Convergence and parallelism in evolution of structures and functions of ferns and other groups of plants

N. M. Derzhavina

Summary. On the basis of own investigations and literature data, the similarity of structures and functions of ferns and unrelated and related species is demonstrated in connection with their adaptation to similar mode of life at the different levels of the organization of plants. Convergence is manifested at the level of organism and organ (similarity of morphological structures: entire fronds and simple leaves; long rhizomes; squamose rhizomes of ferns and imbricate bulbs of flowering plants; shelters for ants and cups accumulating humus; absorbing scales; “complex” polyfunctional buds of rosette ferns with buds of flowering plants; gemmae of mosses and gametophytes of ferns). Convergence at the level of tissue and cells – is in similarity of anatomical structures: spiral thickening of cell walls in root cortical cells in epiphytic Polypodiaceae and velamen in Orchidaceae; multilayered water-storage parenchyma in fronds, rhizomes, tubers of ferns and an analogue tissue in flowering plants; palmate cells of epidermis and mesophyll in sciophytic ferns and sciophytic flowering plants; pyriform epidermal cells in ferns, selaginellas, and sciophytic mosses; protective shielding structures in fern epidermis). Convergence at the functional level – is in indirect parasitism at the cost of fungal symbiont in some epiphytic Polypodiaceae and in Orchidaceae; CAM photosynthesis in some epiphytic and lithophytic ferns, gymnosperms and angiosperms; mycotrophy (mutualistic co-parasitism); poikilohydry.

Key words: adaptatiogenesis, anatomical structures, functional peculiarities, morphological structures.

УДК 582.35:575.833/.4

Convergence and parallelism in evolution of structures and functions of ferns and other groups of plants

N. M. Derzhavina

Key words: adaptatiogenesis, anatomical structures, functional peculiarities, morphological structures.

Summary. On the basis of own investigations and literature data, the similarity of structures and functions of ferns and unrelated and related species is demonstrated in connection with their adaptation to similar mode of life at the different levels of the organization of plants. Convergence is manifested at the level of organism and organ (similarity of morphological structures: entire fronds and simple leaves; long rhizomes; squamose rhizomes of ferns and imbricate bulbs of flowering plants; shelters for ants and cups accumulating humus; absorbing scales; “complex” polyfunctional buds of rosette ferns with buds of flowering plants; gemmae of mosses and gametophytes of ferns). Convergence at the level of tissue and cells – is in similarity of anatomical structures: spiral thickening of cell walls in root cortical cells in epiphytic Polypodiaceae and velamen in Orchidaceae; multilayered water-storage parenchyma in fronds, rhizomes, tubers of ferns and an analogue tissue in flowering plants; palmate cells of epidermis and mesophyll in sciophytic ferns and sciophytic flowering plants; pyriform epidermal cells in ferns, selaginellas, and sciophytic mosses; protective shielding structures in fern epidermis). Convergence at the functional level – is in indirect parasitism at the cost of fungal symbiont in some epiphytic Polypodiaceae and in Orchidaceae; CAM photosynthesis in some epiphytic and lithophytic ferns, gymnosperms and angiosperms; mycotrophy (mutualistic co-parasitism); poikilohydry.

Конвергенция и параллелизм в эволюции структур и функций папоротников и других групп растений

Н. М. Державина

Ключевые слова: адаптациогенез, анатомические структуры, морфологические структуры, функциональные особенности.

Аннотация. На основе собственных исследований и литературных данных выявлено сходство структур и функций папоротников с неродственными и родственными видами на разных уровнях организации растений в связи с их приспособлением к сходному образу жизни. Конвергенция проявилась на организменном и органном уровнях (сходство морфологических структур: цельных вай и листьев, длинных ризомов, чешуйчатых ризомов папоротников и имбрикатных луковиц цветковых растений, дерновинных почек, вместилищ для муравьев и мирмекорий, абсorbирующих чешуй, «сложных» полифункциональных почек розеточных папоротников с почками цветковых растений, выводковых почек мхов и гаметофитов папоротников). Конвергенция на тканевом и клеточном уровнях – это сходство анатомических структур: спиральных утолщений клеток коры корней эпифитных Polypodiaceae и velamen Orchidaceae, многослойной водопоглощающей паренихимы в вайках, ризомах, клубнях папоротников и аналогичной ткани у цветковых, дланевидных клеток.
In the course of adaptatiogenesis, ferns developed secondary, i.e. not inherited from common ancestors, similarity of structures and functions with unrelated and related species in connection with their adaptation to similar mode of life. Conventionally, this similarity is associated with the phenomena of convergence and parallelism.

