

MOSSES OF THE SURROUNDINGS OF THE SALTY LAKES ELTON AND
BASKUNCHAK IN CIS-CASPIAN LOWLAND, SOUTH-EAST EUROPEAN RUSSIA

ФЛОРА МХОВ ОКРЕСТНОСТЕЙ СОЛЯНЫХ ОЗЕР ЭЛЬТОН И БАСКУНЧАК,
ПРИКАСПИЙСКАЯ НИЗМЕННОСТЬ, ЮГО-ВОСТОК ЕВРОПЕЙСКОЙ ЧАСТИ РОССИИ

SVETLANA A. SURAGINA¹, ELENA A. IGNATOVA², ALEXANDER V. POPOV¹,
NINA YU. STEPANOVA³ & MICHAEL S. IGNATOV^{2,3}

СВЕТЛАНА А. СУРАГИНА¹, ЕЛЕНА А. ИГНАТОВА², АЛЕКСАНДР В. ПОПОВ¹,
НИНА Ю. СТЕПАНОВА³, МИХАИЛ С. ИГНАТОВ^{2,3}

Abstract

Elton and Baskunchak Lakes were used as an important source of the sodium chloride for the Russian industry, especially for food, since the Middle Ages. Their peculiar environments received now a conservation status. The moss flora of these two protected territories is described. The territory around Baskunchak Lake in Astrakhan Province is more xeric than that in Elton Lake area in Volgograd Province, despite the latter is situated only 100 km northward from the former. As a result, the moss flora in most types of vegetation around the Elton Lake is more diverse, and several species occurring here are absent at the Baskunchak area. However, the moss flora of Baskunchak area includes a number of epilithic species that are absent in Elton area. Epilites grow near the Baskunchak Lake shore, on Bolshoe Bogdo Mountain, 150 m alt., the highest point in Cis-Caspian lowland, formed of sandstones continuously uplifted by a still growing salt body underneath the mountain. Numerous sinkholes and several caves in the Baskunchak area provide sheltered conditions suitable for mosses. Especially interesting are two larger caves, where ten species were found, nine of them were absent elsewhere in both Elton and Baskunchak areas. The total number of species in Baskunchak and Elton areas are 45 and 35 species, respectively, while without ‘cave species’ the diversity is about equal, 36 and 35 species. The most salt-tolerant mosses at lake shores are *Pterygoneurum subsessile* and *Bryum bicolor*.

Резюме

Озера Эльтон и Баскунчак, расположенные в Прикаспийской низменности, использовались для добычи соли со времен средневековья. В настоящее время территории вокруг них получили охранный статус. В данной статье приводятся данные о флоре мхов этих двух особо охраняемых территорий. Условия в окрестностях озера Баскунчак в Астраханской области более засушливые по сравнению с таковыми в окрестностях озера Эльтон в Волгоградской области, находящегося всего в 100 км к северу от Баскунчака. Поэтому в большинстве типов местообитаний на оз. Эльтон число видов мхов больше, и некоторые из них на Баскунчаке найдены не были. Гора Большое Богдо, 150 м над ур. м., самая высокая точка Прикаспийской низменности, сложенная песчаниками, продолжающая подниматься за счет растущего под ней “соляного купола”, оказывается прибежищем для эпилитов, что компенсирует сокращение здесь числа мхов из-за более засушливого климата. Также в окрестностях оз. Баскунчак имеются многочисленные карстовые воронки, в которых создаются особые защищенные местообитания для мхов. В некоторых из них имеются пещеры, и в двух из них было найдено 10 видов мхов, из которых 9 не удалось найти за пределами пещер ни на Баскунчаке, ни на Эльтоне. Таким образом, общее число видов на Баскунчаке 45, на Эльтоне 35, хотя если исключить эти ‘пещерные виды’, то флоры мхов этих двух территорий оказываются сопоставимыми по богатству: 36 и 35 видов. Наиболее устойчивыми к засолению являются *Pterygoneurum subsessile* и *Bryum bicolor*, которые растут на почве, покрытой коркой соли на берегах обоих озер.

KEYWORDS: bryoflora, xeric mosses, salt-tolerant mosses

¹ – Volgograd State Socio-Pedagogical University, prospekt im. V.I. Lenina, 27, Volgograd 400005 Russia. E-mail: s-suragina@mail.ru; ORCID: (SS) 0000-0003-1516-7316; (AP) 0009-0005-3452-8334

² – Lomonosov Moscow State University, Faculty of Biology, Plant Ecology and Geography Dept., Leninskie Gory Str. 1–12, Moscow 119234 Russia. E-mail: arctoa@list.ru. ORCID: (EI) 0000-0001-6287-5660

³ – Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str., 4, Moscow 127276 Russia. E-mails: ny_stepanova@mail.ru, misha_ignatov@list.ru; ORCID: (NS) 0000-0002-8414-4794; (MI) 0000-0001-6096-6315

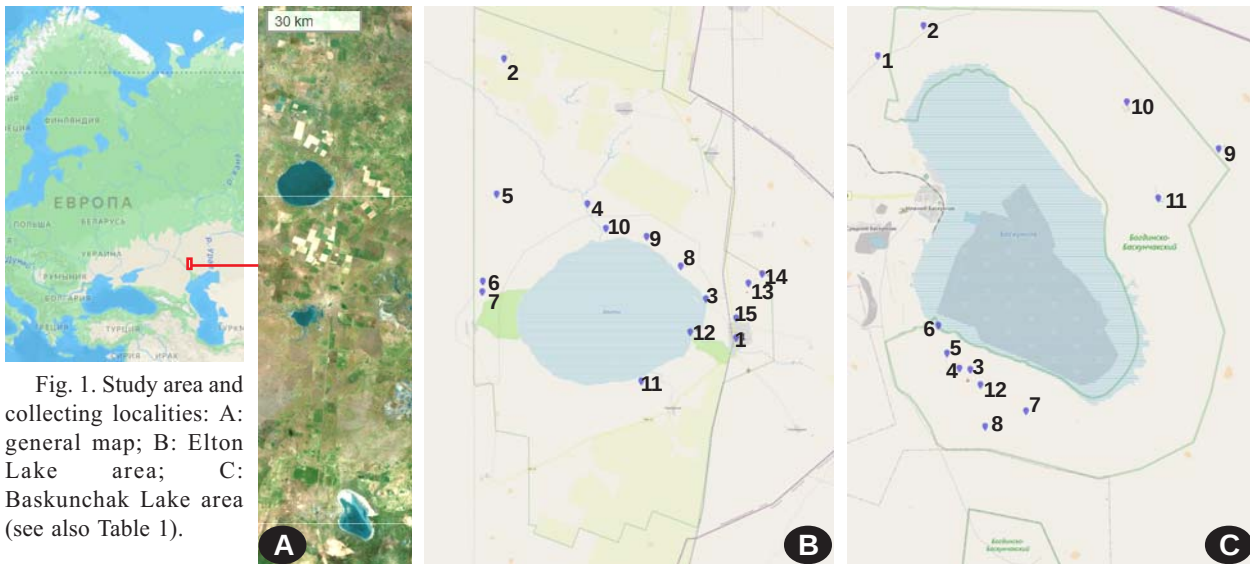


Fig. 1. Study area and collecting localities: A: general map; B: Elton Lake area; C: Baskunchak Lake area (see also Table 1).

INTRODUCTION

Mosses are the plants that cannot tolerate really saline environments, so they lack any marine species, unlike vascular plants and especially Angiosperms. However, few moss species grow on sea shore cliffs experiencing the spray of marine water, and some other mosses occur in inland areas with saline soils. Such mosses are very few, thus raising a special interest to their ecology. For example, the number of studies on the habitats of *Entosthodon hungaricus* seems to be greater compared

to other species: see the review of publications in the paper on this species by Pisarenko *et al.* (2001). A relative rarity of such environments determined the present study of the moss diversity in the areas of two salty lakes, Elton in Volgograd Province and Baskunchak in Astrakhan Province.

