Л.Н. Гумилев атындағы Еуразия ұлттық университетінің ХАБАРШЫСЫ.
BULLETIN of L.N. Gumilyov Eurasian National University.
ВЕСТНИК Евразийского национального университета имени Л.Н. Гумилева.
ISSN: 2616-7034. eISSN: 2663-130X

IRSTI 34.29.15
Research article

https://doi.org/10.32523/2616-7034-2026-155-2-134-148

Comparative analysis of morphological characters of nivicolous myxomycetes of the family Physaraceae in Katon-Karagay and Ile-Alatau State National Nature Parks

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Abstract. This study presents a comparative analysis of morphological characters of nivicolous myxomycetes of the genus *Physarum* Pers. recorded in the Katon-Karagay and Ile-Alatau State National Nature Parks. The aim was to identify diagnostically significant features allowing the delimitation of nivicolous taxa under conditions of high morphological similarity and ongoing taxonomic revision of the family. Material was collected in spring 2025 during active snowmelt in high-mountain regions of Eastern and Southeastern Kazakhstan at elevations of 1570–3180 m a.s.l. Morphological examination of 56 specimens was conducted using light microscopy, focusing on characters of sporocarps, peridium, capillitium, columella, and spores. Four nivicolous taxa were identified: *Badhamia albescens* (Ellis ex T. Macbr.) J.M. García-Martín, J.C. Zamora & Lado, *Nannengaella alpestris* (Mitchel, S.W. Chapm. & M.L. Farr) J.M. García-Martín, J.C. Zamora & Lado, *Physarum nivale* (Meyl.) Mar. Mey. & Poulain, and *Physarum vernum* Sommerf. The most abundant species was *Ph. vernum* (45 specimens), while *N. alpestris*, *Ph. nivale*, and *B. albescens* were represented by 6, 4, and 1 specimens, respectively. The most informative diagnostic characters were the type and shape of fruiting bodies, presence of a stalk, degree and pattern of calcification of the peridium and capillitium, presence and morphology of the columella, and spore size and ornamentation. Specimens of *N. alpestris*, *Ph. nivale*, and *Ph. vernum* generally correspond to their protologues, whereas some Kazakh specimens of *B. albescens* show notable differences, suggesting

Received: 17.05.2026. Accepted: 18.06.2026. Available online: 30.06.2026

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the possible presence of closely related, yet undescribed taxa in the region. The results confirm the high diagnostic value of morphological characters for nivicolous *Physarum* spp. and highlight the perspectives of integrated morphological and molecular studies in Kazakhstan.

Keywords: morphological analysis, high-mountain ecosystems, nivicolous myxomycetes, taxonomy, diagnostic characters, spore ornamentation

Introduction

Plasmodial slime molds (Myxomycetes, Amoebozoa) are a group of amoeboid protists that form macroscopic fruiting bodies—sporocarps—whose morphological characteristics have traditionally served as the basis for their systematics [1,2]. Despite the recent development of molecular phylogenetic method, which were applied as well to Physarales [17], the morphological characteristics of sporocarps remain important for species identification, especially in groups where habitually similar taxa differ in subtle morphological characters.

Among myxomycetes, a distinct ecological guild is the nivicolous, or snowbank myxomycetes, soil-inhabiting species that develop in the spring along the edges of melting snow in mountainous regions of the temperate and subarctic zones. They require a long-lasting snow cover with low positive temperatures, and fruiting upon snow melt when intense solar radiation warms up the soil. Virtually all nivicolous myxomycetes are members of the dark-spored clade, one of the two basal clades of myxomycetes. In addition to their dark spore mass (melanin prevents damage by UV radiation), many nivicolous species are characterized by a dense calcareous peridium, [3,4,7].

According to the latest data, nivicolous myxomycetes account for about 10% of the total species diversity of Myxomycetes and include more than 100 described species, concentrated primarily in the dark-spored families Physaraceae and Didymiaceae [5]. Nivicolous species of the Physaraceae are widely distributed in high-altitude habitats and are characterized by a combination of adaptive morphological similarities and stable diagnostic differences.

Research on nivicolous myxomycetes has been conducted in various mountainous regions of Europe, North Asia, and North America, where their ecological characteristics, seasonal development, and morphological variability have been described [3,4,6–11]. These studies have shown that the structural features of the peridium, capillitia, calcareous deposits, columns, and spores are particularly important for the accurate diagnosis of nivicolous species. However, for the territory of Kazakhstan, such studies remain few and far between and fragmentary [12,13]. The current knowledge of myxomycete diversity in the country is based on records accumulated over more than a century of research, covering different regions and ecological conditions. Nevertheless, many areas remain poorly investigated, particularly high-mountain ecosystems where nivicolous species occur. A recent review of myxomycete records from Kazakhstan summarized the history of research and the currently known species diversity in the country [13]. These data indicate that further studies are needed to improve our understanding of the distribution and ecology of myxomycetes in Kazakhstan. The high-altitude regions of Eastern and Southeastern Kazakhstan, including the Katon-Karagay and Ile-Alatau State National Nature Parks, have not yet been specifically studied from the perspective of the comparative morphology of nivicolous representatives of the Physaraceae family.

