БОТАНИКА И ЭКОЛОГИЯ

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THE APPROACHES TO THE CLASSIFICATION OF LIFE FORMS OF FERN-LIKE PLANTS (POLYPODIOPHYTA, INCLUDING LYCOPODIOPHYTA)

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The life form (LF) of plants reflects their adaptation to past and current soil, climatic, and cenotic conditions of their habitats. A distinctive feature of fern-like plant classifications (Polypodiophyta, including Lycopodiophyta) is the need to consider both the structure of sporophytes and gametophytes. The study of the morphological structures of fern gametophytes, begun in the 19th century by German botanists, revealed the importance of using comparative morphology in approaches to the classification of ferns (Orth, 1936; Goebel, 1928). The methods of spore germination were analyzed by S. Momose (1937 a,b; 1938 a,b,c; 1939; 1941; 1942). The author distinguished three types of germination: centrifugal, tangential, and centripetal. Nayar B.K. and Kaur S. when studying pteridophytes of India proposed a new classification, which reflected all existing types of germination of spores and formation of prothallia. J.E. Warming (1884), when distinguishing the life forms of ferns, distinguished two groups: I main (3 subgroups) the smallest and II main (2 subgroups, 3 types) with many variants and subvariants. The first approaches in our country to the allocation of LF of plants were successfully developed by I.G. Serebryakov for higher angiosperms (Serebryakov, 1964), where spore plants were not considered. The first classification of spore plants (ferns, horsetails and club mosses) was reflected in the works of A.P. Khokhryakov (1976) and Shorina N.I. (1994). When studying ferns of the south of the Russian Far East, O.V. Khrapko (1996) developed a fairly detailed classification that identified 14 morphological types of fronds, 6 types of branching and 15 types of rhizomes, which ultimately identified 15 LF of the above-ground and underground parts of ferns. A number of authors (Halle, Oldeman, 1970; I.I. Gureeva (2001)) proposed the term "architectural model" which is based on a dichotomous key in the consideration of underground rhizomes and contains a large number of models, types, groups, sections, variants, but does not reflect the biomorphological features of the perennial structure for fern's-like plants. According to some authors (Serebryakov, 1964; Raunkiaer, 1934) the concept of modularity in the classification of LF of ferns, which is developed on non-ecological principles, the "architectural model" cannot be recognized as the structural basis of a life form. Raunkiaer developed (1934) a classification in which 131 biomorphs from the main 13 and 185 variants are distinguished. For fern-like plants of the boreal, subtropical and tropical zones, distinguished by the presence of evergreen and tree-like species, we are segregated classification of plant life forms, based on the classification of Ch. Raunkiaer (1934), with additions according to T. Hosokawa (1949) for epiphytic plants, which includes 12 main life forms and 31 variants.

Key words: *pteridophytes; life form; biomorph; classification; ecological principle*

Introduction

The biomorphological characteristics of plants reflect their adaptability to environmental factors. The ecological conditions for the development of flora as a whole can be assessed, for example, using life forms (biomorphs) (Vinkovskaya, 2005). The adaptability of fern-like plants to the entire range of habitat conditions in a given natural area is demonstrated by their life form (LF), which reflects the past impacts of prevailing soil, climatic, and cenotic conditions. This is revealed in the characteristics for the genesis of general and regional floras, their spatial division, and their place in the system of higher-ranking phytochores.

A significant number of classifications of plant life forms formulated. Approaches to identifying biomorphs implemented with varying detail and ranges of coverage of the characteristics of the object of classification. Typically, they reflect a specific set of characteristics. The goal of this study is to summarize existing modifications and concepts of fern-like plant life forms, as well as to propose a unified universal system. Life forms, as part of the biomorphological analysis of flora, are essential for understanding the characteristics of its genesis, spatial division, and place within the system of higher-ranking phytochores (Kamelin, 1973; Mochalov, 2013a). The importance of biomorph analysis is reflected in the works of, for example, H. Raunkiaer (Raunkiaer, 1934), and the general principles were outlined by I.G. Serebryakov (1962, 1964). The composition of the flora itself is largely determined by the presence of a certain number of ecological niches within a territory, on the one hand, and, on the other, by the unique ecological relationships of species to the conditions of the territory (Kamelin, 1973).

Following I.G. Serebryakov, by life form we mean: the general appearance (habitus) of a certain group of plants (including their aboveground and underground organs – underground shoots and root systems), arising during their ontogenesis as a result of growth and development under specific environmental conditions. This habitus historically arises in given soil and climatic conditions as an expression of plant adaptation to these conditions (Serebryakov, 1962).

Pteridophytes in general, like seed plants and gymnosperms, have distinctive features in both structural and anatomical elements. In this context, the adaptive responses of ferns are distinguished not only by physiological characteristics, anatomical, and biomorphological traits that determine the general habitus of plants. These responses, however, lead to adaptation not to a specific environmental factor, but to the entire complex, since factors do not influence it in isolation.

The aim of this study is to analyze existing classifications, modifications and life form concepts of ferns, and to propose a unified universal system for boreal, subtropical and tropical ferns.

Results and discussion

It should be noted that not only sporophytes but also gametophytes were classified.

In his 1884 work "Om Skudbygning, Overvintring og Foryngelse," J. E. Warming first introduced the concept of life form as it applies to plants. He developed a detailed system of LF, classifying plants by lifespan, shoot development cycle, ability to reproduce vegetatively, root system structure, and other biomorphological characteristics. His approach to identifying life forms relied on adaptive traits, and the classification itself consisted of two groups: the first main group – hapaxanthus plants (monocyclic, including annuals, dicyclic-biennials, and pleio-polycyclic perennials) – the smallest; and the second main group – perennial polycarpic plants (two subgroups, three types) with numerous variants and subvariants. His system was distinguished by its great detail and elaboration of plant adaptations to environmental conditions, fully covering the biological types of plants in the forest zone of Europe, and even considering spore-bearing plants, for example, *Lycopodium*: II B 1 xxx. The system proposed by J.E. Warmig consisted of capital Latin letters: A – non-moving plants and B – moving ones. Under the numbers, the author considers the root, which can die or persist throughout life, as well as plants moving above and below ground, subdividing it into Latin (a, b, aa, bb, etc.) and Greek letters (α, β, γ, αα, ββ, etc.). It is rather inconvenient, cumbersome, and replete with both numbers and letters of the Latin and Greek alphabets.