Elton and Baskunchak are famous for their economic value since the ancient time because of important source of the edible salt. Having so unusual environments, the surroundings of the lakes received recently conservation

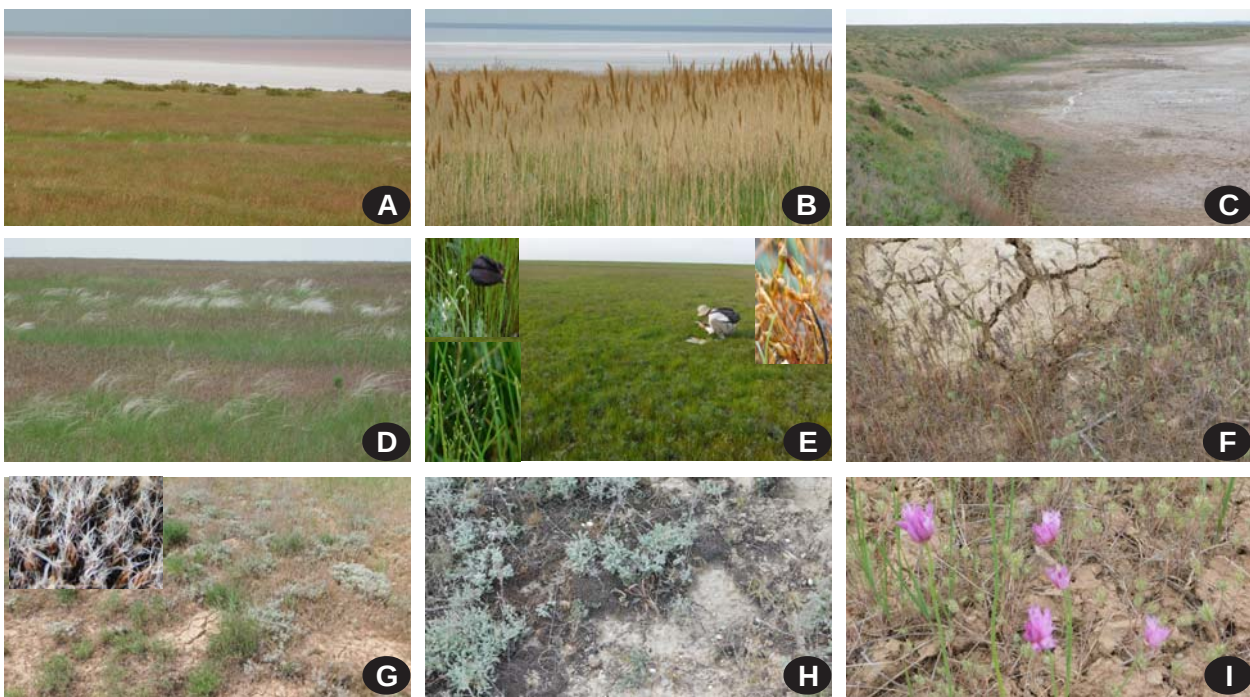


Fig. 2. Elton Lake area: habitats and images of selected species. A & D: *Poa bulbosa*+*Stipa* steppe near the lake (water has a reddish color because of *Dunaliella salina* algae); B: Lake low banks with *Phragmites* (no mosses within); C: Steep lake banks, almost lacking mosses; E: A relatively mesic steppe in shallow depression, with *Fritillaria*, *Cardaminopsis* and minute grass *Zingeria*, and *Entosthodon hungaricus*; F: Bare soil in *Poa bilbosa*+*Eremopyrum* grassland, with *Pterygoneurum* in fissures; G–H: *Amaranthaceae* shrublets and *Artemisia austriaca* dry steppe with *Syntrichia ruralis*; I: *Eremopyrum* + *Allium* dry steppe without mosses.

Table 1. Collecting localities and dates

#	Locality, vegetation / habitat	Coordinates (GPS)	Date
ELTON			
1	Elton settlement, on soil near Park office	49°07'17"N, 46°50'36"E, 10 m alt.	30.IV.2023
2	Grassland with <i>Zingeria</i> , meso-xeric grassland in shallow depression	49°21'45"N, 46°32'17"E, 20 m alt.	30.IV.2023
2a	Shallow depression in dry <i>Festuca</i> dominated grassland	49°22'00"N, 46°32'02"E, 10 m alt.	30.IV.2023
3	Elton Lake bank and the N-faced slope of the dam	49°09'19"N, 46°48'13"E, –10 m alt.	1.V.2023
3a	Elton Lake bank and the N-faced slope of the dam	49°09'19"N, 46°48'13"E, –10 m alt.	4.V.2023
4	Khara River, left bank	49°14'15"N, 46°38'52"E, 20 m alt.	1.V.2023
5	NW of Elton Lake, <i>Poa bulbosa</i> grassland	49°14'41"N, 46°32'15"E, –10 m alt.	1.V.2023
5a	Lanzug Creek	49°14'45"N, 46°31'42"E, 20 m alt.	1.V.2023
6	Presnolimansky Upland W of Elton Lake	49°10'14"N, 46°30'37"E, 30 m	1.V.2023
7	Presny Liman, a grassland	49°09'41"N, 46°30'34"E, 10 m alt.	1.V.2023
8	NE of Elton Lake, a grassland	49°11'01"N, 46°46'14"E, 0 m alt.	2.V.2023
9	N of Elton Lake, a grassland	49°12'33"N, 46°43'32"E, 0 m alt.	2.V.2023
10	Chernavka Creek, steep banks	49°12'58"N, 46°40'19"E, 0 m	2.V.2023
10a	Chernavka Creek, steep banks	49°12'52"N, 46°40'21"E, 0 m alt.	3.V.2023
10b	Chernavka Creek, steep banks	49°12'53"N, 46°40'27"E, 0 m alt.	3.V.2023
11	Malaya Smorogda (also Samaroda) Creek near mouth, <i>Halocnemum</i> vegetation	49°05'03"N, 46°43'07"E, –10 m alt.	2.V.2023
11a	Malaya Smorogda (also Samaroda) Creek near mouth, <i>Atriplex cana</i> vegetation	49°04'58"N, 46°43'24"E, –5 m alt.	2.V.2023
12	Bolshaya Smorogda (also Samaroda) Creek near mouth, <i>Halocnemum</i> vegetation	49°07'36"N, 46°46'58"E, –10 m alt.	2.V.2023
12a	Bolshaya Smorogda (also Samaroda) Creek near mouth, <i>Halocnemum</i> vegetation	49°07'33"N, 46°47'16"E, –10 m alt.	4.V.2023
13	Ulagan Upland	49°10'08"N, 46°51'34"E, 68 m alt.	3.V.2023
13a	SWW of Ulagan Upland, gravely steppe	49°10'16"N, 46°51'44"E, 55 m alt.	3.V.2023
13b	SW of Ulagan Upland, abandoned quarry	49°09'04"N, 46°51'03"E, 40 m alt.	3.V.2023
14	Old abandoned arable fields	49°10'37"N, 46°52'39"E, 55 m alt.	3.V.2023
15	Sand quarry N of Elton settlement	49°08'19"N, 46°50'36"E, 20 m alt.	4.V.2023
BASKUNCHAK			
1	Peshchernaya Ravine	48°16'52"N, 46°47'47"E, 20 m alt.	7.V.2024
1a	Peshchernaya Ravine	48°16'57"N, 46°47'46"E, 10 m alt.	7.V.2024
1b	Kristalnaya Cave	48°16'57"N, 46°47'46"E, 0 m alt.	5.V.2002
2	N of Baskunchak Lake	48°17'39"N, 46°49'34"E, 10 m alt.	7.V.2024
3	Bolshoe Bogdo Mountain	48°08'41"N, 46°51'26"E, 80 m alt.	7.V.2024
3a	Bolshoe Bogdo Mountain	48°08'42"N, 46°51'24"E, 100 m alt.	7.V.2024
3b	Bolshoe Bogdo Mountain	48°08'41"N, 46°51'14"E, 70 m alt.	8.V.2024
3c	Vodyanaya #1 Cave	48°08'41"N, 46°51'26"E, 80 m alt.	4.V.2002
4	Surikov Ravine, upper part	48°08'44"N, 46°50'59"E, 50 m alt.	8.V.2024
5	Surikov Ravine, lower part	48°09'08"N, 46°50'30"E, 30 m alt.	8.V.2024
6	SW of Baskunchak Lake, slopes to lake bar and Kordon Ravine lower part	48°09'51"N, 46°50'09"E, –20 m alt.	8.V.2024
7	E of Bolshoe Bogdo Mountain, dry steppe	48°07'37"N, 46°53'35"E, 10 m alt.	9.V.2024
7a	E of Bolshoe Bogdo Mountain, steppe and upper part of small ravine	48°07'37"N, 46°53'35"E, 10 m alt.	9.V.2024
8	E of Bolshoe Bogdo Mountain, Sherbulak,	48°07'13"N, 46°51'59"E, 10 m alt.	9.V.2024
9	NE of Baskunchak Lake, steppe and hills	48°14'27"N, 47°01'07"E, 0 m alt.	10.V.2024
9a	NE of Baskunchak Lake, sinkhole	48°14'27"N, 46°51'59"E, 0 m alt.	10.V.2024
10	NE of Baskunchak Lake, Karasun Lake	48°15'40"N, 46°57'31"E, 0 m alt.	10.V.2024
11	NE of Baskunchak Lake, Gorkaya River	48°13'12"N, 46°58'53"E, –10 m alt.	10.V.2024
11a	NE of Baskunchak Lake, Gorkaya River	48°13'10"N, 46°58'45"E, –10 m alt.	10.V.2024
12	E of Bolshoe Bogdo Mountain, Krasnaya Balka	48°08'18"N, 46°51'48"E, 30 m alt.	11.V.2024

