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Ferns of the Southwestern Altai as an object of studying the pteridoflora (class Polypodiopsida) of the Kazakhstan Altai

In accordance with the study's objective, the article presents the results of systematic and chorological analyses of ferns of the Southwestern Altai in the Kazakhstan Altai mountains, and also analyzes the specificity of the pteridoflora to soil substrates and moisture. The pteridoflora (class Polypodiopsida) was established as consisting of 32 species, belonging to 12 genera and 9 families. In terms of the number of species, the leading families are Woodsiaceae, Dryopteridaceae, Cystopteridaceae, and Athyridaceae, which together account for over 75.0 % of the total number of species in the study area. The family-species coefficient of the pteridoflora of the Southwestern Altai at the level of 0.28 indicates a low saturation of families with species and its primeval age. The pteridoflora was found to be associated with five distinct geographical areas. Species with a Holarctic distribution were the most prevalent, comprising 68.75 % of the total, suggesting a strong connection to Holarctic floras. According to the growing conditions, ferns are divided into 3 belt-zonal groups: plain-mountain-forest, mountain-forest and high-mountain. The dominant position is occupied by the mountain-forest group — 23 species (71.75 %), growing in coniferous, mixed and small-leaved forests, confined to the mountains in the altitude limit of 900–1700 m above sea level. A specificity of pteridoflora to various types of rocky habitats and cliffs was revealed. According to the requirement for moisture supply of ecotopes, ferns are divided into 6 groups, where the dominant position is occupied by the mesophilic ecomorph, represented by mesophytes — 46.8 % and mesopetrophytes — 37.5 % of the total species composition.

Keywords: habitat, species, Southwestern Altai, pteridoflora, zonal distribution, ecomorph.

Introduction

Fern-like plants (pteridophytes) represent the most numerous group of ancient vascular spore-bearing plants, and their historically formed species composition in a specific territory — pteridoflora — has a relict character. In terms of antiquity, ferns are probably second only to Rhyniophyta and Lycopodiophyta and are approximately the same geological age as Equisetophyta [1]. The antiquity of their origin, along with the complex biology of their development and reproduction, determines their low competitiveness in the formation of modern phytocenoses. The diversity of sporophyte structures and the high polymorphism of ferns often lead to challenges in their systematic identification [2]. Despite the continuous interest of specialists in pteridophytes, the study of their natural-territorial distribution and various aspects of their biology and ecology remains highly relevant, especially in light of increasing economic development and changing climatic conditions [3].

Currently, there are about 300 genera and more than 10,000 species of ferns worldwide. Their greatest species diversity is concentrated in the mountainous tropics of both the Old and New Worlds, particularly in regions with an equatorial or tropical uniformly humid climate, which has remained largely unchanged since the Carboniferous period — the heyday of ferns. In contrast, the boreal regions of the Old and New Worlds are less rich in fern species. In countries with temperate and cold climates, only a few species have survived, having demonstrated the ability to adapt to new environmental conditions. However, many ferns play a significant role in the formation of vegetation cover and have practical uses, including medicinal and decorative purposes [4].

The study of Kazakhstan's flora has received considerable attention over the past decades, with various systematic plant groups identified to varying degrees of detail. In most cases, botanical studies focus on seed plants, which are the most common in modern ecosystems. Ferns have been recognized as an integral spore-bearing component of the vascular plant flora in the analyzed territory or its subdivisions. Studies on ferns in mountainous regions are of particular scientific interest, as mountain systems being the richest in flora serve as reservoirs of the gene pool of ancient relict taxa and centers of biodiversity [5].

All of the above underscores the relevance of conducting comprehensive and in-depth research on the ferns of Kazakhstan's flora in general, and specifically in the Kazakhstan Altai. According to A.A. Sokolov's

interpretation [6], the Kazakhstan Altai includes the Southwestern Altai, characterized by a complex and diverse mountainous landscape, as well as varying soil-climatic and hydrological conditions.

Research objective: to conduct a systematic, chorological analysis of ferns of the Southwestern Altai and to determine some aspects of their ecological and biological indicators to identify development trends and formation conditions.

