play a prominent role in this case seems well founded.

In the present investigation it was demonstrated that leaf anatomy is not simply the result of environmental selection on plants living under mediterranean bioclimates. In addition, phytosociological features of the sclerophyllous *Quercion ilicis* vegetation, as discussed above, seem to cast at least some doubts as to whether this vegetation can be considered a climax community in each case. In our opinion, the problem of identifying the climax vegetation in the Mediterranean Basin should be re-examined on the basis of the ecophysiology of the most significant species.

CONCLUSIONS

Notwithstanding that this study is merely a first attempt that, we hope, might encourage further investigation, two models of leaf anatomy centered on the eco-morphological adaptations of evergreen plants can be proposed:

oleoid leaf – hypostomatic leaves, mainly found on species from the Mediterranean Basin, California, Chile, and from tropical flora; in the mediterranean ecosystems of Australia they are found only among the major genera of *Myrtaceae*;

proteoid leaf – amphistomatic leaves, widely represented in the species from the mediterranean type ecosystems of Australia and southern Africa, mainly as *Proteaceae, Dilleniaceae* and some *Myrtaceae*.

The distribution of stomata is the main eco-morphological adaptation of leaves and determines the distinction between the oleoid and proteoid leaf types, but other characteristics can be taken into consideration.

In the proteoid leaf, e.g. in *Proteaceae*, lignified elements occur in the mesophyll; they cross the leaf and surround the vessels. They can also appear in the palisade layer or under the epidermis. The cuticle is thick, markedly papillose with abundant wax deposits; in addition, the epidermis is heavily thickened and in many cases even multilayered. Stomata appear completely sunken in the epidermis or protected by a thick layer of hair. Finally, the transpiring surface accounts for a large percentage of leaf area. Consequently, the amphistomatic *Proteaceae* leaf can be considered as representing the highest degree of xeromorphism.

The oleoid leaf, by contrast, lacks markedly developed support structures; the cuticle is mostly smooth, the epidermis quite thin and stomata surface relatively small. These conditions are typical of tropical plants but can be also recognized in the most widely diffused plants of mediterranean type ecosystems from the northern hemisphere. In this sense, the eco-morphological adaptations of the leaf in mediterranean species appear to converge with adaptations in tropical flora.

The functional significance of such adaptations can be briefly discussed. On the basis of present knowledge of the factors that affect water evaporation through stomata, the oleoid leaf would appear to be better adapted to water stress because the stomata, which are confined to the lower side of the lamina, are protected from the strongest microclimatic variations. In the proteoid leaf, on the contrary, the stomata of the upper leaf surface are directly exposed during clear days to the repeated and sudden lowerings of atmospheric humidity and to stronger transpiration demand. As a consequence, we would assume that hypostomatic leaves would confer an advantage on plants living under xeric conditions.

In fact, evergreen species of the mediterranean-type ecosystems of the Mediterranean Basin, California and Chile have hypostomatic leaves, and this would appear to accord with the assumed eco-morphological significance of this adaptation. Yet it can be pointed out that in the northern hemisphere and in the tropics (and when found in humid environments) most species generally have oleoid (hypostomatic) leaves.

The proteoid leaf appears to be a feature suited for relatively moist conditions, but this hypothesis is not confirmed by the eco-morphological evidence: in fact, the proteoid leaf is typical of the *Proteaceae*, which are highly adapted to arid climates, and it appears in Australian as well as in southern African species. In southwest Australian flora, where *Proteaceae* undoubtedly show the greatest amount of diversity (ca. 800 species), there are no examples of species adapted to humid environments. Species of the northern hemisphere with amphistomatic leaves are relatively few, but even in this case they occur mainly in arid environments (*Arctosthaphylos* sp. and *Pistacia atlantica*, cfr. Gindel, 1968). This evidence does not accord with the logically-presumed functional significance of the occurrence of stomata on the upper or lower side of leaves, and the evidence further weakens the functional interpretation of hypostomaty as an anatomical adaptation to xeric or desert environments. In fact, it is possible that stomatal distribution are related to the efficiency of other adaptations in successfully dealing with water stress. The more species are efficient in functional terms, the less they need protection from environmental stress. As a consequence, stomata can be exposed to severe environmental conditions when plants have the capability of maintaining an adequate supply of water.

