Plant Systematics and Evolution (2025) 311:6
https://doi.org/10.1007/s00606-024-01926-x

RESEARCH

Contributions to the flora of Kazakhstan, genera *Arthrophytum* and *Haloxylon*

Bektemir B. Osmonali[1,2] · Polina V. Vesselova[1] · Gulmira M. Kudabayeva[1] · Serikbay Ussen[1,2] · Daulet Sh. Abdildanov[1,2] · Nikolai Friesen[3]

Received: 5 March 2024 / Accepted: 27 September 2024 / Published online: 10 February 2025

Abstract

The article discusses the results of comparative analysis of morphological, anatomical and molecular genetic structure of species *Arthrophytum longibracteatum, Arthrophytum balchaschense, and Haloxylon aphyllum*). Morphological-anatomical and molecular genetic methods were used during the study. To clarify the correctness of species identification, the collected specimens were compared with the Type specimen of *Arthrophytum balchaschense* stored at the Institute of Botany and Phytointroduction (AA). Other herbaria specimens of this species stored in the AA herbarium and herbaria collections: MW LE and TASH were also reviewed. With the help of QGIS programme, a map of the location points of the studied specimens was made. The conducted studies allowed to form a proof base of clear belonging of *Arthrophytum balchaschense* to the genus *Haloxylon*. This circumstance became the reason for the necessity of nomenclatural changes consisting in assignment of *Arthrophytum balchaschense* to the genus *Haloxylon* under the name *Haloxylon balchaschense* (Iljin) Osmonali, Veselova & Kudab. This species has a central-eastern-North Turanian distribution, being endemic to the flora of Kazakhstan.

Keywords Anatomy · *Arthrophytum* · Betpakdala · Chenopodiaceae · Endemic species · *Haloxylon* · Hybrid · Molecular genetics · Morphology

Introduction

The genus *Haloxylon* Bunge ex Fenzl of the family Chenopodiaceae (Amaranthaceae s.l.) according to the databases International Plant Names Index (IPNI) and Plants of the World Online (POWO) includes 11 species (*Haloxylon ammodendron* (C.A.Mey.) Bunge ex Fenzl, *H. gracile* (Aellen) Hedge, *H. griffithii* (Moq.) Boiss., *H. multiflorum* (Moq.) Bunge ex Boiss, *H. negevensis* (Iljin & Zohary) L.Boulos, *H. persicum* Bunge, *H. salicornicum* (Moq.) Bunge ex Boiss., *H. schmittianum* Pomel, *H. scoparium* Pomel, *H. tamariscifolium* (L.) Pau, and *H. thomsonii* Bunge ex Boiss.) occur from the Mediterranean to Central Asia inclusive (Zhu et al. 2004; Dong et al. 2016).

Many of these species were previously considered to be members of the genus *Arthrophytum* Schrenk, which, according to IPNI and POWO, currently comprises 8 species (*Arthrophytum balchaschense* (Iljin) Botsch, *A. betpakdalense* Korovin & Mironov, *A. iliense* Iljin, *A. korovinii* Botsch., *A. lehmannianum* Bunge, *A. longibracteatum* Korovin, *A. pulvinatum* Litv., and *A. subulifolium* Schrenk).

In the flora of Kazakhstan (Goloskokov and Polyakov 1960; Baitenov 2001) and Central Asia (Pratov 1972), there are 3 species of the genus *Haloxylon*: *H. ammodendron* (C.A.Mey.) Bunge, *H. aphyllum* (Minkw.) Iljin, and *H. persicum* Bunge. However, according to recent the literature sources, the first two species are combined into *Haloxylon ammodendron* (C.A.Mey.) Bunge ex Fenzl. (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:941607-1), which reduces, in turn, the number of representatives of the genus growing in Kazakhstan. From our point of view, the association of *Haloxylon aphyllum* with *H. ammodendron* is not quite unambiguous. Additional studies are needed here. Since only *H. aphyllum*

Handling Editor: Mike Thiv.

✉ Nikolai Friesen
nfriesen@uni-osnabrueck.de

[1] Institute of Botany and Phytointroduction, Almaty, Kazakhstan

[2] Al-Farabi Kazakh National University, Almaty, Kazakhstan

[3] Botanical Garden of the Osnabruck University, Osnabruck, Germany

is widespread in the area under study, we use this species name in the article. In the deserts of Central Asia, *H. ammodendron*, *H. aphyllum*, and *H. persicum* play an important role in human life, performing, among other things, a protective function (wind control and sand fixation) (Zhu et al. 2004; Dong et al. 2016). In Kazakhstan, species of *Haloxylon* are distributed mainly in Turanian deserts, occurring in all southern and south-eastern regions of the republic (Goloskokov and Polyakov 1960; Pratov 1972).

The development of molecular genetic methods of analysis, now actively used in systematic studies, leads to numerous changes in the taxonomy of almost all groups of plants. Thus, some genera are divided into several genera, and others, on the contrary, are united into one, or species from one genus are considered by systematists within the scope of another genus, hybrid specimens are identified, etc. (Kechaykin et al. 2020; Sumbembayev et al. 2021, 2023a; 2023b; Sukhorukov et al. 2022, 2023a, 2023b; Friesen et al. 2022; Lazkov and Veselova 2022; Terletskaya et al. 2023; Osmonali et al. 2023, etc.).

Considering that morphologically some representatives of genera *Haloxylon*, *Arthrophytum*, and *Anabasis* L., belonging to the same tribe Salsoleae of subfamily Salsoloideae, are very similar at certain stages of their development, the question of determination of their systematic belonging is actual. The present article is devoted to the results of one of such studies.

During expeditionary studies on the flora of the Eastern and north-eastern part of Betpakdala, in particular on the identification of rare and endemic species of this region, we noted a strong similarity between the species *Arthrophytum balchaschense* and *Haloxylon aphyllum*. The similar features that attracted our attention include the spatial arrangement of young green shoots, the structure of bark, and the shape of fruits (in the latter case when examined in detail). Therefore, to clarify the systematic affiliation of the plants we were interested in, we collected their samples not only to replenish herbarium collections but also as material for molecular genetic studies.

To clarify the correct identification for the species as *Arthrophytum balchaschense*, the collected specimens were compared (checked) with the type specimen stored at the Institute of Botany and Phytointroduction (AA) AA0002446. It was once collected and described by M.G.Popov (Popov 1936) as *Anabasis pauciflora* Popov. Almost in the same period, M.M. Ilyin described the species *Anabasis balchaschensis* Iljin (Ilyin, 1936), which was renamed *Arthrophytum balchaschense* (Iljin) Botsch (Botschancev 1954) by V.P. Bochantsev 1954 (Goloskokov and Polyakov 1960). *Anabasis pauciflora* (Pratov 1972) was also added to *Arthrophytum balchaschense* as a synonymy, type specimens were submitted to the V.L. Komarov Botanical Institute in Moscow. V.L. Komarov Botanical Institute in St. Petersburg (LE00054892, LE00054893).

Thus, it was decided to make a molecular genetic analysis and to identify the relatedness of *Arthrophytum balchaschense* with species of the genus *Haloxylon*. One of the most important molecular methods in the study of kinship relations at the supra-species (genus) systematic level is the comparison and analysis of aligned DNA sequences of individual fragments of the genome and plastome of plants. In the study of genome fragments (nuclear DNA), nrITS (internal transcribed spacer) analysis of ribosomal DNA is the most popular. At the same time, in the plastome, a large range of genes and introns is used (Friesen 2007; Osmanali et al. 2023).

Material and methods

The objects of the study are species of genera *Haloxylon* and *Arthrophytum* of family Chenopodiaceae (Amaranthaceae s.l.), growing on the territory of Kazakhstan: *Arthrophytum longibracteatum* Korovin, *Arthrophytum balchaschense* (Iljin) Botsch., and *Haloxylon ammodendron* (C.A.Mey.) Bunge ex Fenzl (*Haloxylon aphyllum* (Minkw.) Iljin). The species *Anabasis salsa* (C.A.Mey.) Benth. ex Volkens was selected as a closely related species to the studied genera occurring directly in the same phytocenoses (Fig. 1). The studied specimens were collected at the same developmental phase for greater reliability of the results. All collection points of the studied species are presented in Table 1.

Herbaria specimens of the species *Arthrophytum balchaschense* of the Institute of Botany and Phytointroduction (AA, MW, LE, TASH, Fig. 3 and Online Resource 1).

Images of herbarium specimens were taken on a Levenhuk DTX RC3 remote-controlled microscope (China).

