

A comparison of structural adaptation in three petrophyte ferns

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Nina M. Derzhavina¹, Nina I. Shorina² and Katsuhiko Kondo³ : **A comparison of structural adaptation in three petrophyte ferns**

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Abstract

Three petrophyte ferns, *Lepisorus thunbergianus* and *Lemmaphyllum microphyllum* (Polypodiaceae) and *Crepidomanes latealatum* (Hymenophyllaceae) were compared on the basis of biomorphological, histological and cytological data as well as characteristics of plastid apparatus. They showed xero-, meso-, hygro-, helio-, scio- and cryo-morphous characteristics in combination. *Lepisorus thunbergianus* was shade tolerant, hydrolabile xeromesophyte, that indicated an intermediate position between homoio- and poikilohydric ferns, an eutroph. *Lemmaphyllum microphyllum* was shade tolerant, hydrolabile, homoiohydric mesophyte with xeromorphous syndrome, an oligotroph. *Crepidomanes latealatum* was a sciophyte, hydrolabile poikilohydric hygrophyte, an oligotroph. They had two alternative strategies of their adaptiogenesis : *Lepisorus thunbergianus* and *Lem. microphyllum* performed an enhanced ability of water retention of the tissues and cells and *C. latealatum* performed an ability to endure a deep dehydration of tissues without loss of viability and displayed restoration of the normal hydrature under favorable conditions. They also indicated similar tendency of adaptiogenesis : They were dwarfish, evergreen, showed changes in mesophyll from an increase of cell density and number of cell layers up to reduction in structure ; and secondary poikilohydry and oligotrophy of epiliphytes in function.

Key words : biomorphological level, chloroplast, petrophyte fern, photosynthetic apparatus, phylogenetic idea.

Investigation of morphology and structure of plant photosynthetic apparatus is necessary to deposit our knowledges on whole range of fundamental and applied problems in the fields of ecology, geography and physiology of plant biology, in the course of global and regional ecological monitoring, as well as in selection and introduction of plants. This approach was successfully applied in studies of flowering plants of different phytogeographical zones (e.g., Mokronosov and Shmakova 1978 ; Pyankov and Kondrachuk 1998, 2003 ; Ivanova and Pyankov 2002 a, b). As a rule, ferns are beyond the field of vision of the botanists in such an aspect. The goal of the present study was a complex quantitative analysis of photosynthetic apparatus of three petrophyte ferns at various levels of their organization and an attempt to answer the question about existence of general trends and differences in adaptiogenesis in these plants. Moreover, a search of

the structural parameters that contribute largely to these differences was conducted.

Materials and methods

Three fern species : *Lepisorus thunbergianus* (Kaulf.) Ching, *Lemmaphyllum microphyllum* C. Presl (Polypodiaceae), and *Crepidomanes latealatum* (Bosch) Copel. (*Trichomanes latealatum* Bosch) (Hymenophyllaceae) were collected in Honshu, Japan by N. I. Shorina and K. Kondo (Table 1). The climate is humid, temperate. Elevations range from 200 to 600 m above the sea level. Annual precipitation is between 1,800 and 2,000 mm with a summer maximum. Potential evaporation is 900 mm. Difference between rainfall and potential evaporation is from 800 to 1,600 mm. Summer air temperature is 22–24°C, average winter air temperature is 8–12°C. Radiation balance is 251.4–293.3 J/m² per year.

The term photosynthetic apparatus is referred

Table 1. Fern species and their collection sites studied

Species	Habitat
<i>Lepisorus thunbergianus</i>	Japan, Kanto District : Ibaragi Prefecture, Suigo-Tsukuba Quasi-National Park, Mt. Tsukuba, on roadside-slope, open rocky site (chasmophyte)
<i>Lemmaphyllum microphyllum</i>	Japan, Chubu District : Aichi Prefecture, Ishimakiyama-Tame Prefectural Nature Park, in <i>Cryptomeria japonica</i> forest associated with <i>Aucuba japonica</i> understory and moss layer (epilithophyte)
<i>Crepidomanes latealatum</i>	Japan, Chugoku District : Hiroshima Prefecture, Hiroshima City, Asa-Kita Ku, Kabe, Watariba, along Ota River, on road-side cliff on Hiroshima Prefectural Road 177, in moss pillow on rock (epilithophyte)

to the whole complex of material structures that participate in photosynthesis in a plant and plant-cover (Goryshina 1989).

The base of the study is the method of analysis of the plant photosynthetic apparatus developed by Mokronossov (1978) and Mokronossov and Borzenkova (1978). The method includes the complex analysis of plant photosynthetic apparatus at various levels of its organization such as a) fronds, b) mesophyll cells and c) plastid apparatus.

Biomorphological characteristics of the species studied were determined according to the method of Serebryakov (1962, 1964), Serebryakova (1980), Shorina (1994) and Gureyeva (2001).

Sections (paradermal and transverse) were made according to the conventional method (Barykina et al. 2000). Conductive elements of xylem, mesophyll of fronds and sclerenchyma were analyzed on macerated material. Anatomical figures were drawn using a drawing arrangement (RA-4, Russia).

In the course of work, we used Siam Mesoplant, a laboratory complex of analysis of morphology and structure of plant photosynthetic apparatus (Department of Plant Physiology, Ural State University, Ekaterinburg). Software of the complex is realized on the basis of algorithms of improving and transformation of images, morphometry of images and stereological reconstruction of cells.

Discoid cuttings were hewn from the middle

parts of 10–20 fronds of middle-aged fern sporophytes, or leaflets were used (in the case of *C. latealatum*), at first scanned, then transferred to 70% ethanol. This material was used for obtaining almost all calculated and measured characteristics (except the frond area).

Quantitative indices :

1. SSFD (specific superficial frond density) – Dry weight of the frond area unit (kg/m^2). Ten discs dried under 105°C were weighed in triplicate. Calculations were conducted by the formula as follows: $\text{SSFD} = \text{Mdr} \times 100/10 \times \text{Sd}$, where Mdr is dry weight of 10 disks (mg) ; Sd is area of a disk (cm^2) ; 100 – coefficient.

2. Ncl – Cell number per frond area unit was determined following maceration of tissues in 20% KOH under $80\text{--}90^\circ\text{C}$ using a Goryaev's hemocytometric chamber ("Krasnogvardeyets", Russia) in 20 replicates in 225 squares and the optic microscope Biolam D-13 ("Lomo", Russia). Calculations were conducted by the formula: $\text{Ncl} = (\text{A} \times \text{V} \times 250 \times 1000) / 225 \times \text{S}$, where A is number of cells in 1 field of chamber ; V is volume of the macerated material ; S is total surface of the disks ; 225 is number of squares in a field of the chamber ; $1/250$ is volume of 1 square of the chamber.

3. Ncp – Number of chloroplasts was determined using a microscope after maceration of disks under heating in 5% solution of CrO_3 in 1 N HCl on water bath under $50\text{--}60^\circ\text{C}$ within 10–15 min. in 30 replicates. Under such an ap-

proach, the error of averages was not more than 5% for most indices.

Measured indices : The following indices were obtained by means of the image analysis system (Macro and Meso modules) :

1. Morphological characteristics of fronds (area, perimeter, lamina length, width, coefficient of shape) in 10–20 replicates.