Ecological approach

The study of the morphological structures of the fern gametophyte, begun in the 19th century by German botanists, led to the recognition of a wide variety of such structures when studying the features of gametophyte development in fern plants (mainly tropical and subtropical species); in addition to the usual heart-shaped gametophytes, asymmetrical, filiform, etc. were described (Goebel, 1877; Burk, 1975). As data on the development of the fern thallus accumulated, researchers repeatedly began to express the opinion that comparative gametophyte morphology can be used in approaches to the classification of ferns (Goebel, 1928; Orth, 1936). Thus, as early as 1898, Helmut Bruchmann, while studying boreal species of the genus *Lycopodium*, described the types of germination and thallus formation: type I (in the light) and type II (underground, without light) (Bruchmann, 1898). Later, the types identified by Bruchmann were used for studies of American club mosses (Brown, 1917) and the ontogenetic features of newly described species of this genus in New Zealand (Chamberlain, 1917).

The first to attempt to analyze the various modes of spore germination was S. Momose (1937 a, b; 1938 a, b, c; 1939; 1941; 1942). His classification included only three types of spore germination: centrifugal (the prothallial filament grows in the direction opposite to the growth of the first rhizoid), tangential (the prothallial filament grows perpendicular to the growth axis of the first rhizoid, and the rhizoid is located in the area of the first cell septum of the basal cell) and centripetal (the prothallial filament develops in the same way as in the tangential type, but the rhizoid is formed on the basal cell). In 1964, Atkinson L.R. and Stokey A.G., while studying species of the families Osmundaceae Martynov, Hymeniphyllaceae Mart., proposed and developed a different system of spore germination types, including two types: bipolar (development of the prothallium in two directions) and tripolar (development of the prothallium in three directions). M. Nishida (1965) attempted to integrate and generalize the systems developed by S. Momose and Atkinson L.R., Stokey A.G. In his understanding, the centripetal type (aspidioid according to Nishida) and tangential (polypodioid) are derivative and can be combined into a tripolar type according to (Atkinson, Stokey, 1964), when considering the type of spore germination of *Ceratopteris* Brongn., he proposed a third type - intermediate. Paying attention to the sequence of the first and subsequent divisions of the protonema cell of the germinating spore, the formation of the first rhizoid, as well as its polarity and the subsequent development of gametophytes (types of prothallia formation), Bal Krishnan Nayar and his student Surjit Kaur (Nayar, Kaur, 1971) proposed a completely new and detailed classification for leptosporangiate spore ferns (Fig. 1) while studying pteridophytes of India.

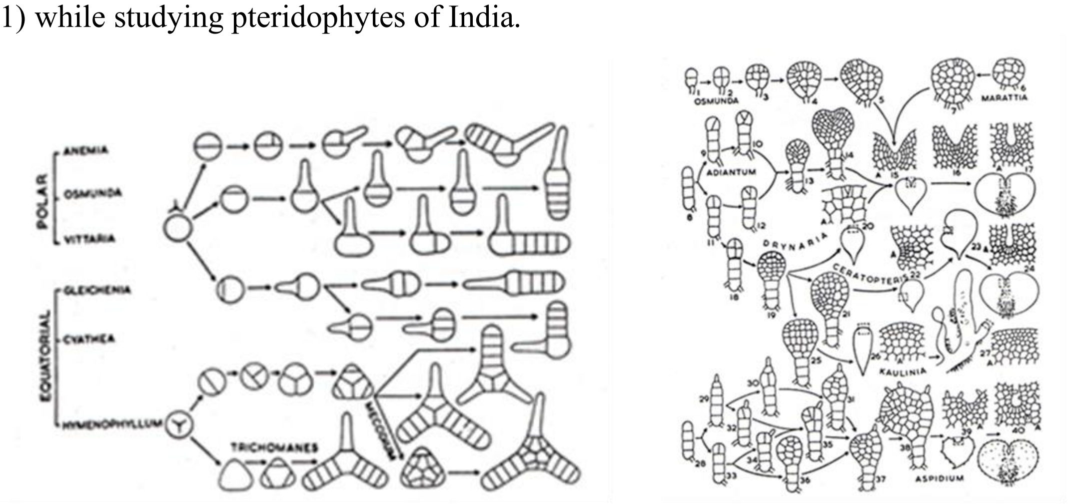

Fig. 1 Scheme of spore germination for leptosporangiate ferns and formation of prothallium (according to Nayar and Kaur, 1969)

In this classification, several types of spore germination and, accordingly, prothallia formation are distinguished in ferns: polar and equatorial, which differ in the plane and sequence of divisions.

In polar germination, the first cell septum in the spore runs parallel to the equatorial plane of the spore, and the elongation of the first rhizoid and the developing prothallium occurs in a plane parallel to the polar axis of the spore. The most common type of polar germination: Vittaria, Anemia, and Osmunda. This Osmunda type is characteristic only of the Osmundaceae family. Five types of equatorial germination are distinguished, differing in the plane and sequence of spore divisions. The septum formed during the first division in the germinating spore is parallel to the polar axis, and the prothallium elongates in a plane parallel to the equatorial plane of the spore. The most common type of equatorial germination: Gleichenia, Cyathea for tree ferns, and Hymenophyllum with the most unusual types (Trichomanes and Mecodium types). Spore germination is a reliable criterion in gametophyte biomorphology, but prothallial development ultimately leads to the characteristic habitual form of the mature thallus (prothallus). Nayar B.K. and Kaur S. identified seven types of prothallial plate formation (Osmunda, Marattia, Adiantum, Drynaria, Ceratopteris, Kaulinia, Aspidium), differing in the location of the meristematic cell and multicellular meristem, the sequence of cell divisions, which ultimately leads to the mature thallus type, which subsequently corresponds to certain taxonomic groups of ferns, and prothallial development itself – to the form of the mature thallus of the group. In our opinion, when studying ferns, attention should first be paid to the structure of the adult sporophyte, as it is the dominant phase in the reproductive cycle. It is a typical terrestrial plant (with some exceptions: *Lomariopsis lineata* (C.Presl) Holttum, which has a constant life form of not only the sporophyte but also the prothallus growing in the water column and is common as an aquarium plant), in which axial organs can be distinguished: stem, rhizome, and leaf-like organs (stem-branches) - fronds. It should also be noted that the sporophyte, unlike the gametophyte, can play a phytocoenotic role (and even, in rare cases, transform biotopes).