On the basis of own investigations (Derzhavina, 2008, 2010, 2012, 2013, 2015a, b) and literature data, we have made an attempt to reveal convergence and parallelism in the evolution of structures and functions of ferns and other plant groups.

Results
Convergences, as well as structural and functional analogies, are manifested both at the level of organism and organ (epimorphological), and at the level of tissue and cell:

A. Morphological structures – formal resemblance between:

1. Entire fronds (species of the genera Pyrrosia, Lemnaphyllum, Lepisorus, etc.) and simple leaves of flowering plants.

2. Long rhizomes of ferns covered by scales (Microgramma lycopodioides, Drynaria volkensii, Polypodium aureum, etc.) and the axes of Lycopodiophyta covered by photosynthetic microphylls having the enation origin Although the scales on fern rhizomes cannot photosynthesize, however, apart from their protective role, they can participate in translocation of water to the cortex of rhizomes in several Indian Pyrrosia species (Nayar, 1961).

3. Tuft biomorphs of ferns (species of Woodsia, Asplenium, Aleuritopteris) and flowering plants (the term “tuft” as applied to ferns is conditional enough; it was proposed by A.P. Khokhryakov (1979) on the principle of formal resemblance of dense arrangement of fronds and dense arrangement of shoots of flowering plants).

In these ferns, effect of extreme environment is compensated in some measure by the processes of polymerization of structures, manifested, primarily, in the formation of the tuft (cespitose) life form. Besides increase of number of terminal buds, abundant branching of rhizomes and dense arrangement of fronds, these ferns are characterized by the persistent stipes of their dead fronds.

These compact structures, besides their main functions, have additional functions as well, which are important in extremal environmental conditions: they protect buds from parching effect of cold wind, high temperatures, excess insolation and transpiration. Dense “brush” of petioles retains fallen fronds, fine soil particles, etc., preventing their blowing-out by wind. Accumulating humus may promote geophytization – embedding of ferns into the substrate with formation of epigeogenic rhizomes. In the opinion of M. T. Mazurenko (1986), “Arctic and Arcto-Alpine ferns represent geophytized tuft plants” hiding either in rock clefs, or below the layer of broken stones.

4. Shelters for ants (in the case of myrmecophily) in epiphytic ferns of the genera Solenopteris and Lecanopteris (Davidson, Epstein, 1989; Johns, 1995) and epiphytic flowering plants Myrmeccodia, Hydnophytum, Myrmedoma, Myrmephytum and Squamellaria (Rubiacaeae), Dischidia (Asclepiadaceae), Tillandsia (Bromeliaceae) (Huxley, 1980).

These plants have mutualistic relations with ants, which colonize the spaces in rhizomes (Lecanopteris, Solenopteris) and air tubers (Hydnophytum, Myrmeccodia – Rubiacaeae), internodes (Myrmecconiaeula, Clerodendrum myrmecophyllum – Verbenaceae), sacciform blisters on leaves – fornicaria (Melastomataceae), etc.

Huxley (1980) noted some convergent similarity of structures inhabited by ants:

1. Presence of water-absorbing structures in them, however, having different origin and morphology. They include additional roots of Dischidia and Solenopteris; “blotches” (small white convex structures in spaces of tubers) in Myrmeccodia, Hydnophytum, etc.; absorbing trichomes in Tillandsia; in Lecanopteris, the whole interior surface of the rhizome may absorb water. However, their functions in myrmecophytes from different biotopes are not elucidated completely.

2. Many myrmecophytes have dark-colored interior surface of the cavities. These cavities are
colonized by ants; possibly, ants need dark places for nesting (Janzen, 1974; ref. in: Huxley, 1980).

3. All ant nests in plants have narrow tunnel-like entrances that open in a horizontal plane. They are arranged like inkpot, what prevents falling out of contents and accumulation of rainwater, as well as decrease amount of incoming light.

It turns out that cohabitation of plants with ants ecologically lifts the restriction on distribution of epiphytes in the conditions of deficit of nutrients and allows them colonizing hostile environments.

Therefore, ants and epiphytes have developed in most cases mutualism on the basis of commensalism. Interspecific interactions of plants and ants may be estimated as topical (they create the environment one another); trophic; fabric (ants use plant material for building of nests); rarely – phorical (in case of myrmecochory).

5. Cups accumulating humus in nest and niche of the genera Asplenium, Drynaria, Platyserium, etc., and flowering plants of the families Araceae, Orchidaceae, Asclepiadaceae, etc.