2. Frond thickness (μm) on transverse sections obtained by a freezing microtome (in ten replicates) and partial tissue volume (a fraction of area of the certain part of the section that falls at this tissue).

3. Chloroplast parameters (μm). Surface area (Scp) and volume (Vcp) were calculated by bidimensional projection indices : $\text{Scp} = b \times A$, where A is mean projection area, coefficient $b = 4$, $\text{Vcp} = (A^2/P) / (b^3 \times \text{Kn})$, where P is mean projection perimeter, factor of proportionality $\text{Kn} = 0.11$.

4. Area (Scl) and volume (Vcl) of cells under microscopical examination of a drop of macerated material (m^2 , m^3). The formulas were the same as in the case of chloroplasts. Depending on the cell shape, the coefficients were : $b = 3.2$ – 4.0 , $\text{Kn} = 0.08$ – 0.11 .

Calculated indices :

1. CVCP – Cellular volume of a chloroplast, or volume of a cell falling at a chloroplast (m^3). $\text{CVCP} = \text{Vcl} / \text{Ncp}$.

2. Total volume of chloroplasts in volume of a cell (%). $\text{Vcp} / \text{Vcl} = (\text{Ncl} \times \text{Vcp} / \text{Vcl}) \times 100$.

3. CLMI – Cellular membrane index, or total area of the surface of external cellular membranes per frond area unit (m^2/m^2). $\text{CLMI} = \text{Ncl} \times \text{Scl}$.

4. CPMI – Chloroplast membrane index, or total area of the surface of external chloroplast membranes per frond area unit (m^2/m^2). $\text{CPMI} = \text{Ncl} \times \text{Scp}$.

5. Mesophyll volume per frond (%). $\text{Vm} = \text{Ncl} \times \text{Vcl} / \text{Vf}$, where Vf is volume of 1 cm^2 of frond surface. Arithmetic mean values were used in tables and diagrams.

Results

Sporophyte morphology

According to the life form (biomorph) classification, middle – aged sporophytes of the ferns studies are erosulate long-rhizomatous (*Lep. thunbergianus* – short-rhizomatous) dorsiventral evergreen herbaceous perennials, hemicryptophytes. Fronds are situated on dorsal side of their rhizomes in two orthostichies. Fronds of *Lep. thunbergianus* and *C. latealatum* are monomorphous (trophosporophylls) in *Lem. microphyllum* – dimorphous (trophosporo- and trophophylls).

The fronds vary significantly in the shape and size. In *Lep. thunbergianus*, they are entire, lanceolate to linear, coriaceous (Fig. 1 A, B). Under water deficit, they roll up, spore-bearing surface being inside. In *Lem. microphyllum*, trophophylls are entire, rounded to obovate, coriaceous; trophosporophylls are narrow-obovate (Fig. 2 A, B).

An abscission layer with strictly determined detachment line develops between the petiole and phyllopede in these two species.

Crepidomanes latealatum has tripinnatisected thin fronds that are able to dry and restore vital activity after moistening (Fig. 3 A, B). *Lem. microphyllum microphyllum* has a maximum thickness of lamina together with minimal frond area in comparison with other species (Table 2).

Lepisorus thunbergianus and *Lem. microphyllum* are characterized by closed venation (Figs. 1 A, B and 2 A). Basal acroscopic veins anastomose with basal basisopic ones. Recurrent inserted veins ending in hydathodes develop there (Mitsuta 1984). Such a venation was regarded by Pichi-Sermolli (1977) as progressive and the most close to reticulate. Venation in *C. latealatum* is open dichotomous (Fig. 3 A).

Additional roots branching up to 3–4th order arise from the ventral side of the rhizomes in the studied species. The rhizome, primordia of fronds and lateral rhizomes, bases of mature fronds, and lateral rhizomes are coated in *Lep. thunbergianus* (Khare 1965) and *Lem. microphyllum* by peltate clathrate scales that vary in size and shape (Figs. 4 B, C and 5 H). *Crepidomanes latealatum* is characterized by dense single-row multicellular trichomes, coating the roots as well.

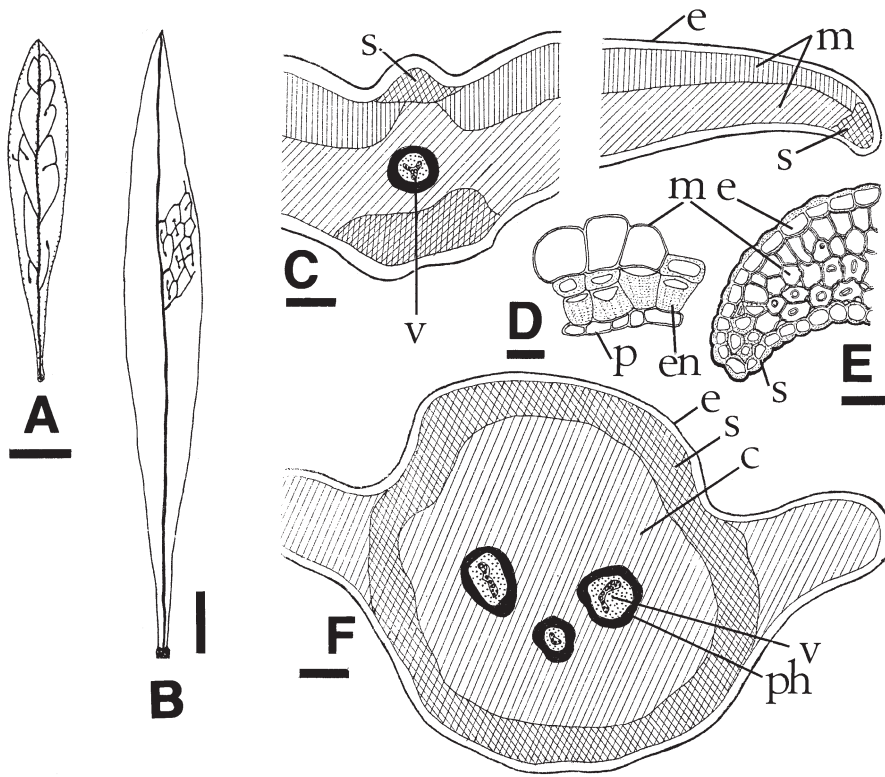


Fig. 1. Differentiation of fronds in *Lepisorus thunbergianus*. A : Frond of immature plant. Bar=3.0 mm. B : Frond of adult plant, which shows the pattern of venation. Bar=6 mm. C : Schematic diagram of transverse section of frond. Bar=0.14 mm. D : Portion of endodermis. Bar=0.02 mm. E : Margin of frond lamina. Bar=0.06 mm. F : Transverse section of petiole. e=epidermis ; m=mesophyll ; v=vascular strand ; en=endodermis ; p=pericycle ; c=parenchyma cells ; ph=cells containing phlobaphenes ; and s=sclerenchyma. Bar=0.14 mm.