Anatomic method

Materials of anatomical sections were fixed in 45% alcohol. The objects of transverse sections were frozen in histological paraffin in special moulds of 15 × 15 mm. Transverse sections of the specimens were made using a "Rotary semi-automatic microtome" (MEDITE M530) with a transverse section thickness of 40 µm. Transverse sections were viewed using a Levenhuk Zoom&Joy microscope (China), images of transverse sections were taken with a Levenhuk D740T 5.1 camera, using LevenhukLite software. Biometric data were also measured using this programme. The mean number and standard error of biometric data were calculated using Microsoft Excel using the data analysis function. The current literature data of closely related species were used to describe the anatomical structure of the studied specimens (Pyankov et al. 1997; Butnik et al. 2001,

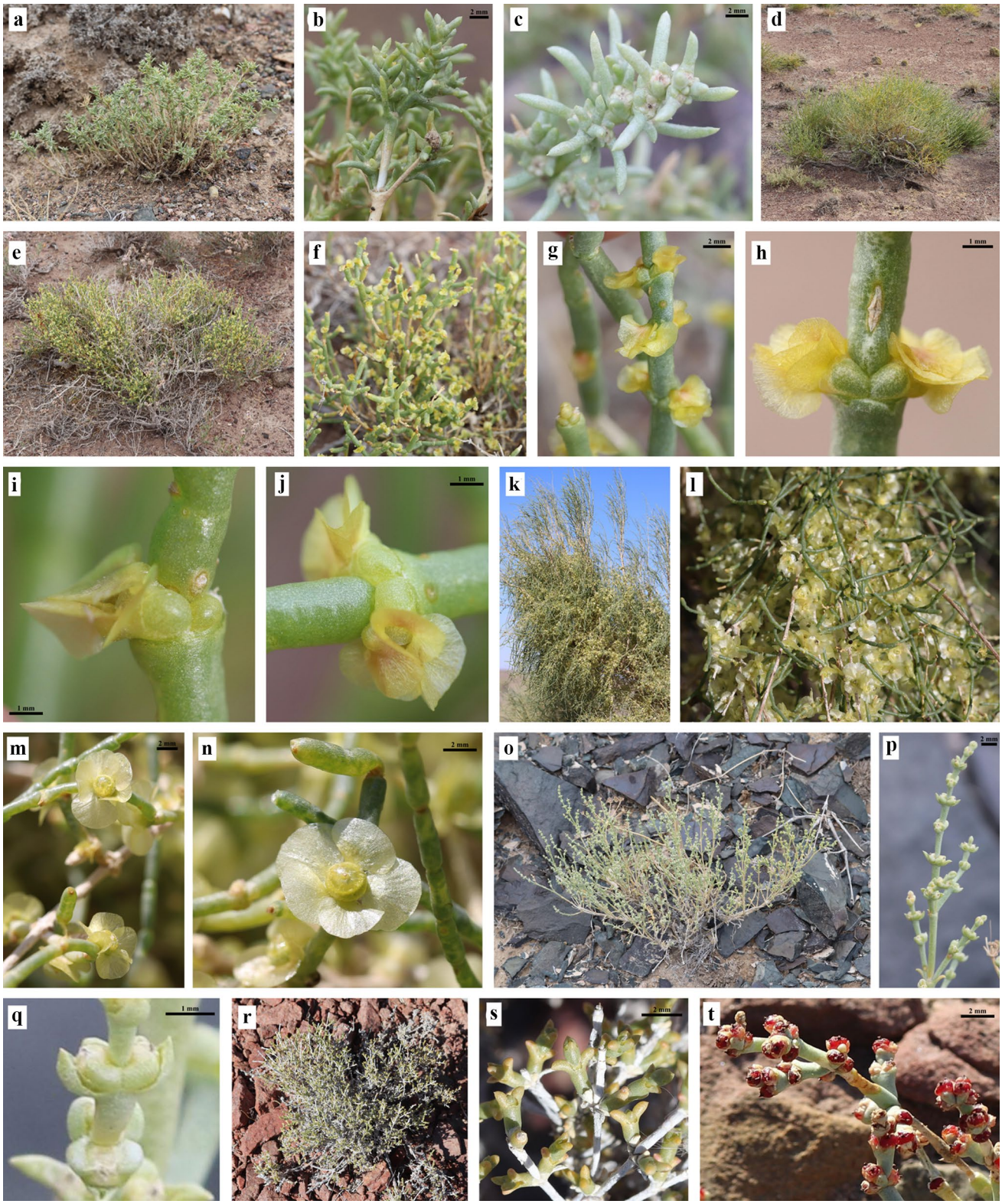

Fig. 1 **a–c** *Arthrophytum longibracteatum*, **d–j** *Haloxylon balchaschense* (*Arthrophytum balchaschense*), **k–n** *Haloxylon ammodendron* (*H. aphyllum*), **o–q** *Arthrophytum* sp. (hybrid), and **r–t** *Anabasis salsa*

Table 1 Origin, source, and GenBank accession numbers of sequences used for phylogenetic analyses

Accession	Name	Coordinates	Voucher	rITS	rps16 intron
B58	*Haloxylon balchaschense (Arthrophytum balchaschense)*	46.108889 N 73.254167 E	AA0003148	OR906301	OR913002
B59	*H. balchaschense*	46.356389 N 73.815278 E	AA0003149	OR906302	OR913003
B60	*Arthrophytum longibracteatum*	43.545556 N 78.591944 E	AA0003150	OR906303	OR913004
B61	*A. longibracteatum*	43.472778 N 79.010833 E	AA0003151	OR906304	OR913005
B62	*Arthrophytum sp*	43.472778 N 79.010833 E	AA0003152	OR906305	OR913006
B63	*Anabasis salsa*	45.366389 N 73.665833 E	AA0003153	OR906306	–
B64	*A. salsa*	46.186667 N 73.597778 E	AA0003154	OR906307	–
B66	*A. salsa*	46.041667 N 73.628056 E	AA0003155	OR906308	–
B67	*A. salsa*	46.319722 N 73.593889 E	AA0003156	OR906309	–
B70	*A. salsa*	44.629722 N 74.461944 E	AA0003157	OR906312	OR913008
B71	*A. salsa*	46.041667 N 73.628056 E	AA0003158	OR906313	–
B68	*Haloxylon aphyllum*	46.101667 N 73.276389 E	AA0003159	OR906310	OR913007
B69	*H. aphyllum*	44.629722 N 74.461944 E	AA0003160	OR906311	–

2017; Voznesenskaya et al. 2013; Zhaglovskaya et al. 2015; Schüssler et al. 2016; Osmonali et al. 2020).

Molecular genetics methods

DNA from leaves dried with silica gel was extracted using the NucleoSpin Plant II Mini kit (MACHEREY–NAGEL GmbH & Co. KG). The ITS fragment was amplified using ITS-A (Blattner 1999) and ITS-4 (White et al. 1990) primers. The chloroplast fragment rps16 intron was amplified using the primers rps16f-rps16r2 described by Shaw et al. (2007).

Amplification and sequencing

To perform the PCR, the amplification protocol for Red Mix was used, involving a 20 µl reaction mixture with 2×HS Taq Mix Red (Biozym Scientific GmbH, Germany), where the mix was 1 µl each of direct primer and reverse primer, 10 µl Red Mix, and 8 µl H_2. The amplified products were tested by electrophoresis on a 1.5% agarose gel stained with ethidium bromide. The DNA fragments were visualized under UV light on a Gel I X20 Lmager (INTAS Science Imaging Instruments GmbH, Germany) and documented using a Mitsubishi P93D printer (Mitsubishi Elec. Corp., Japan). The PCR products were sent for sequencing to Microsynth SeqLab (Göttingen, Germany; www. microsynth.seqlab.de). The sequences from all individuals were manually edited in Chromas Lite 2.1 (Technelysium Pty Ltd., South Brisbane, QLD, Australia) and aligned with ClustalX (Thompson et al. 1997); the alignment was manually corrected using MEGA7 (Kumar et al. 2016). Alignments of ITS and CP DNA fragments including own sequences and selected sequences from NCBI GenBank see on the Online Resource 2.

Phylogenetic analyses

Both datasets (nrITS and the cpDNA markers) were analysed separately through Fitch parsimony with the heuristic search option in PAUP version 4.0 b10 (Swofford 2002) with MULTREES, TBR branch swapping, and 100 replicates of random addition sequence. Gaps were treated as missing data. The consistency index (CI) was calculated to estimate the amount of homoplasy in the character set (Kluge and Farris 1969). The most parsimonious trees returned by the analysis were summarized in one consensus tree using the strict consensus method. Bootstrap support (BS) was performed using 1,000 pseudoreplicates to assess the support of the clades (Felsenstein 1985). Bayesian phylogenetic analyses were also performed using MrBayes 3.1.23 (Ronquist and Huelsenbeck 2003). The sequence evolution model was chosen by following the Akaike information criterion (AIC) obtained from jModelTest2. Two independent analyses with four Markov chains were run for 10 million generations, sampling trees every 100 generations. The first 25% of the trees were discarded as burn-in. The remaining 150,000 trees were combined into a single dataset, and a majority-rule consensus tree was obtained, along with posterior probabilities (PP).