In nest epiphytes, leaves (fronds) form a kind of funnel, where humus is accumulated and water is retained (Araceae, Orchidaceae, ferns – Asplenium nidus, Drynaria meyeniana). This substrate is transperced by abundant intermingled roots, resembling a bird’s nest and supplying the plants with water and nutrients. Bracket epiphytes (Conchophyllum – Asclepiadaceae, ferns Drynaria laurantii, species of the genus Platyserium, etc.) accumulate humus and retain water in the spaces between leaves or fronds (having the shape of brackets) and tree bark.

6. Squamose rhizomes of ferns, whose axes are covered by long persisting, imbricate thickened frond bases (phyllo- or trophopodia) with a storage function (Athyrium filix-femina, Polystichum braunii, Dryopteris filix mas, etc.) and imbricate bulbs of flowering plants (Shorina, 2000).

7. Absorbing scales on fronds of some ferns of the family Polypodiaceae (Polypodium hirsutissimum, P. squaliidum, P. plopoedioideus, Pleopeltis angusta) (Ogura, 1972) and on leaves of flowering plants (Bromeliaceae). L. Müller, G. Starmecker, S. Winkler (1981) proved that these trichomes were the analogues of water-absorbing scales of Bromeliaceae and likewise consist of living cells of stalk and dead cells of central disk, ring and wing. These scales absorb water through lignified cells of central disk, ring and wing and transport it inside the frond through the stalk cells.

8. “Complex” polyfunctional buds of rosette ferns such as those in flowering plants. Complexity of buds in such ferns is ensured by presence of multiple fronds at different phases of morphogenesis near the apex.

Chamaephytic ferns – Matteuccia struthiopteris, Osmunda asiatica periodically develop abortive fronds (cataphylls), which closely surround the terminal bud, ensuring its protection along with scales on unexpanded fronds. Such buds are called “closed buds” (Shorina, 2000). Although buds of other rosette ferns, for example, such as Athyrium filix-femina, have no specialized cataphylls and can be formally considered open buds, nevertheless, they have additional protection in the form of trophopodia of assimilating fronds covered by large filmy scales, as well as petioles of dead fronds. Moreover, such buds perform not only the function of regular reproduction, but, in the case of frond damage, they can form a new portion of fronds, becoming the analogues of proleptic and dormant buds of flowering plants. At the same time, in comfortable conditions, vigorous sporophytes can give rise to two generations of fronds, and in that case, the terminal bud becomes an analogue of the enrichment bud (Shorina, 2000).

9. Gemmae of mosses and gametophytes of ferns of the families Hymenophyllaceae, Vittariaceae (Surova, 1978). Here, formal resemblance is often based on different morphological structures.

B. Anatomical structures – formal resemblance between:

1. Spiral thickening of cell walls in root cortical cells in epiphytic Polypodiaceae (Schneider, 1996), Asplenium (et al., 2011) and velamen in Orchidaceae;

2. Multilayered water-storage (specialized and non-specialized) parenchyma in fronds (Derzhavina, 2008), rhizomes, tubers of ferns and an analogue tissue in flowering plants.

In most ferns (Lemmaphyllum microphyllum, Microsorum punctatum, Pyrrosia longifolia, etc.), as well as in cryptic succulents-angiosperms (Zygophyllum, Nitraria) (Gamaley, Shiroyedmaka, 1988), succulentization proceeds on the basis of polyfunctionality of chlorenchyma; and water storage may be a function of either hypodermis only, or palisade parenchyma, or spongy parenchyma, or the mesophyll as a whole. Judging by literature data, species of the genera Pyrrosia (Nayar, 1961; Hovenkamp, 1986) and Platyserium (Boyer, 1964; Froebel, Strank, 1981), inhabiting seasonal tropical climate, already have a specialized water-storage parenchyma.

However, among ferns, there are no highly specialized leaf succulents like Crassulaceae,
Aizoaceae with fleshy cylindrical, etc., leaves, massive specialized water-storage parenchyma, high water-retaining power, and many other characteristics. In general, ferns are, in our opinion, “leaf” subsucculents or cryptic succulents. V. R. Filin (1995) used the term “semisucculents” for the fronds of Ophioglossum vulgatum with high water content. In contrast to typical leaf succulents, they retain water poorly, but absorb it quickly;

3. Palmate cells of epidermis and mesophyll in sciophyte ferns and sciophyte flowering plants (Lotova, Timonin, 1989); pyriform epidermal cells in ferns, selaginellas, and sciophyte mosses (Razdorsky, 1949; Singh, 1963);

4. Protective shielding structures in fern epidermis (crystals of calcium salts, as in Aizoaceae) (Ogura, 1972) and various trichomes and glands (trichomes at the lower surface in the genera Ceterach, Pyrrosia, Platycerium; glands in species of the genera Aleuritopteris, Cheilanthes, etc.) like that in flowering plants.