The LF system proposed and developed by Christen Christensen Raunkiaer (1934) and later published with all identified groups and keys by I. Ellenberg & D. Mueller-Doubois (1967) has undeniably contributed to the development of the concept of biomorphology both in Russia and abroad. This classification differs from previous works in its simplicity, clarity, and completeness. The system is based on the spatial arrangement of renewal buds and their ability to survive unfavorable seasons. The author initially developed it for boreal plants, and only after 1930 revised it for all vegetation zones of the earth: boreal, subtropical, and tropical. Moreover, only five main types of LF were listed, not 13 as intended by the author (phanerophytes P, chamaephytes Ch, hemicryptophytes H, geophytes G, therophytes T, lianas L, hemiepiphytes EL, epiphytes E, false hydrophytes Hyd, thallo-chamaephytes Th Ch, thallo-hemicryptophytes Th H, thallo-therophytes Th T, thallo-epiphytes T E). It should be noted that Christen Christensen Raunkiaer listed 131 biomorphs out of the 13 main ones and 185 variants related primarily to angiosperms in his classification. He did not consider all biomorphs in detail, which is why epiphytic plants were poorly represented in the LF spectrum, a point he later made.

T. Hosokawa proposed a system of LFs for epiphytic plants. Plants are classified according to the main environmental factors that significantly influence them (Hosokawa, 1949). In this case, these are two factors related to water and light. Life forms are clearly distinguished that are adaptations to the water factor, such as succulent (xerophilous form), and others, such as hygromorphic (tuberous character and membranous leaves). Life forms in relation to the light factor are those plant species that manage to increase the perceptible area of light to obtain it sufficiently. This includes the following adaptations: elongated internodes, mostly sympodial shoots, or elongated monopodia with shortened internodes or axes. Two groups of epiphytes are distinguished: 1 – typical epiphytes and 2 – false epiphytes. Next, the subdivision into Fi subgroups: plants with very thin mesophyll (mainly the Hymenophyllaceae family) was considered. The relationship with the substrate and the position of dormant buds on the rhizome were examined: D – woody and shrubby epiphytes separated from the substrate; Mc – primarily herbaceous plants in which renewal buds are located near the apex; SV – vines in which the connection with the substrate is lost in adulthood; Se – succulent epiphytes. Epiphytes with creeping rhizomes were classified as Rr, plants with shortened rhizomes that did not grow as actively represented the Rd life form, rosette epiphytes without rhizomes or stems – F, etc.

The first approaches in our country to identifying LF for boreal species were successfully developed by I.G. Serebryakov for angiosperms plants (Serebryakov, 1964), where the author distinguished four main divisions (woody, semi-woody plants, terrestrial and aquatic herbs), but did not consider fern-like plants, although they could be placed in the divisions of terrestrial and aquatic herbs, and woody - tropical and subtropical representatives (Fig. 2).

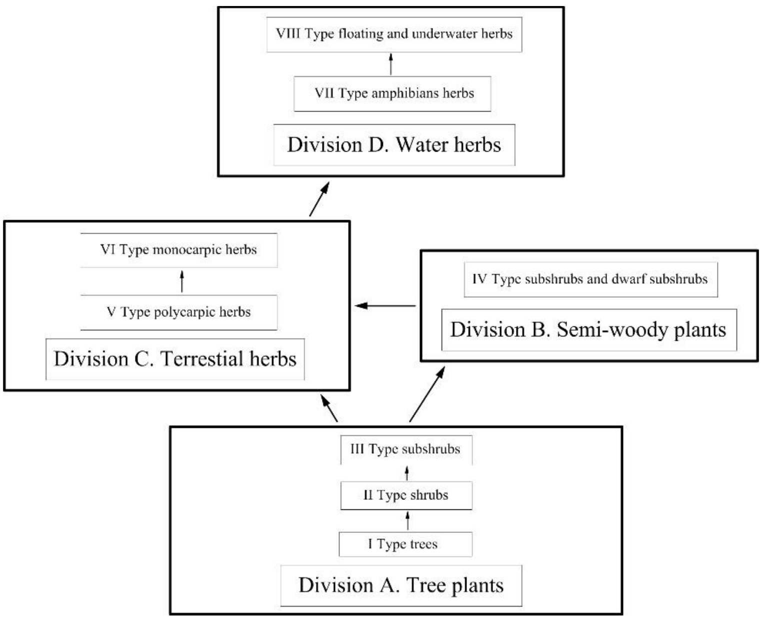

Fig. 2 Scheme of divisions according to I.G. Serebryakov (1962)

It should be noted that some aspects of the overwintering of renewal buds, as well as the LF identified by Ch. Raunkiaer (hemicryptophytes, cryptophytes), were considered by the author to be not entirely justified. Distinguishing the large divisions A, B, C, and D, he emphasized that the evolutionary system of LF ends with herbaceous plants – the monocarpic type (which complete their life cycle in one or more years), while D – aquatic herbs, were not considered in detail due to the wide diversity of life forms.

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The classification of the LF for ferns, as well as horsetails and club mosses, received special attention in the works of A.P. Khokhryakov (1976), who argued that existing classifications of plant LF (vascular) cannot be applied to higher spore-bearing vascular plants. According to A.P. Khokhryakov strikingly distinguished pteridophytes from angiosperms, which possess typical shoots, various types of shoot formation, axillary buds, etc. (Khokhryakov, 1976, 1979, 1981). In his classification, he distinguished LF by dividing them into 10 levels of quantitative and qualitative polymerization, from the precellular level to the shoot level. Regarding ferns, the preshoot and shoot levels are important, where quantitative polymerization of preshoots is expressed as an increase in frond concentration per unit rhizome length, considering the rhizome, in this system, as a homologue of the syntelome. The system of life forms was constructed from rhizomes: long-rhizome and rosette, then the position relative to the substrate was considered – plagiotropic or orthotropic, etc. Finally, the frond structure (annual, perennial, rooting, or not), the presence/absence of stolons and brood buds (Khokhryakov, 1981). Despite the author's intention to propose a system for all spore-bearing and cryptogamic plants, it very incompletely and indirectly reflects the necessary diagnostic features, and from the perspective of biomorph evolution.

