Contribuţii Botanice, **II, 1997-1998**
Grădina Botanică "Alexandru Borza"
Cluj-Napoca

HISTO-ANATOMICAL ORGANIZATION OF THE LEAF BLADE OF DIFFERENT GYMNOSPERM SPECIES

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Abstract. The relationship between the structural basis of physiological processes and the abiotic factors of the environment is convincingly illustrated in the case of gymnosperm species that populate various terrestrial habitats. From among the leaves of the 17 gymnosperm species that have been studied microscopically in native and stained cross sections, 4 relevant structural varieties have been chosen to be presented in this communication. They represent the heliophylic equifacial leaf blade that may be both amphystomatic or hypostomatic , the xerophylic reversed dorsiventral leaf type, which is in the same time epistomatic, as well as the homogenous and the dorsiventral blade types, with or without an internal layer of horizontally disposed hialin parenchyma and a sclerenchymatic hypodermal region.

Introduction.

The internal structure of the leaf blade reflects a broad adaptive plasticity to the environmental conditions, especially in relation with the light and water status of the habitats in which the leaves develop and in which the entire plant lives. The leaf structure of the most common conifers is relatively well known, but the histological organization of the leaf blade of many other gymnosperm species remains largely unknown. This is the main reason why this study proposes to reveal the main histo-anatomical features of leaf blades that exist in gymnosperms, reflecting the structural basis of adaptation to local environmental conditions [1,2,3].

In relation with the direction and intensity of illumination, as well as with the available water content of the biotope, the structure of the leaf blades may be dorsiventral, equifacial, homogenous, reversed dorsiventral and monofacial. These types differ in the histological structure of the mesophyll, and in the arrangement of stomata on the two surfaces. The arrangement of the vascular tissues in the veins, and the location and number of secretory chanels do not depend on the environmental factors [5,7,9].

Material and Methods.

Fully developed leaves were collected from at least five different branches of plants belonging to 17 gymnosperm species: *Araucaria bidwilli* Hook., *Araucaria excelsa* R. Br., *Ceratozamia robusta* Miq., *Cryptomeria japonica* D.Don., *Cycas circinalis* L., *Cycas revoluta* Thunb., *Encephalartos ferox* Kirstenbosch, *Ginkgo biloba* L., *Gnetum gnemon* L., *Juniperus squamata* Buch.H., *Larix decidua* Mill., *Metasequoia glyptostroboides* Hu *et* Cheng, *Podocarpus falcatus* R. Br. *et* Merb., *Podocarpus neriifolia* D.Don., *Taxus baccata* L., *Thuja occidentalis* L. and *Torreya californica* Torr [4]. Some of the leaves were examined microscopically in native cross sections and epidermal peels immediately after collection, the other sections were fixed and stained simultaneously with Congo red and chrysoidine G, while some other cross sections were metachromatically stained with toluidine blue [6,10].

Results and Discussion.

Gymnosperm leaves are mostly perennial, remaining on the stem for many seasons, enduring shorter or longer dry and cold periods. In almost all of the17 species that have been examined, despite of their morphological and anatomical diversity, the leaves are sclerophylls, they have an extremely thick cuticle and the cells of their epidermis and hypodermis have thick and impermeable walls. Oftenly these leaves contain abundant secondary metabolites (mainly terpenes) that make them unpalatable. Conifer leaves have only a few forms, being represented by needles or forming a shieldlike covering of small flat scales on the stems. Other gymnosperms, especially the genera that inhabit the Southern Hemisphere, possess rather large leaves or broad scales held away from the stem [8].

The main anatomical properties of the leaf blades of the 17 gymnosperm species that have been examined are shown in table 1.

Four of the most interesting structural types of leaf blades have been selected in order to present the main histo-anatomical characteristics that ensure the survival of gymnosperm species in specific habitats.