According to the way of rhizome branching, all studied species are acrogenous ferns in the sense of Goebel (1928) and Troll (1937). *Lepisorus thunbergianus* and *Lem. microphyllum* are characterized by a modification of the *Polygonum*-type branching. Here, lateral rhizomes are initiated irregularly (in contrast to *Niphobolus adnascens* that was used by Troll as an example under consideration of such a variant of branching), usually at the middle of "internode" or at almost opposite position in respect of one of the fronds. According to Hagemann (1976), this is the *Stenochlaena*-type of branching (Figs. 4 D, E, F and 5 A, B). A modification of the *Davallia*-type of branching is typical to *C. latealatum*. In this case, the bud takes almost axillary position shifting slightly toward the apex of the main axis (Fig. 6 A). Such a branching was regarded

by Troll (1937) as transitional to the axillary one.

Sporophyte anatomy

The vascular system of *Lep. thunbergianus* and *Lem. microphyllum* rhizomes is presented by a dictyostele that practically correspond to the *Polypodium*-type stele according to Verdoorn (1938) and Ogura (1972) and by protostele in *C. latealatum* (Figs. 4 A, 5 D, E and 6 B).

Fronds of the three studied species differ in structure, tissue ratio and quantitative indices. Fronds of *Lep. thunbergianus* and *Lem. microphyllum* are hypostomatal, the stomatal apparatus of *Lep. thunbergianus* is anomocytic (Cotthem 1970) and that of *Lem. microphyllum* cyclocytic (Sen and Hennipman 1981). The mesophyll belongs to the dorsiventral type (Vasilevskaya and Butnik 1981) and consists of 6–9

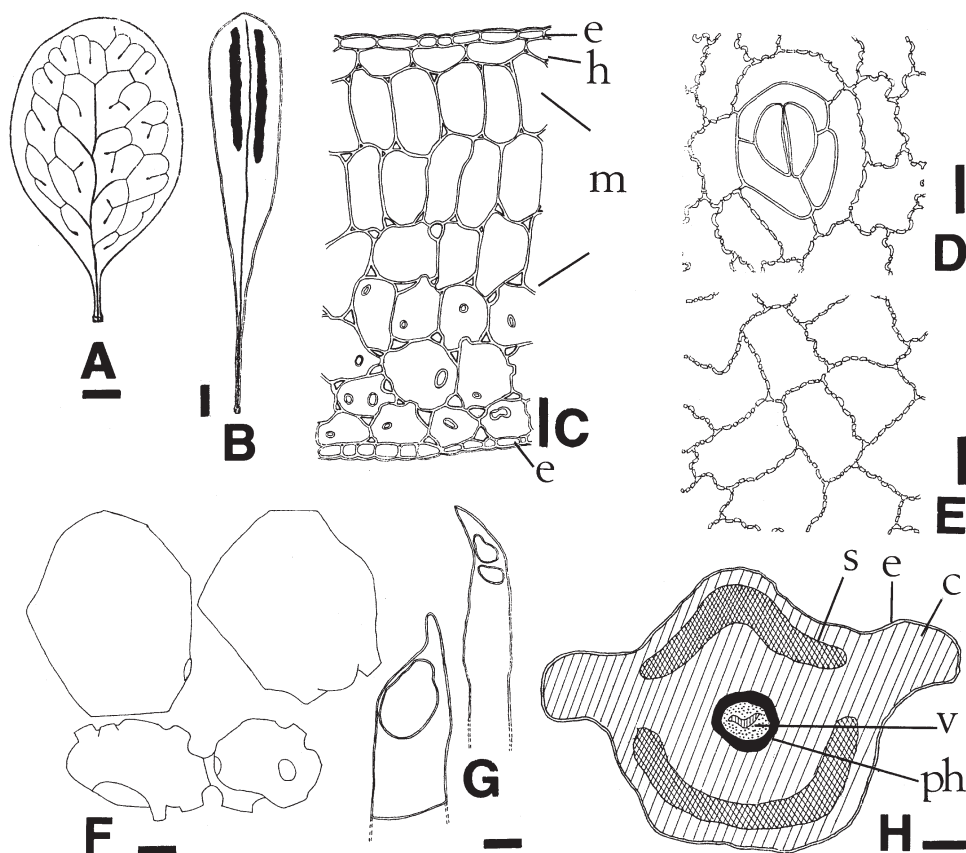


Fig. 2. Fronds in *Lemmaphyllum microphyllum*. A : Sterile frond which shows venation pattern. Bar=2.8 mm. B : Trophosporophyll. Bar=2.8 mm. C : Transverse section of the frond lamina. Bar=0.06 mm. D : Abaxial epidermis. Bar=0.04 mm. E : Adaxial epidermis. Bar=0.04 mm. F : Mesophyll cells. Bar=0.04 mm. G : Tracheal element with perforation. Bar=0.04 mm. H : Transverse section of petiole in the middle. Bar=0.1 mm. h=hypodermis ; see Fig. 1 for the explanations of other abbreviations.

layers of cells (Figs. 2 C, D, E and 7 A, D, E).

Transverse section of *Lem. microphyllum* frond shows comparatively small epidermal cells without chloroplasts compressed dorsiventrally. Their external walls are covered by cuticle and thickened. One-layered hypodermis is situated subepidermally. Below the hypodermis, there are 3-4-layers of large oval cells of the palisade tissue that turn gradually to the oval cells of spongy tissue with many small protuberances and intercellular spaces (Fig. 2 C, F). An interesting peculiarity of this species is the presence of pitted vessels with simple perforations in

fronds together with tracheids (Fig. 2 G).

Fronds of *Lep. thunbergianus* have 2-3-layered palisade mesophyll and spongy tissue consisting of rounded or oval cells lesser in size than in *Lem. microphyllum*, with protuberances (Fig. 7 A, B). The chloroplasts are situated parastrophically. The epidermis consists of comparatively large cells without chloroplasts covered by cuticle that is especially thick on external walls. At the frond margin, there are strands of non-lignified fibers of sclerenchyma that appear to ensure rolling-up of the frond under water deficit (Fig. 1 E).