Most representatives of the Physaraceae family were historically classified within the broad genus *Physarum* Pers. However, modern molecular phylogenetic studies have revealed the

polyphyly of this genus as traditionally understood and have led to a revision of the systematic placement of several species [14–17]. In particular, *Physarum albescens* Ellis ex T. Macbr. was transferred to the genus *Badhamia* Berk., *Physarum alpestre* Mitchel, S.W. Chapm. & M.L. Farr to *Nannengaella* J.M. García-Martín, J.C. Zamora & Lado., and *Ph. nivale* (Meyl.) Mar. Mey. & Poulain will, perhaps with further revisions, be transferred to *Aethaliopsis* Zopf.[17]. These changes, caused by the rule of monophyly for a valid taxonomic unit, underscore the need to reassess the morphological characteristics of the nivicolous taxa in light of current understanding of the Physaraceae system.

In Kazakhstan, the study of nivicolous myxomycetes is of particular relevance, as the country's mountain ecosystems are characterized by a wide range of elevations, diverse slope exposures, and prolonged snow cover in certain high-altitude regions. These factors create favorable habitats for snowmelt species; however, their species diversity and morphological variability remain insufficiently studied. For the first time, a comparative analysis of the morphological characteristics of nivicolous representatives of the Physaraceae family is being conducted for the territories of the Katon-Karagai and Ile-Alatau State National Nature Parks, which helps fill a research gap regarding this group in Kazakhstan.

This study examines four nivicolous taxa of the Physaraceae family: *Badhamia albescens* (Ellis ex T. Macbr.) J.M. García-Martín, J.C. Zamora & Lado, *Nannengaella alpestris* (Mitchel, S.W. Chapm. & M.L. Farr) J.M. García-Martín, J.C. Zamora & Lado*, Physarum nivale* and *Physarum vernum* Sommerf, identified within the Katon-Karagay and Ile-Alatau State National Nature Parks. The aim of the study is to conduct a comparative analysis of their morphological characteristics and to identify the most consistent features relevant for the diagnosis, taxonomic interpretation, and further study of nivicolous myxomycetes in Kazakhstan.

Materials and research methods

The data for this study were collected during the snowmelt period in the Katon-Karagai and Ile-Alatau State National Nature Parks, located in the mountainous regions of Eastern and Southeastern Kazakhstan.

Field research was conducted within the Katon-Karagay State National Nature Park in the Sarymsak River valley, on the gentle northern and eastern slopes of the Sarymsak Range, and in the vicinity of the village of Katon-Karagay, from May 4 to 8, 2025. Collections were made at elevations of 1,570–1,880 m above sea level.

Within the Ile-Alatau State National Nature Park, research was conducted on the northern slopes of the Zailiyskiy Alatau, including the Medeu Gorge, adjacent valleys, the slopes of Mount Shymbulak, and the area around Big Almaty Lake, from April 26 to May 1, 2025. Samples were collected at elevations ranging from 1840 to 3180 meters above sea level.

Specimens of nivicolous myxomycetes from the family Physaraceae were chosen for comparative analysis. The samples were identified based on the morphological concept of species, using the identification keys and descriptions provided in the work by Poulain et al. [18]. Air-dried sporocarps were studied using a Keyence VHX 7000 stereomicroscope (Keyence Corporation, Osaka, Japan) and a Leica DM2500 microscope (Leica Mikrosysteme Vertrieb GmbH, Wetzlar, Germany). Temporary microscopic slides were prepared by placing fragments of fruiting bodies with capillitium and spores in a drop of water on a microscope slide. Spore size was measured for 50 spores per sample (excluding spore ornamentation), and values are given as the mean ± standard deviation. The examined specimens were deposited in the private herbarium of M.

Schnittler (abbreviation: sc). The taxonomy in this study follows the nomenclatural database Nomenmyx [19] (Lado et al. 2005–2026).

Results

The study identified four nivicolous taxa of the Physaraceae family: *Badhamia albescens* (= *Physarum albescens*), *Nannengaella alpestris* (= *Physarum alpestre*), *Physarum nivale*, and *Physarum vernum*.

A total of 56 samples were analyzed. The most common species was *Physarum vernum*, with 45 samples, accounting for the majority of the material studied. *Nannengaella alpestris* was represented by 6 samples, *Physarum nivale* by 4 samples, and *Badhamia albescens* by 1 sample.

The data obtained indicate an unbalanced representation of the studied taxa in the collected material. Within the studied areas (Katon-Karagay and Ile-Alatau national parks), P. vernum was the most frequently encountered species. This may suggest a wider ecological range and greater adaptability of this species to local nivicolous conditions, although further research is needed to test this hypothesis.

The results of the study of the morphological characteristics of the identified species are presented in the descriptions below and in Table 1.