The leaflets of *Cycas circinalis* are typical sclerophylls and the organization of the mesophyll exhibits heliophylic characteristics. Under the epidermal layer covered by a thick waxy cuticle there is a discontinuous sclerenchymatic hypodermis, consisting of two compact rows of lignified cells in front of the vascular bundle (Fig.1). The adaxial palisade parenchyma has higher cells than the abaxial one, and between these two layers the mesophyll contains a large number of horizontally elongated parenchyma cells only with a few chloroplasts. The

intercellular spaces are much smaller than in a typical spongy parenchyma. The fundamental tissue which surrounds the vascular bundle of the vein has no photosynthetic function, but it can store large amounts of water and organic nutrients.

Tab. 1. Structural characteristics of the mature leaf blade of 17 gymnosperm species

Species	Type of structure	Number of veins	Type of stomatal disposure	Number of secretory canals	Position of secretory canals
Araucaria bidwilli Hook	dorsiventral	many	hypostomatic	many	between the veins
Araucaria excelsa R.Br.	equifacial	one	amphystomatic	4	on the 4 edges
Ceratozamia robusta Miq.	dorsiventral	many	hypostomatic	0	-
Cryptomeria japonica D.Don.	homogenous	one	amphystomatic	1	under the vein
Cycas circinalis L.	equifacial	one	hypostomatic	0	-
Cycas revoluta Thunb.	equifacial	one	hypostomatic	0	-
Encephalartos ferox Kirstenbosch	dorsiventral	many	hypostomatic	many	between the veins and near the edges
Ginkgo biloba L.	dorsiventral	many	hypostomatic	many	between the veins
Gnetum gnemon L.	dorsiventral	many	hypostomatic	0	-
Juniperus squamata Buch.H.	reversed dorsiventral	one	epistomatic	1	under the vein
Larix decidua Mill.	homogenous	one	epistomatic	0	-
Metasequoia glyptostroboides Hu *et* Cheng	dorsiventral	one	hypostomatic	3	under the vein and near the lateral edges
Podocarpus falcatus R.Br. *et* Merb.	homogenous	one	amphystomatic	1	under the vein
Podocarpus neriifolia D.Don.	dorsiventral	one	hypostomatic	0	-
Taxus baccata L.	dorsiventral	one	hypostomatic	0	-
Thuja occidentalis L.	reversed dorsiventral	one	hypostomatic	1	under the vein
Torreya californica Torr.	dorsiventral	one	hypostomatic	1	under the vein