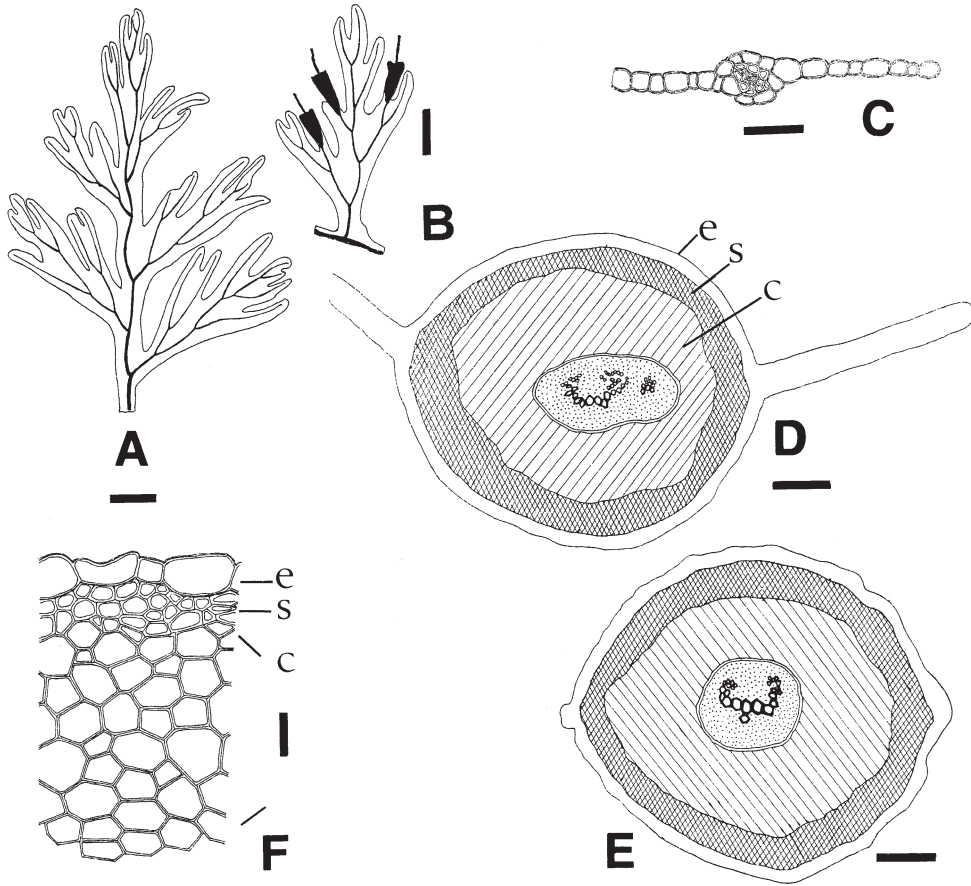


Fig. 3. Lamina in *Crepidomanes latealatum*. A : Pinna (segment) of 1st order. Bar=2 mm. B : Pinna (segment) of 2nd order with spore-bearing structures. Bar=2 mm. C : Portion of transverse section of frond. Bar=0.06 mm. D : Transverse section of petiole below the lamina. Bar=0.1 mm. E : Transverse section of petiole at base. Bar=0.1 mm. F : Portion of transverse section of petiole. Bar=0.1 mm. See Fig. 1 for the explanations of abbreviations.

Fronds of *C. latealatum* have no stomata and intercellular spaces. On transverse section, the frond lamina consists of 1 layer of parenchymatous cells (Fig. 3 C) with chloroplasts in apostrophic and epistrophic positions.

Frond petioles differ in shape in transverse sections, in size of epidermal cells, shape of sclerenchymatous strands and pattern of distribution of conductive elements of xylem (Figs. 1 F, 2 H and 3 E, F). The endodermal cells of *Lep. thunbergianus* and *Lem. microphyllum* contain phlobaphenes.

Calculated and measured indices of photosynthetic apparatus vary significantly in the studied species (Tables 2 and 3).

The maximum frond density (dry weight of

area unit) was observed in *Lep. thunbergianus*, correspondingly, it has the highest number of cells and chloroplasts per frond area unit (Ncl, Ncp). In *Lem. microphyllum*, the maximum thickness of frond lamina and minimal frond area as compared to other species were detected, the frond density and number of cells per frond were lower than in *Lep. thunbergianus*, but cell volume was the highest. *Crepidomanes latealatum* was characterized by highest frond area but minimal values of SSFD, numbers of cells and chloroplasts, as well as volume of cells and chloroplasts.

Large number of chloroplasts in cells of *Lep. thunbergianus* results in high value of chloroplast membrane index (CPMI) and comparatively

Table 2. Quantitative structural indices of photosynthetic apparatus

No	Index	<i>Lepisorus thunbergianus</i>		<i>Lemmaphyllum microphyllum</i>	<i>Crepidomanes latealatum</i>
1	Fronde area (Sf) m ²	4.9×10 ⁻⁴		1.1×10 ⁻⁴	11.5×10 ⁻⁴
2	Fronde thickness (Tf) m	520.2×10 ⁻⁶		587.9×10 ⁻⁶	69.3×10 ⁻⁶
3	Weight of fronde area unit, (SSFD) kg/m ²	773.3×10 ⁻⁴		426.6×10 ⁻⁴	74.1×10 ⁻⁴
4	Cellular volume (Vcl) m ³	45.0×10 ⁻¹⁵	99.3×10 ⁻¹⁵	386.4×10 ⁻¹⁵	24.2×10 ⁻¹⁵
		p	s		
5	No. of chloroplasts per cell (Ncp)	98.2	75.5	86.1	49.7
		p	s		
6	No. of cells per 1 m ² (Ncl)	44.1×10 ⁷	61.4×10 ⁷	47.4×10 ⁷	16.9×10 ⁷
		p	s		
7	Volume of chloroplast (Vcp) m ³	232.5×10 ⁻¹⁸		181.5×10 ⁻¹⁸	98.2×10 ⁻¹⁸
8	No. of chloroplasts per 1 m ² (Ncp)	4.3×10 ¹⁰	4.6×10 ¹⁰	4.08×10 ¹⁰	0.8×10 ¹⁰
		p	s		
		8.9×10 ¹⁰			

p, palisade tissue ; s, spongy tissue.

high CLMI. The highest value of CLMI was detected in *Lem. microphyllum*, that has largest mesophyll cells, but the total chloroplast volume was minimal in this species. *Crepidomanes latealatum* was characterized by higher total chloroplast volume per cell volume (Vcp/Vcl) in comparison with *Lem. microphyllum* despite the minimal values of derivative indices.

Significant differences were detected between the species under comparison of the cell surface/cell volume ratio (Sc/Vcl). It was the highest in *C. latealatum* with its parenchymatous cells without protuberances. The lowest values of this index were found in *Lem. microphyllum* where mesophyll is composed of mainly large-celled spongy tissue with short cellular protuberances. *Lep. thunbergianus* was intermediate in respect of this index.

The total fraction of chlorenchyma in the studied species varied from 5.9–31.2% of the total fronde volume (Vm), and its maximum value was observed in *Lem. microphyllum*.

Discussion

It is known that plants are distributed throughout a plant community in concordance with gradient of environmental conditions. Ways

and mechanisms of plant adaptation within a climatic region are diverse. Adaptations take place at various levels of organization, from biochemical to phytocenological. In this connection, evaluation of cenotic position of the studied species may partially elucidate their affiliation to one or another ecological group.

Lepisorus thunbergianus is a short-rhizomatous small fern inhabiting chinks and cracks in rocky sites (chasmophyte). Such ecotopes are distinguished by specific edaphic and microclimatic conditions similar to such under the forest canopy (Porter 1994). Open rocks being the habitat of this species may be exposed to heavy insolation and difference of daily and night temperatures. Main limiting environmental factors for this species appear to be the surplus solar radiation and water deficit.