In our opinion, anatomical structure must be also rethought in terms of heredity and phylogenetic relationships. Tropical climates have existed since the time of the origin of Angiosperms, whereas mediterranean-type climates appeared relatively recently, in the late Tertiary (Axelrod, 1975). The presence of oleoid leaves is therefore an ancient feature of evergreen broad-leaved plants that developed under tropical conditions in humid environments and in the absence of water stress: consequently, hypostomaty cannot be considered as an adaptation to summer drought specific to plants living in mediterranean climates.

In Meusel's opinion, evergreen broad-leaved plants are either sclerophyllous (in dry habitats) or laurophyllous (in humid habitats). This distinction is chiefly made on the basis of exterior features rather than on quantitative data. The evidence collected in the present investigation seems to exclude a real difference among hypostomatic leaves of any type, and it appears impossible to distinguish a mediterranean group only on the basis of xeromorphic characteristics. In this sense we would exclude the oleoid leaf from the sclerophyll category and limit the true definition of the sclerophyllous leaf to the proteoid type.

The problem can be also considered from a phylogenetical point of view. There seems to be a basic difference between flora from the southern hemisphere and from other parts of the world:

oleoid groups of tropical origin – these are composed of broad-leaved trees with hypostomatic leaves but in different measure provided with sclerophyllous adaptations which prevail in the flora of mediterranean-type ecosystems.

proteoid groups of gondwanian origin – these are composed of broad-leaved woody plants that generally have amphistomatic and highly sclerophyllous leaves.

The probability of a common origin for both types appears very low because of large differences at the level of eco-morphological adaptations, geographical distribution and membership in different taxonomic groups. It therefore seems that the flora of gondwanian origin may have a completely different origin from other evergreen Angiosperms. This can be supposed, at least for

Proteaceae and other southern species, but a different condition can be hypothesized for *Myrtaceae*; these have Australia as a principal centre of diversity but are also widely diffused in the tropics. Representatives of this family retain the main features of tropical flora, but amphistomatism appears as a secondary condition in Australian representatives with ericoid leaves, e.g., in *Calothamnus, Hypocalymma* and *Melaleuca*. The gondwanian flora orginated under cold conditions, so amphistomatism, a typical feature of gondwanian flora, cannot be considered as an adaptation to xeric conditions.

We can therefore conclude that evergreen broad-leaved woody plants have a different origin and belong to two distinct phyla, the gondwanian and the tropical, and that the xeromorphic features that appear in representatives of five mediterranean type ecosystems are mainly superficial; they seem to be the effect of convergence and do not seem to be based on a common phyletic origin for these plant groups.

SUMMARY

The present study is concerned with what can be considered the most important eco-physiological adaptation of mediterranean woody flora, sclerophylly. The purpose of the present work is to provide a general picture of leaf structure as it relates to biogeographic distribution of evergreen broad-leaved species. The main objectives are to clarify the characteristics of sclerophylly and laurophylly to test if sclerophylly can be assumed as the basis for the identification of the mediterranean climax community; to gain a better understanding of eco-morphological convergence among mediterranean ecosystems; and to assess phylogenetic constraints on tropical and mediterranean evergreen flora.

Sclerophylly characterises evergreen species in mediterranean environments and implies an increase in leaf consistency, i.e., a "leaf hard and coriacious, breaking when folded.

Indeed, sclerophylly is mainly considered as the most important physiognomic feature involved in the evolutionary convergence of the five, largely disjunct mediterranean ecosystems. This opinion goes back to the earliest ecological literature. Convergence, formulated in a more evolutionary context as a major theme of comparative research on plant form and function in central Chile and in California, has gained great momentum during the last few decades. As a result of these studies a number of paradigms that emphasize the significance of the convergent versus the non-convergent features of sclerophyllous mediterranean vegetation have been put forth.

Despite these efforts and the large body of eco-physiological literature that deals with sclerophyllous species, sclerophylly is still an empirical term, which practically implies that any plants with leaves hard to the touch should be included in the sclerophyllous category. In fact, hard-leaved plants are also found outside mediterranean climates: in wet tropical zones and even beyond the arctic circle.