Studying bracken cenopopulations allowed N.I. Shorina to identify three types of rhizomes in the rhizosphere: elongated, shortened, and transitional (Fig. 3), and several variants of bud arrangement on the dorsoventral rhizome – apical or lateral, with numerous subdivisions for both rhizomes and buds (Shorina, 1981). The conducted research formed the basis for the classification of life forms of leptosporangiate ferns (1994) (Fig. 4).

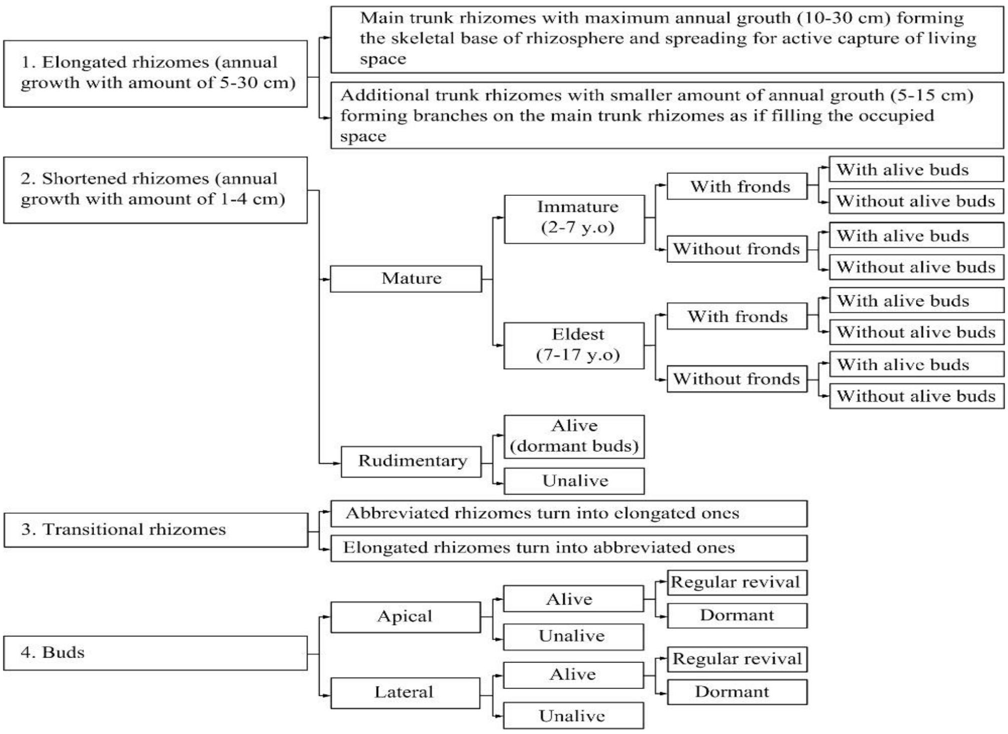

Fig. 3 Variants of rhizomes and buds of *Pteridium aquilinum* (L.) Kuhn (according to Shorina, 1981)

The proposed system proved to be quite complex, developed only for boreal fern species, where it combined phytocoenotic characteristics, vegetative motility, the location of renewal buds relative to the substrate, and borrowed terms from Ch. Raunkiaer, among others. However, it was also unclear to many botanists, for example, groups: implicitly polycentric, acentric; sections: ascending rosette, oblique rosette, diffuse rosette, ascending rosette, etc. This has always presented biomorphologists with difficulties in classifying LF. The identified class, wandering ferns, had no subclasses, groups, or sections and included annual or biennial species.

In studying ferns in the southern Russian Far East (RFE), O.V. Khrapko uses his own LF system, which identifies life-form groups based on the structural features of the perennial parts (rhizomes) and short-lived parts of ferns (fronds). The author identifies a large number of both types and groups of above-ground and underground parts of ferns, significantly complicating the use of the classification (Khrapko, 1996).