Jan Grzybek (1973) observed crystals of calcium oxalate on frond surface in Polypodium vulgare. In Aizoaceae, calcium crystals in epidermis act as a kind of matte glass, decreasing intensity of insolation reaching chlorophyll-bearing cells (Udalova, 1980). It is possible to suppose that they can have such a protective function in ferns as well.

Lower frond side in species of Pyrrosia, Platycerium is covered by dense blanket of dead stellate trichomes, in Ceterach officinarum – by brown clathrate scales with imbricate arrangement. In Aleuritopteris argentea, upper side of frond blades has spring green color, lower side is silvery-white due to secretory bicellular trichomes excreting waxy substance (Nayar, 1962, 1963; Derzhavina, 2006), which forms powder-like deposition. This adaptation allows fronds restraining excessive transpiration and, possibly, possesses shielding protective properties in conditions of high insolation.

C. Functional peculiarities

1. Indirect parasitism at the cost of fungal symbiont in some epiphytic Polypodiaceae (Pyrrosia piloselloides and P. nummularifolia) and in Orchidaceae (Ruinen, 1953). Hazard of epiphytic invasion consists not only in coating of stems and branches of phorophytes by roots, rhizomes and rhizoids of epiphytes, but also in infection by mycorrhizal fungi, which turn to parasites in the new host. According to J. Ruinen, infection of phorophytes by symbiotic fungi (epiphytic invasion) takes place in the rhizosphere, and the larger the surface of stem and branches covered by roots, the higher is the possibility of infection by symbiotic fungi. Infection leads usually to moderate and increasingly serious tracheomycosis (damaging of tracheas by fungal hyphae), accompanied by tylosis and blocking of vessels by gum

2. CAM photosynthesis in some epiphytic and lithophytic ferns, gymnosperms (Schulze et al., 1976) and angiosperms.

After discovery of CAM metabolism in species of the family Polypodiaceae – Pyrrosia adnascens, P. confluentes, P. dielsii, P. longifolia, Drymoglossum piloselloides (two latter species have CAM invariably, irrespective of ecological conditions), Dictimia brownii (Wong, Hew, 1976; Winter et al., 1983; Ong et al., 1986), Microsorium punctatum, Polypodium crassifolium and lithophyte Platycerium veitchii (Holttum, Winter, 1999), and Vittariaceae (Martin et al., 2005, etc.) and investigation of different aspects of ecological physiology of other ferns (Griffiths, 1989; Kluge et al., 1989, etc.), a hypothesis about the origin of some ferns with different types of metabolism was proposed.

M. Kluge et al. (1989) noted that CAM does not allow epiphyte succulent ferns to withstand long drought periods, but that it is useful in improvement of carbon and water balance within short periods of water deficit. It is quite consistent with habitat conditions of these ferns in humid tropical forests, where the sun shines usually before midday, and it rains in the afternoons for a few hours, i.e., an alternation of wet and dry conditions takes place (“pulse type of water supply”) with circadian rhythmicity.

3. Mycotrophy (mutualistic co-parasitism) in ferns of the families of Polypodiaceae, Hymenophyllaceae, etc., and in angiosperms of the families of Ericaceae, Orchidaceae, etc., as well as in clubmosses. Of 426 spore plants studied, 43 % were obligate mycotrophs, and only 9 % – facultative mycotrophs (Wang, Qiu, 2006).

It is known that all Ophioglossaceae are obligate mycotrophs (Filin, 1978b), though they depend on mycorrhiza in different ways. Gametophytes of Hymenophyllaceae are facultative mycotrophs in natural conditions (Surova, 1978), gametophytes of clubmosses – obligate mycotrophs (Filin, 1978a).

Furman (1959; ref. in: Johansson, 1974), who took up a problem of mycotrophy, found, on the one hand, the contacts between roots of Orchidaceae, Bromeliaceae, Pteridophyta and mycelium, on the other hand, – only free-standing mycelium.

I. V. Kruger, I. L. Poponina (1979) studied mycosymbiotic structures in 35 fern species. They
found no non-mycorrhizal ferns. According to
the degree of mycotrophy, ferns were divided into
several groups: the level of mycorrhizal infection –
more than 30 %, 20–30 %, less than 20 %. They
found that the sporophytes of Polydium
vulgare (Poly podiaceae), Pteridium aquilinum
(L.) Kuhn. (Hypolepidaceae), Gymnocarpium
dryopteris (L.) Newm. (Athyriaceae), Phegopteris
connectilis (Michx.) Watt (Thelipteridaceae) had
vesicular arbuscular endotrophic mycorrhiza with
Endogonium fungi. No mycorrhiza was found in
gametophytes of these species. Infection of roots, in
opinion of these authors, comes from the soil due
to chlamydospores and sporocarps of Endogonium
fungi that hibernate in the soil.