Species from the subfamily Salicornioideae were selected as an outgroup: *Halostachys belangeriana* (Moq.) Botsch., *Halocnemum strobilaceum* (Pall.) M.Bieb., *Kalidium caspicum* (L.) Ung.-Sternb., and *K. foliatum* (Pall.) Moq.

Results

As a result of expeditionary research, samples of species *Arthrophytum longibracteatum* (2 populations), *Haloxylon balchaschense* (*Arthrophytum balchaschense*, 2 populations), *Haloxylon ammodendron* (*H. aphyllum*, 2 populations), *Arthrophytum* sp. (hybrid, 1 population), and Anabasis salsa (6 populations) were attracted for study. The main points of the studied samples are located in the northwestern part of Lake Balkhash, which corresponds to the north-eastern edge of the territory of the Betpakdala floristic district. With the help of QGIS programme, a map of the location points of the studied specimens was made (Fig. 2).

Typical materials of the studied species are in herbaria collections of Almaty (AA) and St. Petersburg (LE). A total of 70 herbarium specimens were analysed, based on which a distribution map of *Haloxylon balchaschense* (*Arthrophytum balchaschense*) was made (Fig. 3). The map shows its locality points according to the data of specimen labels from 4 large herbaria collections (AA, MW, LE, and TASH). The red ring on the map shows the point of the first description of the species (locus classicus), from where type materials were collected. The black ring marks the points of own collections of this species (Fig. 3).

Morphology

For visual assessment of the similarity and difference of species of *Arthrophytum longibracteatum*, *Haloxylon balchaschense* (*Arthrophytum balchaschense*), and *Haloxylon ammodendron* (*H. aphyllum)*, their main morphological characters reflected on the photos of the viewed specimens were analysed. In particular, the following were considered: leaf arrangement, branching of young shoots, and fruit wings (Fig. 4).

Anatomy

Three species were selected for comparative anatomical analysis: *Arthrophytum longibracteatum, Haloxylon balchaschense (Arthrophytum balchaschense), and Haloxylon ammodendron (H. aphyllum)*. In *Arthrophytum longibracteatum*, anatomical slices of leaves and stems were studied. In contrast, in the other two species, slices of only young shoots with assimilation cells were studied, as they have no leaves.

The cross-sectional thickness for all specimens was 40 µm. Thinner slices could not be made due to the succulent origin of the studied species, the water-bearing cells of which rupture at smaller slice thicknesses (Fig. 5).

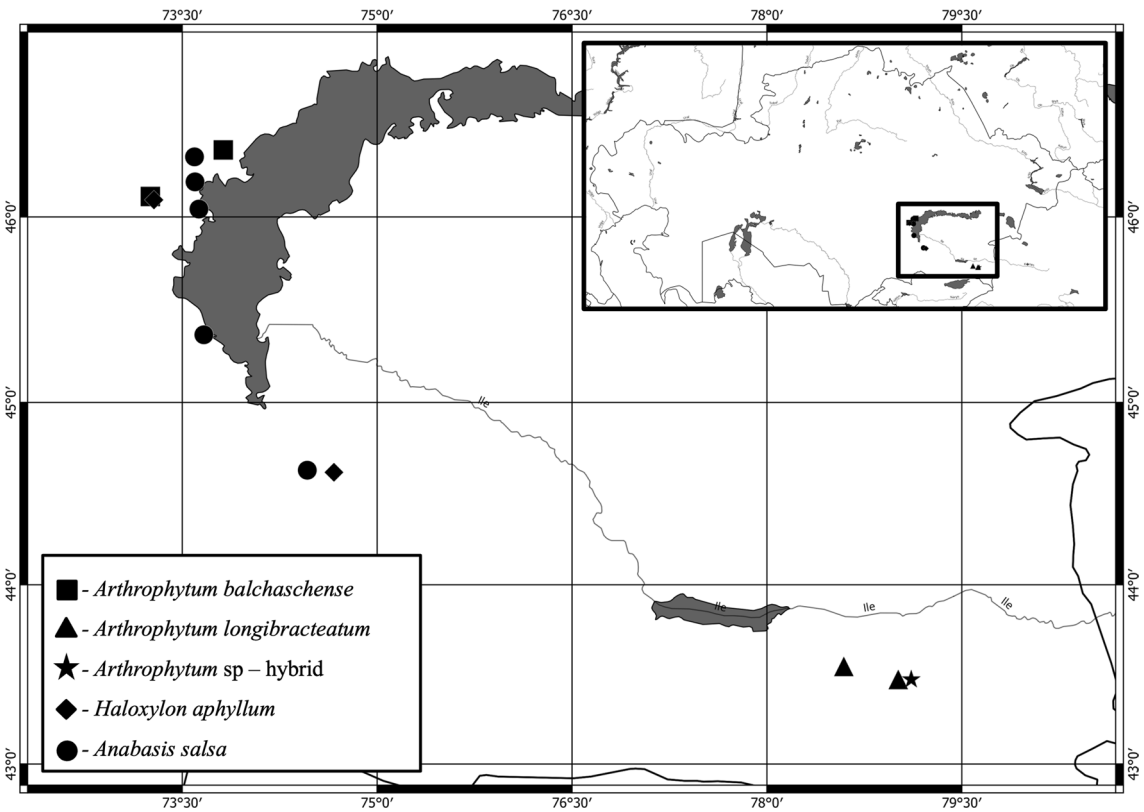

Fig. 2 Distribution map of the samples studied

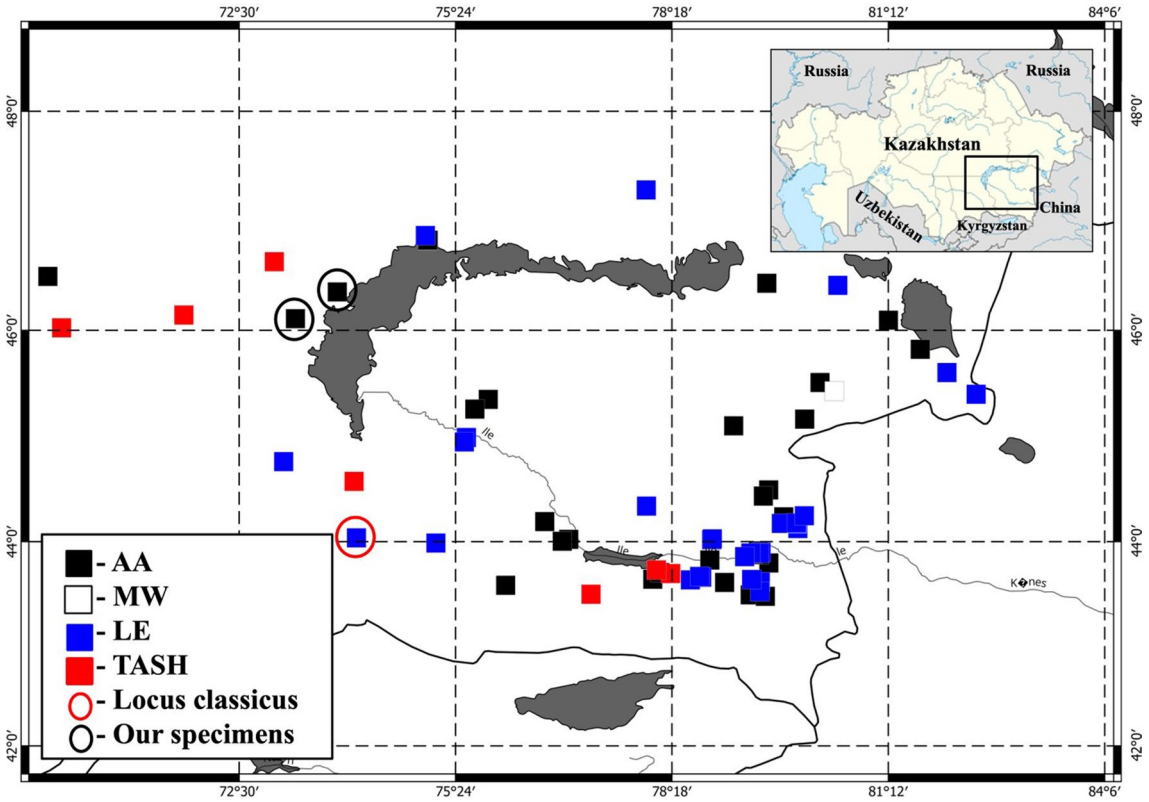

Fig. 3 Map of *Haloxylon balchaschense* (*Arthrophytum balchaschense*) localities according to the studied herbarium specimens (Table 2)

The following anatomical structures are indicated in transverse anatomical sections: epidermis, palisade mesophyll, cranz cells, drusa, water-bearing cells, xylem, phloem, collenchyma, sclerenchyma, parenchyma cells, parenchyma of the core, and vascular bundle. The biometric data are presented in Table 3.