Lemmaphyllum microphyllum is an inhabitant of flat rocky surfaces (epilithophyte) whose roots often penetrate into the chinks. Biotic factors affecting life of this fern are shading and interaction with mosses. The genus *Lemmaphyllum* is mainly composed of tropical epiphytic ferns. *Lemmaphyllum microphyllum* appears to find similar environmental conditions on rocks in northern regions of its chorological area. A weak

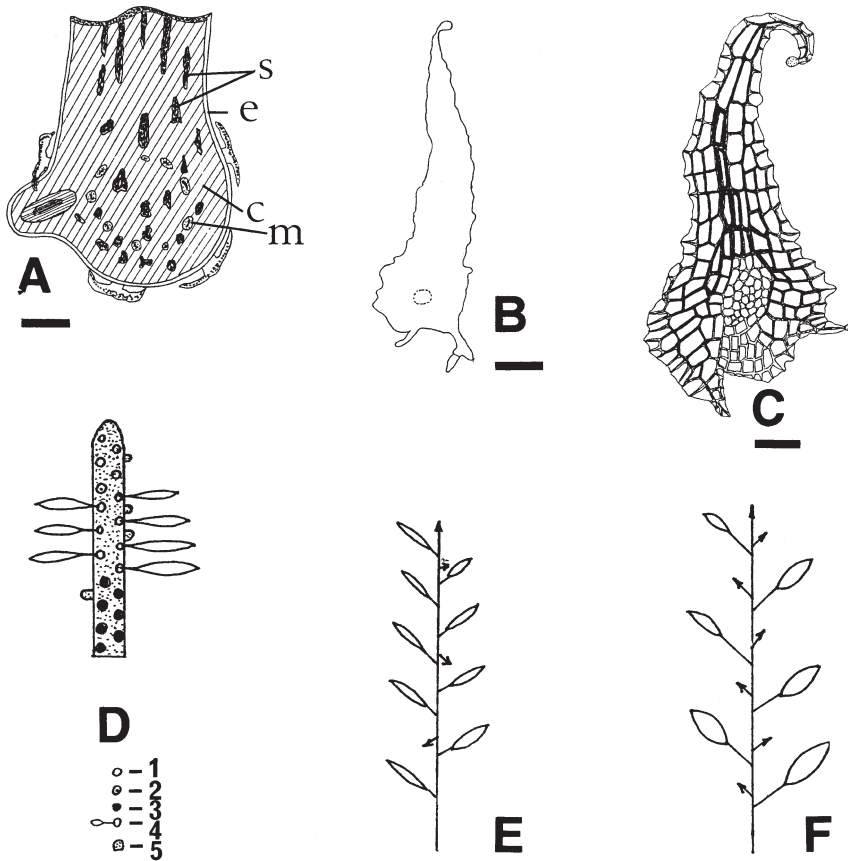


Fig. 4. Rhizomes in *Lepisorus thunbergianus*. A : Cross section of rhizome at phyllopede. Bar=0.4 mm. B : Rhizome scales at a young stage. Bar=0.2 mm. C : Rhizome scale at the mature stage. Bar=0.2 mm. D : Schematic diagram of rhizome structure (dorsal side). 1=frond primordium; 2=dormant primordium; 3=phyllopede of falling frond; 4=frond; and 5=primordium of lateral rhizome. E : Schematic diagram of rhizome branching in *Lep. thunbergianus*. F : Schematic diagram of rhizome branching in *Niphobolus adnascens* (after Troll 1937). See Fig. 1 for the explanations of abbreviations.

link in its ecological demands may be possibly water stress, excess and deficient insolation.

Crepidomanes latealatum is an inhabitant of shady rocks (epilithophyte) colonizing them only together with mosses (bryophilous species) that form green carpet promoting water accumulation and retention. Extraordinary influence of any of the main environmental factors may be fatal for this tender fern. Usually, members of the Hymenophyllaceae colonize sites with sufficiently humid microclimate, air immobility and considerable shading. However, according to the information of Surova (1978), low temperatures are not a limiting factor in the northward distribution of these ferns.

Taking into account only analysis of habitats,

these ferns may be a priori attributed to the following groups in respect of the main environmental factors : *Lep. thunbergianus* is a heliophilous mesoxerophyte, *Lem. microphyllum* is a shade-tolerant mesophyte or xeromesophyte, *C. latealatum* is a sciophilous hygrophyte.

In the present paper, we make an attempt to evaluate the ways of adaptation of the studied species to the environmental conditions at various levels of plant organization : biomorphological, histological, cellular and at the level of the plastid apparatus.

I. Biomorphological level :

1) Formation of such biomorphs that allow to colonize predominantly stony habitats. *Lepisorus*

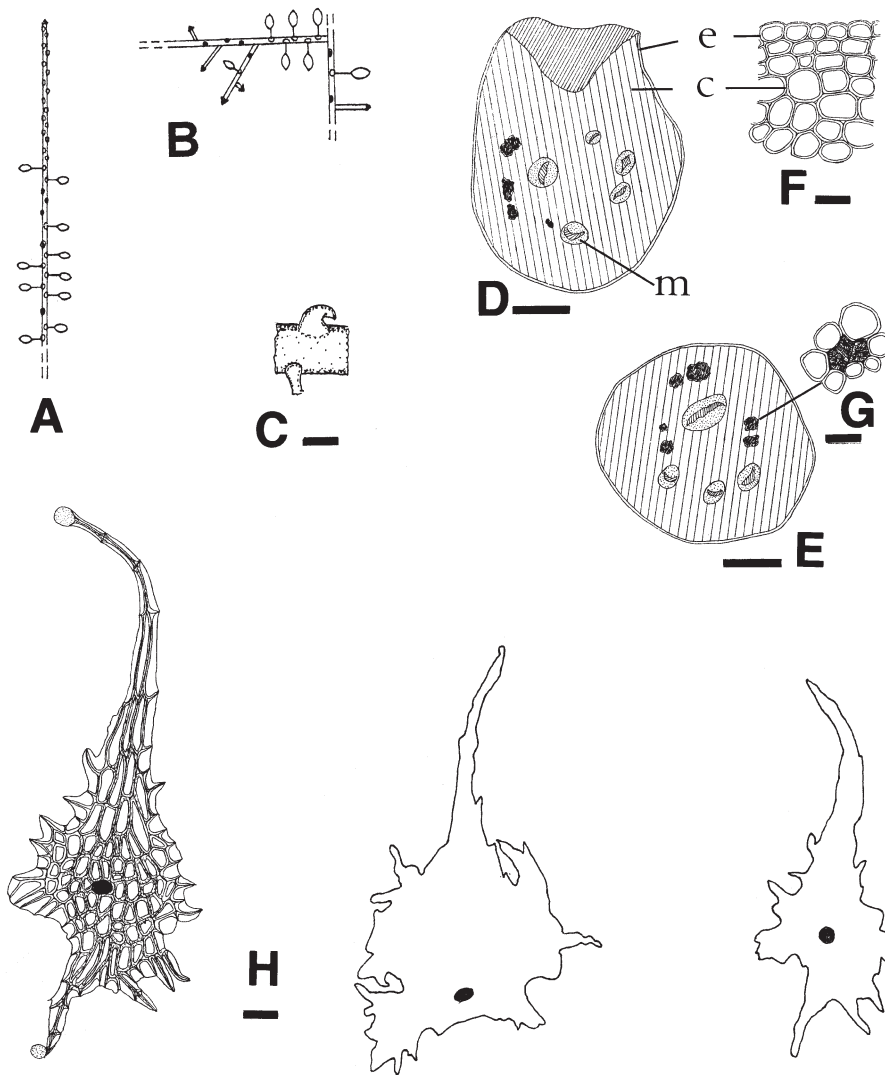


Fig. 5. Rhizomes in *Lemmaphyllum microphyllum*. A : Schematic diagram of rhizome structure (dorsal side), which does not include the root. B : Schematic diagram of rhizome branching. C : Portion of rhizome with frond primordium and fragment of root. Bar=0.4 mm. D : Cross section of rhizome at phyllopede. Bar=0.2 mm. E : Cross section of rhizome at internode. Bar=0.2 mm. F : Portion of rhizome cortex. Bar=0.04 mm. G : Rhizome sclerenchymatous strand. Bar=0.04 mm. H : Scales on rhizome. Bar=0.12 mm. See Fig. 1 for the explanations of abbreviations and Fig. 4 for the explanations of the numbers.