Experimental

The study focuses on a set of fern species found in the flora of the Southwestern Altai, inhabiting all typical habitats within this mountainous region.

The mountain structure of the Southwestern Altai consists of a system of high ridges ranging from 1,500 to 2,800 meters above sea level, while low-mountain and foothill areas are situated at elevations of 500–700 meters. The climate is sharply continental, characterized by cold, long winters, hot summers, and significant temperature fluctuations throughout the day, seasons, and year. Annual precipitation varies from 400–550 mm in the western part to 1,500 mm at the upper forest line in the eastern and northeastern parts of the region [7].

To achieve the research objectives, we relied on the results of long-term field studies conducted in the Ivanovsky, Ubinsky, Ulbinsky, Koksinsky, Lineisky, and Kholzun ridges. Additionally, we examined herbarium collections housed in the herbarium fund of the RSE on the Right of Economic Management "Altai Botanical Garden" (acronym ABG) and utilized publications by the garden's staff [8–11]. The floristic survey of the study area was conducted using the route-reconnaissance method [12], which provided data on fern species composition. The taxonomic analysis follows the classification of V.K. Nayar [13], with modifications based on A.I. Shmakov [14]. To study the natural-territorial distribution of the pteridoflora of the Southwestern Altai, a chorionomic approach was applied. This approach is based on the principle that each species is associated with a specific phytochorion (a unit of floristic zoning), such as a floristic kingdom or region. The alignment of a species' distribution with particular phytochorions determines the classification of its range [15]. The type of range is established on a broad geographic scale, distinguishing species characteristic of an entire hemisphere (e.g., Holarctic) or specific geographic regions (Eurasian, North American-Asian, Asian). The range group further defines the species' confinement to a specific zone or vegetation belt [16]. The classification of fern distribution patterns in the flora of the Western Altai follows the principles proposed by A.S. Mochalov et al. [2] in their analysis of Ural ferns. From an ecological perspective, ferns were analyzed based on their moisture requirements and preferred substrate type [15].

The nomenclature of genera and species primarily follows the Global Biodiversity Information Facility (GBIF) database [17].

Results and Discussion

A review of scientific publications established that the flora of the Kazakhstan Altai includes 41 species of ferns from the class Polypodiopsida, representing 14 genera and 10 families [18–22]. As a result of our research and a critical revision of the available literature data [9] on ferns (Polypodiopsida) in the Southwestern Altai, which is part of the Kazakhstan Altai, we identified a pteridoflora comprising 32 species from 12 genera and 9 families. This accounts for 78.05 % of the fern species diversity in the Kazakhstan Altai (Table).

T a b l e

The composition of systematic groups of ferns (class Polypodiopsida) found in the South-West Altai

#	Family	Amount (count)		% of total species
		genera	species	
1	Polypodiacaceae–Polypody family	1	2	6.25
2	Hypolepidaceae — Hypolepis family	1	1	3.12
3	Aspleniaceae — Spleenwort family	1	2	6.25
4	Thelipteridacea–Marshfern family	2	2	6.25
5	Athyridaceae — Ladyfern family	1	4	12.50
6	Cystopteridaceae — Bladderfern family	2	6	18.75
7	Onocleodaceae — Sensitivefern family	1	1	3.12
8	Woodsiaceae — Clifffern family	1	7	21.88
9	Dryopteridaceae– Woodfern family	2	7	21.88
	TOTAL	12	32	100

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In the family-genus spectrum of ferns in the Southwestern Altai, three families contain two genera each (Dryopteridaceae, Cystopteridaceae, Thelypteridaceae), while the remaining six families each include a single genus. The family-genus coefficient of the pteridoflora is 0.75. Regarding the number of species composing the pteridoflora of the Southwestern Altai, the most species-rich families are Woodsiaceae, Dryopteridaceae, and Athyriaceae, each represented by seven species. The second-largest family is Cystopteridaceae, with six species, followed by Athyridaceae, which includes four species. The families Polypodiaceae, Aspleniaceae, and Thelypteridaceae each contain two species, while the remaining two families are represented by a single species. The family-species coefficient of the pteridoflora in the Southwestern Altai is 0.28. Thus, in taxonomic terms, the leading families with the highest number of species are Woodsiaceae, Dryopteridaceae, Cystopteridaceae, and Athyridaceae, accounting for 21.88 %, 21.88 %, 18.75 %, and 12.50 %, respectively, of the total species diversity. Together, these families comprise more than 75 % of the total fern species in the Southwestern Altai, while all other families collectively make up 25 % of the species composition.