Molecular phylogeny

Sequencing of nrITS and chloroplast (rps16 intron) fragments was performed for 5 species, one of which is of hybrid origin. The ITS sequencing tree is made using the studied samples and supplemented with samples from the NCBI database. In the tree, our samples are highlighted in bold. Colour highlighting shows the generic affiliation (*Haloxylon, Arthrophytum, and Anabasis*) of the species (Fig. 6). It should be noted that the nrITS fragments in the genus Haloxylon are identical for all species of the genus. In contrast, the chloroplast fragments are more or less different according to the analyses. For detailed species distinction (scattering among species), a full genomic analysis of chloroplast fragments is needed. An attempt at of amplifying and sequencing herbarium specimens of other species of the genus *Arthrophytum* was unsuccessful because, unfortunately, the DNA in the succulent green parts of the plants was already severely degraded due to prolonged drying of the herbarium. For the chloroplast tree, rps16 intron sequences were used (Fig. 7). In both analyses (ITS and plastids), sequences of *Arthrophytum balchaschense* did not differ from *Haloxilon* species. We also sequenced IGS trnQ-rpS16, but it did not work properly; the sequencing data were unsuitable for analysis. *Arthrophytum* sp. (Accession B62) is isolated between clades of *Arthrophytum* and *Haloxilon* in ITS tree and in the plastid tree, clearly in the clade with *Arthrophyton longibracteatum*.

Discussion

Screening of literature data and available herbarium specimens revealed that *Haloxylon balchaschense* (*Arthrophytum balchaschense*) has a central-eastern-North Turanian range. In the north, it reaches the south-eastern part of the Kazakhstan Shallow Foothills; in the east (along the foothill deserts) it penetrates into the western part of the Dzungarian Alatau; in the west, it is found in the Pribalkhashie and eastern spurs of Betpakdala; in the south, it is confined to the desert-stony foothills of the Zailiyskiy Alatau (Iljin, 1936; Goloskokov and Polyakov 1960; Pratov 1972; Safronova 2010; Kamelin 2017) (Fig. 3). The species is endemic to Kazakhstan

Table 2 Label data of studied herbarium specimen of *Haloxylon balchaschense*

Floristic area	Label data	Coordinates	Collectors	Date of collection
Herbarium AA				
Betpakdala	Northern shore of Balkhash, Kounrad, rocks of the hills	N 46.833208 E 75.025421	*Popov M.G.*	9 Sep 1935
	Northern Pribalkhashie Kounrad. Slope of a hillside	N 46.831128 E 75.034423	*Popov M.G.*	5 Oct 1935
	Western Betpak-Dala. Tamgaly-jar tract, at the foot of a chink, near a spring on solonchaks	N 46.499924 E 69.935850	*Kubanskaya Z.V.*	22 Aug 1946
Zailiyskiy Alatau	Zailiyskiy Alatau. Bala-Boguty mountains. Stony-takyr sub-mountain (Pri Iliyskiy) desert to the east of Sary-bulak village	N 43.701164 E 78.138586	*Popov M.G.*	8 Aug 1937
	Zailiyskiy Alatau. Boguty mountains. Stony foothills near Charyn settlement	N 43.880985 E 79.385366	*Popov M.G.*	30 Aug 1937
	Zailiyskiy Alatau. Sub-mountainous Iliysk plain. Pebbles near the settlement of Charyn	N 43.911074 E 79.460137	*Popov M.G.*	31 Aug 1937
	Alma-Ata region, Chilik district, Syugatinskaya intermountain valley, between Kara-Kaili and Turaigyr mountains	N 43.637392 E 78.043003	*Kubanskaya Z.V.*	22 Sep 1961
Dzungarian Alatau	North-eastern spurs of the Dzungarian Alatau. Plateau between Jalanshkul and Alakul. Gammada	N 45.168451 E 80.079059	*Goloskokov V.P.*	17 Jun 1949
	South-eastern spurs of Dzungarian Alatau. Ulkun-Kalkan mountains near Kokbastau spring. Along the southern stony slopes of hills	N 45.105143 E 79.127147	*Goloskokov V.P.*	14 Jun 1956
	Southern spurs of Dzungarian Alatau, east of Altyn-Emel pass. Kum-Tekey tract, on loams	N 43.823053 E 78.807564	*Kurochkina L.Y.*	7 Sep 1958
	Dzungarian gate in the bed of the Chindaly r., on a rubbly grass. Gammada	N 45.823817 E 81.628129	*Kurochkina L.Y.*	29 Aug 1959
	Alma-Ata region. Panfilov district, southern gentle slopes of Mataiyu mountains	N 44.238521 E 79.798914	*Kubanskaya Z.V.*	1 Aug 1960
	Southern spurs of the Dzhungarian Alatau. Koibyn Canyon on the way to Koktal. Along the feather-coloured exposed slopes	N 45.512905 E 80.284769	*Goloskokov V.P.*	5 Jul 1971
Balkhash-Alakol	Alma-Ata region. 45 km east of Chilik r. Iliysk rubbly desert	N 43.578271 E 76.071998	*Bochantsev V.P.*	24 Sep 1953
	Lower course of the Charyn r. Uroch. Sary-Togoy. Along the saline ancient terrace on the left bank of the river	N 43.874304 E 79.467443	*Goloskokov V.P.*	18 Jun 1955
	Alma-Ata region, north of the village of Uzun-Tam. Uzun-Tam	N 46.437031 E 79.571535	*Godvinsky M.I.*	11 Jun 1958
	Gammada on the south-east shore of Lake Alakul near the 3rd border post. Stony solonchaks	N 43.606044 E 79.006038	*Gamayunova A.P*	19 Jul 1958
	Eastern Pribalkhashie. South-East of Lake Alakul. Gammada at the foot of g. Aktu	N 46.094847 E 81.201398	*Kurochkina L.Y.*	1 Oct 1958

Table 2 (continued)

Floristic area	Label data	Coordinates	Collectors	Date of collection
	Eastern Pribalkhashie. North-East of Lake Jalanash-Kul. Jalanash-Kul. On rubbly loams	N 43.470871 E 79.551979	*Kurochkina L.Y.*	1 Oct 1958
	Eastern Pribalkhashie. Dzungarian gates. Lenkol valley. On rubbly loams	N 45.354522 E 75.838042	*Kurochkina L.Y.*	2 Oct 1958
	Gammada between the Ili River and the Ketmen Ridge. Ketmen. Between the Charyn and Chundzha s	N 43.485079 E 79.349004	*Kurochkina L.Y.*	11 Oct 1958
	Alma-Ata region. Alakul district. Dzungarian gate. Plain. Soils grey-brown	N 44.003914 E 76.829767	*Mikheeva N.N.*	9 Jul 1959
	Alma-Ata region. Panfilov district, intermountain valley of Matay, and Ulken-Kalkan and Kishi Kalkan mountains. On grey-brown solonchak soils and solonchaks	N 44.496126 E 79.596407	*Kubanskaya Z.V.*	25 Jul 1960
	Alma-Ata region. Panfilov district, intermountain valley of Matai and Ulken-Kalkan mountains, tract. Kosbastau, on solonchak soils	N 44.437322 E 79.524996	*Kubanskaya Z.V.*	27 Jul 1960
	Alma-Ata region. Uygur district, vicinity of Tas-Kara-Su settlement, on saline soils	N 44.193021 E 76.595442	*Kubanskaya Z.V.*	13 Aug 1960
	Alma-Ata region. Uygur district, on the road from Chunji to Temirlik river, On saline grey-brown soils	N 43.794614 E 79.598984	*Kubanskaya Z.V.*	17 Aug 1960
	Alma-Ata oblast. Iliyskiy district, hilly sands of Ulkun-Kum, in interbuggy depressions	N 44.022154 E 76.916819	*Kubanskaya Z.V.*	22 Oct 1960
	The right bank of the middle course of the Ili River. Upland terrace opposite Ayak-Kalkan resort. On solonchaks	N 45.263001 E 75.658508	*Goloskokov V.P.*	6 Jun 1971
Herbarium MW				
Dzungarian Alatau	North-eastern spurs of Dzungarian Alatau, plateau between Jalankul and Alakul	N 45.432703 E 80.476828	*Goloskokov V.P.*	17 Jun 1959
Herbarium LE				
Dzungarian Alatau	Semirechensk region, between Kunchy hills and Ayaguzom river, solyanka steppe	N 44.126599 E 79.986995	*Korzhinsky S.I.*	23 Jul 1890
	South-east of Sary-Kulsuk	N 44.341550 E 77.959714	*Shishkin B.K.*	24 Jun 1914
	Taldykorgan near the gammady at the foot of the Altyn-Emelya pass near Baschiy village	N 44.018413 E 78.830979	*Bochantsev V.P.*	19 Aug 1927
	Taldykurgan oblast. Kum-tekei tract of the eastern Altyn-Emel pass, on loamy and brushy soils along watercourses and volcanoes of the foothill plain	N 44.026560 E 78.840936	*Kurochkina L.Y.*	7 Oct 1958