thunbergianus with its short rhizomes becomes possibility to occupy chinks between stones, clefts where humus (decaying plant remains, transferred soil particles) is accumulated. Moreover, rocks with chinks are a good accumulator of water (Walter 1968 a, b). The most favourable edaphic conditions for petrophytes are there (Gureyeva 2001). *Lemmaphyllum microphyllum* and *C. latealatum* have correspondingly long

branching rhizomes creeping along flat surface of stones with small amount of drifted soil on them (oligotrophy).

2) Small plant size (nanism) and leaf surface reduction are traditionally regarded as xeromorphic characters (Butnik et al. 1991). However, xeromorphosis-like characters may be a result of not only water stress but also "peinomorphosis" (Greb 1957) : inadequate nitrogen supply (es-

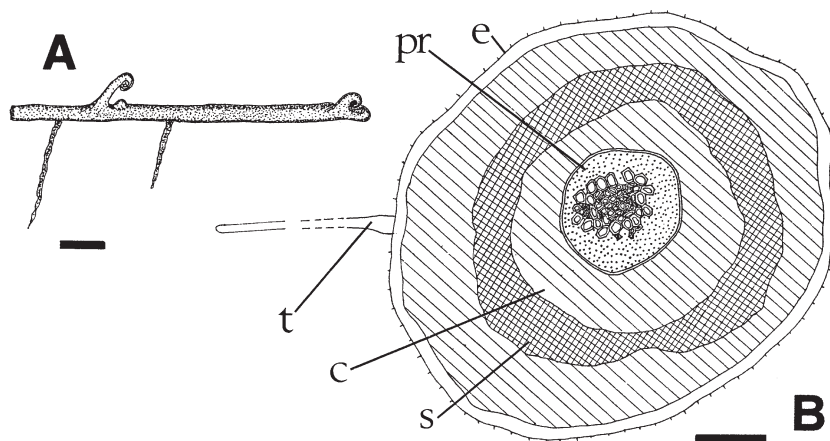


Fig. 6. Rhizomes in *Crepidomanes latealatum*. A : Distal part of rhizome of which trichomes are removed. Bar=3 mm. B : Cross section of rhizome. Bar=0.08 mm. pr=protosteles and t=trichome ; see Fig. 1 for the explanations of other abbreviations.

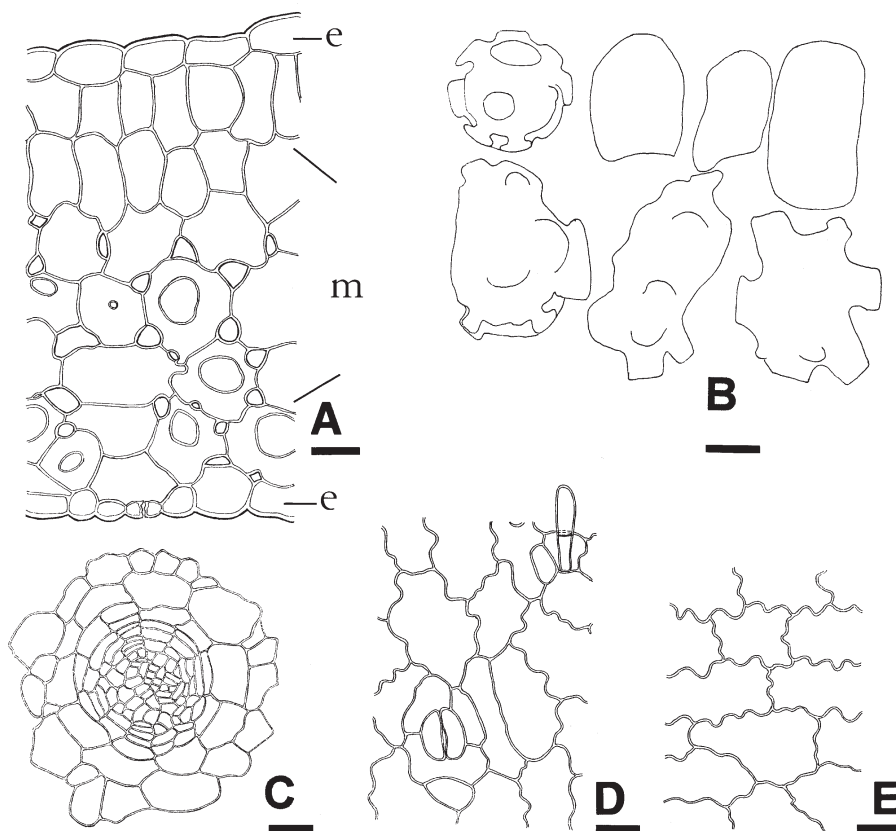


Fig. 7. Lamina anatomy in *Lepisorus thunbergianus*. A : Transverse section of frond lamina. Bar=0.04 mm. B : Cells of mesophyll (macerated material). Bar=0.02 mm. C : Cells of adaxial epidermis surrounding hydathode. Bar=0.04 mm. D : Abaxial epidermis. Bar=0.04 mm. E : Adaxial epidermis. e=epidermis. Bar=0.04 mm.

pecially in the case of oligotrophic ferns), soil overmoistening, etc.

3) Multiple-sected fronds such as in *C. latealatum* ensure the maximum surface of contact with the environment whose hydrature determines in many ways water supply of this fern what enhance the intensity of photosynthesis.

4) Evergreen nature of fronds (all the species).

5) Ability to roll up spore-bearing surface inside (*Lep. thunbergianus*).

6) Ability to fall at anabiosis (poikilohydry) (*C. latealatum*) or to endure short-term dehydration (*Lep. thunbergianus*).

7) Dense cover of scales and trichomes serving possibly not only as a protective means but also in preventing excess transpiration.

II. Cyto-histological level :

1) Thickness of lamina. It is known that thick and hard leaves are absolutely impenetrable to solar radiation (Larcher 1978), mesomorphous leaves pass 10–20% of solar radiation, and very thin leaves up to 40%. The highest pellucidity is noted in the region of the spectrum with high reflectivity. The minimal thickness of frond laminas in *C. latealatum* has possibly adaptive significance in its habitats with extremely lowered light availability and allows to use the light of low intensity effectively. This is promoted to a considerable degree by apostrophic and epistrophic position of chloroplasts in the cells.

A series of experiments in leaf-bearing woody plants (Malkina and Kovalev 1974 ; Malkina 1975 ; Zelniker 1978, in Goryshina 1989) shows that intense light stimulates growth of cells in height that results in formation of a sun leaf with densely packed mesophyll and thickened lamina. But in this case superficial growth of a leaf becomes delayed, so small leaves develop, i.e., intense development of the palisade tissue compensates diminution of the leaf lamina in heliomorphic xerophytes (Vassilevskaya 1950). Thick frond laminas as in *Lep. thunbergianus* with high proportion of dorsiventral mesophyll appear to ensure effective usage of light of high intensity.