Taxonomy and morphological comparison of species

Badhamia albescens (Ellis ex T. Macbr.) J.M. García-Martín, J.C. Zamora & Lado, Persoonia 51: 109–110 (2023) ≡ Physarum albescens Ellis ex T. Macbr., N. Amer. Slime-moulds, ed. 2: 86 (1922) = Leocarpus fulvus T. Macbr., N. Amer. Slime-moulds: 82 (1899) = Physarum rubronodum G.W. Martin, J. Wash. Acad. Sci. 38(7): 238 (1948)

Study area: Kazakhstan, East Kazakhstan Region, Katon-Karagai District, Katon-Karagai State National Nature Park: Sarymsak River valley, open meadow in a cedar forest, on dry grass and leaves, 49.09531 N, 85.65785 W, 1828 m a.s.l., May 5, 2025, leg. M. Schnittler and O.N. Shchepin, sc37823.

This is one of the most easily recognizable species of the Physaraceae family, known for its stalk, the light, creamish yellowish-ochre or even golden color of its peridium, and the numerous bright yellow capillitium nodules. In classic representatives of this species, the fruiting bodies are usually sporocarps, with sporangia that are ovoid or globose, often on a thin, slender brown stalk. The hypothallus is brown and clearly defined. The peridium is double: the outer layer is dense and calcified to varying degrees, while the inner layer is thin and membranous. The capillitium is well-developed, colorless, reticulate, tubular, with yellow calcareous nodules. The spores are dark in color, with a warty ornamentation.

The sample studied is distinguished by a number of characteristics from both the classic form of *B. albescens* [18,20] and the specimens of *Badhamia* aff. *albescens* discovered in the Ile-Alatau National Park in 2013 [13]. Fruit bodies consist of irregularly shaped sporocarps and short plasmodiocarps, sessile or on a short brown stalk (Fig. 1A). The color of the capillitium also differs: in the studied specimen, the capillitium filaments are pale brown in both reflected and transmitted light, rather than colorless (Fig. 1B). The spores are dark brown in bulk, violet-brown in transmitted light, uniformly warty, and have a diameter of (10.4–) 11.2–12.5 (–13.1) μm (Fig. 1C), which is consistent with classical descriptions.

The combination of a stalk, a distinct hypothallus, and a typical physaroid capillitium with bright yellow nodules reliably distinguishes this species from other nivicolous species of the Physaraceae.

Despite its external distinctiveness, recent genetic data suggest that the name *B. albescens* encompasses a complex of closely related biological species [21]. Therefore, this species is important as a model organism for discussing the stability of traditional morphological traits in nivicolous myxomycetes and the dispersal capacity of cryptic soil protist species [21,22].