The low saturation of families with genera and species indicates the ancient origin of ferns in the Southwestern Altai. It is well known that the older a florogenetic element is the fewer species it tends to contain [23]. The presence of many families and genera represented by only one or two species in the fern flora of the Southwestern Altai is characteristic of the flora of the northern regions of the Holarctic floristic kingdom as a whole [24].

The current distribution of these elements reflects the historical process of flora formation. In the chorological analysis, the ferns of the Southwestern Altai were classified into five chorological groups (Fig. 1).

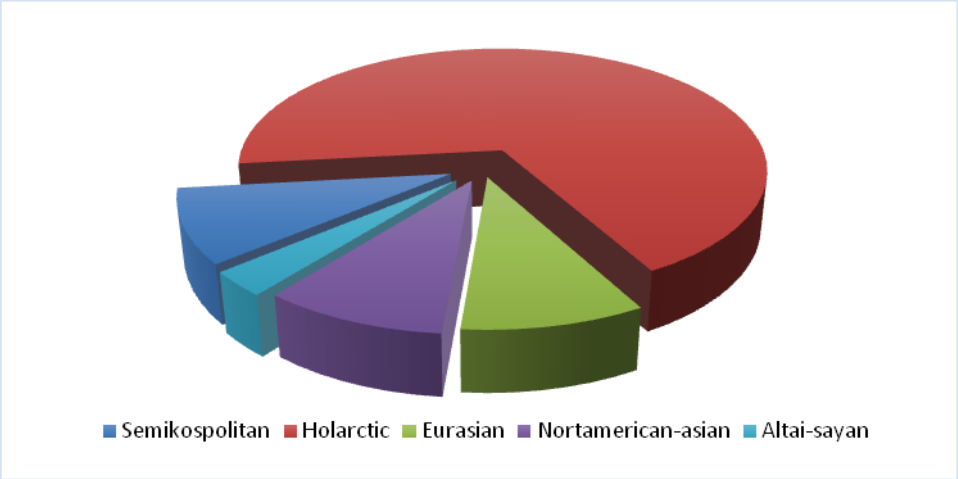

Figure 1. Fern habitats of the South-West Altai

1) Semicosmopolitan Group. This group is represented by three species (9.37 %) that are widely distributed in the Northern Hemisphere and extend into the Southern Hemisphere: *Pteridium aquilinum* (L.) Kuhn, *Asplenium trichomanes* L., *Cystopteris fragilis* (L.) Borb.;

2) Holarctic Group. This group includes 22 species (68.75 %) that are found across the Northern Hemisphere, specifically in Eurasia and North America: *Asplenium septentrionale* (L.) Hoffm., *A. ruta-muraria* L., *Athyrium filix-femina* (L.), *A. monomachii* (Kom.) Kom., *Cystopteris dickeana* R. Sim., *C. montana* (Lam.) Bernh., *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *D. cristata* (L.) A. Gray, *D. expansa* (C. Presl) Fraser-Jenkins et Germy, *D. dilatata* (Hoffm.) A. Gray, *D. filix-mas* (L.) Schott, *D. fragrans* (L.) Schott, *Gymnocarpium continentale* (Petrov) Pojark., *G. dryopteris* (L.) Newman, *Phegopteris connectilis* (Michx.) Watt, Roth., *Polystichum braunii* (Spenn.) Fée, *P. lonchitis* (L.) Roth, *Polypodium vulgare* L., *Thelypteris palustris* Schott, *Woodsia alpina* (Bolton) Gray, *W. ilvensis* (L.) R. Br., *W. glabella* R. Br.;