M. Kessler et al. (2010), who studied 126
species of ferns and clubmosses from Malaysia
and Sulawesi, found mycorrhiza in 109 species for
the first time. Here, most species had arbuscular
mycorrhiza.

Orchidaceae, known to be obligate mycotrophs
at early stages of their development; however,
it is little known, to what extent mycorrhiza are
important in the nutrition of mature plants, and
the available data are controversial (Benzing, 1987).

4. Poikilohydry

of ferns of the family
Polypodiaceae (Pyrrisia, Platycerium, Polyodium
polypodioides, etc.), Hymenophyllaceae,
Cheilantheaceae, Aspleniacese (Ceterach
officinarum), Schizaceae (Anemia rotundifolia,
A. tomentosa), etc., and angiosperms of
the genera Ramondia, Haberlea (Gesneriaceae),
Myrothamnus (Myrothamnaceae), Chamaegigas
(Serophulariaceae), etc., clubmosses (Selaginella
trisulcata), mosses and other organisms (Stuart,
1968; Kessler, Siorak, 2007).

This complex phenomenon – capability to
withstand extremal and long-lasting dehydration
and life in condition of water deficit – anhydrobiosis
(Oppenheimer, Halevy, 1962) was poorly known in
ferns and represented in few publications.

E. Rouschal (1938) damaging that dangerous
changes in the palisade parenchyma cell volume in
Ceterach officinarum were prevented due to
two mechanisms: longitudinal collenchyma-like
thickenings of some cell walls and gelification of
dehydrated vacuoles, rich in catechin-like tannins.
He noted the facts of extremal resistance of
C. officinarum to water loss. In the experiments,
fronds lost water more than 98 % of total
saturation without apparent injury. Experiments of
H. Oppenheimer and A. Halevy (1962) confirmed
these data. In the cells of palisade parenchyma,
in most angiosperms, intended for excretion of excess water from fronds, may be considered as an example of convergence. Whereas, emergence of a new adaptive role in hydathodes of epiphyte ferns – intake of water – as an example of paracorvergence. Hydathodes in *Platycerium stemaria* and *P. angolense* combine two functions: guttation and participation in intake of water (Boyer, 1964).

Change of storage function of rhizomes to the function of intake of nutrients and water in case of transition of ferns to myrmecophily makes these structures to be paracorvergent to storage structures of flowering plants – rhizomes, tubers, bulbs, etc.

There are numerous examples of parallelism. For instance, development of similar tufted biomorphs in ferns within the families Aspleniaceae, Woodsiaceae, which occupy similar ecological niches; presence of similar structural types of fronds in the genera and species of a single family, inhabitants of similar biotopes: *hydromorphic* – Ceratopteris cornuta and *C. thalictroides*; *hygromorphic* – *Adiantum capillus-veneris*, Crepidomanes latealatum, etc.; *mesomorphic* – species of the genera *Asplenium*, *Microgramma*, *Polypodium*, *Phyllitis*, *Platycerium*, etc.; *subxeromorphic* – in species of the genera *Pyrrosia*, *Ceterach*, *Lepisorus*, *Aleuropteris*, etc.; *subsucculent* – *Antrophyum* (Vittariaceae) (Gladkova, 1978), *Pyrosla*, *Platycerium*, *Lemmaphyllum*, *Microsorium* (Polypodiaceae) (Derzhavina, 2008); CAM photosynthesis in species of a single genus *Pyrosla*, etc.

Enhancement of ecological expansion in this group of organisms took part, probably, due to epectomorphoses (Iordansky, 1990) – development of such wide-spectrum adaptations, which affect dispersal (expansion of ranges) and broadening of ecological amplitude of ferns markedly. At that, their structural and functional level does not change, i. e., epectomorphoses does not lead to morphophysiological progress or regress, but allow ferns to expand old or occupy new ecological niches.

**Conclusion**

The carried out research convinces that in the morphofunctional systems of fern the most mobile adaptive structures are, first of all, fronds. Individual structural components (mesophyll, cells, etc.) of this heterogeneous adaptive complex are connected by complex communications among themselves and with other elements of various systems of an organism (rhizomes, roots).

The functional variability of fern sporophytes is manifested primarily in the phenomenon of secondary poikilohydry, as a reaction to the seasonal climate with long dry seasons, and in succulentization as a reaction to the conditions of a humid tropical climate in which short-term dryness alternates with heavy showers, as well as mycotrophy – the conjugate evolution of ferns and fungi, whose adaptive value consists in effective adaptation of organisms to the environment in the conditions of the competition.