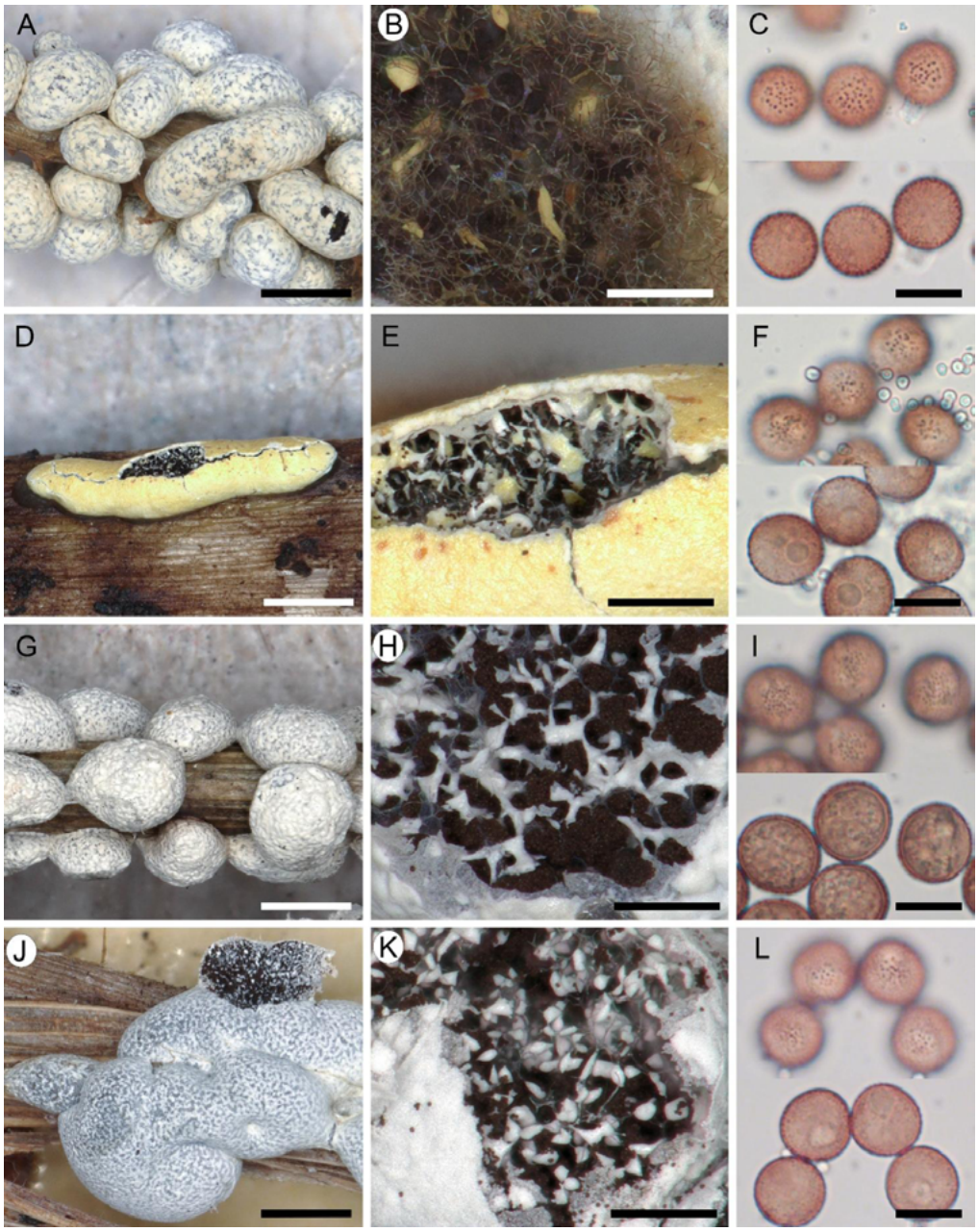

Figure 1. Badhamia albescens (sc37823) A–C; Nannengaella alpestris (sc37814) D–F; Physarum nivale (sc37801) G–I; Physarum vernum (sc37707) J–L. Fruiting bodies (A, D, G, J); details of the peridium and capillitium (B, E, H, K); spores in transmitted light (C, F, I, L). Scale bars: A, D, G, J = 1000 μm; B, E, H, K = 200 μm; C, F, I, L = 10 μm.

Nannengaella alpestris (Mitchel, S.W. Chapm. & M.L. Farr) J.M. García-Martín, J.C. Zamora & Lado, Persoonia 51: 110 (2023) ≡ Physarum alpestre Mitchel, S.W. Chapm. & M.L. Farr, Mycologia 78(1): 68 (1986)

Study area: Kazakhstan, Almaty, Ile-Alatau State National Nature Park: valley 450 m northeast of the dam in front of the Medeu Stadium, on dry grass, 43.14865 N, 77.06855 W, 1,934 m a.s.l., April 26, 2025, leg. M. Schnittler, O.N. Shchepin, Yu.K. Novozhilov, and Zh. Azirakhmet, sc37678; 43.14867 N, 77.06847 W, 1,940 m a.s.l., sc37660; East Kazakhstan Region, Katon-Karagai District, Katon-Karagay State National Nature Park: Sarymsak River valley, open meadow in a cedar forest, on dry grass, 49.10930 N, 85.66324 W, 1667 m a.s.l., May 5, 2025, leg. M. Schnittler and O.N. Shchepin, sc37814; 49.10918 N, 85.66302 W, 1669 m a.s.l., sc37819; 49.10881 N, 85.66271 W, 1,690 m a.s.l., sc37817; 49.10810 N, 85.66250 W, 1682 m a.s.l., May 7, 2025, sc37851.

This is a typical plasmodiocarpous nivicolous species with a thick, heavily calcified outer peridium. The morphological characteristics of the studied specimens correspond to the protologue [23] (Fig. 1D–F). Fruit bodies are most often clustered or densely grouped; plasmodiocarps are usually more or less elongated, often curved and branched, sometimes forming labyrinthine structures up to 40 mm long; rarely, sessile, cushion-shaped sporocarps are present. The color of the peridium varies from cream-yellow and canary-yellow to ivory. The hypothallus is thin, membranous, transparent, colorless or pale yellow, and usually becomes calcified along the margin of the fruiting bodies. The peridium is double: the thick outer layer is smooth, brittle, corky-calcareous, white, and covered with a yellow transparent membrane as a third layer; the inner layer (the true peridium) is thin, membranous, transparent, and splits irregularly. The capillitium is dense, reticulate, of the badhamoid type in the lower part, with large, branched nodes; above, it is physaroid, with transparent filaments; the nodes vary from large, angular, and branching to small, spindle-shaped, shiny, yellow, ivory-colored, or pale cream. The columella is well-developed, calcified, white, yellow, or creamy white, often forming a central ridge along the plasmodiocarp. Spores are black in bulk, dark purplish-brown in transmitted light, warty, (9.0–) 10.3–11.5 (–12.0) μm in diameter.

The reclassification of this species into Nannengaella is well supported by its strong calcification, well-developed calcareous columella, and the general morphological characteristics of representatives of this clade as described in the revision by García-Martín et al. [17].

Nannengaella alpestris is reliably distinguished from other nivicolous species of the family Physaraceae by its elongated plasmodiocarpous fruiting bodies, combined with a strongly calcareous yellow or cream-colored peridium and abundant yellowish, angular or branching lime nodes.

Physarum nivale (Meyl.) Mar. Mey. & Poulain, in Poulain, Meyer & Bozonnet, Les Myxomycètes: 551 (2011) ≡ Badhamia panicea var. niviale Meyl., Bull. Soc. Vaud. Sci. Nat. 56: 66 (1925)

Study area: Kazakhstan, East Kazakhstan Region, Katon-Karagay District, Katon-Karagay State National Nature Park: Sarymsak River valley, on dry grass, 49.11287° N, 85.66566° E, 1619 m a.s.l., 04 May 2025, leg. M. Schnittler and O.N. Shchepin, sc37797; 49.11269° N, 85.66648° E, 1611 m a.s.l., sc37801; 49.1119011° N, 85.66550418° E, 1635 m a.s.l., sc37804; 49.09341° N, 85.65755° E, 1844 m a.s.l., 05 May 2025, sc37827.