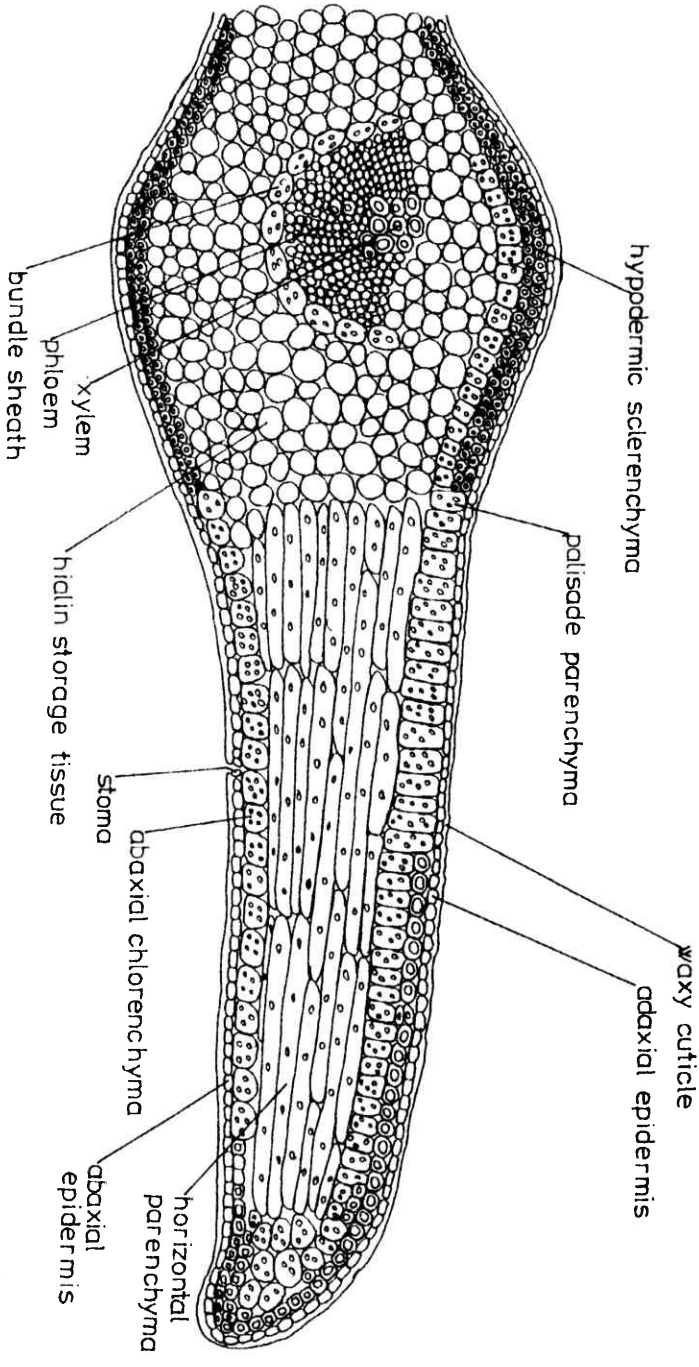

Fig.1. Structural scheme of a representative fragment of the cross section of a leaflet of *Cycas circinalis* L.

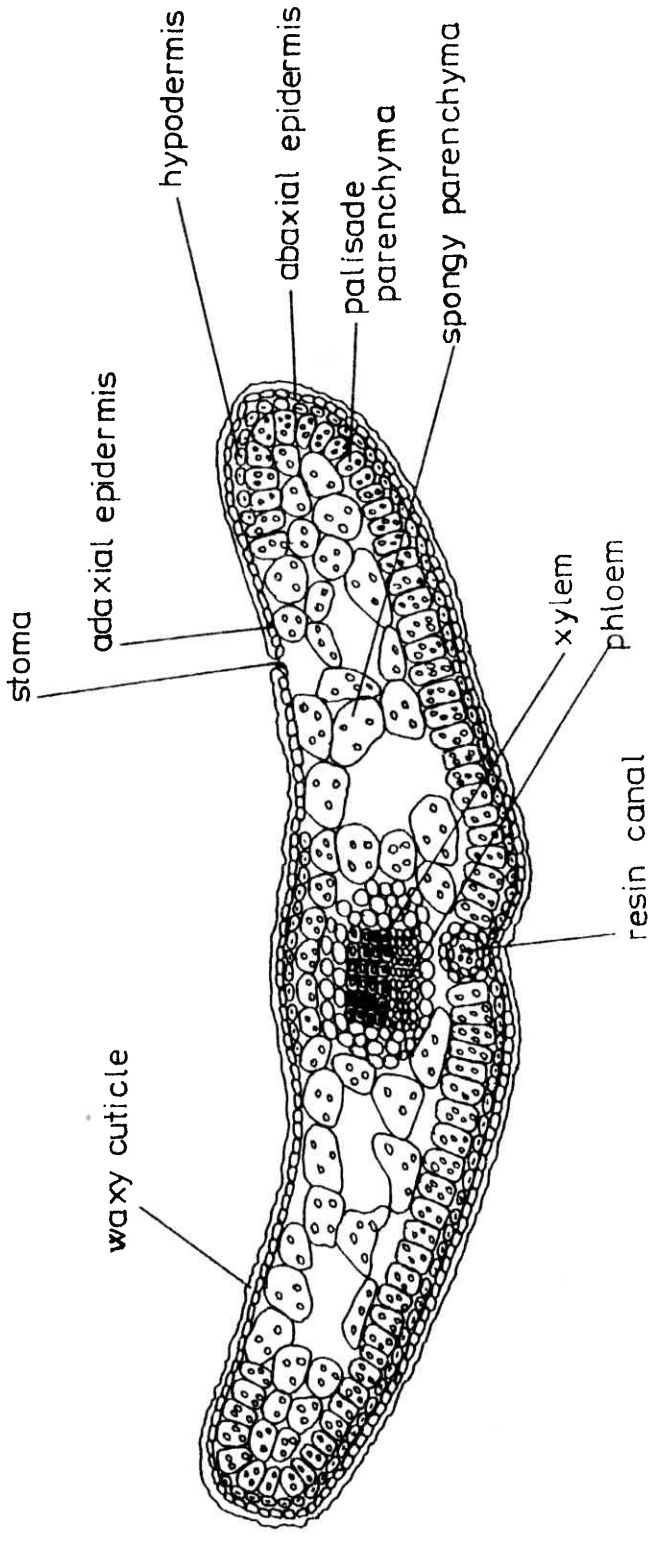

Fig. 2. Histo-anatomical scheme of the leaf blade of *Juniperus squamata* Buch.H.