Table 2 (continued)

Floristic area	Label data	Coordinates	Collectors	Date of collection
	Southern spurs of Dzungarian Alatau, Kaybyn River Canyon on the Koktal road	N 44.175294 E 79.766248	*Goloskokov V.P.*	5 Jul 1971
Zailiyskiy Alatau	Semirechenskaya oblast, Jarkent district Kara-Tuma-Sary-Chagan	N 44.174900 E 79.974331	*Minson A.*	22 Aug 1910
	Semireka oblast Jarkent district, Urta-kuduk	N 44.177547 E 79.972529	*Minson A.*	23 Aug 1910
	Semireka oblast, Jarkent uyezd, between Dubin village and Ili river. Dubin and Ili river sands	N 44.249077 E 80.074498	*Sapozhnikov V.V.* and *Shishkin I.B.*	2 Jul 1912
	Zailiyskiy Alatau, foothill Ili desert. Gamada at the foot of Boguty mountains near Charyn settlement	N 43.656028 E 78.698521	*Popov M.G.*	31 Aug 1937
	Zailiyskiy Alatau, sub-mountainous Priili desert. Gammada at the foot of the Byuguti mountains	N 43.630730 E 78.547035	*Popov M.G.*	31 Aug 1937
	Zailiyskiy Alatau, sub-mountainous Priili desert. Gammada at the foot of the Byuguti mountains	N 43.664458 E 78.671331	*Popov M.G.*	31 Aug 1937
	Almaty oblast Uygur district near Garyn village salian-rocky desert	N 43.855629 E 79.274219	*Borisova A.G.* and *Ilyin M.M*	26 Dec 1937
	Middle reaches of the Charyn River of Mount Katu with rocky plumes near the temporary stream bed	N 43.890770 E 79.356587	*Goloskokov V.P.*	21 Jun 1955
	Taldykurgan oblast, Jarkent basin west part, Desert 8 km east of Sary-Ozek Jarkent highway. Solonchak depression among tar desert	N 44.994926 E 75.545910	*Bochantsev V.P.*	20 Aug 1955
	Almaty region Jarkent Basin, left bank of the Ili River, 40 km east of Charyn village on the road to the village of Yenlik. Yenlik. Clay solanschiks with saxaul	N 44.179271 E 79.968666	*Grubov V.I.* and *Lubarsky N.*	22 Aug 1955
	Priili Deserts East of the Charyn River and West of the Chunzhi river	N 45.606401 E 81.985297	*Kurochkina L.Y.*	11 Oct 1958
	Priilii deserts 20 km Chunzhi, along the river Charyn. Along watercourses of gammads	N 45.402638 E 82.376495	*Kurochkina L.Y.*	11 Nov 1958
	East Kazakhstan, Ili River basin, Chundja foothill highway, 11 km to the north of Chundja. Pscha-pebble desert	N 44.179271 E 79.968666	*Grubov V.I.* and *Bachantsev V.P.*	2 Aug 1960
	Chunja village, Ulken-Kum sands, pre-sand plain, Almaty region	N 43.634923 E 79.368419	*Kubanskaya Z.V.*	22 Oct 1960
	Near the village of Charyn	N 43.888904 E 79.466756	*Bochantsev V.P.*	2 Apr 1976
Betpakdala	Northern Pribalkhashie, Kounrad, slope, hills	N 46.877018 E 74.996429	*Popov M.G.* and *Rubtsov N.I.*	5 Oct 1935
	Northern Pribalkhashie, Kounrad, slope, hills	N 46.875291 E 74.995625	*Bochantsev V.P.*	1 Apr 1976

Table 2 (continued)

Floristic area	Label data	Coordinates	Collectors	Date of collection
Balkhash-Alakol	Ili River valley Raskum sands	N 44.994926 E 75.545910	*Bochantsev V.P.*	28 Aug 1915
	Kishi-Alakul coastal strip	N 46.417359 E 80.523065	*Cherniakova E.*	7 Sep 1930
	Ili River valley between Chundja and Tas-Karasu villages, Rubble semi-desert	N 44.953032 E 75.517644	*Rodin L.*	23 Oct 1931
	Eastern Pribalkhashye north-eastern Jalanashkul (Dzungarian Gate) gammada	N 45.606401 E 81.985297	*Kurochkina L.Y.*	1 Oct 1958
	Dzungarian Gate, rubbly desert	N 43.897976 E 79.493442	*Kurochkina L.Y.* and *Годвинский М.И.*	2 Oct 1958
	Semipalatinsk region, 35 km NNW of Akbotay railway station Pribalkhash plain 12 km 10 km from Ayak-Karaul	N 47.290780 E 77.953740	*Vasilevich V.I., Lavrenko E.M.* and *Rachkovskaya E.I.*	7 Aug 1966
Moyinkum	Djambyl Mountains. Chacharly ridge. Saline pazhbina	N 44.765965 E 73.096358	*Drobov V.P.* and *Gomolitsky P.*	1 Jun 1926
Chu-Ili	South Kazakhstan Chui district, Chu-Ili mountains	N 43.986902 E 75.136967	*Drobov V.* and *Gomolitsky P.*	1 Jun 1926
	Chu River valley between Sarybulak spring and Gullevka settlement	N 44.036614 E 74.071533	*Mironov B.* and *Ilyin M.M.*	28 Aug 1933
Herbarium TASH				
Chu-Ili	Chui district. Djambul mountains, saline depths	N 44.577829 E 74.040411	*Drobov V.P.* and *Gomolitsky P.*	1 Jun 1926
Zailiyskiy Alatau	Almaty okr. Yenbekshikazakh district, vicinity of Lake Boraldai salt pans	N 43.491573 E 77.214686	*Bochantsev P.B.*	29 Aug 1928
	Almaty oblast, Yenbekshikazakh district Istimbet-kul lake and Chilik river sands and takyrs	N 43.692488 E 78.283106	*Bochantsev P.B.*	16 Feb 1937
	Almaty region, Chilik district, bumpy sands of Ulken Kum, pre-sand plain	N 43.727466 E 78.092001	*Kubanskaya Z.V.*	25 Oct 1960
Betpakdala	East Betpakdala, Sary-Bulak clay-rubble remnants	N 46.634971 E 72.971155	*Mironov B.*	7 Aug 1933
	East Betpakdala near Aral-tobe hill, opening hills	N 46.142883 E 71.759695	*Mironov B.*	13 Sep 1933
	West Betpakdala, edge of wet salt marsh	N 46.024074 E 70.119904	*Mironov B.* and *Paziy V.*	4 Jun 1936

(Osmonali et al. 2019), prefers rubbly, clayey solonchak deserts, and rarely enters sands (Iljin, 1936; Goloskokov and Polyakov 1960; Pratov 1972; Kubentayev et al. 2024).

The main difference between the morphology of *Arthrophytum longibracteatum* and the other two leafless species is the presence of developed leaves. The similarity of the morphological structure of *Arthrophytum balchaschense* and *Haloxylon aphyllum* (Figs. 1 and 4) is manifested in the structure of stems (young shoots), the spatial arrangement of which relative to the stems is 45º–50º, whereas in *Arthrophytum longibracteatum* young shoots, stems and leaves are arranged at an angle of 30º–40º. At the same time, young shoots of *Arthrophytum balchaschense* are larger (2040.2 ± 33.51 µm) than those of *Haloxylon*

Fig. 4 Morphological characters (herbarium specimens): **a–c** *Arthrophytum longibracteatum*, **d–e** *Haloxylon balchaschense,* **f–g** *Haloxylon aphyllum*. **a–c**, **e**, **g** leaf arrangement; **d**, **f** fruit wings

aphyllum (1809.4 ± 11.51 µm) (Table 2). In *Arthrophytum longibracteatum* these values are much smaller: In young shoots they are 1581.9 ± 75.35 µm, and the leaf diameter is 1139.9 ± 4.22 µm.