The surprising uniformity of anatomical characterstics of evergreen laurophylls from the Canary Islands and of evergreen woody species from the mediterranean basin made it impossible to draw a clear boundary between the two leaf types, and induced a wider investigation into evergreen species from tropical to humid subtropical zones, and from warm temperate humid zones to the five mediterranean regions of the world.

Of the most representative species in the five mediterranean areas of the world and in the tropical, subtropical and warm temperate zones, 146 evergreen species were selected for inclusion in this study.

Various features are related to leaf scleromorphism, but in this investigation only the ones most affected by high temperatures, strong illumination and hydric deficit have been considered. The following characteristics have been examined in relation to their function under conditions of water stress:

the development and shape of the upper and lower cuticle; mechanical structures and the occurrence of collenchyma; decreasing size of epidermic cells; palisade development; position, size and density of stomata, etc.

Transverse sections from selected mature leaves were cut and treated with dyes and observed under an optical microscope. Dimensions were measured using a micrometrical eyepiece.

Micrometrical data made possible the construction of a matrix composed of 23 characteristics for 146 species. The matrix was processed using Wildi-Orloci software.

Two main clusters are identified. It can be assumed that stomata size and position, combined with mechanical structures, are the main causes of divergence observed among the species studied. This is not simply a divergence between laurophylls and sclerophylls. Rather, the two main groups identified correspond to hypostomatic species, both tropical and mediterranean, from the northern hemisphere, and to mediterranean amphistomatic species from the southern hemisphere.

Notwithstanding that this study is merely a first attempt to encourage further investigation, two models of leaf anatomy centered on the eco-morphological adaptations of evergreen plants can be proposed:

oleoid leaf – hypostomatic leaves, mainly found on species from the Mediterranean Basin, California, Chile, and from tropical flora; in the mediterranean ecosystems of Australia they are found only among the major genera of *Myrtaceae*;

proteoid leaf – amphistomatic leaves, widely represented in the species from the mediterranean type ecosystems of Australia and southern Africa, mainly as *Proteaceae, Dilleniaceae* and some *Myrtaceae*.

The distribution of stomata is the main eco-morphological adaptation of leaves and determines the distinction between the oleoid and proteoid leaf types, but other characteristics can be taken into consideration.

In the proteoid leaf, e.g. in *Proteaceae,* lignified elements occur in the mesophyll; they cross the leaf and surround the vessels. They can also appear in the palisade layer or under the epidermis. The cuticle is thick, markedly papillose with abundant wax deposits; in addition, the epidermis is heavily thickened and in many cases even multilayered. Stomata appear completely sunken in the epidermis or protected by a thick layer of hairs. Finally, the transpiring surface accounts for a large percentage of leaf area. Consequently, the amphistomatic leaf of *Proteaceae* can be considered as representing the highest degree of xeromorphism.

The oleoid leaf, by contrast, lacks markedly developed support structures; the cuticle is mostly smooth, the epidermis quite thin and stomata surface relatively small. These characteristics are typical of tropical plants but can be also recognized in the most widely diffused plants of mediterranean type ecosystems from the northern hemisphere. In this sense the eco-morphological adaptations of the leaf in mediterranean species appear to converge with adaptations in tropical flora.

In our opinion, anatomical structure must be also rethought in terms of heredity and phylogenetic relationships. Tropical climates have existed since the time of the origin of Angiosperms, whereas mediterranean-type climates appeared relatively recently, in the late Tertiary. The presence of oleoid leaves is therefore an ancient feature of evergreen broad-leaved plants that developed under tropical conditions in humid environments and in the absence of water stress; consequently, hypostomaty cannot be considered as an adaptation to summer drought specific to plants living in mediterranean climates.

In Meusel's opinion, evergreen broad-leaved plants are either sclerophyllous (in dry habitats) or laurophyllous (in humid habitats). This distinction is chiefly made on the basis of exterior features rather than

on quantitative data. The evidence collected in the present investigation seems to exclude a real difference among hypostomatic leaves of any type, and it appears impossible to distinguish a mediterranean group only on the basis of xeromorphic characteristics. In this sense we would exclude the oleoid leaf from the sclerophyll category and limit the true definition of the sclerophyllous leaf to the proteoid type, in which morphological structures are genetically fixed.