The maximum thickness was detected in *Lem. microphyllum* fronds but their thickening is re-

lated to an increase of cell area and volume (Vcl) rather than development and compaction of palisade tissue (Table 2). Some authors that studied arctic and high-altitude plants (e.g., Bubolo 1984 ; Goryshina 1987 ; Miroslavov and Kravkina 1990 ; Miroslavov et al. 1998 ; Pyankov and Kondrachuk 1998, 2003) showed that large thickness of the leaf lamina being a result of increase in size of the palisade tissue cells is characteristic for cryophilous species.

2) Presence of an abscission layer in fronds of *Lep. thunbergianus* and *Lem. microphyllum* appears to ensure a possibility to shed the fronds in the case of extreme situation.

3) Comparatively small epidermal cells of *Lem. microphyllum* compressed dorsiventrally appear to enhance frond permeability to light and serve as light filter in conditions of shading, but at lesser extent than in *Lep. thunbergianus*. This character is regarded by Vassilyeva and Vassilyev (1988) as an indicator of non-optimal water relations.

4) Presence of cuticle on the epidermal surface that lowers the transpiration intensity is regarded as a xeromorphous character. Vassilyeva and Vassilyev (1988) pointed out that this is a character of evergreen plants of various habitats.

5) Presence of hydathodes in plant leaves as in *Lep. thunbergianus* and *Lem. microphyllum* is regarded by Goryshina (1979) as meso- and hygromorphous trait. Hydathodes promote elimination of excess water and salts from the plant.

6) As mentioned above, *Lem. microphyllum* characterized by a single adaxial layer of hypodermal cells. On an example of some *Pyrrosia* species, it was demonstrated that the hypodermis has water-accumulating properties (Hovenkamp 1986). Pautov (2002) considers that the hypodermis protects the leaf primordium against dehydration in the species of *Populus*. There is an opinion (Lidfors 1896 ; Guttenberg 1927) that it serves as a site of transitory accumulation of the storage nutrients. According to the opinion of other authors (Barykina and Chubatova 1980), this is a structural adaptation of ecological nature caused by long life-span of leaves that contribute to the lowering of transpiration under dry conditions as well to protection against heavy cooling and heating. It is possible that

this tissue in *Lem. microphyllum* may serve in that way.

7) *Lemmaphyllum microphyllum* has the mesophyll with slightly developed palisade tissue and prominent spongy parenchyma with large number of intercellular spaces. This tissue not only regulates gas exchange but also enhances absorption of radiation due to its multiple scattering in intercellular spaces (Kultiasov 1982) and possibly has water-accumulating function. As it is known, spongy tissue in sun leaves is composed of cells that are smaller than in shade leaves and have numerous chloroplasts and no protuberances. From this point of view, *Lep. thunbergianus* may not be considered a "pure" heliophyte, i.e., cells of its spongy tissue have a great number of protuberances as in *Lem. microphyllum*.

8) *Lemmaphyllum microphyllum* and *Lep. thunbergianus* are characterized by comparatively dense net of veins per unit of the frond area that is traditionally regarded as an xeromorphic trait. However, Vassilyeva and Vassilyev (1988) demonstrated that dense net of veins is combined with low transpiration in some mangrove plants as well as in plants of tropical rainforest, i.e., venation is not always an indica-

tor of xeromorphism.

9) Higher specialization of conductive elements of *Lem. microphyllum* (presence of vessels) serves probably a purpose of ensuring the maximum photosynthetic activity of the frond and associated transpiration.

Quantitative and measured indices :

1) Cell size. As it is known, unfavourable environmental factors (water deficit) cause delay of cell elongation and lead to the formation of small-celled tissues (Mokronosov 1978). According to Vassilevskaya (1950), growth of leaves of xerophytes completes quickly (microphyllly), and a characteristic feature of their photosynthetic apparatus is development of the palisade tissue. In this case, the relative chloroplast volume (Vcp) and number of chloroplasts (Ncp) increase. This feature we have observed on the example of *Lep. thunbergianus* (Table 2). At a lesser degree, these correlations are expressed in *Lem. microphyllum*. Increase of dry weight of the frond area unit (SSFD) is related to the small-celled tissue structure. The maximum values of SSFD were noted in *Lep. thunbergianus*, two times lesser values in *Lem. microphyllum* and the minimal ones in *C. latealatum*.

Table 3. Derivative structural indices of photosynthetic apparatus

No	Index	<i>Lepisorus thunbergianus</i>		<i>Lemmaphyllum microphyllum</i>	<i>Crepidomanes latealatum</i>
1	Cell volume per 1 chloroplast (CVCP) m ³	458.7×10 ⁻¹⁸	1314.8×10 ⁻¹⁸	4488.1×10 ⁻¹⁸	487.6×10 ⁻¹⁸
		p	s		
2	Total volume of chloroplasts in the volume of cell (Vcp/Vcl) %	50.7	17.6	4	20.2
		p	s		
3	Chloroplast membrane Index (CPMI) m ² /m ²	8.3	8.9	6.7	0.8
		p	s		
4	Cellular membrane index (CLMI) m ² /m ²	4.3	9.3	16.1	2.3
		p	s		
5	Cell surface / cell volume ratio (F/V) m	0.21×10 ⁻⁶	0.15×10 ⁻⁶	0.09×10 ⁻⁶	0.56×10 ⁻⁶
		p	s		
6	Volume of mesophyll in leaf (Vm) %	3.8	11.7	31.2	5.9*
		p	s		

*photosynthetic tissue is considered. p, palisade tissue ; s, spongy tissue.

2) High values of the chloroplast volume (Vcp) in all studied species as compared to flowering plants lie within the limits typical for sciophytes. This may be explained in the light of phylogenetic ideas about the organization of photosynthetic apparatus (Silayeva 1986). In the row Lycopodiophyta – Equisetophyta – Polypodiophyta – Gymnospermae – Angiospermae, there is a trend toward diminishing of the size of chloroplasts along with an increase of their number per cell.

3) As it was demonstrated on large number of flowering plants (Mokronossov and Shmakova 1978), the modal values of cell volume (Vcl) in mesophytes are several times higher than those in xerophytes. Therefore, the cell volume per chloroplast (CVCP) is sharply lowered in xerophytes (Table 3). Hence, the cell volume occupied by the plastids (Vcp/Vcl) is approximately two times larger in xerophytes. These correlations are clearly observed in *Lep. thunbergianus* (xeromorphous traits) and *Lem. microphyllum* (mesomorphous traits).

4) The values of chloroplast membrane index (CPMI) and the number of chloroplasts (Ncp) per leaf area unit are usually low in sciophilous plants and high in xerophytes. These values increase in the row *C. latealatum* – *Lem. microphyllum* – *Lep. thunbergianus* but in *Lep. thunbergianus* they are lower than in xerophilous flowering plants.