Physarum nivale is a nivicolous species forming relatively small sessile sporocarps and short, densely clustered plasmodiocarps. The examined specimens collected in Katon-Karagay National Park correspond to the protologue in their main morphological characteristics [24,25] (Fig. 1G–I). The fruiting bodies are usually rounded, sometimes kidney-shaped, and more rarely worm-like elongated; the base is often distinctly compressed. The peridium is greyish, with scat-

tered calcareous thickenings. The capillitium is well developed, reticulate, of the badhamioid type, with large angular and branching nodes densely filled with calcareous granules and connected by thin, hyaline capillitial threads free of lime. The spore mass is dark brown; the spores are finely and evenly verrucose, (11.0–) 11.7–13.1 (–13.9) μm in diameter. Macroscopically, the species strongly resembles Physarum vernum, but differs in the more rounded outline of the sporocarps, which only exceptionally form short plasmodiocarps, stronger calcification of the capillitium, and darker spores with a paler side [18]. In its barcodes, both species differ strongly [13].

Physarum nivale belongs to a group of species whose taxonomic placement will probably be revised in the near future. For now, it is retained in the genus Physarum; however, its phylogenetic position indicates a close relationship to the type species of the genus Aethaliopsis [17].

Physarum vernum Sommerf., Syst. Mycol. 3: 146 (1829) ≡ Badhamia verna (Sommerf.) Rostaf., Sluzowce monogr. 145 (1874)

Study area: Kazakhstan, Almaty, Ile-Alatau State National Nature Park: steep lateral ravine with a small stream, ca. 600 m south of the dam above the Medeu stadium, right side, along the road to Shymbulak, near snow patches, on dry grass, 43.14527° N, 77.05899° E, 1900 m a.s.l., 26 April 2025, leg. M. Schnittler, O.N. Shchepin, Yu.K. Novozhilov and Zh. Azirakhmet, sc37672; snow patches in open woodland of Picea schrenkiana, small lateral valley above a steep gorge, near snow patches, on dry grass, 43.12724° N, 77.05270° E, 2312 m a.s.l., 27 April 2025, sc37686; 43.12719° N, 77.05297° E, 2307 m a.s.l., sc37687; 43.12699° N, 77.05305° E, 2300 m a.s.l., sc37688; 43.12720° N, 77.05274° E, 2322 m a.s.l., sc37692; 43.12718° N, 77.05269° E, 2318 m a.s.l., sc37693; 43.12821° N, 77.05091° E, 2315 m a.s.l., sc37694; 43.12713° N, 77.05295° E, 2313 m a.s.l., sc37695; snow patches in open woodland of Picea schrenkiana, open meadows in the upper part of the valley, near snow patches, on dry grass, 43.12574° N, 77.05403° E, 2331 m a.s.l., sc37696; 43.12509° N, 77.05408° E, 2342 m a.s.l., sc37698; northern slope, left side of the valley across the road, ca. 3.2 km south-southeast of the dam, large open meadows, near snow patches, on dry grass, 43.12494° N, 77.07485° E, 2255 m a.s.l., 29 April 2025, sc37704; 43.12210° N, 77.07536° E, 2279 m a.s.l., sc37706; 43.11986° N, 77.07563° E, 2298 m a.s.l., sc37691; northern slope, left side of the valley across the road, ca. 4.2 km south-southeast of the dam, alpine meadows with deep erosion depressions, near snow patches, on dry grass, 43.11854° N, 77.07418° E, 2376 m a.s.l., sc37707; 43.11504° N, 77.07335° E, 2434 m a.s.l., sc37725; northern slope, left side of the valley across the road, ca. 2.8 km south-southeast of the dam, small open meadows among open woodland of Picea schrenkiana Fisch. & C.A.Mey, near snow patches, on dry grass, 43.12800° N, 77.07323° E, 2195 m a.s.l., sc37711; 43.12802° N, 77.07327° E, 2194 m a.s.l., sc37712; 43.12749° N, 77.07333° E, 2215 m a.s.l., sc37713; 43.12746° N, 77.07333° E, 2215 m a.s.l., sc37715; 43.12753° N, 77.07327° E, 2231 m a.s.l., sc37716; 43.12748° N, 77.07332° E, 2207 m a.s.l., sc37719; 43.12508° N, 77.07415° E, 2247 m a.s.l., sc37721; 43.12484° N, 77.07457° E, 2237 m a.s.l., sc37722; 43.12398° N, 77.07542° E, 2257 m a.s.l., sc37724; 43.12802° N, 77.07334° E, 2201 m a.s.l., sc37728; 43.12486° N, 77.07458° E, 2247 m a.s.l., sc37734; 43.12479° N, 77.07465° E, 2253 m a.s.l., sc37735; gentle southern slope above the upper cable car station, below the summit of Shymbulak, near snow patches, on dry grass, 43.11718° N, 77.11378° E, 3169 m a.s.l., 30 April 2025, sc37753; 43.11766° N, 77.11414° E, 3183 m a.s.l., sc37755; steep southern slope below the middle cable car station, near the upper forest limit, near snow patches, on dry grass, 43.11979° N, 77.09930° E, 2802 m a.s.l., sc37749; road from Shymbulak village, near the tourist base, gentle western slopes, isolated snow patches in clearings of open woodland of Picea schrenkiana, near snow patches, on dry grass, 43.11375° N, 77.07751° E, 2431 m a.s.l., 1 May 2025, sc37776; 43.11375° N, 77.07755° E, 2438 m a.s.l., sc37777; 43.11345° N, 77.07768° E, 2444 m a.s.l., sc37779; 43.11342° N, 77.07770° E, 2444 m a.s.l., sc37781.