Besides, external morphological similarity of fruit wings (Fig. 4) is observed in *Arthrophytum balchaschense* and *Haloxylon aphyllum* species. However, in *Haloxylon aphyllum*, wings are located perpendicularly relative to the fruit base, in *Arthrophytum balchaschense*, they bend inwards, thus covering the fruit itself. To some extent such arrangement of wings has external similarity with the similar character of such species of genus *Anabasis* as *A. truncata* (Schrenk) Bunge and *A. aphylla* L.

Comparative analysis of anatomical structure also showed similarity between *Arthrophytum balchaschense* and *Haloxylon aphyllum* species. Thus, the thickness of the epidermis in *Arthrophytum balchaschense* was 31.88 ± 1.20 µm, while in *Haloxylon aphyllum*, it was 30.66 ± 0.99 µm. In *Arthrophytum longibracteatum* species, this layer was thinner in leaves 21.3 ± 1.00 µm, and on the contrary, it was thicker in stem 35.94 ± 1.55 µm. The thickness of palisade mesophyll in the first species is 34.14 ± 0.96 µm, in the second—60.4 ± 1.45 µm, in the third—74.19 ± 7.42 µm (leaf), 59.8 ± 1.75 µm (stem). According to this index, all species are well differentiated from each other (Fig. 5). The thickness of cranial cells of the species considered varies between 3–4 µm, with the lowest values observed in *Arthrophytum balchaschense* at 15.88 ± 0.56 µm and the highest in *Arthrophytum longibracteatum* at 19.26 ± 0.55 µm (leaf). The aquifer (water-bearing cells) is most well represented in the two compared species than in *Arthrophytum longibracteatum*. These data are also consistent with the smaller size of young shoots in this species. At the same time, despite the fact that *Arthrophytum balchaschense* exceeds the similar indicators of *Haloxylon aphyllum* in the size of the stem transverse section, they are smaller than those of *Haloxylon aphyllum* (495.14 ± 12.94 µm) in the size of layers of some tissues, including the water-bearing layer (361.07 ± 16.81 µm). As for other layers (except sclerenchyma), in *Arthrophytum balchaschense* they have a larger size than in *Haloxylon aphyllum*.

According to the results of molecular genetic analyses, *Arthrophytum balchaschense* is close to *Haloxylon aphyllum*, as well as other species of the genus *Haloxylon*. Given that all species lined up almost in the same lineage according to ITS sequences (Fig. 6), we can say that this fragment is the same for all species of the genus *Haloxylon*. At the same time, given the small number of phylogenetic works directly related to the studied specimens, it is difficult to judge the formation of this group (Pyankov et al. 2001; Sukhorukov 2014; Dong et al. 2016; Schüssler et al. 2016; Sukhorukov et al 2018; Wang et al 2022). But the fact that the ITS sequencing fragment of *Arthrophytum balchaschense* appeared to be within *Haloxylon* species proves the generic

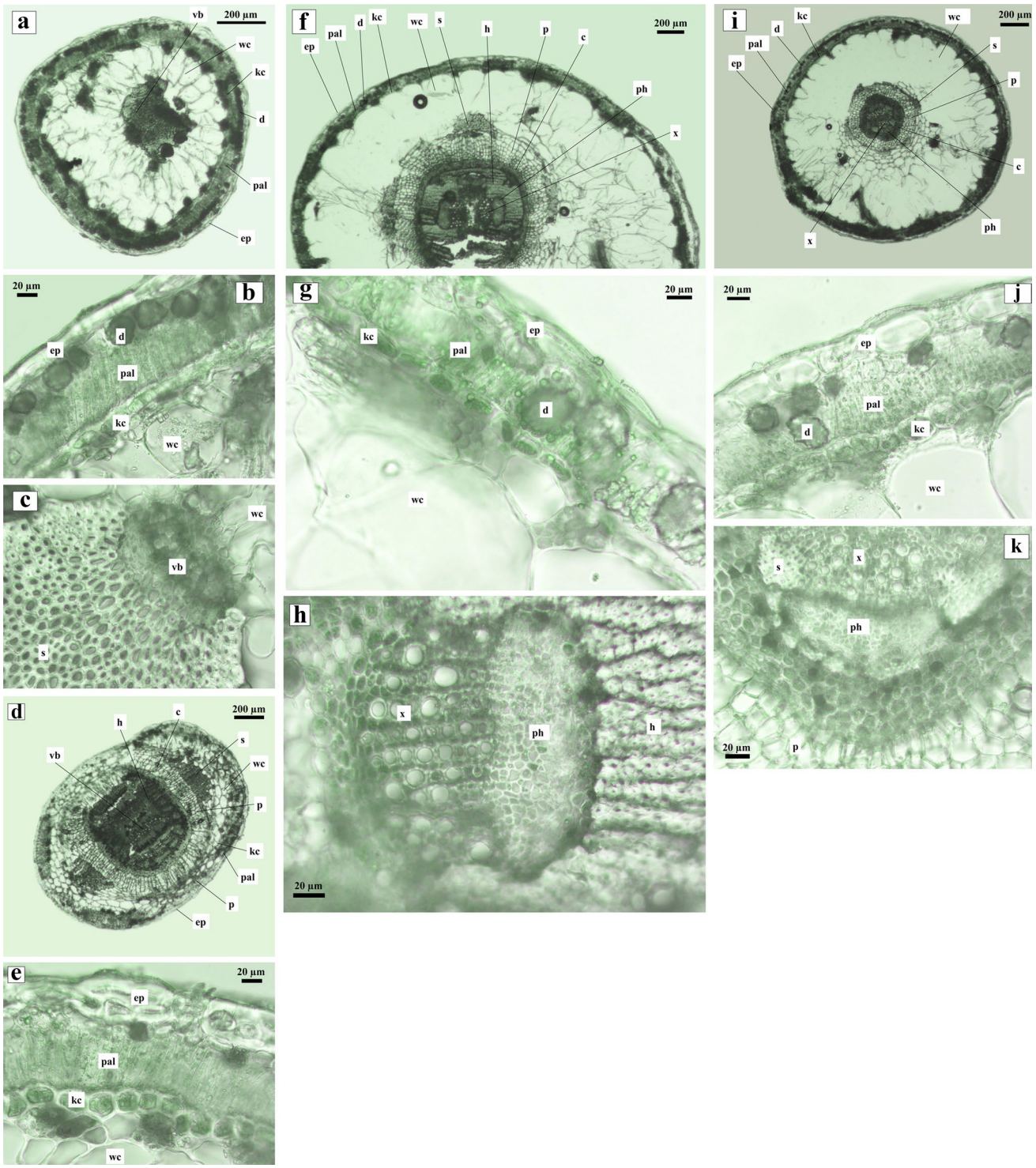

Fig. 5 Comparative anatomical structure of the studied species: **a–e** *Arthrophytum longibracteatum* (**a–c**—leaf, **d–e**—stem), **f–h** *Haloxylon balchaschense (Arthrophytum balchaschense)*, and **i–k** *Haloxylon ammodendron* (*H. aphyllum*). *EP* epidermis, *PAL* palisade chlorenchyma, *Kc* kranz cell, *D* druza, *Wc* water-bearing cell, *X* xylem, *Ph* phloem, *C* collenchyma, *S* sclerenchyma, *P* parenchyma cells, *H* core parenchyma, and *Vb* vascular bundle

Table 3 Biometric data on the anatomical structure of the studied species: 1—*Haloxylon balchaschense;* 2—*H. aphyllum;* 3—*Arthrophytum longibracteatum* (leaves); 4—*Arthrophytum longibracteatum* (stem)

No	Cross-sectional diameter, µm	Epidermis thickness, µm	Length of palisade mesophyll, µm	Kranz cell thickness, µm	Thickness of water-bearing cells layer, µm	Diameter of water-bearing cells, µm	Parenchyma µm	Sclerenchyma µm	Core diameter µm	Drill diameter µm
1	2040.2 ± 33.5	31.88 ± 1.2	34.14 ± 0.96	15.88 ± 0.5	361.07 ± 16.8	74.42 ± 4.27	146.64 ± 3.6	45.18 ± 1.1	585.64 ± 6.8	31.98 ± 1.0
2	1809.4 ± 11.5	30.66 ± 0.9	60.4 ± 1.45	17.89 ± 1.6	495.14 ± 12.9	68.88 ± 9.47	87.99 ± 4.7	51.98 ± 2.1	260.45 ± 4.1	22.24 ± 2.6
3	1139.9 ± 4.2	21.3 ± 1.0	74.19 ± 7.42	19.26 ± 0.5	276.33 ± 21.8	99.73 ± 14.1	–	–	–	29.22 ± 1.4
4	1581.9 ± 75.3	35.94 ± 1.5	59.8 ± 1.75	21.19 ± 0.7	226.88 ± 18.8	59.68 ± 7.3	145.13 ± 4.6	62.31 ± 1.5	732.7 ± 20.7	–

affiliation of this species (Fig. 6). Chloroplast fragments also confirm this result (Fig. 7). In addition, the rps16 intron sequence of *Haloxylon aphyllum* B68 differs from that of *Haloxylon ammodendron* from Genbank (OR251181, NC_027668), which confirms the need for a more thorough analysis of the relationships between these species.