3) North American-Asian Group. This group is represented by three species (9.37 %): *Athyrium sinense* Rupr., *Polypodium sibiricum* Sipliv., *Woodsia calcarea* (Fomin) Shmakov;

4) Eurasian Group. This group includes three species (9.37 %): *Athyrium distentifolium* Tausch ex Opiz, *Cystopteris sudetica* A. Braun & Milde, *Woodsia heterophylla* (Turcz. ex Fomin);

5) Altai-Sayan Group. This group is represented by a single species (3.14 %), an Altai-Sayan endemic, *Cystopteris altajensis* Gureeva. This species was described from Siberia (Altai); type locality: "Altai Krai, Turochaksky District, Lake Teletskoye, lower reaches of the Bolshie Chili River, shaded rock niches" [25].

Thus, the ferns of the Southwestern Altai are predominantly represented by Holarctic species (68.75 %). The high proportion of Holarctic ferns indicates extensive connections between the local flora of the Southwestern Altai and the floras of the Holarctic. Additionally, the presence of cosmopolitan species within the pteridoflora suggests its antiquity.

We identified zonal-altitudinal groups based on species distribution within specific ecological zones or altitudinal belts. Accordingly, the ferns of the Southwestern Altai were classified into three zonal-altitudinal groups: plain-mountain-forest, mountain-forest, and high-mountain. The high-mountain group comprises species growing above the forest line in subalpine meadows, rocky screes, and well-lit rock outcrops, with a vertical distribution range of 1,800–2,200 m above sea level. This group includes five species (15.65 %): *Athyrium distentifolium*, *Woodsia acuminata*, *W. asiatica*, *W. ilvensis*, and *W. heterophylla*. The mountain-forest group is the most species-rich, comprising 23 species (71.75 %) and encompassing a highly heterogeneous assemblage. Species within this group occur across the entire mountain-forest belt (900–1,700 m a.s.l.), predominantly in sparse coniferous and mixed forests. Representative species include *Athyrium filix-femina*, *A. monomachii*, *A. sinense*, *Botrychium lunaria*, *Dryopteris expansa*, *Matteuccia struthiopteris*, *Gymnocarpium dryopteris*, *Phegopteris connectilis*, *Polystichum braunii*, *P. lonchitis*, and *Pteridium aquilinum*. In the lower and middle mountain belts, *Dryopteris carthusiana* and *D. filix-mas* are found in shaded coniferous forests, whereas *Woodsia calcarea*, *Polypodium vulgare*, and *P. sibiricum* inhabit crevices of shaded, moss-covered, moist rock formations and granitoid outcrops. Meanwhile, *Asplenium septentrionale*, *A. trichomanes*, *Cystopteris altajensis*, *C. fragilis*, *C. dickeana*, *Dryopteris fragrans*, and *Gymnocarpium continentale* occur in illuminated rock crevices and rocky slopes. The plain-mountain-forest group is associated with both zonal vegetation (foothill coniferous and mixed forests) and intrazonal vegetation, including swamps, marshy meadows, riverbanks, and streams. This group comprises four species (12.5 %) distributed within an altitudinal range of 600–900 m a.s.l.: *Asplenium ruta-muraria*, *Cystopteris sudetica*, *Dryopteris cristata*, and *Thelypteris palustris*.

The observed zonal distribution of ferns in the study area aligns with the findings of A.I. Shmakov [26]. Analyzing the pteridoflora of the Altai, Tien Shan, and Semirechye, Shmakov demonstrated that most ferns are restricted to mountain systems, with only a few extending into lowland areas. This distribution pattern is closely linked to the evolutionary history of ferns, which were originally associated with forest vegetation. Over time, due to climatic shifts, certain species evolved adaptations that enabled them to colonize open, rocky environments. This explains the presence — albeit in limited numbers — of high-altitude species.

Ecological analysis of flora, including pteridoflora, involves assessing species' relationships with environmental conditions. Typically, this analysis examines species' affinity to factors such as moisture levels, rocky substrates, and calcium-rich soils [24].