The leaf of *Juniperus squamata* covers the stem with its adaxial surface, which means that it is illuminated mainly on its abaxial side. This peculiar disposure to light leads to a reversed dorsiventral structure, which is very rarely found in plants. The palisade parenchima develops only on the abaxial side of the mesophyll, and it is interrupted by the resin chanel situated under the vein. The spongy parenchima of the adaxial mesophyll region shows rather large intercellular spaces, which communicate with the pore of the few stomata disposed randomly in the adaxial epidermis (Fig.2) . The vein has approximately the same number of tracheids and sieve cells.

The leaf blade of *Araucaria excelsa* has a romboidal cross section and it may be considered equifacial, its mesophyll showing a radial simmetry (Fig.3). All around the mesophyll there is a continuous layer of sclerenchymatic hypodermis, which prevents water loss and provides a good thermic isolation. The periphery of the mesophyll is occupied by a regular row of palisade cells with many chloroplasts, and this tissue surrounds an internal parenchyma with large cells that are elongated towards the adaxial and the abaxial poles. The only criterium for establishing these poles is the arrangement of the two vascular tissues in the vein, the xylem being always closer to the adaxial face than the phloem. The elongated parenchyma cells seem to store large quantities of water.

The cross section of the leaf of *Podocarpus neriifolia* reveals a typical dorsiventral and hypostomatic structure, with an adaxial palisade parenchyma and a well represented spongy parenchyma, rich in horizontally elongated large cells. The epidermis has a very thick and waxy cuticle. The cells of the sclerenchymatic hypodermis exhibit extremely thick cell walls. The vein consists of a large number of xylem and phloem vessels, and under the phloem there is a layer of angular collenchyma, which is a very rare tissue in leaves of gymnosperms (Fig.4). The entire structural organization indicates that this leaf has a very intense metabolism, needs high photon flux densities and can resist to longer periods of moderate drought.

Conclusions.

Adaptation to different light and water conditions of the habitats leads to specific internal organizations of the leaf blade of gymnosperm species. The dorsiventral and reversed dorsiventral structure can be found in leaves that are strongly illuminated from only one side, while a uniformly intense illumination determins the equifacial organization of the heterogenous mesophyll. Sclerophylls possess a very thick cuticle, a well developed sclerenchymatic hypodermis, many vascular elements and very large parenchyma cells disposed in the internal region of the