status. The protected area of the Elton Nature Park (since 2001) includes 1060.40 km², with partly protected surroundings 149 km² (since 2024). Bogdo-Baskunchak Strict Nature Reserve covers 184.78 km² (since 1997). Some botanical and zoological exploration has been conducted for the various groups on plants, animals, and vegetation (Safronova, 2005, 2006, 2012; Kalyuzhnaya, 2007). However, mosses of the Elton and Baskunchak areas were never the subject of a special floristic exploration.

Occasional collections from these areas were accumulated in herbaria, e.g. specimen of *Syntrichia caninervis* collected at Bogdo in 1926 by S.G. Grigoriev (det. L.I. Savicz, LE); then botanists from Moscow (Belyanina, 1984), Volgograd (V.A. Sagalaev, 1992, and I. Zemlyanskaya, 1997, 1999), and Tolyatti (V.V. Sinyakina, 1990) collected few samples deposited in MHA. The first large collection of mosses, 30 species, in Baskunchak

area was gathered by Suragina in 2002 near Bogdo Mountain and in several caves in that area, which were published within the annotated list of mosses of Astrakhan Province (Suragina *et al.*, 2002).

The present study is the first bryological exploration of the total territories of protected areas around Elton and Baskunchak lakes, describing species diversity in main vegetation types. Though the distance between two lakes is only 100 km, the Baskunchak area is more xeric. We combine data on mosses of both territories in one publication to provide differences in ecology for some characteristic species.

STUDY AREA

Elton and Baskunchak are the largest lakes with the sodium chloride deposits in the European Russia. They are situated in Cis-Caspian lowland, at 17 m and 21.6 m below sea level, covering area 152 km² and 106 km², re-

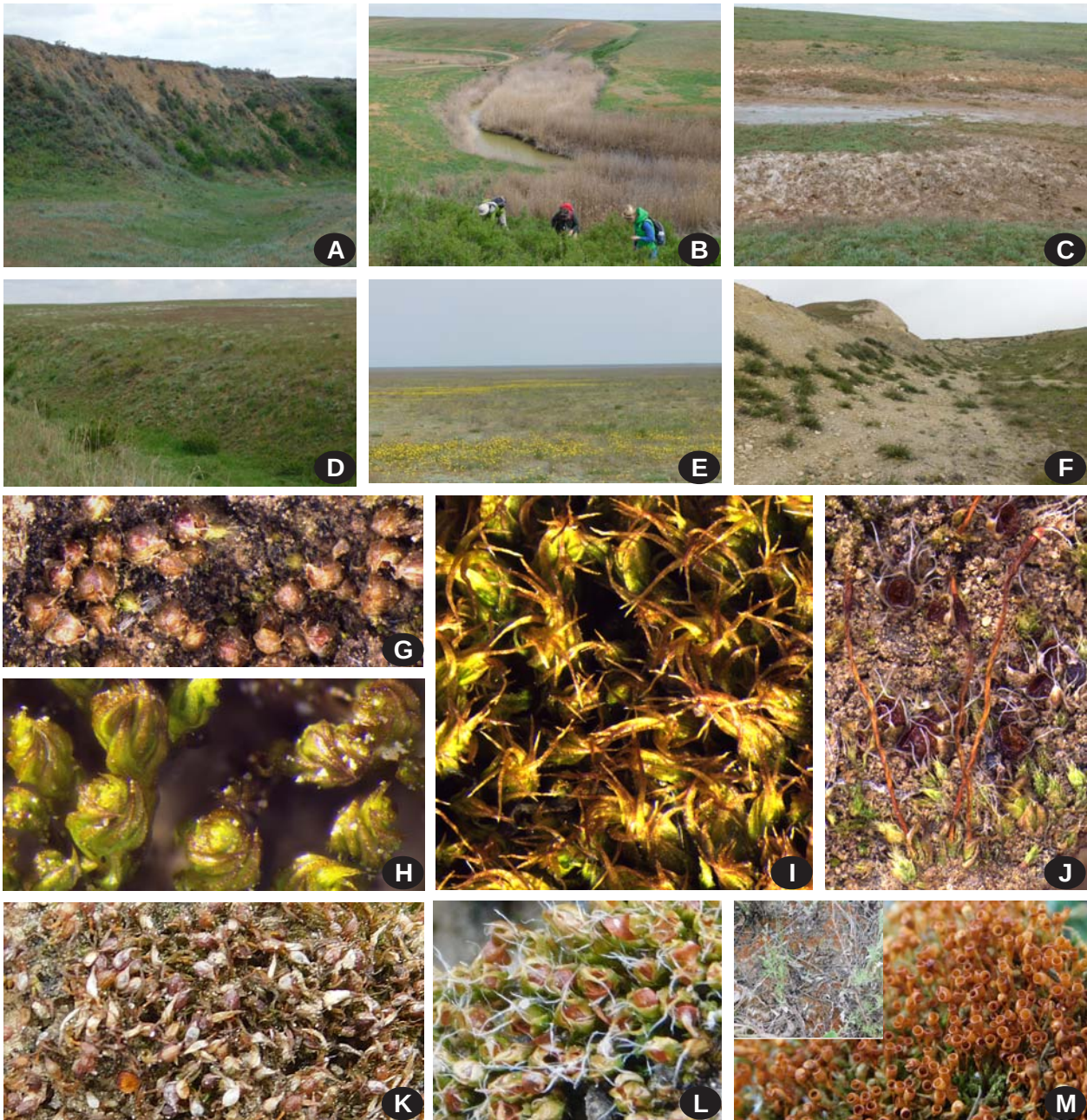


Fig. 3. Elton Lake area: habitats and images of selected species. A: Steep slope to Chernavka Creek valley, with high diversity of mosses near its base under scattered small shrub canopy; B: Khara River, *Spiraea* and *Caragana* shrubs, with a rather diverse moss species diversity under them; C: Lanzug Creek, temporarily flooded; D: ravine with gentle grassy slopes, with few mosses, including *Tortula acaulon*; E: abandoned field, invaded recently by *Lagoseris*, with a high diversity of mosses (*Acaulon triquetrum*, *Microbryum curvicolle*, etc.); F: Ulagan hill, with dry gravelly soil, with scattered *Pterygoneurum* spp. and *Aloina rigida*; G: *Acaulon triquetrum*; H: *Pseudocrossidium hornschruchianum*; I: *Ceratodon purpureum* var. *conicus*; J: *Tortula lindbergii*; K: *Microbryum curvicolle*; L: *Pterygoneurum subsessile*; M: *Physcomitrium arenicola*.

spectively (Fig. 1). The depth of Elton is up to 1.5 m in spring, and only 5–7 cm in summer, while in Baskunchak the deepest place is 3 m, but the median depth is zero, so in summer the lake looks as a giant piece of salt and only in spring the shallow water covers its surface.