Apparently, competition with flowering plants for the same resources in similar habitats was for ferns the evolutionary factor that led to the diversification of their ecological niches, specialization of types, convergence, structural and functional analogies, the flash of biodiversity and increase the adaptive level of many taxa.

**REFERENCES**

Anthelme F., Abdoulkader A., and Viane R. 2011. Are ferns in arid environments underestimated? Contribution from the Saharan mountains. *J. Arid Environments* 75: 516–523.

Benzing D. H. 1987. Vascular epiphytism: taxonomic Participation and adaptive diversity. *Ann. Miss. Bot. Gard.* 74(2): 183–204.

Boyer Y. 1964. Contribution a la étude de l’ecophysiologie de deux fougéres épiphytiques: *Platycerium stemaria* et *P. angolense*. *Ann. Sci. Nat. Ser.* 12(5): 87–228 [In French].

Davidson D. W., Epstein W. W. 1989. Epiphytic Associations with Ants. In: *Vascular Plants as Epiphytes*. Ed. U. Luettge. Springer–Verlag, Berlin, Heidelberg, 200–229 pp.

Derzhavina N. M. 2006. Biomorfologiya i anatomiya ravnosporykh paporotnikov (epilitov, epifitov, zemnovodnykh i vodnykh) v svyazi s adaptaciogenezom (Biomorphology and anatomy of homosporous ferns (epilithophytes, epiphytes, amphibious and aquatic) in connection with adaptatiogenesis: Abstract of the thesis of the Dr.Sci.Biol. Moscow, 50 pp. [In Russian]. (Державина Н. М. Биоморфология и анатомия равнospоровых папоротников (эпилитов, эпифитов, земноводных и водных) в связи с адаптациогенезом: Автореф. дис. ... докт. биол. наук. М., 2006. 50 с.).

Derzhavina N. M. 2008. Types of mesophyll in fern fronds and variants of their structural variability. In: *Perspectives in Pteridophytes*. Eds S. C. Verma, S. P. Khullar, H. K. Cheema. Bishen Singh Mahendra Pal Singh, Dehradun, India, 227–241 pp.
Convergence and parallelism

Derzhavina N. M. 2010. Ecological classification of vascular epiphytes. Indian Fern J. 27: 32–52.

Derzhavina N. M. 2012. Adaptation of ferns to epiphytic mode of life: a case of Platycerium willinckii and Asplenium nidus. Indian Fern J. 29: 164–182.

Derzhavina N. M. 2013. Evolutionary restrictions and compensatory adaptations in homosporous ferns. Indian Fern J. 30: 255–267.

Derzhavina N. M. 2015a. Adaptation of epilithic ferns on different levels of structural organization. Contemporary Problems of Ecology 8(2): 141–147.

Derzhavina N. M. 2015b. Adaptive Strategies of homosporous Helophytic and Hydrophytic ferns. Contemporary Problems of Ecology 8(5): 560–573.

Filin V. R. 1978a. Lycopodiaceae. In: Zhizn rasteniy [Plant life. Ed. by A. L. Takhtajan]. Prosveshcheniye, Moscow, 4: 104–112 [In Russian]. (Филин В. Р. Семейство Lycopodiaceae // Жизнь растений / Под ред. А. Л. Тахтаджина. М.: Просвещение, 1978а. Т. 4. С. 104–112).

Filin V. R. 1978b. Ophioglossaceae. In: Zhizn rasteniy [Plant life. Ed. by A. L. Takhtajan]. Prosveshcheniy, Moscow, 4: 171–175 [In Russian]. (Филин В. Р. Семейство Ophioglossaceae // Жизнь растений / Под ред. А. Л. Тахтаджина. М.: Просвещение, 1978б. Т. 4. С. 171–175).

Filin V. R. 1995. Serpent’s-tongue (Ophioglossum vulgatum). In: Biological flora of the Moscow region. Eds. V. N. Pavlov, V. N. Tikhomirov. MGU–Argus, Moscow, 11: 4–36 [In Russian]. (Филин В. Р. Указник обыкновенный // Биол. флора Моск. обл. / Под ред. В. Н. Павлова и В. Н. Тихомирова. Вып. 11: М.: Изд-во МГУ; Изд-во «Аргус», 1995. С. 4–36).

Froebel H. A., Strank K. J. 1981. Zum Wasserhaushalt von Platycerium Desv. Beitr. Biol. Pflanzen 56: 275–291.