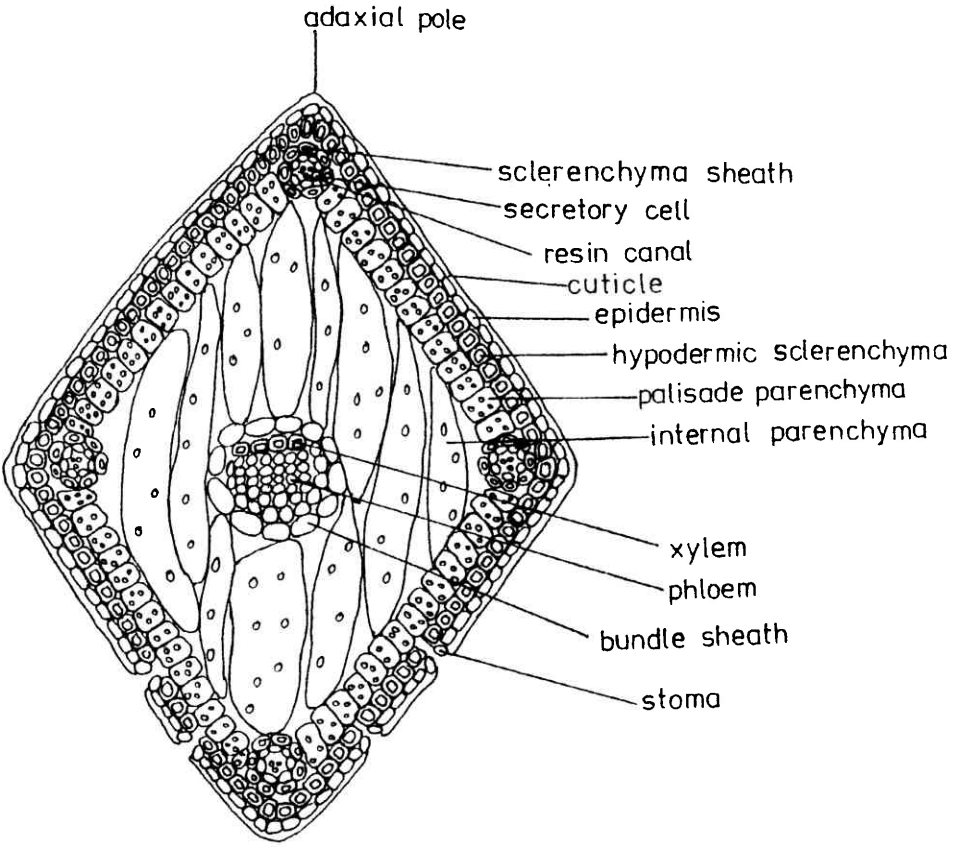

Fig. 3. Internal organization of the leaf of *Araucaria excelsa* R.Br.