During the studies, other important points were noted in the structure of the phylogenetic trees obtained. According to ITS fragments, hybridogenic specimen B62 of *Arthrophytum* sp (Fig. 6) was located between species of genera *Arthrophytum* and *Haloxylon*. By chloroplast fragments, the hybridogenic specimen was close to *Arthrophytum longibracteatum* (Fig. 7), while by morphological structure of leaves they differ. It is not possible to discuss the formation of the hybrid in question due to insufficient evidence. However, with a varying degree of probability, it can be assumed that the parents of this specimen are *Arthrophytum longibracteatum* and *Haloxylon* sp. (possibly *Arthrophytum balchaschense*). The study of this specimen B62 *Arthrophytum* sp. (hybrid) (coordinates 43.472778 N 79.010833 E) requires a full-fledged study within the whole population.

The next point worthy of attention, in our opinion, is the fact that *Salsola oppositifolia* Desf., currently understood as *Soda oppositifolia* (Desf.) Akhani (Rudov et al. 2020)), in the ITS tree showed relative closeness to the genera *Arthrophytum*, *Haloxylon*, and *Anabasis* than to Salsola (Fig. 6). In terms of chloroplast tree, it appeared very close to the genus *Arthrophytum* (Fig. 7), as noted previously (Schüssler et al. 2016). In addition, comparing the presented photos of the species in the GBIF (Global Biodiversity Information Facility) database https://www.gbif.org/species/11364737 and Plantarium https://www.plantarium.ru/page/view/item/72511.html, we can say that Soda oppositifolia is habitually very similar to species of the genus *Arthrophytum*.

Conclusion

The results of the conducted comparative analysis of morphological, anatomical, and molecular genetic structure of *Arthrophytum longibracteatum, Arthrophytum balchaschense,* and *Haloxylon ammodendron* (*H. aphyllum*) species allowed to form a proof base of clear belonging of *Arthrophytum balchaschense* to the genus *Haloxylon*. This circumstance became the reason for the necessity of nomenclatural changes consisting in assignment of *Arthrophytum balchaschense* to the genus *Haloxylon* under the name *Haloxylon balchaschense* (Iljin) Osmonali, Veselova & Kudab. This species has a central-eastern-North Turanian distribution, endemic to Kazakhstan's flora.

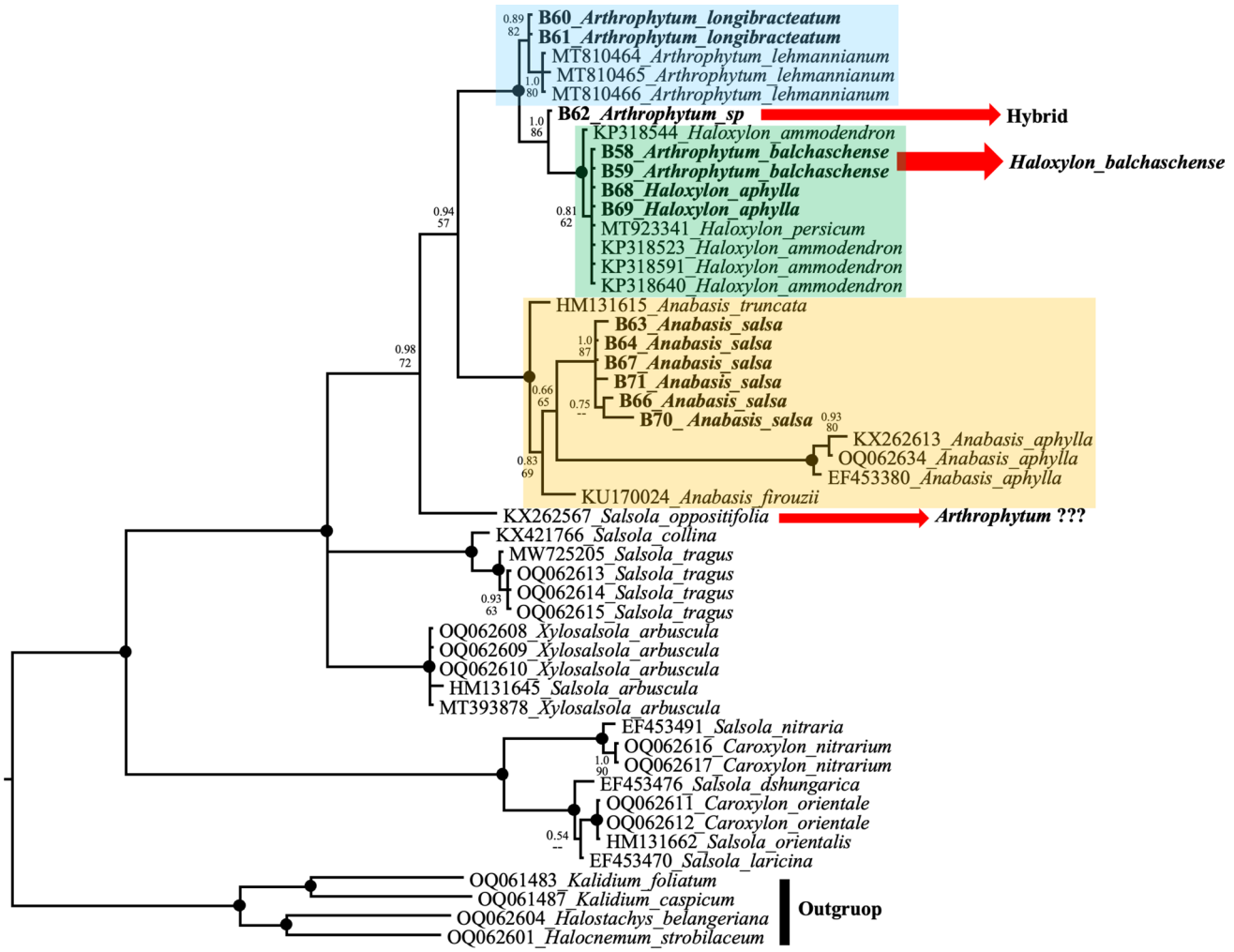

Fig. 6 ITS tree of species of the genus *Haloxylon, Arthrophytum,* and *Anabasis*. The joint presence of Bayesian with a probability greater than 0.98 and bootstrap support greater than 95% is indicated by a black dot. The samples we investigated are highlighted in bold. The following data were obtained by running the data through the JModeltest software: GTR + I + G, -lnL 2647.49996, AIC 5470.999920, and weight 0.654477

Taxonomical treatment

Haloxylon balchaschense (Iljin) Osmonali, Veselova & Kudab., **comb. nova** ≡ *Anabasis balchaschensis* Iljin, V.L.Komarov (ed.), Fl. URSS 6: 299. 1936 (rossice); et Acta Inst. Bot. Acad. Sc. URSS, Ser. I. Fasc. 2, 131. 1936 (latine) ≡ *Arthrophytum balchaschense* (Iljin) Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 85. 1954.—LECTOTYPE: Songoria, am Tschu. (LE 01248297) (Fig. 8).

= *Anabasis pauciflora* Popov, V.L.Komarov (ed.), Fl. URSS 6: 879. 1936.