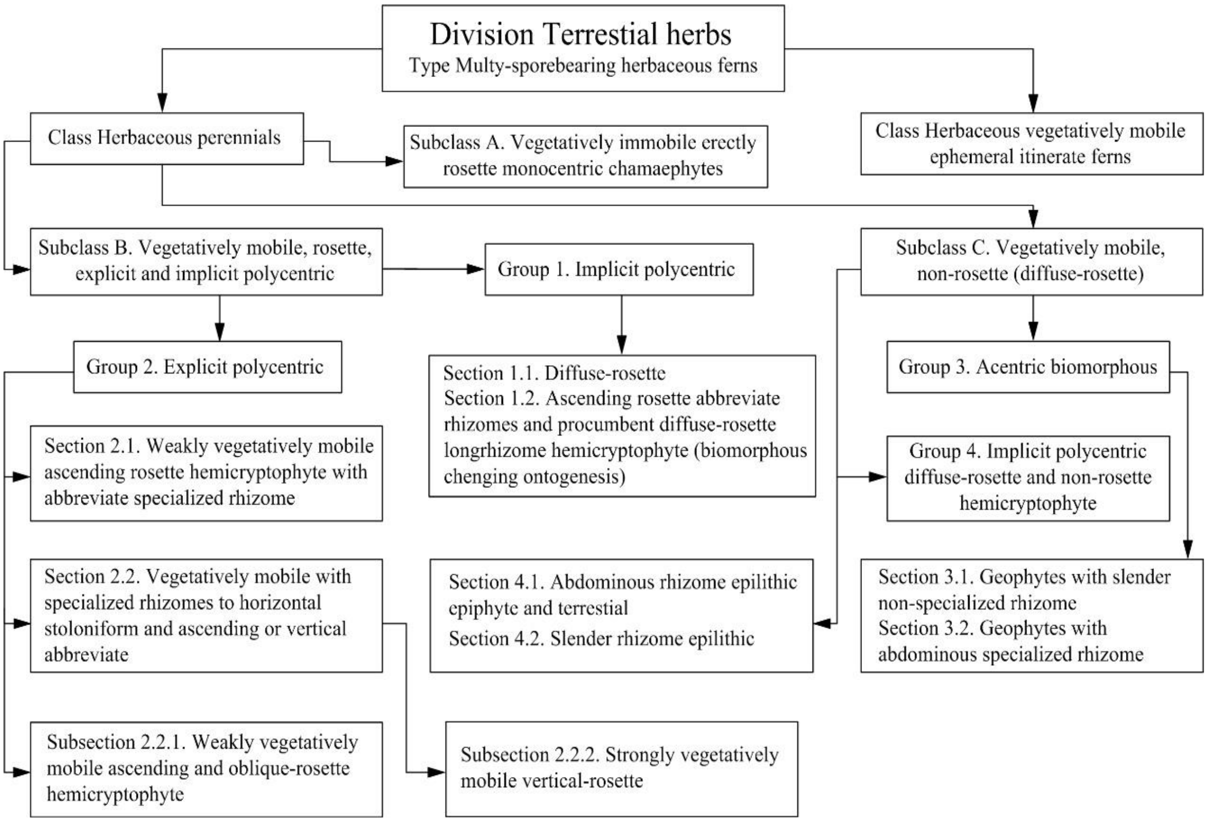

Fig. 4 Structure of life forms by N.I. Shorina (1981)

Seven types were identified in the plagiotropic rhizome group, and six types in the ascending and orthotropic group, grouped according to the direction of rhizome growth. Names were assigned based on characteristic representatives of ferns (Adiantum, Onoclea, Lunathyrium, Dryopteris). Furthermore, frond types were also proposed based on characteristic representatives (Osmunda, Camptosorus, Athyrium, Polypodium, etc.), which, for non-specialists, presented considerable difficulties in identifying life forms (Fig. 5). At that time, the author noted 84 species in the pteridophyte flora of the Russian Far East, which belonged to 14 morphological frond types; 6 branching types; and 15 rhizome types, ultimately identifying 15 life forms.

Model approach

Beginning in the late 1970s, a new term, "architectural model," emerged, coined by French scientists in relation to tropical woody plants (Halle and Oldeman, 1970) and later (Halle and Oldeman and Tomlinson, 1978), which fails to reflect the biomorphological and ecological structural features of ferns.

The essence of the proposed model boils down to the activity of the tree's apical meristems, which ultimately form systems of shoots – modules, within the structure of a mature plant. Architectural models are not related to plant size, and their development is not influenced by environmental factors. Consequently, they do not reflect bioecological and evolutionary characteristics, and the term is fundamentally "technocratic."

Developing the theory of metamerism based on the proposed idea of plant structural units by Halle and Oldeman (1970) and comparing various groups (ferns, gymnosperms, angiosperms), I.S. Antonova (1999) examines ferns from the perspective of "structural units," i.e., modularity.

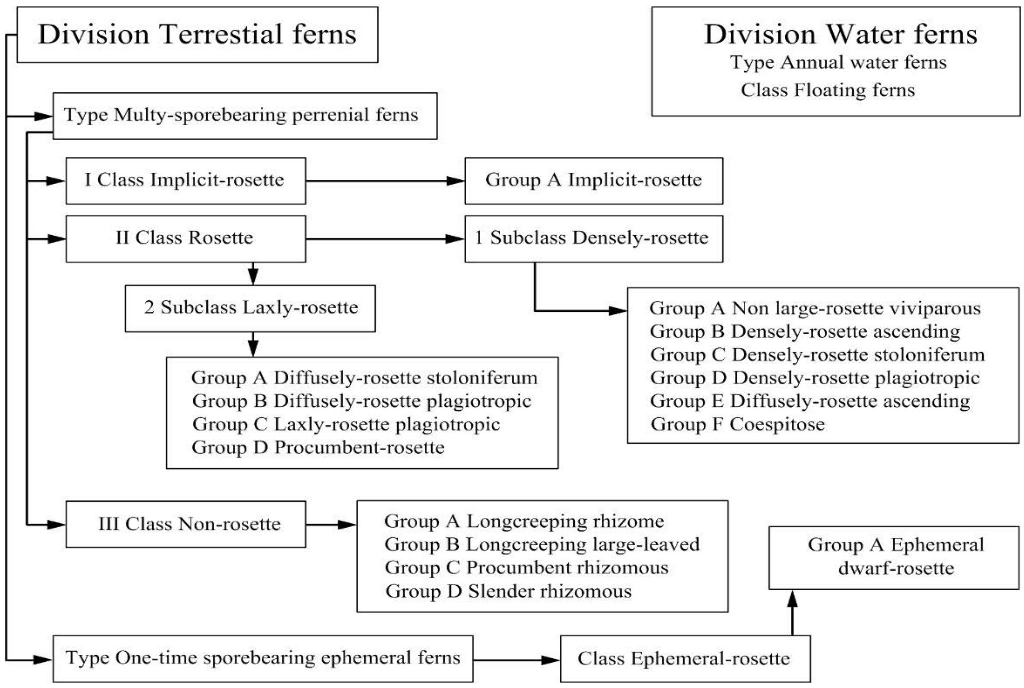

Fig. 5 Structure of life forms according to O.V. Khrapko (1996)

Studying the structure of six short-rhizome ferns across three life forms according to Khokhryakov (1981), she developed, as in the works of N.I. Shorina (1988), a modular theory of objects as "hierarchically organized multilevel structures...various formations of the aboveground part of the plant" (Antonova, Lagunova, 1999: p. 49). In short-rhizome ferns, the authors reduced metamerism to the modularity of complexes consisting of sections of the phyllopodia spiral, i.e., an elementary shoot system. Unfortunately, this classification was not further developed for pteridophytes.