The underground “salty masses” caused the uplifting in the lake proximities; thus, in 4–5 km north-east from Elton Lake there is the Ulagan hill, 68 m above sea level, the highest point in Volgograd Province east of Volga River,

and it continues uplifting for ca. 2 mm a year. In Baskunchak area, the Bolshoe Bogdo Mountain (hereafter Bogdo) is 150 m above sea level (at base ca. 5 × 3 km). It is the highest point of the Cis-Caspian Lowland, that continues uplifting for ca. 0.8 mm a year, raising Permian and Jurassic sandstones and Triassic variegated strata.

In 1980–90, the mean annual temperature in Elton and Baskunchak was ca. +8°C and annual precipitation was 300 mm in Elton and 270 mm in Baskunchak. However,

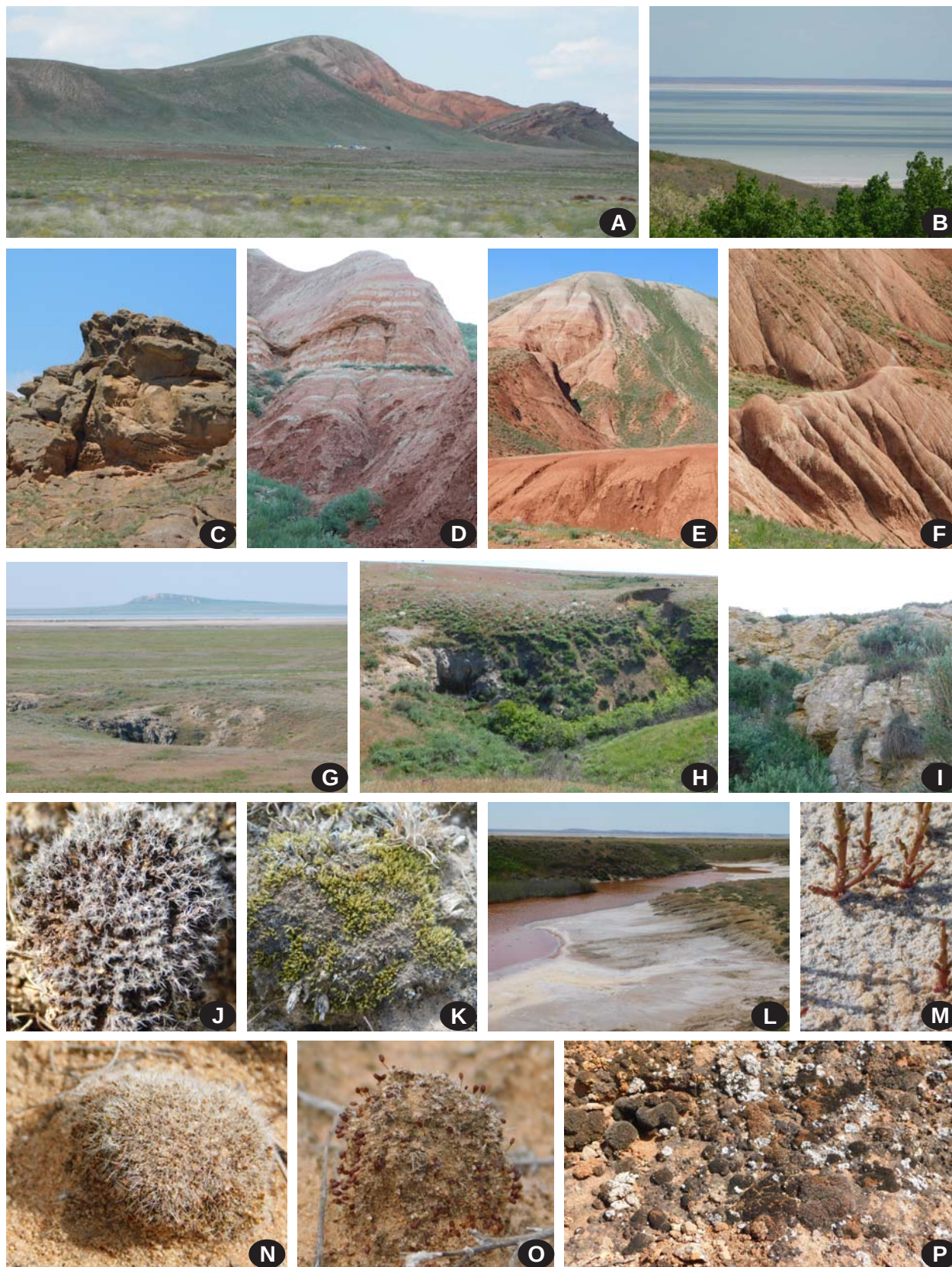


Fig. 4. Baskunchak Lake area: habitats and images of selected species. A: Bogdo Mountain, dry *Stipa* steppe in front view; B: Baskunchak Lake, temporary with water layer above salt, that is exposed and matted in summer, resulted in striped appearance; C–F: sandstones and variegated strata of slopes of Bogdo Mt.; G–I: karst sinkholes; J: *Syntrichia caninervis*; K: *Bryum caespitium*; L: Gorkaya River, the only tributary to Baskunchak Lake; M: *Salicornia*, on pure NaCl, forming monospecific vegetation at lake shore; N–P: cushions approaching to ball-shaped due to wind erosion, of *Pterygoneurum subsessile* (N), *P. ovatum* (O), *Grimmia plagiopodia* (P).

in 2001–2011, in Baskunchak the mean temperature raised up to +9.9°C and annual precipitation raised to 334 mm (Amosov, 2012), while maximal temperature reached +44°C and minimal one was –36° (Amosov, 2012).

The dwarf semishrub and bunch-grass steppe (desert-steppe) vegetation prevails in both areas, with abundant occurrence of *Artemisia lercheana*, *A. santonica*, *A. pauciflora*, *Bassia prostrata*, *Tanacetum achilleifolium*, *Camphorosma monspeliaca*, *Festuca valesiaca*, *Agropyron desertorum*, and *Stipa sareptana*. Soils in Baskunchak area are at places sandy, where more commonly occur *Stipa lessingiana*, *S. pennata*, *Agropyron desertorum*, *A. fragile*, *Koeleria glauca* and *Artemisia marschalliana*. In dry steppes, a relatively large mosses *Syntrichia ruralis* and *S. caninervis* form at places a significant cover. The most frequent mosses in such communities are also *Pterygoneurum subsessile*, *P. ovatum*, and *Bryum caespitium*, though they rarely grow in abundance.

Grasslands in shallow depressions among flat steppe may have a more mesophytic, with the minute grass of the genus *Zingeria* (Elton area), but such vegetation type is very rare.

In Elton area, shrub vegetation (*Spiraea* spp., *Prunus spinosa*, *Rosa* spp., *Prunus tenella*, *Caragana* spp.) occurs on ravine slopes, and the larger and steeper the slope is, the more diverse are mosses in such communities. On gentler slopes to shallow depressions, under the same shrubs, a dense grass cover develops, so mosses are scattered if any in such habitats.

Scattered trees of *Eleagnus*, *Populus*, *Ulmus*, and *Malus* occur in few most sheltered and wet places in both Elton and Baskunchak areas; however, we were unable to find even scanty, depauperate mosses on their trunks, and no mosses were found on soil under their canopy as well. Likewise, there were no mosses on banks of brooks and creeks.

On the shores of Elton and Baskunchak lakes, monodominant communities of *Salicornia* without any other plants occur, while at some distance from the shore, they are replaced by hyperhalophytic dwarf semishrub vegetation of *Halocnemum strobilaceum*, *Halimione verrucifera*, and *Limonium suffruticosum*. Selected vegetation types of Elton area are illustrated in Figs. 2 and 3, and of Baskunchak in Fig. 4.