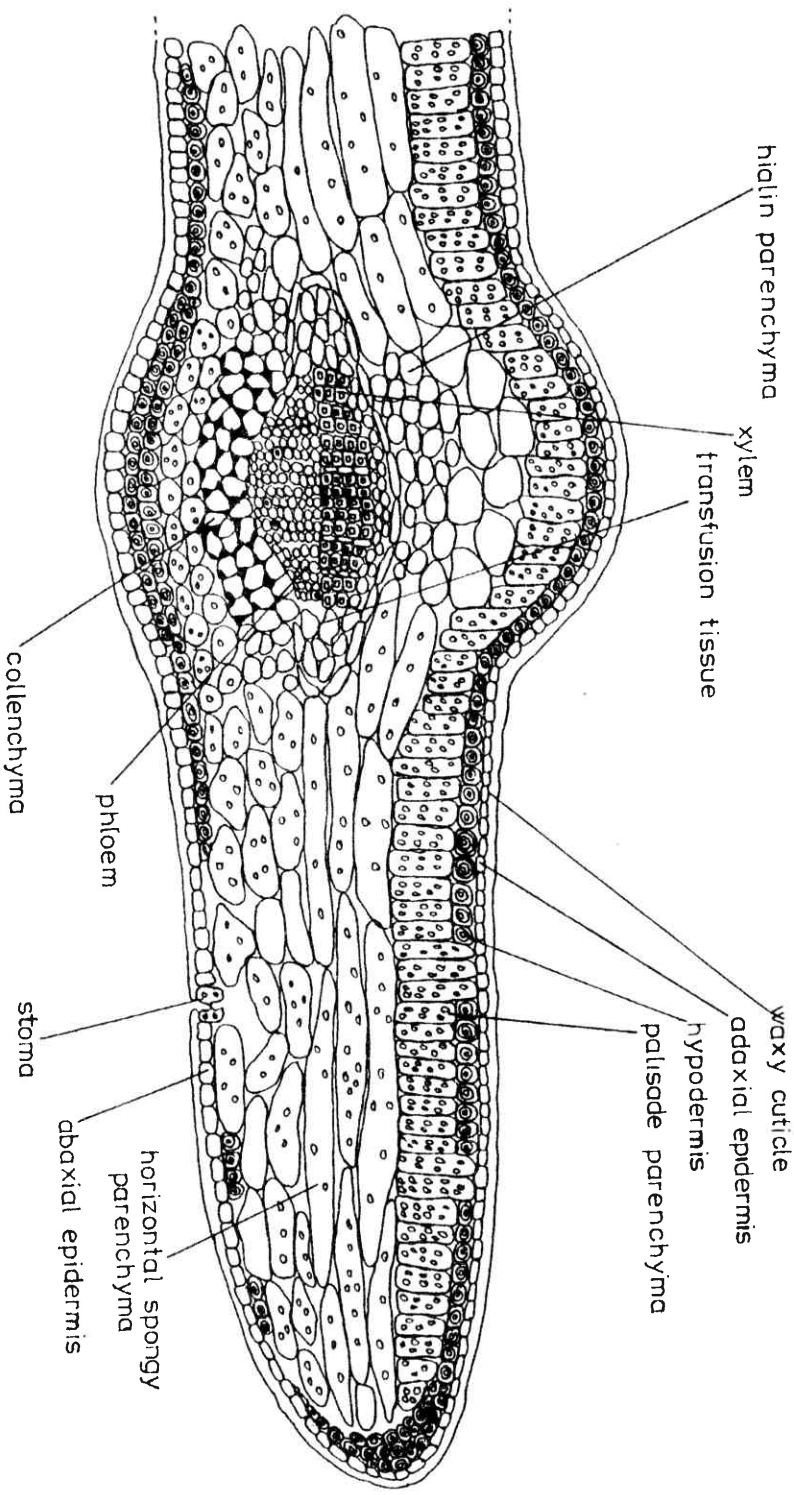

Fig.4. Fragment of the leaf blade of *Podocarpus nerrifolia* D.Don., represented in cross section.

mesophyll, ensuring the storage of high amounts of water. The leaves of *Cycas circinalis* have two different palisade layers and a hialin parenchyma. The reversed dorsiventral leaf of *Juniperus squamata* exhibits stomata only on the adaxial surface. In *Araucaria excelsa* the mesophyll has a rather radial simmetry, while the dorsiventral leaf blade of *Podocarpus neriifolia* exhibits large horizontal aquous parenchyma cells.

Acknowledgement

We would like to thank to the botanists of the "Alexandru Borza" Botanical Garden for providing many of the biological samples used in this work.

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ORGANIZAREA HISTO-ANATOMICĂ A LIMBULUI FOLIAR LA DIFERITE SPECII DE GIMNOSPERME

(Rezumat)

Varietatea structurală a frunzei celor 17 specii de gimnosperme examinate reflectă adaptarea evolutivă la diferite condiţii hidrice şi fotice. În frunzele caduce (de *Larix decidua* şi de *Ginkgo biloba*) predomină caracterele de heliofilie, iar în cele persistente se accentuează trăsăturile structurale ale xerofiliei fiziologice: cerificarea pronunţată a cuticulei, densitatea mică a stomatelor, sclerenchimatizarea hipodermei, prezenţa celulelor acvifere în interiorul mezofilului, lignificarea epidermei. Pe baza structurii histologice a limbului foliar, cele mai rezistente specii la seceta fiziologică sunt *Encephalartos ferox*, *Thuja occidentalis* şi *Araucaria excelsa*. În frunza numeroaselor specii (ex. *Podocarpus neriifolia*, *Araucaria bidwilli*, *Cycas circinalis*,

Ceratozamia robusta, *Ginkgo biloba*) ţesutul asimilator lacunos este înlocuit de un parenchim orizontal cu celule turgescente şi spaţii intracelulare înguste, adeseori lipsit de cloroplaste (parenchim hialin cu rol acvifer). Colenchimul lipseşte din majoritatea frunzelor examinate. În funcţie de direcţia şi intensitatea iluminării din cursul dezvoltării ontogenetice a frunzelor, acestea pot avea structură dorsiventrală (ex. *Araucaria bidwilli*), omogenă (ex. *Araucaria excelsa*), ecvifacială (ex. *Cycas revoluta*) sau invers-dorsiventrală (ex. *Thuja occidentalis*, *Juniperus squamata*). În privinţa dispunerii stomatelor, unele frunze ecvifaciale sunt hipostomatice (ca şi cele dorsiventrale), iar altele amfistomatice (ca şi cele cu mezofil omogen), pe când frunzele cu anatomie invers-dorsiventrală sunt epistomatice.