This approach was further developed in the work of I.I. Gureeva (2001). The system is built in the likeness of a dichotomous key and contains a large number of models, types, groups, sections, and variants (Fig. 6). In this case, a classification of underground rhizome structures and their branching patterns is presented. The patterns are identified based on the arrangement of meristems on the fern "rhizome," which leads to different types of branching, for example, acrogenic or phyllogenous, as in the works noted by K. Goebel (1928) and W. Troll (1937), or dichotomous, as demonstrated by R.J. Mueller (1982) in studying the branching of the Asian fern genus *Lygodium*. This structure includes 35 names and, in its hierarchical division: architectural type (3), architectural model (5), groups (3), sections (10), and variants (14). This makes the classification practically impossible to visualize and represent; it is very difficult to understand and use. As analysis shows, there is currently no convenient, univalent classification of life forms, with simple notations and abbreviations, that could be easily used to describe the biomorphological features of ferns.

Over several decades, Raunkiaer's (1934) life form system has become one of the most frequently used classifications due to its simplicity and universality across various vegetation types (Adamson, 1939; Cain, 1950). As noted by V.N. Golubev (1977), where he discussed plant life forms, classifying LF by a single integral feature is fundamentally universal. For these reasons, Raunkiaer's (1934) classification is widely used to study the impacts of environmental changes on different vegetation types (Harrison et al., 2010; Marini et al., 2011) and to investigate plant biogeographical traits (Danin & Orshan, 1990; Pavon et al., 2000; Irl et al., 2020).

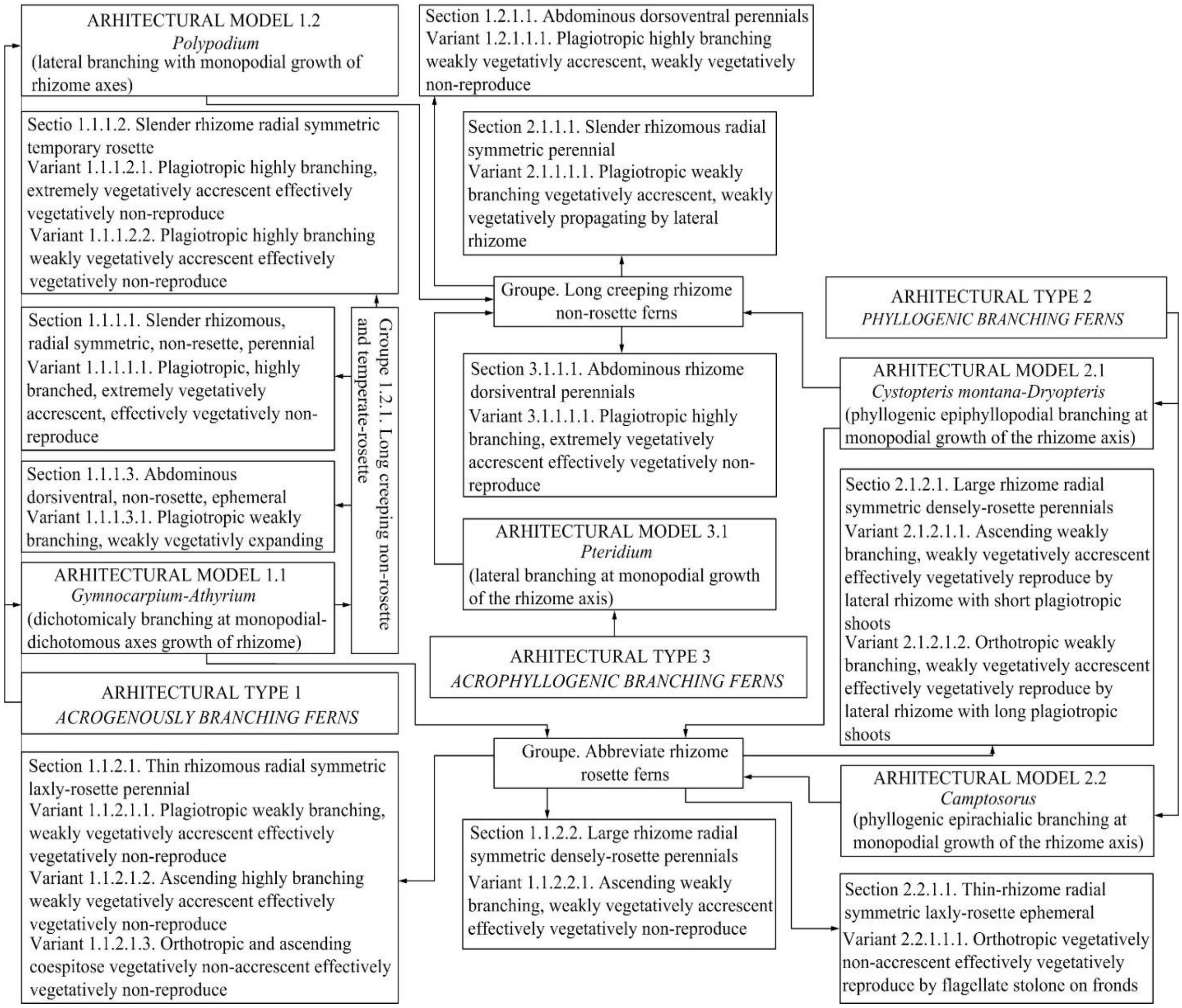

Fig. 6 Structure of life forms according to Gureeva I.I. (2001)

More recently, Raunkiaer LF have also been proposed as indicators defining local resilience strategies of plant communities, especially in island ecosystems (Ottaviani et al., 2020; Conti et al., 2022). Understanding the diversity and distribution of functional traits and plant LF has a wide focus in macroecological and biogeographical studies (Violle et al., 2014). The relationship between Raunkiaer life forms and vegetation type has been extensively studied both in the last century (Raunkiaer, 1934; Adamson, 1939; Cain, 1950) and in modern studies: their variations along altitudinal gradients have been described in spatially restricted areas (Irl et al., 2020; Matteodo et al., 2013). Other studies have also shown large-scale distribution of plant traits (related to growth forms, or altitudinal ones) along climatic gradients (Moles et al., 2009; Olson et al., 2018).