METHODS AND MATERIALS

In order to reach a reasonably complete moss flora exploration, the field trips were conducted in Elton in 2023 and in Baskunchak in 2024, both in late spring (Table 1), when sporophytes are developed in most species, and also because the summer drought makes mosses partly damaged and difficult to find, considering also the strong winds covering their tufts with the fine dust.

The localities for more detailed studies were selected based on general habitat diversity. The most common

types of steppe vegetation were observed in many places at short stops; however, in such habitats, mosses are usually represented by *Bryum caespitium*, *Syntrichia ruralis*, *S. caninervis*, and *Pterygoneurum subsessile*, rarer by few other species, or at places we failed to find even a single moss. Therefore the special attention was addressed to a selected localities with steep eroded slopes, sites with rocky substrates, wetter places closer to lake shores, etc., so each vegetation type enriched in moss species diversity was more closely investigated. Collections are kept in MHA, with duplicates in MW and VOLG.

Some nearby collecting sites are combined in maps in Fig. 1, and in further discussion we consider localities as combined, meaning one number is one locality. The collection of Suragina in 2002 and few other herbarium specimens are included in the analysis of species distribution. The less known species and those which are difficult to identify are commented and illustrated using the present collections.

RESULTS

The records of species from the main collecting localities are shown in the Table 2. Species names are given according to Brinda & Atwood (2026). In total, 52 species were revealed in study area in the course of studies in 2023–24, with addition of the previous data published by Suragina *et al.* (2002). The moss flora of Elton area includes 35 species and of Baskunchak area 45 species; however, in the latter area, nine species were collected only in deep caves in karst sinkholes, so in general their moss diversity is almost equal.

DISCUSSION

Widespread species in Elton and Baskunchak

Like in many other xeric regions, the widespread species are few. Only nine species in Elton and Baskunchak areas can be referred to rather common species, which are defined here as occurring at least in half of the studied localities. Among them, only three species, *Bryum caespitium*, *Pterygoneurum ovatum* and *P. subsessile*, are common in both areas. Three species are common in Elton area only (*Entosthodon hungaricus*, *Physcomitrium arenicola*, and *Syntrichia ruralis*) and three species are common in Baskunchak area only (*Encalypta vulgaris*, *Pseudocrossidium hornschiuchianum*, and *Syntrichia caninervis*).

A comparison of species which are common in each area proves that the environments of Elton area are more mesic. Especially contrasting is the abundance of *Entosthodon hungaricus* and *Physcomitrium arenicola* in Elton and their rarity or absence in Baskunchak. These representatives of the family Funariaceae are mesic plants, having leaves with large, thin-walled cells; they can tolerate xeric environments largely because of their ephemeral life strategy. Spring time, when snow is melting, is sufficient for their rapid development, capsules maturing and spore spreading.

¹ – names of vascular plants follow Skvortsov (2006) and Reshetnikova (2018, 2026).

Table 2. Distribution of moss species in localities of Elton and Baskunchak areas (cf. Fig. 1 and Table 1); specially markets records from Krystallnaya Cave (1K) and Vodyanaya #1 Cave (3V).

Species	Elton	Baskunchak
<i>Acaulon triquetrum</i>	4, 10, 14	1, 6, 8, 9
<i>Aloina aloides</i>	10	---
<i>Aloina rigida</i>	13	---
<i>Amblystegium serpens</i>	---	1K
<i>Barbula unguiculata</i>	4, 10, 13	1, 3, 6, 9
<i>Brachytheciastrum collinum</i>	10	1
<i>Brachytheciastrum velutinum</i>	4	---
<i>Brachythecium rutabulum</i>	---	1K
<i>Bryoerythrophyllum recurvirostrum</i>	---	1K
<i>Bryum argenteum</i>	4, 13, 15	4, 6, 7
<i>Bryum caespiticeum</i>	2, 3, 4, 5, 6, 7, 8, 9, 10, 13, 14	1, 3, 5, 6, 7, 8, 9, 12
<i>Bryum capillare</i>	9	2
<i>Bryum creberrimum</i>	14	1K
<i>Bryum dichotomum</i>	1, 11, 12	5
<i>Bryum kunzei</i>	5, 12	6
<i>Bryum lonchocaulon</i>	---	8
<i>Bryum moravicum</i>	---	1K
<i>Bryum pseudotriquetrum</i>	---	6
<i>Bryum subapiculatum</i>	---	6
<i>Bryum violaceum</i>	4, 10	---
<i>Ceratodon purpureus</i>	2, 4, 5, 7, 13, 14	3, 4, 5, 7, 8, 9, 10
<i>Didymodon rigidulus</i>	---	1K, 3V
<i>Didymodon vinealis</i>	---	1K, 3V, 8
<i>Encalypta vulgaris</i>	10	1, 2, 3, 4, 5, 7, 9, 11, 12
<i>Entosthodon fascicularis</i>	---	11
<i>Entosthodon hungaricus</i>	2, 3, 4, 5, 6, 8, 10, 11	1, 5, 6, 7, 11
<i>Entosthodon pulchellus</i>	4, 10	1, 3, 8, 9
<i>Funaria hygrometrica</i>	3, 4, 5, 10, 15	6, 7
<i>Grimmia anodon</i>	---	1, 3, 5, 12
<i>Grimmia laevigata</i>	---	12
<i>Grimmia plagiopodia</i>	---	3, 4, 12
<i>Grimmia pulvinata</i>	---	1
<i>Leptobryum pyriforme</i>	---	1K
<i>Microbryum curvicolle</i>	4, 10	1, 3, 4, 5, 9
<i>Physcomitrium arenicola</i>	2, 3, 4, 5, 6, 7, 10, 11	---
<i>Platydictya jungermannioides</i>	---	3V
<i>Pseudocrossidium hornschiianum</i>	8, 10, 13	1, 3, 6, 7, 8, 9, 11
<i>Pterygoneurum ovatum</i>	1, 3, 4, 5, 6, 7, 8, 10, 13, 14, 15	1, 3, 4, 5, 6, 7, 12
<i>Pterygoneurum subsessile</i>	3, 4, 5, 7, 8, 10, 11, 12, 13	1, 3, 4, 5, 6, 7, 9, 11, 12
<i>Pterygoneurum volgensse</i>	2, 3, 10	1
<i>Schistidium sinensiapocarpum</i>	---	1K
<i>Streblotrichum convolutum</i>	4	12
<i>Syntrichia caninervis</i>	3, 4, 5, 7, 10, 13, 15	1, 2, 3, 4, 5, 6, 8, 9, 10
<i>Syntrichia pseudohandelii</i>	10	12
<i>Syntrichia ruralis</i>	2, 3, 4, 6, 7	3, 12
<i>Tortula acaulon</i>	2, 4, 5, 6, 9, 10	1, 3, 4, 6, 7
<i>Tortula lindbergii</i>	3, 4, 10, 13, 14	1, 11
<i>Tortula mucronifolia</i>	8, 10	---
<i>Tortula muralis</i>	3, 11, 14	1, 3, 5, 8, 12
<i>Tortula protobryoides</i>	2, 4, 5, 6, 8, 10, 14	1, 5, 7, 8, 9
<i>Weissia cf. brachycarpa (ster)</i>	10	---
<i>Weissia longifolia</i>	4	2, 3

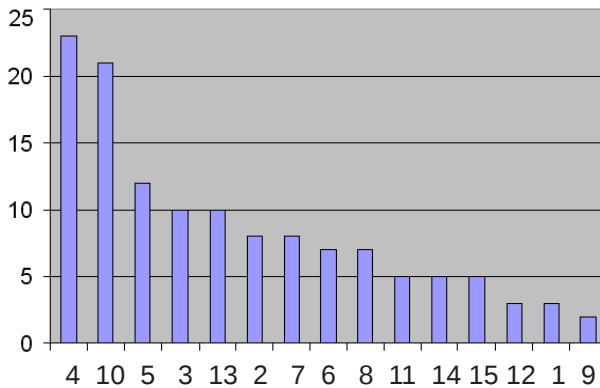


Fig. 5. The species diversity in Elton area (locality numbers shown below bars are according to Table 1). The maximal diversity is 23 species in Khara River (#4); 21 species, in Chernavka Creek (#10). Other localities possess a considerably lower species diversity: 12, in Lanzug Creek (#5); 10 on Elton lake dam and nearby lake banks (#3) and in Ulagan Upland (#13).