Gamaley Yu. V. 1978. Structural types of desert plants. In: Pustynyi Zaatlaskyoy Gobi. Kharakteristika rasteniy-dominiantov [Deserts Transaltai Gobi: Characteristics of dominant plants]. Nauka, Leningrad, 45–67 pp. [In Russian]. (Гамалей Ю. В., Шейровдамба Ц. Структурные типы пустынных растений // Пустыни Заалтайской Гоби. Характеристика растений-доминантов. Л.: Наука, 1988. С. 45–67).

Gladkova V. N. 1978. Vittarioideae. In: Zhizn rasteniy [Plant life. Ed. by A. L. Takhtajan]. Prosveshcheniy, Moscow, 4: 194–195 [In Russian]. (Гладкова В. Н. Vittarioideae // Жизнь растений / Под ред. А. Л. Тахтаджина. М.: Просвещение, 1978. Т. 4. С. 194–195).

Griiffiths H. 1989. Carbon Dioxide Concentrating Mechanisms and the Evolution of CAM in Vascular Epiphytes. In: Vascular Plants as Epiphytes. Ed. U. Lüttge. Springer-Verlag, Berlin Heidelberg, 42–81 pp.

Gryzhev J. 1973. Biological and phytochemical investigations on Polypodium vulgare L. I. Anatomical analysis. Acta Biol. Cracov. Ser. Bot. XVI(1): 29–35.

Holtum J. A. M., Winter K. 1999. Degrees of crassulacean acid metabolism in tropical epiphytic and lithophytic ferns. Australian Journal of Plant Physiology 26(8): 749.

Hovenkamp P. 1986. A monograph of the genus Pyrrosia (Polypodiaceae). E. J. Brill, Leiden University Press, (Leiden Botanical Series, vol. 9), 280 pp.

Huxley C. 1980. Symbiosis between ants and epiphytes. Biol. Rev. 55: 321–340.

Iordansky N. N. 1990. Evoluciya kompleksnykh adaptacij [Evolution of complex adaptations]. Nauka, Moscow, 310 pp. [In Russian]. (Иорданский Н. Н. Эволюция комплексных адаптаций. М.: Наука, 1990. 310 с).

Iordansky N. N. 1994. Makroevoluciya: sistemnaya teoriya [Macroevolution: a system theory]. Nauka, Moscow, 112 pp. [In Russian]. (Иорданский Н. Н. Макроэволюция: системная теория. М.: Наука, 1994. 112 с).

Johnsson D. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeogr. Suec. 59: 1–136.

Johns R. J. 1995. Lecanopteris lomarioides (Polypodiaceae). Bot. mag. Kew. 12: 89–95.

Kessler M. et al. 2010. A survey of the mycorrhization of Southeast Asian ferns and lycophytes. Plant Biology 12: 788–793.

Kessler M. & Siorak Y. 2007. Desication and rehydration Experiments on Leaves of 43 Pteridophyte Species. Amer. Fern J. 97(4): 175–185.

Khokhryakov A. P. 1979. Life forms of pteridophytes, their origin and evolution. Izvestiya Akademii nauk SSSR. Seriya biologicheskaya [Proceedings of the Russian Academy of Sciences. Biology] 2: 251–264 [In Russian]. (Хокхряков А. П. Жизненные формы папоротникообразных, их происхождение и эволюция // Изв. АН СССР. Сер. биол., 1979. № 2. С. 251–264).

Kluge M., Avadhani P. N., Goh C. J. 1989. Gas Exchange and Water Relations in Epiphytic Tropical Fern. In: Vascular Plants as Epiphytes. Ed. U. Lüttge. Springer-Verlag, Berlin Heidelberg, 87–107 pp.

Kruger I. V., Poponina I. L. 1979. Mycosymbiotrophy of ferns and some problems of their biology. In: Mikoriza rasteniy: respublikanskie sbornik nauchnykh trudov [Plant Mycorrhiza: the Republican collection of scientific works]. Perm, 19–25 pp. [In Russian]. (Крюгер И. В., Попонина И. Л. Микосимбиотрофизм папоротников и некоторые вопросы их биологии // Микориза растений: республ. сб. науч. тр. Пермь, 1979. С. 19–25).

Leroux O., Baghnevskaya Zarworna A., Rambe S. K., Knox J. P., Marcus S. E., Bellefroid E., Stubbe D., Chabbert B., Habrant A., Claeyts M., Viane R. L. L. 2010. Non-lignified helical cell wall thickenings in root cortical cells of Aspleniacae (Polypodiaceae): histology and taxonomical significance. Ann. Bot. (Oxford) 107: 195–207.
Lotova L. I., Timonin A. K. 1989. Sravnitelnaya anatomiya vysshikh rasteniy: uchebno-metodicheskoie posobie [Comparative anatomy of higher plants: study guide]. Izdatelstvo MGU, Moscow, 80 pp. [In Russian]. (Лотова Л. И., Тимошин А. К. Сравнительная анатомия высших растений: учебно-метод. пособие. М.: Изд-во Моск. ун-та, 1989. 80 с.).