However, only a few studies have been conducted that have analyzed in detail large-scale patterns of plant LF within individual biogeographic regions (Taylor et al., 2023) and habitat types (Blasi et al., 1990; Loidi et al., 2021). That is, the LF proposed and developed by Ch. Raunkiaer still have not lost their relevance, i.e., their universality, and can be perfectly used to distinguish those of ferns, both in temperate climates and in countries with a tropical and subtropical climate. We disagree with the statement of Smith (1913) that the structure of LF proposed by Ch. Raunkiaer did not contain data on pteridophytes: *Salvinia*, *Isoetes*, and tree ferns were included as examples. When identifying certain biomorphs that are quite complex in their assignment to a particular group, it is possible to combine biomorph groups, creating a new one: E-H, E-Ch, Th-Ch, H-E (epiphytes-hemicryptophytes, epiphytes-chamaephytes, therophytes-chamaephytes, non-micryptophytes-epiphytes), especially since the possibility of such manipulations is indicated in the articles of foreign researchers (Smith, 1913; Stanley, 1950; Ellenberg I. & Mueller-Doubois D., 1967). But it should be noted that Raunkiaer's studies mainly reflect higher angiosperms, and epiphytic plants are not fully studied. T. Hosokawa (1949), while studying the life form spectra of Micronesia and adjacent islands, proposed a system of LF of epiphytic plants based on the system of Raunkiaer (1934), which can be perfectly used in working with representatives of the pteridoflora of the tropics and subtropics, especially since he adhered to the system of Raunkiaer. From the proposed system of LF for epiphytic plants, the following abbreviations proposed by T. Hosokawa can be used for epiphytic ferns: F, F-H, Rr, Rd, Fi-Rr, Fi-Rd and, in addition, they can be integrated with the designations of Ch. Raunkiaer: Rr-H as described earlier. In addition, the constant inconvenience regarding the definition/description of fern rhizomes, short-rhizome, long-rhizome, thin-rhizome, etc., disappears, since Ch. Raunkiaer's classification includes the abbreviations caespitose, herbaceous, reptant, scapose (Table).

Table

A variant of the unified classification for ferns

PHANERO-PHYTES	NP (Nanophanerophytes)	Phanerophytes with trunks up to 2 m
	Mi P (Microphanerophytes)	Phanerophytes with trunks from 2 to 5 m
	Mes P (Mesophanerophytes)	Phanerophytes with trunks from 5 to 50 m
CHAMAE-PHYTES	Ch herb (Herbaceous chamaephytes)	Plants with renewal buds near the ground surface, buds located at a height of no more than 30-50 cm, herbaceous chamaephytes, perennial evergreen / deciduous
	Ch herb rept (Herbaceous chamaephytes reptant)	Plants with renewal buds near the ground surface, buds no higher than 30-50 cm, creeping herbaceous chamaephytes, perennial evergreen/deciduous
	f Ch herb pulv (Flat Herbaceous chamaephytes pulvinate)	Plants with renewal buds near the ground surface, buds no higher than 30-50 cm, cushion-shaped herbaceous chamaephytes, perennial evergreen/deciduous
	Ch poik (Poikilohydrous chamaephytes)	Plants with renewal buds near the ground surface, buds no higher than 30-50 cm, poikilohydric herbaceous chamaephytes, arid habitats, perennial evergreen
	Ch herb rept-met T rept (Herbaceous chamaephytes reptant–Reptant therophytes)	Plants with renewal buds near the ground surface, with buds no more than 30-50 cm high, are herbaceous recumbent chamaephytes, or creeping annuals. During dry periods, they may die off completely and behave as annuals
HEMI-CRYPTOPHY TES	eH coesp (Caespitose hemicrypto-phytes sparingly evergreen)	Plants with renewal buds at ground level and protected by litterfall are turfy hemicryptophytes, or evergreens
	eH rept (Reptant hemicry-ptophytes sparingly evergreen)	Plants whose renewal buds are at ground level and protected by litterfall, creeping hemicryptophytes, evergreens
	H ros (Scapose hemicryptophytes rosette)	Plants whose renewal buds are at ground level and protected by litterfall, rosette hemicryptophytes, evergreens
	hyd H rept (Aquatic hemicryptophytes reptant)	Aquatic hemicryptophytes, creeping
	hyd H caesp (Aquatic hemicryptophytes caespitose)	Aquatic hemicryptophytes, turfy
HEMI-CRYPTOPHY TES-EPIPHYTES	eH rept–Rd (Reptant hemicryptophytes sparingly evergreen–*Reptata densa)	Plants with renewal buds at ground level and protected by litterfall are creeping hemicryptophytes, evergreens – creeping epiphytes with fronds densely located on the rhizome, with renewal buds on creeping rhizomes near the substrate surface
	e H rept–Rr (Reptant hemicryptophytes sparingly evergreen–*Reptata remota)	Plants with renewal buds at ground level and protected by litterfall are creeping hemicryptophytes, evergreens – creeping epiphytes with fronds widely spaced on the rhizome, with renewal buds on creeping rhizomes near the substrate surface