A relative abundance of *Syntrichia ruralis* (common in Elton, rarer in Baskunchak) and opposite relative abundance in Baskunchak of more xerophilous *S. caninervis* is also revealing: the former species occurs in most regions of Russia, whereas the latter very rarely crosses the northern limit of the steppe zone. *Encalypta vulgaris* also rarely penetrates into the forest zone; it is common on open calcareous soil, chalk and other calcareous rock outcrops.

Even more interesting is distribution of *Pseudocrossidium hornschruchianum* in the studied areas. This is more southern and western species in European Russia, with northern limit in Volgograd Province. Being common and locally abundant in Baskunchak area, it was found only in three localities in Elton area, being associated there with a number of other southern xerophytic mosses: *Tortula lindbergii*, *Aloina aloides*, *Microbryum curvicaule*, *Entosthodon puchellus*, *E. hungaricus*, and *Acaulon triquetrum*. In these localities were also found an endemic of Cis-Caspian lowland *Pterygoneurum volgensse*, a rare southern species *Syntrichia pseudohandelii* (see more about it in Ignatova *et al.*, 2026) and *Aloina aloides*, known in Russia outside the Caucasus only in Elton area. Among moderately common species also occurring with the above-mentioned mosses are *Tortula protobryoides*, *T. acaulon*, *Aloina rigida*, and *Encalypta vulgaris* (the latter species was found only once in Elton area, whereas in Baskunchak area it is fairly common). Since the group of these species needs to be mentioned below, we denote it as ‘*Acaulon–Microbryum* group’.

Hotspots of moss diversity in Elton and Baskunchak

Among the studied localities in Elton area, a noteworthy is the highest species diversity in only two places: on steep, permanently eroded soil bank of the Khara River, the largest tributary of the Elton Lake, and on slopes to Chernavka Creek, with the especially strongly winding riverbed (Fig. 5).

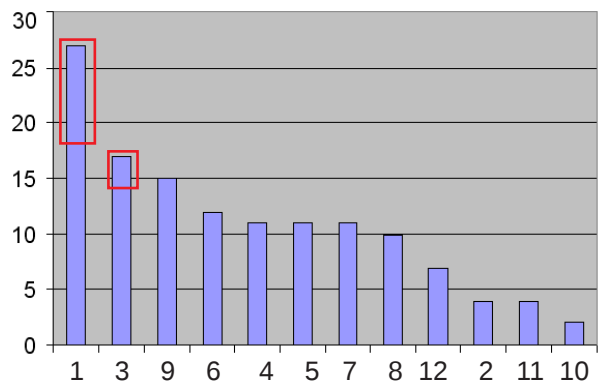


Fig. 6. The species diversity in Baskunchak area (locality numbers shown below bars are according to Table 1). The maximal diversity is 27 species in Peshchernaya ravine, including Krystallnaya Cave (#1); 17, in Bogdo Mountain, including Vodyanaya #1 Cave (#3); 15, in hills and sinkhole area NW of Baskunchak Lake (#9); 12, at bank of Baskunchak lake at Kordonnaya ravine and in its lower course (#6). Red boxed mark species found in caves only.

In Baskunchak area, the number of species may look as having a superficially similar distribution (Fig. 6). However, the situation there is markedly different: subtracting the species found only in caves (red boxes in Fig. 6), the number of species per locality appears more even.

This difference has a simple explanation in the number of watercourses inflowing to the lakes. The Elton Lake has seven tributaries, including Khara River, the largest among others (Fig. 3B) and Chernavka Creek (Fig. 3A), one of the smallest, but forming steep slopes in narrow valley. The species of ‘*Acaulon–Microbryum* group’ are the best represented in these two localities. Some of Elton tributaries are flooded only temporary, e.g. Lanzug Creek (cf. Fig. 3C). The Baskunchak Lake has only one tributary, the Gorkaya River (Fig. 4L). The slopes to this river and nearby ravines, however, are too dry and windy, thus not contributing considerably to the moss species diversity. The low river banks have in many sites saline soils with *Halocnemum* dominated vegetation.

Sheltered areas in Baskunchak are very different from those in Elton. First of all, these are Bogdo Mountain cliffs and steep slopes and, second, the karst sinkholes, continued in some of them into caves.

Bogdo is a spectacular hill with rocky substrates (Fig. 5A); however, even in narrow valleys on its slopes in many places no bryophytes were found, apparently due to an easily eroded soil (Fig. 5D, E). Its cliffs are shaped by wind erosion, and bryophytes are rarely present only in deep cracks and under overhangs, where solitary cushions of *Tortula muralis* and *Grimmia anodon* are able to survive. Other mosses in Bogdo area occur only in stream beds with very rarely running water. Acidophilous epiliths *Grimmia anodon*, *G. plagiopodia*, and *G. laevigata* occur in such habitats, being accompanied at places by *Tortula muralis*, *Pterygoneurum subsessile*, *P. ovatum*, *Syntrichia caninervis*, *S. pseudohandelii*, and *Weissia longifolia*.



Fig. 7. *Syntrichia caninervis* variation. A–B: plants from soft gypsum in a karst sinkhole bottom, developing rhizoid gemmae (B, magnified in inset); C–D: most common habitat and habit on open rock faces; E & H: upper parts of leafy shoots, dry; F: upper part of male shoot; G: upper part of female shoot; I: plant with sporophyte, dry.

Mosses mentioned for Elton area as a specific complex of species growing on steep, eroded slopes, including *Acaulon triquetrum*, *Microbryum curvicolle*, *Entosthodon pulchellus*, *Tortula lindbergii* and some others, were found in Baskunchak area in two types of habitats. One of them is Surikov Ravine, the biggest one on Bogdo Mountain, situated on its north-western side. However, its slopes are formed by sandy soil, covered by grass vegetation; they are not especially steep, having few places with bare soil where the species of ‘*Acaulon–Microbryum* group’ can grow, which causes their rarity in this locality.

Other habitats for this species complex are karst sinkholes; they are numerous in Baskunchak area. However, only the large ones maintain any moss diversity: for example, *Acaulon triquetrum* was found only in four sinkholes and *Microbryum curvicolle* in three ones. In many smaller sinkholes, *Syntrichia caninervis* was the only moss species; it grew in a broad range of habitats, including

wet, paste-like masses in sinkhole bottom and holes in dry rock outcrops on sunny slopes (Fig. 7). In wetter places its plants were largely buried in gypsum, they looked depauperate and sometimes developed rhizoid gemmae, whereas at the border of sinkhole they were well developed, looking so different that it was difficult to believe that such plants may represent the same species.

Many sinkholes in Baskunchak area possess caves, mostly not big, sometimes inhabited by wolves. Some outstandingly large caves were studied in 2002 by botanists from Volgograd, with the help with moss collecting from the speleologist I.V. Golovachev, who gathered mosses in Krystalnaya Cave at depth of 10–12 m. The cave entrance is almost vertical, thus sunlight at that depth is sufficient for the moss growth. This collection includes nine species: *Amblystegium serpens*, *Brachythecium rutabulum*, *Bryoerythrophyllum recurvirostrum*, *Bryum creberrimum*, *B. moravicum*, *Didymodon rigidulus*, *D. vinealis*, *Lepto-*