It was also demonstrated that sclerophylly is not the result of environmental selection on plants living under mediterranean bioclimate. In our opinion, the problem of identifying the climax vegetation in the Mediterranean Basin should be reexamined on the basis of the ecophysiology of the most significant species.

RÉSUMÉ

Cette recherche concerne ce que l'on peut considérés comme l'adaptation ecophysiologique la plus importante de la flore méditerranéenne, le sclérophyllie. Le but de ce travail est de présenter une image générale de la structure de la feuille dans le cadre de la distribution biogéographique des espèces latifoliées. Nous voulons clarifier les caractéristiques de la sclérophyllie et de la laurophyllie pour vérifier si la sclérophyllie peut être prise comme base pour l'identification de la communauté climax méditerranéenne; nous voulons comprendre la convergence écomorphologique dans les écosystèmes méditerranéens; enfin, nous voulons examiner les contraintes phylogénétiques sur les flores méditerranéennes et tropicales à feuilles persistantes.

La majorité des observations ont démontré que beaucoup de plantes dans les conditions arides possèdent des particularités structurales dans l'anatomie de la feuille pour lesquelles Monfort a proposé le mot "xéromorphisme". La sclérophyllie est un cas particulier de xéromorphisme qui caractérise les espèces à feuilles persistantes dans les milieux méditerranéens. La sclérophyllie implique une augmentation de la consistance de la feuille, c'est-à-dire, "une feuille dure et coriace qui se brise quand elle est pliée".

En effet, dès le début des études sur cette question, la sclérophyllie a généralement été considérée comme la caractéristique physionomique la plus importante dans la convergence évolutif des cinq écosystèmes méditerranéens disséminés dans le monde. La convergence, qui a été formulée dans un contexte évolutionniste comme le thème le plus important de la recherche comparée sur la fonction et la forme des plantes dans le centre du Chili et en Californie, a récemment acquis un importance fondamentale. Comme résultat de ces études, un certain nombre de paradigmes soulignant l'importance des caractéristiques convergentes de la végétation méditerranéenne sclérophylle ont étés proposés.

Malgré ces efforts et le corpus de textes écophysiologique assez impressionnant qui traitent des espèces sclérophylles, la sclérophyllie est encore aujourd'hui un terme empirique qui suggère que toutes les plantes avec des feuilles coriaces au toucher sont du type sclérophylle. Mais en effet les espèces à feuilles coriaces se trouvent aussi en dehors des milieux méditerranéens: dans les zones tropicales humides et même au delà du cercle arctique.

L'uniformité surprenante des caractéristiques anatomiques des laurophylles à feuilles persistante de les Îles Canaries et les espèces ligneuses à feuilles persistantes du bassin méditerranéen a rendu possible une nette distinction entre les deux types de feuilles (De Lillis and Valletta 1985), et a rendu nécessaire un recherche plus approfondie sur les espèces à feuilles persistantes des régions tropicales à régions humides subtropicales, et des régions chaudes tempérés humides à les cinq zones méditerranéennes de la planète. 146 des espèces à feuilles persistantes plus représentatives de ces régions ont été choisies pour cette recherche.

Des caractéristiques variées sont liées à la sclérophyllie, mais dans cette recherche on n'a pris en considération les plus affectées par des températures élevées, par une forte illumination, et par un déficit hydrique. Les caractéristiques suivantes ont été examinées:

le développement et la forme de la cuticule supérieure et inférieure; les structures mécaniques et la présence de collenchyme; la taille des cellules épidermiques; le développement de la palissade; la position, taille et densité des stomates, etc.

Des sections transversales de feuilles mures sélectionnées ont été faites, traitées avec des colorants et observées avec un microscope optique. Les dimensions ont été mesurés avec un oculaire micrométrique. Ces données ont rendu possible la construction d'une matrice composée de 23 caractéristiques pour les 146 espèces. La matrice a été analyser en utilisant un logiciel Wildi-Orloci.