The analysis of fern distribution in the Southwestern Altai revealed a distinct preference for rocky substrates, a pattern consistent with pteridofloras of other mountainous regions, particularly Southern Siberia [25]. Of the total species composition, 17 species (53.12 %) are confined to various rocky habitats and cliffs. As noted by I.I. Gureeva [25], small-sized species with compact rhizomes were commonly found in crevices, where microclimatic conditions — such as temperature and moisture regimes — resemble those of forest understories, while light spectra approximate those of open landscapes. In the Southwestern Altai, this group includes all species of the genus *Woodsia* (*W. acuminata*, *W. alpina*, *W. asiatica*, *W. calcarea*, *W. ilvensis*, *W. glabella*, *W. heterophylla*), as well as *Asplenium septentrionale* and *A. trichomanes*.

On flat surfaces of granitoid outcrops with minimal soil accumulation, we recorded the presence of *Cystopteris fragilis*, *C. dickeana*, *Polypodium sibiricum*, and *P. vulgare*. Additionally, *Athyrium distentifolium* and *Dryopteris fragrans* were observed on large Kurums (rock streams).

Based on moisture requirements, four major plant ecomorphs are traditionally distinguished concerning water regimes: xerophytes, mesophytes, hygrophytes, and hydrophytes. Intermediate groups that account for subtle variations in moisture availability are also recognized in floristic analyses [27].

The species of the studied pteridoflora were divided into 6 groups, which represent variations of 3 main ecomorphs (Fig. 2).

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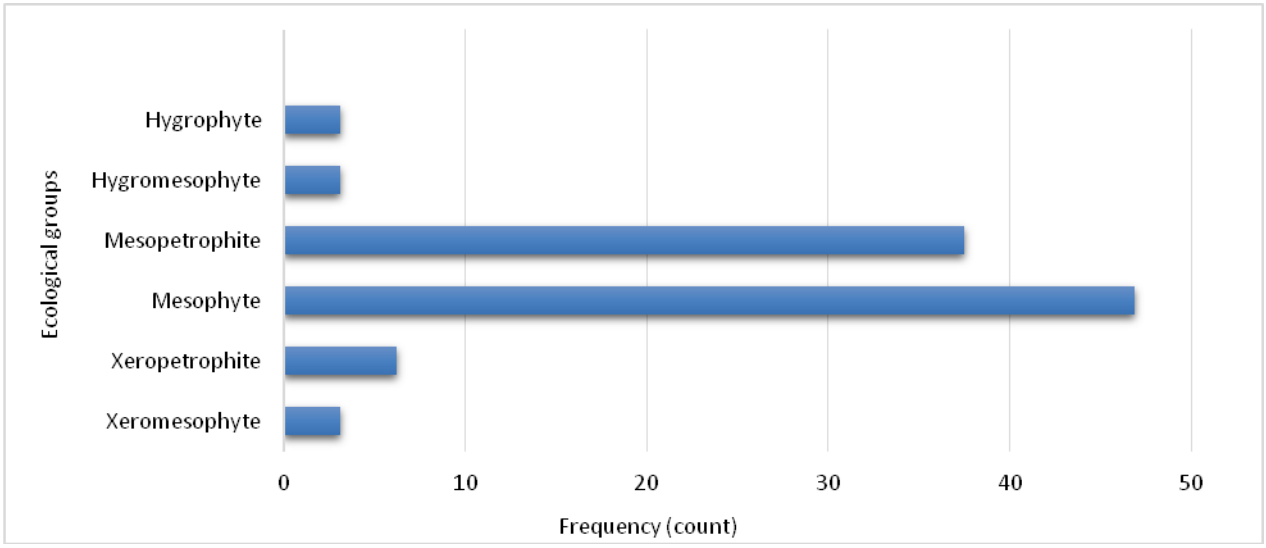

Figure 2. Distribution of the Southwestern Altai pteridoflora by moisture requirements

1. The xerophilicecomorph of ferns in the Southwestern Altai is scarce due to the biological and evolutionary characteristics of pteridophytes, represented by three species (9.37 %): *Woodsia asiatica* — a xeromesophyte (3.125 %), and *Asplenium septentrionale* and *Woodsia heterophylla* — xeropetrophytes (6.25 %). These species are confined to habitats with periodic or constant (but minor) moisture deficits, exhibiting high physiological drought tolerance yet responding positively to additional moisture under conditions of good drainage [28].