5) It is known (Ivanova and Pyankov 2002 a) that the more is the cell surface/cell volume (F/V) ratio the more is the rate of diffusion of CO₂ from intrafoliar space to the chloroplasts (carboxylation sites). *Crepidomanes latealatum* with its fronds with one-layered lamina and, correspondingly, without intrafoliar space has the maximum values of that index and *Lem. microphyllum* with its thick fronds has the minimal ones (Table 3).

6) The total fraction of leaf chlorenchyma (%) is usually high in the conditions of high level of light and optimal water supply. The fraction of mesophyll in a leaf decrease along with an increase of shading (Ivanova and Pyankov 2002 b). These data are confirmed by our investigations: *C. latealatum*, an inhabitant of the most shady biotopes has the minimal value of this index.

The maximum value is detected in *Lem. microphyllum* possessing thickest frond laminas where spongy tissue greatly contributes to the assimilation potential of mesophyll (Table 3).

Thus, the present investigation revealed xero-, meso-, hygro-, helio-, scio- and cryomorphous traits existing in diverse combinations in the studied species at various levels of their organization.

1. Xero-heliomorphous traits (joined, i.e. are usually in combination).

a) Organismic level : nanism, reduction of the frond area, coriaceous fronds (*Lem. microphyllum*, *Lep. thunbergianus*) ; ability of fronds to roll up by means of sclerenchymatous strands (*Lep. thunbergianus*) ; an evergreen phenorhythmotype, dense cover of trichomes and scales (all the species) ; poikilohydry (*C. latealatum*).

b) Tissue level : relatively thick frond laminas, dorsiventral mesophyll, presence of an abscission layer, cuticle, dense net of veins per frond area unit (*Lem. microphyllum*, *Lep. thunbergianus*) ; presence of hypodermis and vessels (*Lem. microphyllum*).

c) The level of cells and plastid apparatus : pycnomorphous structure (compact cell packing) and small cell size, large number of cells (Ncl) per frond area unit, high values of SSFD, CPMI (*Lep. thunbergianus*) ; parastrophic position of chloroplasts, relatively high volume and number of chloroplasts (Ncp) (*Lem. microphyllum*, *Lep. thunbergianus*), small epidermal cells (*Lem. microphyllum*).

2. Sciomorphous traits : hypostomaty, relatively small number of stomata per frond area unit, sinuous epidermal cell walls, protuberances of spongy mesophyll cells, high values of the chloroplast volume (Vcp) (*Lep. thunbergianus*, *Lem. microphyllum*) ; minimal values of the cell surface/cell volume ratio (F/V) (*Lem. microphyllum*) ; multiple-sected fronds with thin lamina, reduction of mesophyll (small amount of chlorenchyma in the frond), low values of CPMI and number of chloroplasts (Ncp) (*C. latealatum*).

3. Mesomorphous traits : differentiation of the mesophyll onto palisade and spongy tissue (*Lep. thunbergianus*, *Lem. microphyllum*) ; large cells,

relatively high values of cell volume (Vcl), CVCP and CLMI (*Lem. microphyllum*).

4. Hygromorphous traits : presence of hydathodes (*Lep. thunbergianus*, *Lem. microphyllum*) ; obligate bryophily, one-layered lamina, absence of stomata and cuticle, open dichotomous venation, low values of SSFD, poikilohydry (*C. latealatum*).

5. Cryomorphous traits : small coriaceous fronds, presence of intercellular air spaces (*Lep. thunbergianus*, *Lem. microphyllum*), large cells, low values of the cell surface/cell volume ratio (F/V), presence of hypodermis (*Lem. microphyllum*).

The obtained data allow to correct our suppositions concerning affiliation on the studied ferns to certain ecological groups. In respect of light regime of the biotope, *Lem. microphyllum* and *Lep. thunbergianus* have plastic demands and probably may be named shade-tolerant plants. As for water balance, *Lep. thunbergianus* has both mesomorphous and xeromorphous traits but the latter in greater amount than in *Lem. microphyllum*. Therefore, the former fern may probably be considered xeromesophyte but not mesoxerophyte as it was supposed, the second fern-mesophyte with a xeromorphous syndrome.

Moreover, the both species possess rather wide ecological valence in respect of environmental humidity : they are able to withstand both scanty water supply due to xeromorphy and conditions of increased hydrature by eliminating excess water through the hydathodes ; therefore, they are hydrolabile plants. *Lemaphyllum microphyllum* is homoiohydric, *Lep. thunbergianus* being able to withstand short-term dehydration has an intermediate position between homoio- and poikilohydric ferns. Such polyfunctionality of fronds is effective when these plants grow at risk.

Cell hydrature in *C. latealatum* is practically the same as the hydrature of environment. Therefore, it is a hydrolabile poikilohydric hygrophyte. In relation to the factor of light, it is a sciophyte.

Apparently, the optimum strategy for *Lep. thunbergianus* and *Lem. microphyllum* in the course of adaptiogenesis was enhancement of water retention ability of tissues and cells, and

for *C. latealatum*-ability to endure a deep dehydration of tissues without loss of viability and to restore the normal hydrature under favourable conditions.

In respect of the soil richness, *Lep. thunbergianus*, an inhabitant of chinks, may be named an eutroph, and the epilithophytes *C. latealatum* and *Lem. microphyllum* – oligotrophs.

Thus, a comparison of 3 species of petrophyte ferns shows that they have similar trends of adaptiogenesis at the level of organization of photosynthetic apparatus. At the structural level, it matters in size reduction (due to frond length lowering), evergreen nature, structural changes in mesophyll (from an increase of cell density and number of cell layers up to reduction), at the functional level-secondary poikilohydry and oligotrophy (in epilithophytes). The causes of the adaptive differences are possibly related to heredity (Walter 1968 a, b), origin of the species, ways of dispersal, modern configuration of their chorological areas, ecological niche specificity.

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- ニーナ M. ジェルジャビナ¹・ニーナ I. ショリナ²・近藤勝彦³：岩生シダ3種の構造的適応に関する比較
- 岩生シダ植物のウラボシ科ノキシノブとマメツタ、コケシノブ科アオホラゴケについて生形態学的、解剖学的、細胞学的ならびに色素体特徴を分析し、比較をした。それら3種は、乾生、中生、湿生、陽生、陰生、氷生の各形態を組み合わせた特徴を示した。極東ロシアにも分布するノキシノブは耐陰性で、恒水性と変水性シダとの中間型を示す水分不安定中乾性特徴を示し、富栄養性であった。マメツタは耐陰性で、乾生形態傾向をもつ水分不安定、恒水性中生植物であり、貧栄養性であった。また、アオホラゴケは陰生形態、水分不安定変水性湿性形態を示し、貧栄養性であった。それら3種は二者択一的適応生成戦略をもっていた。ノキシノブとマメツタは組織や細胞の水分保持増強能力があることを示した。そして、アオホラゴケは植物体組織の極度の脱水に耐えられる能力をもつことを示した。そして、水分が生活に必要な条件に戻ったとき、もとの普通の水分保持に戻すことを示した。また、それら3種はともに矮小性、常緑性、葉肉中の細胞の高密度化から、細胞層の多重化、組織の縮小化まで、互いに類似した適応構造を示した。さらに耐変水性と岩表生植物としての貧栄養性特性を予想させる。
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