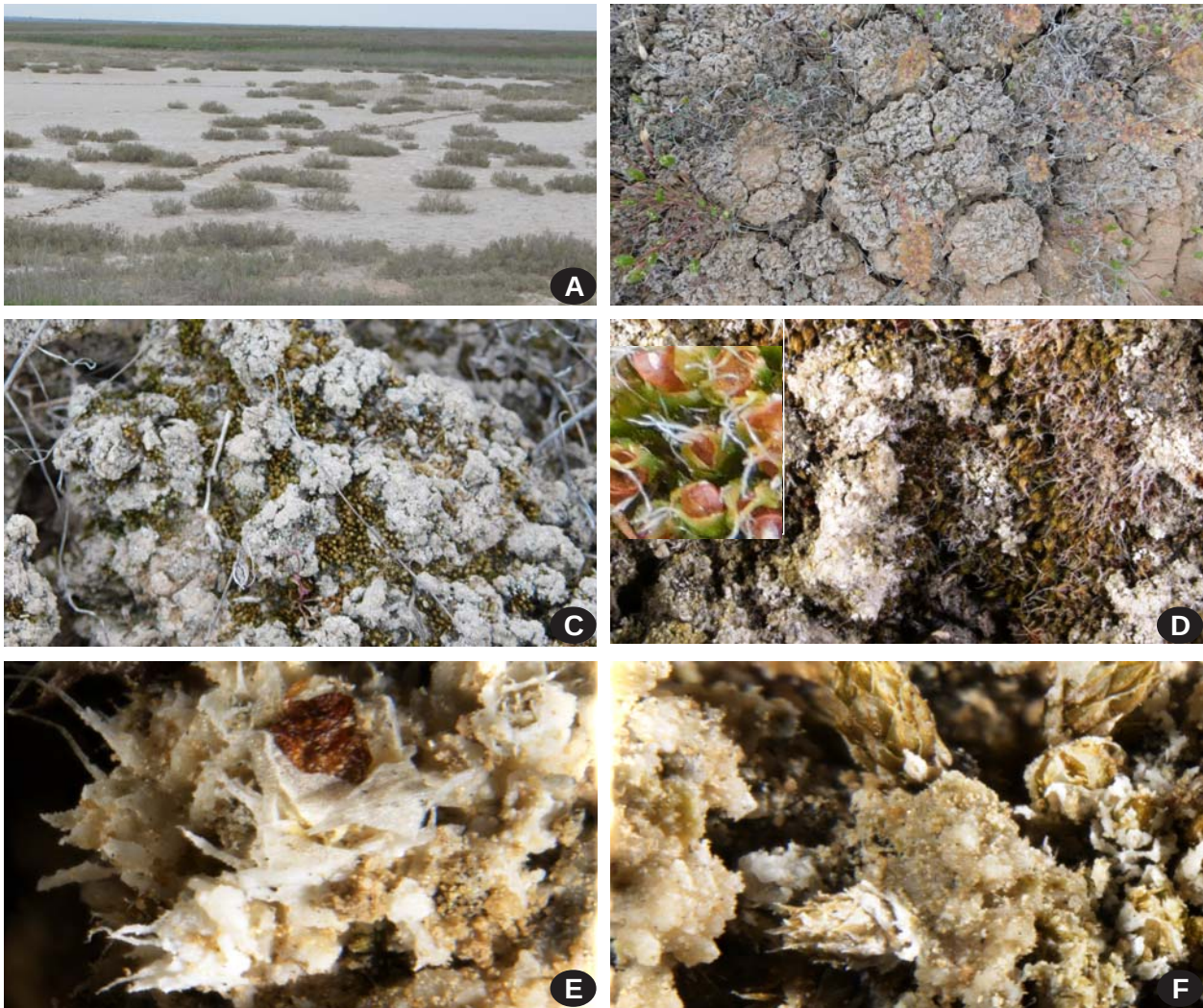


Fig. 8. *Halocnemum strobilaceum* communities on wet salty shore of Elton Lake (locality 12, Bolshaya Smorogda). A: general view; B–D: soil pieces with salt deposits, with *Pterygoneurum subsessile*; E: *P. subsessile* strongly covered by salt, but still able to produce sporophytes; F: *Bryum dichotomum* plants encrusted by salt.

bryum pyriforme, and *Schistidium sinensiapocarpum*. Most of them were not found in other places either in Baskunchak or Elton area. Only *Didymodon vinealis* was found outside the caves in one steppe locality; this species and *Didymodon rigidulus* were also found in another cave, Vodyanaya #1. Only in the latter cave, *Platydictya jungermannioides* was collected (also in 2002).

Salt-tolerant mosses

The poorest in moss species diversity are salty habitats at lake shores. The shore of Baskunchak lake is covered by sodium chloride crust, where only *Salicornia* can survive (Fig. 3M). Further zones with a somewhat less salinity were described by Ilyin (1927) for Elton lake area, where the vegetation of the shore transits to less halophytic types with the zone dominated by *Halocnemum*, Fig. 8A. In Elton area, these communities were both wet and mesic, while in the lower course of Gorkaya River, the only tributary of Baskunchak Lake, *Halocnemum* occurs mostly on more raised terraces. The wetter *Halocnemum* vegetation on

Elton Lake banks is conspicuous, especially by salt ridges intermingling the clayish soil surface (Fig. 8). The most common moss here is *Pterygoneurum subsessile*; it develops abundant sporophytes and often has unusually light green leaves (Fig. 8D), not dark greyish- or blackish-brown, common in xeric habitats in the study areas (its identity with more 'typical' specimens of the species were confirmed by molecular barcoding, cf. Fedosov *et al.*, 2025). The plants of *P. subsessile* are encrusted with salt (Fig. 8E), and a similar crust occurs also on *Bryum dichotomum* plants (Fig. 8F).

COMMENTS ON SELECTED SPECIES

Acaulon triquetrum – this species is here at the northern border of its distribution in East European sector; it grows on bare soil on slopes, rarer in flat areas: on abandoned field in Elton and in karst sinkholes in Baskunchak area, almost always with sporophytes (Fig. 3G).

Aloina aloides was found as a single tuft at the base of slope to Chernavka Creek in Elton area (Fig. 3A), to-

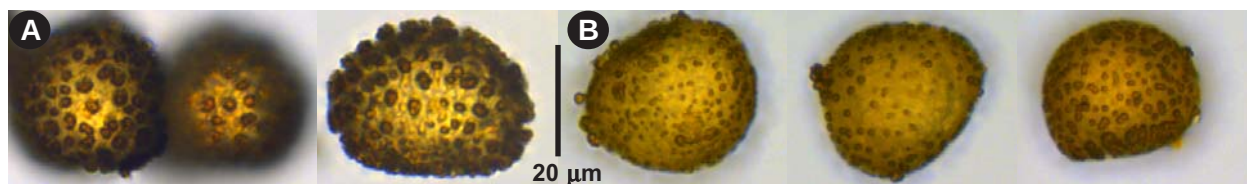


Fig. 9. Spores of *Physcomitrium arenicola* (A) and *Entosthodon hungaricus* (B), showing difference in ornamentation and dimensions, making possible species identification in poorly preserved capsules.