Martin Sh. L., R. Davis, P. Protti, Teng-Chiu Lin, Shin-Hwe Lin, C. E. Martin. 2005. The occurrence of Crassulacean acid metabolism in epiphytic ferns, with an emphasis on the Vittariaceae. International J. of Plant Sciences 166(4): 623–630.

Mazurenko M. T. 1986. Biomorfologicheskiye adaptacii rasteniy Kraynego Severa [Biomorphological adaptations of Far North plants]. Nauka, Moscow, 209 pp. [In Russian]. (Мазуренко М. Т. Биоморфологические адаптации растений Крайнего Севера. М.: Наука, 1986. 209 с.).

Müller L., Starnecker G., Winkler S. 1981. Zur Oekologie epiphytischer Farne in Südbrasilien I. Saugschüppen. Flora 171: 55–63.

Nayar B. K. 1961. Ferns of India. Studies in Polypodiaceae. VII. Pyrrlosia Mirbel. J. Indian. Bot. Soc. 40: 144–186.

Ogura Y. 1972. Comparative anatomy of vegetative organs of the Pteridophytes. Borntraeger, Berlin–Stuttgart, 502 pp.

Ong B. L., Kluge M., Friement V. 1986. Crassulacean acid metabolism in the epiphytic ferns Drymoglossum piloselloides and Pyrrlosia longifolia: studies on the responses to environmental signals. Plant Cell. Environ. 9: 547–557.

Oppenheimer H. R., Halevy A. H. 1962. Anabiosis of Ceterach officinarum Lam. et DC. Bull. Res. Counc. of Israel 3: 127–147.

Razdorskі V. F. 1949. Anatomiya rasteniy [Plant anatomy]. Sowetskaya nauka, Moscow, 524 pp. [In Russian].

Rouschal E. 1938. Eine Physiologische Studie an Ceterach officinarum. Flora 132: 305–318.

Ruinen J. 1953. Epiphytosis. A second view on epiphytism. Ann. Bogoriensis 1(2): 101–157.

Schneider H. 1996. The Root Anatomie of Ferns: a comparative Study. In: Pteridology in Perspective. Royal Botanic Gardens, Kew, 271–283 pp.

Schulze E. D., Ziegler H., Stichler W. 1976. Environmental control of crassulacean acid metabolism in Welwitschia mirabilis Hook. Fil. in its range of natural distribution in the Namib desert. Oecologia 24(4): 323.

Shorina N. I. 2000. Morphology of buds and rhizomes of ferns. In: Rasteniya v prirodе i kul'ture [Plants in Nature and Culture]. Dalnauka, Vladivostok, 2: 124–138 [In Russian]. (Шорина Н. И. Морфология почек и корневищ папоротников // Растения в природе и культуре. Владивосток: Дальнаука, 2000. Т. 2. С. 124–138).

Singh T. C. N. 1963. An anatomical and ecological study of some ferns from Mussoorie (North-Western Himalayas). J. Indian Bot. Soc. 42(4): 475–543.

Stuart Tim S. 1968. Revival of Respiration and Photosynthesis in Dried Leaves of Polypodium polypodioide. Planta (Berlin) 83: 185–206.

Surova T. D. 1978. Hymenophyllaceae. In: Zhizn rasteniy [Plant life. Ed. by A. L. Takhтajan]. Prosveshcheniye, Moscow, 4: 218–222 [In Russian]. (Сурова Т. Д. Hymenophyllaceae // Жизнь растений / Под ред. А. Л. Тахтаджяна. М.: Просвещение, 1978, Т. 4. С. 218–222).

Usalova R. A. 1980. Aizoaceae. In: Zhizn rasteniy [Plant life. Ed. by A. L. Takhтajan]. Prosveshcheniye, Moscow, 5: 350–353 [In Russian]. (Удалова Р. А. Aizoaceae // Жизнь растений / Под ред. А. Л. Тахтаджяна. М.: Просвещение, 1980, Т. 5. С. 350–353).

Wang B., Qiu Y.-L. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16: 299–363.

Winter K., Wallace B. J., Stocker G. C., Rocksandic Z. 1983. Crassulacean acid metabolism in austalian vascular epiphytes and some related species. Oecologia 57, 1–2: 129–141. DOI: 10.1007/BF00379570.

Wong Y. S. & Hew C. S. 1976. Diffusive resistance, titrable acidity, and CO₂ fixation in two tropical epiphytic ferns. Amer. Fern. J. 66: 121–124.