Deux regroupements principaux ont été identifiés. Il semble que la taille et la position des stomates, en combinaison avec les structures mécaniques, sont les causes les plus importants de la divergence parmi les espèces qui ont été étudiées. Il ne s'agit pas simplement d'une divergence observée entre sclérophylles et laurophylles. Au contraire, les deux groups identifiés correspondent aux espèces hypostomatiques – tropicales et méditerranéennes – de l'hémisphère nord, et aux espèces amphistomatiques méditerranéennes de l'hémisphère sud.

Malgré le fait que cette étude simplement une première tentative pour encourager d'autres recherches, on peut proposer deux modèles d'anatomie de la feuille, basés sur les adaptations écomorphologique des plantes à feuilles persistantes:

la feuille oleoide — les feuille hypostomatiques, très répandues dans les espèces du Bassin Méditerranéen, de la Californie, du Chili, et dans la flore tropicale; dans les écosystèmes méditerranéens de l'Australie, elles se trouvent seulement dans les genres *Myrtaceae* les plus importants;

lafeuille proteoide – les feuilles amphistomatiques, très répandues dans les espèces des écosystèmes méditerranéens d'Australie et d'Afrique méridionale, généralement présentes comme *Proteaceae, Dilleniaceae* et quelques *Myrtaceae*.

La répartition des stomates est la principal adaptation écomorphologique des feuilles et détermine la division en feuilles protéides et feuilles oléides, mais il-y-a aussi d'autres caractéristique à considérer. Dans la feuille protéoide – dans les *Proteaceae*, par exemple – des éléments ligneux se trouvent dans le mésophylle; ils traversent la feuille et entourent les vaisseaux. Ils peuvent aussi se trouver dans la couche de la palissade ou sous l'épiderme. La cuticule est épaisse, papillose, et contient des dépìts abondants de cire; de plus, l'épiderme est très épais et

souvent avec des couches multiples. Les stomates sont enfoncés dans l'épiderme ou protégés par une couche épaisse de poils. Enfin, la superficie transpirante constitue un pourcentage élevé de la surface de la feuille. En conséquence, la feuille amphistomatique des *Proteaceae* peut être considérée comme ayant le degré le plus représentatif de xéromorphisme.

Par contre, les structures de support développées manquent dans la feuille oléoide; la cuticule est généralement lisse, l'épiderme est plutôt mince, et la surface couverte par les stomates relativement petite. Ces conditions sont typiques des plantes tropicales, mais on peut aussi les reconnêtre dans les espèces plus répandus des écosystèmes du type méditerranéen de l'hémisphère nord. En ce sens, les adaptations écomorphologiques de la feuille des espèces méditerranéennes semblent converger avec les adaptations de la flore tropicale.

Nous pensons que la structure anatomique doit être aussi repensée en termes de rapports héréditaires et phylogénétiques. Les climats tropicaux ont existé dès l'époque de l'origine des Angiospermes, alors que les climats du type méditerranéen sont apparus relativement récemment, à la fin de l'époque Tertiaire. La présence des feuilles oléoides est donc une caractéristique ancienne des plantes latifoliées à feuilles persistantes qui se sont développées dans les conditions tropicales des milieux humides et sans déficit hydrique; en conséquence, l'hypostomatisme ne peut pas être considéré comme étant une adaptation spécifique des plantes méditerranéennes au déficit hydrique de l'été.

Selon Meusel, les plantes latifoliés à feuilles persistantes sont ou sclérophylles (dans les habitats secs) ou bien laurophylles (dans les habitats humides). Cette distinction est faite sur la base des caractéristiques externes plutôt que de donnés quantitatives. Les résultats de nos recherches semblent exclure une différence réelle entre les feuilles hypostomatiques de toute sorte, et de plus il semble impossible de distinguer un regroupement méditerranéen uniquement sur la base des caractéristiques xéromorphiques. En ce sens, nous pourrions exclure la feuille oléoide de la catégorie des sclérophylles et limiter la vraie définition de la feuilla sclérophylle au type protéoide, dans lequel les structures morphologiques sont donnés génétiquement.

Nous avons aussi démontré que la sclérophyllie n'est pas le résultat de la sélection du milieux sur des plantes typiques des bioclimats méditerranéens. Selon nous, le problème de l'identification de la végétation climax dans le Bassin Méditerranéen doit être repensé en base de l'écophysiologie des espèces les plus importants.

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INDEX OF THE SPECIES STUDIED

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