Kazakhstan, East Kazakhstan Region, Katon-Karagay District, Katon-Karagay State National Nature Park: descent along the Sarymsak River valley, middle part of the valley, near snow patches, on dry grass, 49.11545° N, 85.66699° E, 1576 m a.s.l., 4 May 2025, leg. M. Schnittler and O.N. Shchepin, sc37810; 49.11289° N, 85.66557° E, 1619 m a.s.l., sc37796; 49.11158° N, 85.66478° E, 1621 m a.s.l., sc37805; 49.11041° N, 85.66426° E, 1642 m a.s.l., sc37807; 49.11043° N, 85.66413° E, 1646 m a.s.l., sc37809; middle part of the valley, near snow patches, on dry grass, 49.10930° N, 85.66326° E, 1667 m a.s.l., 5 May 2025, sc37816; 49.10918° N, 85.66300° E, 1666 m a.s.l., sc37822; 49.10811° N, 85.66252° E, 1686 m a.s.l., 7 May 2025, sc37853; ascent along the Sarymsak River valley, upper part of the valley, near snow patches, on dry grass, 49.09338° N, 85.65749° E, 1845 m a.s.l., 5 May 2025, sc37825; 49.09336° N, 85.65751° E, 1850 m a.s.l., sc37826; 49.09337° N, 85.65761° E, 1842 m a.s.l., sc37829.

This is a widespread nivicolous species, usually forming short, sinuous, irregularly shaped plasmodiocarps, greyish-white due to abundant calcium carbonate. The morphological characteristics of the specimens examined by us correspond to the protologue [26] (Fig. 1J–L). The plasmodiocarps are variable in shape, confluent, but do not form distinctly sinuous structures; individual fruiting bodies are slightly rounded-flattened, smooth, and, when fused, form broad patches. The peridium is very thin and fragile, dehiscing irregularly and later partly disappearing. A stalk is absent. The capillitium is reticulate, densely branched, physaroid, composed of white calcareous nodes, angular or fusiform, connected by thin hyaline threads; sometimes, due to their shortening, it becomes almost badhamioid in appearance. The spores are dark brown in mass, pale violet-brown in transmitted light, (11.1–) 11.8–12.4 (–12.5) μm in diameter.

Physarum vernum is morphologically closest to Physarum nivale; however, it differs from this species by the predominance of large, irregularly shaped plasmodiocarps closely appressed to one another, a more physaroid capillitium with predominantly non-calcareous threads bearing small angular or fusiform nodes, and paler spores.

The phylogenetic position of Ph. vernum remains unknown and requires further study, but the two specimens (sc30257 and 30091) clustering with Physarum nivale in García-Martín [17] were now revised as Ph. nivale.

Table 1

Comparative table of morphological characters

Species	*Badhamia albescens*	*Nannengaella alpestris*	*Physarum nivale*	*Physarum vernum*
Type of fruiting bodies	sporangia, usually clustered, medium to very large colonies	predominantly narrow, elongated plasmodiocarps, often curved, branched, sometimes labyrinthiform; nearly always with small colonies	sporocarps and short plasmodiocarps, medium to large colonies	usually clustered, irregularly shaped plasmodiocarps, more rarely sessile sporocarps, often in large colonies
Stalk	often short, weak	absent	absent	absent
Size of fruiting bodies	small to medium	0.3–1 mm wide, 0.3–0.5 mm high, up to 40 mm long	small	small to large (0.4–0.8 cm) plasmodiocarps

Peridium color	pale yellow, golden, ochre-yellow	cream-yellow, canary-yellow, ivory-colored	greyish to whitish	greyish to whitish
Peridial calcification	abundant, in irregular patches	lime forms a continuous dense crust	abundant, in irregular patches	abundant, in irregular patches
Columella	absent	well-developed, convex, extending along the base of the entire plasmodiocarp, white, yellow, or cream-colored	absent	absent
Capillitium	reticulate, physaroid, with yellow fusiform or angular lime nodes	reticulate, badhamioid in the lower part and physaroid above; nodes yellowish, large and angular or small and fusiform	reticulate, badhamioid, with large branching white lime nodes	reticulate, physaroid, with white fusiform or angular lime nodes connected by thin hyaline threads; locally almost badhamioid
Spores	dark brown in mass, violet-brown in transmitted light, evenly verrucose, (10.4–) 11.2–12.5 (–13.1) μm in diameter	dark brown in mass, pale violet-brown in transmitted light, (11.1–) 11.8–12.4 (–12.5) μm in diameter	dark brown in mass and in transmitted light, finely and evenly verrucose, (11.0–) 11.7–13.1 (–13.9) μm in diameter	moderately dark to dark violet-brown; spores 9.4–18.1 μm in diameter, with variable ornamentation; specimens corresponding to f. parvisporum have spores 11–12 μm in diameter.