2. The mesophilic ecomorph occupies a dominant position in the studied flora and is represented by two groups: mesophytes and mesopetrophytes, demonstrating the prevalence of pteridophytes in moderately moist habitats. Some species exhibit tolerance to slightly drier conditions, while others prefer higher humidity levels. The mesophyte group is confined to moderately humid habitats in dark coniferous, broadleaf, mixed, and small-leaved forests, less frequently occurring in rocky forest glades covered with moss, wet forest meadows, and swamp edges. This group includes 15 species (46.87 %): *Athyrium distentifolium, A. filix-femina, A. monomachii, A. sinense, Cystopteris montana, C. sudetica, Dryopteris carthusiana, D. expansa, D. dilatata, D. filix-mas, Gymnocarpium dryopteris, Matteuccia struthiopteris, Phegopteris connectilis, Polystichum braunii, Pteridium aquilinum.* The mesopetrophyte group consists of ferns inhabiting shaded and humid environments in coniferous and mixed forests, on ledges beneath cliffs, and in rock crevices and scree habitats. In the Southwestern Altai, 12 species (37.5 %) are classified as typical mesopetrophytes: *Asplenium trichomanes, Cystopteris dickeana, C. fragilis, Gymnocarpium continentale, Polystichum lonchitis, Polypodium sibiricum, P. vulgaris, Woodsia acuminata, W. alpina, W. calcarea, W. ilvensis, W. glabella, Polystichum lonchitis.*

3. The hygrophilicecomorph of ferns in the Southwestern Altai is characterized by a high demand for soil moisture, preferring damp and wet habitats. This ecomorph includes two species: *Dryopteris cristata* (3.12 %) — a hygromesophyte, and *Thelypteris palustris* (3.12 %) — a true hygrophyte, growing in waterlogged meadows.

Thus, the ecological analysis demonstrated that ferns in the studied area are strictly confined to specific habitats and do not exhibit significant ecological diversity.

Conclusions

1 In the Southwestern Altai, 32 species from 12 genera and 9 families of ferns belonging to the class Polypodiopsida have been recorded. The dominant families are Woodsiaceae, Dryopteridaceae, Cystopteridaceae, and Athyriaceae, collectively comprising 75.0 % of the total pteridoflora species composition. The richest genera, accounting for 62.5 % of the species diversity, are Woodsia, Dryopteris, and Cystopteris.

2 The pteridoflora of the Southwestern Altai is predominantly formed by species with wide distribution ranges, particularly Holarctic species (22 species, 68.75 %), indicating a broad connection between the local

fern flora and the floras of the Holarctic region. The ancient origin of the pteridoflora in the Southwestern Altai is supported by the presence of genera represented by only one or two species.

3 The phytocoenotic confinement of the pteridoflora of the Southwestern Altai is categorized into three zonal-belt groups: plain-mountain-forest, mountain-forest, and high-mountain, ranging in elevation from 900 to 2200 m above sea level. Among these, the mountain-forest component is the most dominant, comprising 23 species (71.75 %).

4 The majority of pteridoflora species in the Southwestern Altai (53.12 %) are associated with various rocky habitats and cliffs. In terms of moisture preference, ferns are represented by three ecomorphs: xerophilic, mesophilic, and hygrophilic. Species growing under moderate moisture conditions prevail, with mesophytes accounting for 15 species (46.87 %) and mesopetrophytes for 12 species (37.5 %).