- gether with mosses of ‘*Acaulon–Microbryum* group’.
- A. rigida* was collected only in Ulagan (Elton area) in dry windy place, on exposed gravelly soil (Fig. 2I).
- Amblystegium serpens* surprisingly was found nowhere excepting Kristalnaya Cave (Baskunchak area), where it was represented by few sterile shoots.
- Barbula unguiculata* occurs mainly in the same localities with *Acaulon*, *Microbryum*, *Pseudocrossidium*, and *Entosthodon puhlillus*, but it was also found on sandy soil banks with *Bryum caespitium*.
- Brachytheciastrum collinum* in Elton area was found only on steep slope to Chernavka Creek, and in Baskunchak area only in Peshchernaya Balka; in both localities it formed extensive mats.
- B. velutinum* – only one small collection was made under *Spiraea* shrubs on slope to Khara River in Elton area.
- Brachythecium rutabulum* – the species was collected in a cave at 10 m deep from the entrance, after which the cave form a vertical tube of ca. 15 m; the place used to have enough light, so the plants formed rather large mat with dense foliage and even mature deoperculate sporophytes.
- Bryum argenteum* – in Elton area, grows on various soil banks on slopes and in disturbed places; in Baskunchak area, was found only once in disturbed site in open dry steppe.
- B. caespitium* is very common in dry steppes and occasionally grows in a wide range of other habitats; sporophytes were seen in more mesic places.
- B. capillare* – very rare, found in wetter sites in ravine and at slope base.
- B. creberrimum* – two findings: one in abandoned field, another one in the cave.
- B. dichotomum* – sporadic in a broad range of habitats, including saline soil (Fig. 8).
- B. kunzei* – in dry steppe, rare.
- B. lonchocaulon* – in Baskunchak area in one sinkhole, on wet bottom.
- B. moravicum* – in Baskunchak area, in Kristalnaya cave, at 10 m deep.
- B. pseudotriquetrum* – at base of steep slope to the Baskunchak Lake bar.
- B. subapiculatum* – in Baskunchak area, on soil on slope and near a small karst sinkhole.
- B. violaceum* – in Elton area, on steep grassy slope, near a rodent hole.
- Ceratodon purpureus* – sporadically occurs in moderately dry steppes and on slopes. In most places the plants form extensive populations. Having leaves with strongly ex-
- current costae, such plants resemble not *Ceratodon* but *Didymodon* species (Fig. 3I). In wetter places plants with sporophytes were collected, with capsules inclined to horizontal, as in most common morphs of this species, despite their leaves have a strongly excurrent costae.
- Didymodon rigidulus* – in Baskunchak area, in Kristalnaya and Vodyanaya caves.
- D. vinealis* – in Baskunchak area, found with the previous species in two caves and also once in a sinkhole.
- Encalypta vulgaris* – in Baskunchak area, this species occurs on ravine slopes, banks of Gorkaya River, and sinkhole walls; in Elton area, it was found only on slopes to Chernavka Creek together with species of ‘*Acaulon–Microbryum*’ group.
- Entosthodon hungaricus* – this species was previously thought to be infrequent in Volgograd Province; however, in May in Elton area we found it in most visited localities: at lake shore, in wetter places in steppe and temporary watercourses, and in some other places; in Baskunchak area it was seen fewer times, growing in small groups in wetter places. In Elton area, this species occasionally co-occurs with *Physcomitrium arenicola*; sometimes it is difficult to distinguish them, especially when the capsules are old. In this case, moderately finely vs. coarsely papillose spores provide their reliable distinction (Fig. 9).
- E. pulchellus* – grows mainly with species of ‘*Acaulon–Microbryum*’ group.
- Funaria hygrometrica* – in Elton area, it was found in more or less wet habitats (e.g., Fig. 3C), on lake dam and in quarry bottom; in Baskunchak area, it is rare, growing at base of slopes to the lake and to Gorkaya River (Fig. 4L).
- Grimmia anodon* – on sandstone outcrops and cliffs in Bogdo Mountain, and on cliffs in the lower part of Surikov Ravine; grows with *Tortula muralis* in extremely xeric conditions.
- G. laevigata* – Baskunchak area, one collection of I. Zemlyanskaya (1997), mixed with *Encalypta vulgaris* and *Tortula muralis*.
- G. plagiopodia* – Bogdo Mountain and immediate surroundings, on rocks along brooks (Fig. 4G).
- Grimmia pulvinata* – Baskunchak area, on boulder in dry steppe near the sinkhole with caves.
- Leptobryum pyriforme* – Baskunchak area, in Kristalnaya cave at 10 m deep, with *Bryoerythrophyllum recurvirostrum*.
- Microbryum curvicolle* – in Elton area, only in two localities with well represented species of ‘*Acaulon–Mi-*



Fig. 10. *Tortula lindbergii* (A–E, G–I) and *T. mucronifolia* (F). A: plant, dry; B: plants, wet; C: peristome; D–E: costa in upper part of leaf, with shallow projections of ventral epidermis; F–I: costa transverse section, showing smooth ventral epidermis in *T. mucronifolia* and papillose cells on ventral side of costa in *T. lindbergii*, which has also conspicuous dorsal stereid band.

crobryum' group; in Baskunchak area, in ravines near Bogdo Mountain, and in few karst sinkholes.

Physcomitrium arenicola – this is the only species which is fairly common in Elton area and totally absent in Baskunchak area. Its habitats are similar to those of *Entosthodon hungaricus*. Growing in depressions in dry steppe, it occasionally forms conspicuous orangish patches (Fig. 3M).

Platydictya jungermannioides – Baskunchak area, found once in Vodyanaya cave at 1 m from the entrance.

Pseudocrossidium hornschi – in Baskunchak area, this species occurs on ravine slopes, sometimes in abundance, and in sinkholes; in Elton area, it is contrastingly rarer, found only in the locality with maximally diverse mosses of the '*Acaulon–Microbryum*' group, and in Ulagan. This species is very variable in leaf shape: in wet places in sinkhole bottom, its leaves are lanceolate, while on dry slopes of shallow ravines and in dry steppe they are ovate-triangular (Fig. 3H).

Pterygoneurum ovatum – common in steppe (Fig. 4O), on bare soil on slopes, and on rock outcrops; often grows intermixed with *P. subsessile*, and sometimes intermediate morphotypes, with cup-shaped capsules on setae 1–2 mm long, are observed.

P. subsessile – this species is probably the most common in both areas, well tolerating dry steppe environments, where it grows hidden in soil cracks; it is also most

salt-tolerant, growing alone or with *Bryum bicolor* in salty habitats on lake shores (Fig. 8). In windy places, its dense cushions can be semiglobose or even ball-shaped (Fig. 4N).

P. volgensae – this is a very rare species, growing in small groups on bare soil, especially where the species of '*Acaulon–Microbryum*' group are well represented. The species was previously referred to *P. lamellatum*; however, its distinctions, including genetic ones, appeared to be sufficient for its recognition as a separate species (Fedosov *et al.*, 2025).

Schistidium sinensiapocarpum (reported by Suragina *et al.*, 2002 as *S. apocarpum*) was found in Baskunchak area in Kristalnaya Cave.

Streblotrichum convolutum – very rare in both areas, found as a small admixture to other terrestrial mosses.

Syntrichia caninervis – this species is fairly common in Baskunchak area and less abundant in Elton area. It is discussed in more details by Ignatova *et al.* (2026).

S. pseudohandelii – this species was identified by Kramer (2023) in collection of I. Zemlyanskaya from Bogdo area. It is discussed in detail by Ignatova *et al.* (2026).

S. ruralis – common and at places abundant in steppes in Elton area and in more mesic grasslands in Baskunchak area.

Tortula acaulon – this species grows sporadically both in Elton and Baskunchak areas on moderately dry

slopes of ravines, among grasses or on disturbed soil, usually in small amount.

Tortula lindbergii and *T. mucronifolia* – the record of the latter species by Suragina *et al.* (2002) actually belongs to the former one. The difference between these species was scarcely understood at the time of that publication. However, they differ considerably in structure of ventral epidermis of costa in the distal leaf part. In *T. lindbergii*, the cells above the guide cells are convex and papillose, which can be observed even without leaf transverse section (Fig. 10D, E), whereas in *T. mucronifolia* cells on the ventral side of costa are smooth (Fig. 10F). *Tortula lindbergii* commonly co-occurs with the species of ‘*Acaulon–Microbryum*’ group in both areas (Fig. 3J), while *T. mucronifolia* grows in a wetter habitats, and it was found only in Elton area.

T. muralis – this species is the most troublesome in the study area. Growing on sandstone closer to the top of Bogdo Mountain, usually in fissures or under overhangs, it is represented by small and rigid plants, having leaves with variable hyaline awns, sometimes even lacking. However, its plants on gypsum in sinkholes are much larger, they have broad leaves with slightly recurved margins and long, delicate, flexuose hyaline awns. Plants growing on concrete of artificial constructions are somewhat different from both of above-mentioned morphotypes. The most morphologically deviated plants from sinkholes were sequenced for nrITS, and no difference from other GenBank accessions of *T. muralis* were revealed.

T. protobryoides – in Elton and Baskunchak areas; this species grows mainly where the species of ‘*Acaulon–Microbryum*’ group occur: on ravine slopes, under *Spiraea* shrub canopy, and on abandoned fields.

Weissia cf. *brachycarpa* – found once of slope of ravine to Chernavka Creek valley, on bare soil on steep slope. It was collected without sporophytes, so its certain identification was impossible; however, its rather short perichaetial leaves exclude *W. longifolia*.

W. longifolia – in Elton area, it was collected once under *Spiraea* on slope to Khara River; in Baskunchak area, a single collection was made in ravine on Bogdo Mountain slope.

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