Discussion

During the study conducted in Katon-Karagay and Ile-Alatau State National Nature Parks, four nivicolous species of the family Physaraceae were recorded out of the seven known to science: Badhamia albescens, Nannengaella alpestris, Physarum nivale, and Physarum vernum. Two of these species (Physarum nivale and Nannengaella alpestris) are new records for Kazakhstan, while the other two (Badhamia albescens and Physarum vernum) were recently published as new records for the country [13]. The remaining species, Nannengaella alpina (Meyl.) J.M. García-Martín, J.C. Zamora & Lado (= Physarum alpinum Meyl.), Craterium andinum (Meyl.) J.M. García-Martín, J.C. Zamora & Lado (= Physarum andinum Meyl.), and Badhamia alpina G. Lister, were not found during the present study.

The examined specimens of Nannengaella alpestris, Physarum nivale, and Ph. vernum possess sets of characters typical of these species and fully correspond to their protologues. This result demonstrates the stability of diagnostically important morphological characters known for these species. At the same time, the specimen of Badhamia albescens found in Katon-Karagay National Nature Park in 2025 differs both from the specimens found in Ile-Alatau National Nature Park in 2013 [13] and from the classical forms of B. albescens known from the mountain systems of Europe and North America [18]. These differences are substantial enough to suggest that some specimens from Kazakhstan may belong to a species of Badhamia unknown to science, close to the heterogeneous species complex of B. albescens.

The differences revealed among the studied taxa confirm the particular diagnostic value of several morphological characters for distinguishing nivicolous species of the family Physaraceae. The most informative characters for species delimitation are the type and shape of the fruiting body, the presence of a stalk, the pattern of lime distribution in the peridium and its color, as well as the degree of calcification and color of the capillitium. However, as the latter two characters

are connected to lime deposition, which may be completely absent under suboptimal conditions, they are not well pronounced in all specimens. All these characters have also previously been considered as key for the diagnosis of representatives of Physaraceae [17,27].

Comparison of the obtained data with current taxonomic concepts shows that classical morphological characters of myxomycetes require careful interpretation because of frequent cases of convergent evolution [28–30]. The transfer of Physarum albescens to the genus Badhamia and Physarum alpestre to the genus Nannengaella confirms that the traditional broad concept of the genus Physarum does not fully reflect the real phylogenetic relationships within Physaraceae [17]. Therefore, similar morphological characters in nivicolous species may be associated not only with phylogenetic relatedness, but also with convergent adaptation to similar ecological conditions.

For Kazakhstan, such studies are of particular importance, since nivicolous myxomycetes of the country's high-mountain regions remain insufficiently studied. The results of the present work add to the knowledge of the morphological diversity of representatives of Physaraceae in the mountain ecosystems of Eastern and South-Eastern Kazakhstan. In addition, the detection of a potentially new species within the Badhamia albescens complex confirms the high taxonomic potential of the region and the need for further research.

Thus, the comparative analysis showed that morphological characters remain an important tool for diagnosing nivicolous representatives of Physaraceae; however, they should be considered together with modern molecular phylogenetic data [30]. The main conclusion of the study is that the examined taxa have stable morphological differences that allow species to be distinguished and their taxonomic position to be clarified.

Conclusion

The system of the family Physaraceae is currently undergoing rapid revision. Multigene phylogenetic data have already shown that the traditional broad concept of the genus *Physarum* does not reflect natural evolutionary relationships, and that a considerable proportion of nivicolous species have been or will be reassigned to other genera. Nevertheless, the morphological differences among the nivicolous taxa considered here generally retain their high diagnostic value and allow them to be reliably distinguished through careful analysis of the fruiting bodies, as well as enabling the detection of species potentially new to science.

The results of this study confirm the promise of further research on nivicolous myxomycetes in Kazakhstan, especially when using an integrated approach combining morphological and molecular genetic methods.

Author Contributions

ZA — investigation, formal analysis, writing — original draft preparation. OS — conceptualization, investigation, data processing, formal analysis, methodology development, visualization, writing — original draft preparation. MS — conceptualization, investigation, data collection, methodology development. GA — conceptualization, investigation, data processing. RB — conceptualization, funding acquisition.

Funding

The study was carried out with financial support from the Ministry of Science and Higher Education of the Republic of Kazakhstan under grant number AP23489210 ("Study of the species and genetic diversity of nivicolous myxomycetes in Eastern and Southern Kazakhstan").

Acknowledgments

The authors express their gratitude to Prof. Yu.K. Novozhilov for his participation in the field studies.