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Оңтүстік-Батыс Алтайдың папоротниктері қазақстандық Алтайдың птеридофлорасын (Polypodiopsida класы) зерттеудің нысаны ретінде

Мақалада қойылған мақсатқа сәйкес Оңтүстік-Батыс Алтайдағы қазақстандық Алтай папоротниктерінің жүйелік және хорологиялық талдау нәтижелері келтірілген, сондай-ақ птеридофлораның топырақ субстраттарына және ылғалмен қамтамасыз етілуіне байланысты таралу ерекшеліктері зерттелген. Зерттеу нәтижесінде птеридофлораның (Polypodiopsida класы) 32 түрден, 12 туыстан, 9 тұқымдастан тұратыны анықталды. Түр саны бойынша басым тұқымдастар — Woodsiaceae, Dryopteridaceae, Cystopteridaceae, Athyriaceae, олардың үлесі зерттелген аймақтағы жалпы түрлер санының 75 %-дан астамын құрайды. Оңтүстік-Батыс Алтай птеридофлорасының тұқымдас-түр коэффициенті 0,28 деңгейінде анықталып, оның түрлік құрамының тұқымдастарға қатысты аз қаныққандығын және көне флора екенін көрсетеді. Птеридофлора 5 таралу типіне жатқызылды, олардың ішінде голарктикалық түрлер (68,75 %) басым, бұл флораның Голарктика аймағымен байланысын айғақтайды. Өсу жағдайлары бойынша папоротниктер 3 биіктік-белдеу топтарына бөлінді: жазықтық-таулы-орманды, таулы-орманды және биік таулы. Оның ішінде таулы-орманды топ (23 түр, 71,75 %) басым, олар қылқан жапырақты, аралас және ұсақ жапырақты ормандарда, теңіз деңгейінен 900-1700 м биіктікте таралған. Сонымен қатар птеридофлораның әртүрлі тасты мекендер мен жартас субстраттарына ерекше бейімделуі анықталды. Ылғалмен қамтамасыз етілуіне байланысты папоротниктер 6 экологиялық топқа бөлінді, олардың ішінде мезофильді экоморфа басым: мезофиттер — 46,8 %, мезопетрофиттер — 37,5 %.

Кілт сөздер: таралу аймағы, түр, Оңтүстік-Батыс Алтай, птеридофлора, биіктік-белдеулік таралу, экоморфа.

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Папоротники Юго-Западного Алтая как объект изучения птеридофлоры (класс Polypodiopsida) Казахстанского Алтая

В статье, согласно поставленной цели, приведены результаты систематического и хорологического анализов папоротников Юго-Западного Алтая в пределах Казахстанского Алтая, а также проанализирована приуроченность птеридофлоры к почвенным субстратам и по отношению к увлажнению. Установлена птеридофлора (класс Polypodiopsida**)** в составе 32 видов, из 12 родов,9 семейств. По числу видов к ведущим семействам относятся Woodsiaceae, Dryopteridaceae, Cystopteridaceae, Athyridaceae, доля которых составляет свыше 75,0 % от общего числа видов исследуемой территории. Семейственно-видовой коэффициент птеридофлоры Юго-Западного Алтая равный 0,28 свидетельствует о низкой насыщенности семейств видами и указывает на ее древний возраст. Установлено, что птеридофлора относится к 5 типам ареалов, где доминирующую позицию занимают виды с голарктическим распространением — 68,75 %, что свидетельствует о связи с флорами Голарктики. По условиям произрастания папоротники распределились по 3 поясно-зональным группам: равнинно-горно-лесной, горно-лесной и высокогорной. Главенствующее положение занимает горно-лесная группа — 23 вида (71,75 %), произрастающие в хвойных, смешанных и мелколиственных лесах, приуроченных к горам в высотном пределе 900-1700 м н. у. м. Выявлена специфическая приуроченность птеридофлоры к разного рода каменистым местообитаниям и скалам. По требованию к влагообеспеченности экотопов

папоротники распределились на 6 групп, где доминирующую позицию занимает мезофильная экоморфа, представленная мезофитами — 46,8 % и мезопетрофитами — 37,5 % от общего видового состава.

Ключевые слова: ареал, вид, Юго-Западный Алтай, птеридофлора, поясно-зональное распределение, экоморфа.

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