Continuation of the table

GEOP-HYTES	G rhiz (Rizome-geophytes)	Renewal buds are found on underground plant organs, such as rhizomes. Rhizome-bearing geophytes
	c G rad (Root-budding geophytes rain-green)	Renewal buds are found on underground plant organs, such as rhizomes. Root-sprouting geophytes
THERO-PHYTES	ear T caesp (Caespitose therophytes spring-green)	Plants that survive unfavorable periods in the form of spores. Caespitose spring-green therophytes
THEROPHY-TESCHAMA-EPHYTES	met T rept–Ch herb rept (Reptant therophytes winter-green–Chamaephytes reptant evergreen)	Evergreen creeping therophytes are evergreen creeping chamaephytes. This life form is present in biomes with a pronounced dry period, when plants die off completely.
LIANAS	d Gl (Geophytic lianas spread climbers)	Geophytic creeping vines
	el Gl (Geophytic lianas tendril climbers)	Geophytic vines that climb using tendrils
	st Gl (Geophytic lianas winding climbers)	Geophytic climbing vines
EPIPHYTES	F (Stabiligemmi-epiphyta fascicularis)	Sedentary canister-type epiphytes
	Rd (Mobiligemmi-epiphyta reptata densa)	Creeping epiphytes with fronds densely located on the rhizome, with renewal buds on creeping rhizomes near the substrate surface
	Rr (Mobiligemmi-epiphyta reptata remota)	Creeping epiphytes with fronds widely spaced on the rhizome, with renewal buds on creeping rhizomes near the substrate surface
	Se (Stabiligemmi-epiphyta succulenta)	Succulent-type non-motile epiphytes
	Fi–Rd (Epiphyta unistrato-cellularis–Mobiligemmi-epiphyta reptata densa)	Creeping epiphytes with a thin leaf blade (one cell layer) with fronds densely located on the rhizome, with renewal buds on creeping rhizomes near the substrate surface
	Fi–Rr (Epiphyta unistrato-cellularis–Mobiligemmi-epiphyta reptata remota)	Creeping epiphytes with a thin leaf blade (one cell layer) with fronds widely spaced on the rhizome, with renewal buds on creeping rhizomes near the substrate surface
EIPIHYTES-CHAMAE-PHYTES	F–Ch herb (Stabiligemmi-epiphyta fascicularis–Herbaceous chamaephytes)	Sedentary epiphytes of the canister type, herbaceous chamaephytes, perennial evergreen/deciduous
EPIPHYTES-HEMICRY-PTOPHYTES	Rr-eH rept (Mobiligemmi-epiphyta reptata remota–Reptant hemicryptophytes sparingly evergreen)	Creeping epiphytes with fronds widely spaced on the rhizome, with renewal buds on creeping rhizomes near the substrate surface, creeping hemicryptophytes, evergreen
	F–H ros (Stabiligemmi-epiphyta fascicularis–Scapose hemicryptophytes rosette)	Stationary epiphytes of the canister type, rosette hemicryptophytes, evergreen
HYDRO-PHYTES	kHyd nat (Kormo-hydrophyta natantia)	Floating hydrophytes

Thus, summing up the results of our study of existing classifications of plant LF, we note the following key points. Considering that life forms reflect adaptations that arose during ontogenesis as a result of growth and development under specific environmental conditions, this habitus historically emerges in given soil and climatic conditions as an expression of plant adaptability to these conditions, we believe an ecological approach to classifying LF is more justified than a "modular" approach. The very concept of modularity, which is developed on non-ecological principles of the "architectural model," cannot be recognized as the structural basis of the LF system, and the identification of "architectural types" based on the activity of meristems has no ecological or adaptive meaning, since a plant organism cannot be considered without indicators of adaptation to its environment, since we are talking about adaptation not to a single factor, but to a whole complex of environmental factors. Furthermore, it is impossible to consider a species from a position where "each species represents a unique system of ecological and biological adaptations and can be considered a separate life form" (Golubev, 1968: p. 1092).

The system of the Raunkiaer's LF (1934) does not lose its relevance in our time and is suitable for the allocation of LF of pteridophytes, and additions by T. Hosokawa (1949) on epiphytic plants complement this system, taking into account the characteristics of fern-like plants of the boreal, subtropical and tropical growth zones, we propose to allocate 4 main and 8 combined LF, a total of 32 biomorphs.

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Калюжный С.С., Шевчук О.М. К вопросу о классификации жизненных форм тропических и субтропических видов папоротникообразных растений // Бюллетень Государственного Никитского ботанического сада. – № 158. – С. 44-58

Жизненная форма (ЖФ) папоротникообразных растений (Polypodiophyta, включая Lycopodiophyta) является отражением приспособленности к прошлым и существующим почвенно-климатическим и ценотическим условиям местообитаний. Анализ созданных к настоящему времени классификаций папоротникообразных показывает вовлеченность как спорофитов, так и гаметофитов. В частности, исследование морфологических структур гаметофитов папоротников, начатое в XIX веке еще немецкими ботаниками, выявило важность использования сравнительной морфологии при подходах к классификации папоротникообразных растений (Orth, 1936; Goebel, 1928). Различные способы прорастания спор были проанализированы S. Momose и отражены им в многочисленных публикациях (1937 a, b; 1938 a, b, c; 1939; 1941; 1942). Nayar B.K., Kaur S при изучении папоротникообразных растений Индии предложили новую классификацию. Варминг Й.Э. (1884) при выделении жизненных форм папоротников выделял две группы: I главная (3 подгруппы) самая малая и II главная (2 подгруппы, 3 типа) со множеством вариантов и подвариантов. Первые подходы в нашей стране по выделению ЖФ успешно были развиты И.Г. Серебряковым для высших цветковых растений (Серебряков, 1964), где не рассматривались споровые растения. Первая классификация споровых растений (папоротников, хвощей и плаунов) нашей страны нашла отражение в работах А.П. Хохрякова (1976) и Шориной Н.И. (1994). При Изучение папоротников Юга Российского Дальнего Востока О.В. Храпко была разработана достаточно подробная классификация: выделено 14 морфологических типов вай, 6 типов ветвления и 15 типов корневищ, что в итоге выделило 15 жизненных форм по надземным и подземным частям папоротников (Храпко, 1996). Рядом авторов (Halle, Oldeman, 1970 И.И. Гуреевой (2001) был предложен термин «архитектурная модель», которая базируется на основе дихотомического ключа в рассмотрении подземных корневищ и содержит большое количество моделей, типов, групп, секций, вариантов, но не отражает биоморфологических особенностей строения многолетних структур папоротникообразных растений. По мнению некоторых исследователей, (Серебряков, 1964; Raunkiaer, 1934) концепция модульности при классификации жизненных форм папоротникообразных, которая развита на не экологических принципах «архитектурная модель» не может признаваться структурной основой жизненной формы. Раункиером разработана (1934) классификация, в которой выделены 131 биоморфа из основных 13 и 185 вариантов. Нами предложена объединенная классификация жизненных форм растений, базирующаяся на классификациях Ch. Raunkiaer, с дополнением по T. Hosokawa (1949). Разработанная система жизненных форм Ch. Raunkiaer не теряет своей актуальности и может быть использована большинством ботаников в наше время, и прекрасно подходит для выделения жф папоротникообразных растений, а дополнения T. Hosokawa по эпифитным растениям только усиливают данную систему.

Ключевые слова: *папоротникообразные растения; жизненная форма; биоморфа; классификация; экологический принцип*