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Катонқарағай және Іле-Алатауы мемлекеттік ұлттық табиғи парктері аумақтарындағы Physaraceae тұқымдасына жататын нивальды миксомицеттердің морфологиялық белгілеріне салыстырмалы талдау

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Аңдатпа. Бұл зерттеуде Катонқарағай және Іле-Алатауы мемлекеттік ұлттық табиғи парктері аумағында анықталған *Physarum Pers.* туысына жататын нивальды миксомицеттердің морфологиялық белгілеріне салыстырмалы талдау жүргізілді. Жұмыстың мақсаты – морфологиялық ұқсастығы жоғары және тұқымдастың таксономиялық қайта қаралуы жалғасып жатқан жағдайда нивальды таксондарды ажыратуға мүмкіндік беретін диагностикалық маңызды белгілерді анықтау. Зерттеу материалы 2025 жылдың көктемінде Шығыс және Оңтүстік-Шығыс Қазақстанның биік таулы аймақтарында қардың белсенді еру кезеңінде, теңіз деңгейінен 1570–3180 м биіктікте жиналды. Жарық микроскопиясы әдісімен 56 үлгіге морфологиялық зерттеу жүргізіліп, спорокарптардың, перидийдің, капиллицийдің, колумелланың және споралардың белгілеріне ерекше назар аударылды. Нивальды миксомицеттердің төрт таксоны анықталды: *Badhamia albescens* (Ellis ex T. Macbr.) J.M. García-Martín, J.C. Zamora & Lado, *Nannengaella alpestris* (Mitchel, S.W. Chapm. & M.L. Farr) J.M. García-Martín, J.C. Zamora & Lado, *Physarum nivale* (Meyl.) Mar. Mey. & Poulain және *Physarum vernum* Sommerf. Ең көп кездескен түр *Ph. vernum* болды (45 үлгі), ал *N. alpestris, Ph. nivale* және *B. albescens* сәйкесінше 6, 4 және 1 үлгімен ұсынылды. Ең маңызды диагностикалық белгілер ретінде жемісті денелердің типі мен пішіні, аяқшасының болуы, перидий мен капиллицийдің әктену дәрежесі мен сипаты, колумелланың болуы мен морфологиясы, сондай-ақ споралардың мөлшері мен орнаментациясы анықталды. *N. alpestris, Ph. nivale* және *Ph. vernum* үлгілері жалпы алғанда өздерінің бастапқы сипаттамаларына сәйкес келеді, ал *B. albescens* түрінің кейбір қазақстандық үлгілері айтарлықтай айырмашылықтар көрсетіп, өңірде әлі сипатталмаған жақын туыстас таксондардың болуы мүмкін екенін көрсетеді. Алынған нәтижелер нивальды *Physarum* өкілдері үшін морфологиялық белгілердің жоғары диагностикалық маңызын растайды және Қазақстандағы кешенді морфологиялық әрі молекулалық зерттеулердің болашағы зор екенін көрсетеді.

Түйін сөздер: морфологиялық талдау, биік таулы экожүйелер, Қазақстан, таксономия, диагностикалық белгілер, споралардың орнаментациясы

Сравнительный анализ морфологических признаков нивальных миксомицетов семейства Physaraceae на территориях Катон-Карагайского и Иле-Алатауского государственных национальных природных парков

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Аннотация. В настоящем исследовании представлен сравнительный анализ морфологических признаков нивальных миксомицетов рода *Physarum* Pers., выявленных на территории Катон-Карагайского и Иле-Алатауского государственных национальных природных парков. Целью работы являлось выявление диагностически значимых признаков, позволяющих разграничивать нивальные таксоны в условиях высокой морфологической сходности и продолжающейся таксономической ревизии семейства. Материал был собран весной 2025 года в период активного снеготаяния в высокогорных районах Восточного и Юго-Восточного Казахстана на высотах 1570–3180 м над уровнем моря. Морфологическое исследование 56 образцов проведено с использованием световой микроскопии с акцентом на изучение признаков спорокарпов, перидия, капиллиция, колумеллы и спор. Выявлено четыре нивальных таксона: *Badhamia albescens* (Ellis ex T. Macbr.) J.M. García-Martín, J.C. Zamora & Lado, *Nannengaella alpestris* (Mitchel, S.W. Chapm. & M.L. Farr) J.M. García-Martín, J.C. Zamora & Lado, *Physarum nivale* (Meyl.) Mar. Mey. & Poulain и *Physarum vernum* Sommerf. Наиболее многочисленным видом оказался *Ph. vernum* (45 образцов), тогда как *N. alpestris, Ph. nivale* и *B. albescens* были представлены соответственно 6, 4 и 1 образцом. Наиболее информативными диагностическими признаками оказались тип и форма плодовых тел, наличие ножки, степень и характер обызвествления перидия и капиллиция, наличие и морфология колумеллы, а также размеры и орнаментация спор. Образцы *N. alpestris, Ph. nivale* и *Ph. vernum* в целом соответствуют своим протологам, тогда как некоторые казахстанские образцы *B. albescens* демонстрируют заметные отличия, указывающие на возможное присутствие в регионе близкородственных, ещё не описанных таксонов. Полученные результаты подтверждают высокую диагностическую ценность морфологических признаков для нивальных представителей рода *Physarum* и подчёркивают перспективность комплексных морфологических и молекулярных исследований в Казахстане.

Ключевые слова: морфологический анализ, высокогорные экосистемы, Казахстан, таксономия, диагностические признаки, орнаментация спор

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