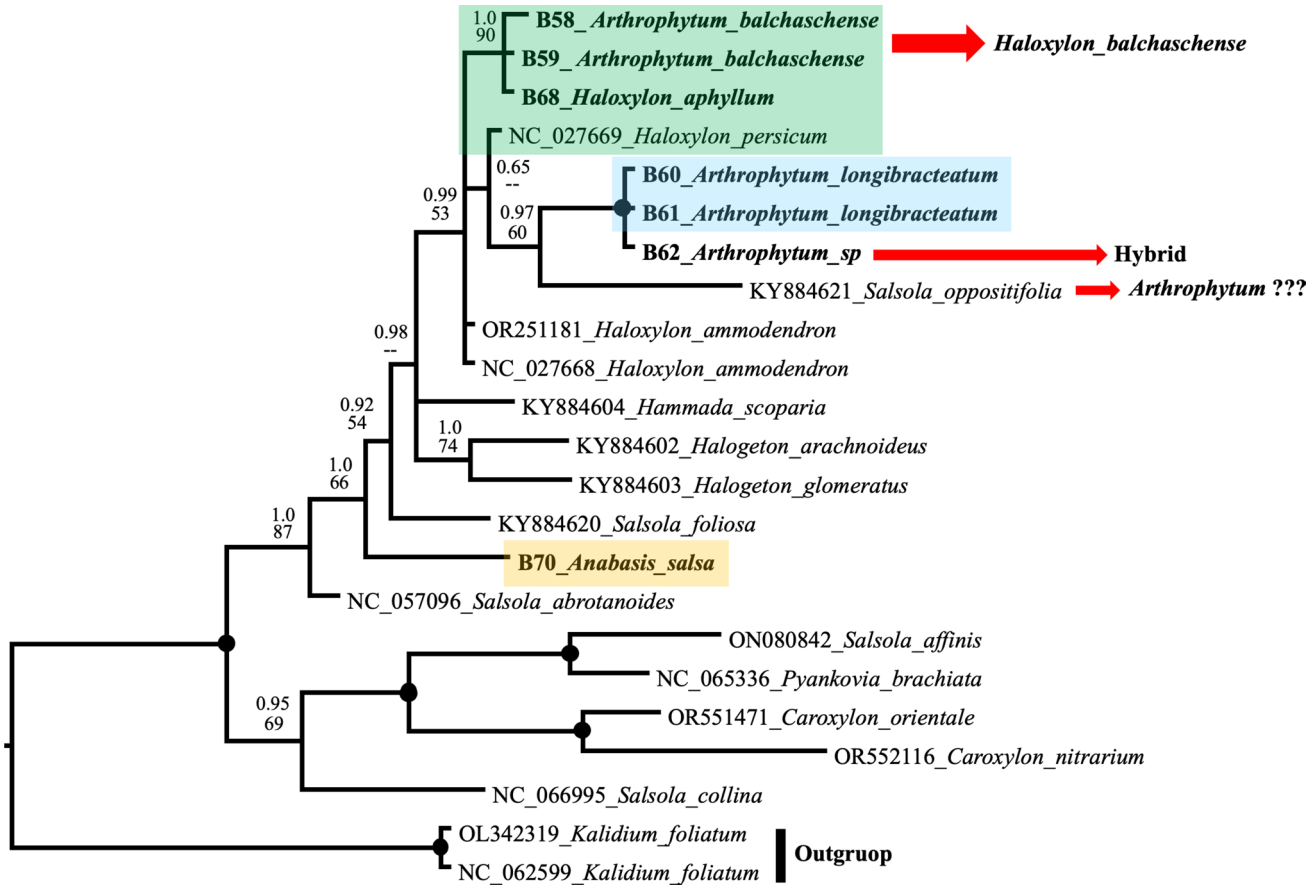

Fig. 7 Plastiden tree (rps16 intron) species of the genus *Haloxylon, Arthrophytum,* and *Anabasis*. The joint presence of Bayesian with probability greater than 0.98 and bootstrap support greater than 95% is indicated by a black dot. The samples we investigated are highlighted in bold. The following data were obtained by running the data through the JModeltest software: GTR + I, -lnL 2293.37211, AIC 4692.744220, and weight 0.237090

Fig. 8 Lectotype of *Haloxylon balchaschensen*

Information on Electronic Supplementary Material

Online Resource 1. Label data of studied herbarium specimen of *Haloxylon balchaschense*.
Online Resource 2. Alignments of ITS and CP DNA fragments including own sequences and selected sequences from NCBI GenBank.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00606-024-01926-x.

Acknowledgements This research has been funded by the Science Committee of the Ministry of Education and Science of the Republic of Kazakhstan (Grant No. AP19679078—Studying the species diversity of ecotone territory of north-eastern Betpakdala for preserving the relict gene pool of Kazakhstan arid flora).

Author contribution BBO presented molecular genetic studies, writing, and coordination of the article for publication. PVV and GMK

developed the concept and design of the research, organizing an expedition trip, collecting material for subsequent work, and writing an article. US and DSA prepared morpho-anatomical studies. NF performed conceptualisation, formal analysis, data processing, data curation, writing, reviewing, and editing. All co-authors participated in interpreting the results and writing the final manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

References

Baitenov MS (2001) The genus *Kalidium* Moq. Flora of Kazakhstan. Genus complex flora. Almaty 2:72

Blattner FR (1999) Direct amplification of the entire ITS region from poorly preserved plant material using recombinant PCR. Biotechniques 27:1180–1186

Botschancev VP (1954) *Arthrophytum balchaschense* (Iljin) Botsch. Bot Mater Gerb Bot Inst Komarova Akad Nauk SSSR 16:85.

Butnik AA, Duschanova GM, Yusupova DM, Abdullaeva AT, Abdinazarov SH (2017) Types leaf mesophyll species of Chenopodiaceae Vent. Central Asia and their role in the monitoring of desertification. J Novel App Sci 6:13–21

Butnik AA, Ashurmetov OA, Nigmanova RN, Payzieva SA (2001) Ecological anatomy of desert plants in Central Asia. Half–shrubs, shrubs. Tashkent Fan 2:132

Dong W, Xu C, Li D, Jin X, Li R, Lu Q, Suo Z (2016) Comparative analysis of the complete chloroplast genome sequences in psammophytic *Haloxylon* species (Amaranthaceae). PeerJ 4:e2699. https://doi.org/10.7717/peerj.2699

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791. https://doi.org/10.2307/2408678

Friesen N, Grützmacher L, Skaptsov M, Vesselova P, Dorofeyev V, Luferov AN, Turdumatova N, Lazkov G, Smirnov SV, Shmakov AI (2022) *Allium pallasii* and *A. caricifolium*—surprisingly diverse old steppe species, showing a clear geographical barrier in the area of lake Zaysan. Plants 11:1465. https://doi.org/10.3390/plants11111465

Friesen N (2007) Molecular methods, used in Plant Systematic. AsBuka-Press, Barnaul (**In Russian**)

Goloskokov VP, Polyakov PP (1960) Chenopodiaceae. In: Pavlov NV (ed) Flora of Kasakhstan. Academy of Sciences of the Kazakh SSR, Alma-Ata, pp 198–359

Ilyin MM (1936) The family Chenopodiaceae. In: Schischkin, VK (ed) Flora of the URSS VI. Academiae Scientiarum URSS, Mosqua, Leningrad, pp 3–354 (**in Russian**)

Kamelin RV (2017) Flora of coloured clays of Middle Asia (brief analysis and problems of genesis). Turczaninowia 20:125–151

Kechaykin AA, Batkin AA, Sitpayeva GT, Vesselova PV, Osmonali BB, Shmakov AI (2020) New data on genus *Potentilla* L. (Rosaceae Juss.) in the flora of Kazakhstan. Turczaninowia 23:32–40

Kluge AG, Farris JS (1969) Quantitative phyletics and the evolution of anurans. Syst Biol 18:1–32. https://doi.org/10.1093/sysbio/18.1.1

Kubentayev SA, Alibekov DT, Perezhogin YV, Lazkov GA, Kupriyanov AN, Ebel AL, Izbastina KS, Borodulina OV, Kubentayeva BB (2024) Revised checklist of endemic vascular plants of Kazakhstan. PhytoKeys 238:241–279. https://doi.org/10.3897/phytokeys.238.114475

Kumar S, Stecher G, Tamura K (2016) Mega 7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molec Biol Evol 33:1870–1874. https://doi.org/10.1093/molbev/msw054

Lazkov GA, Vesselova PV (2022) On two species of *Dracocephalum* L. (Lamiaceae). Turczaninowia 25:52–57

Osmonali BB, Vesselova PV, Kudabayeva GM, Skaptsov MV, Shmakov AI, Friesen N (2023) Phylogeny and flow cytometry of the genus *Kalidium* Moq. (Amaranthaceae s.l.) in Kazakhstan. Plants 12:2619. https://doi.org/10.3390/plants12142619

Osmonali BB, Vesselova PV, Kudabaeva GM (2019) Distribution peculiarities of endemic species from the family Chenopodiaceae Vent. of Kazakhstan flora. Probl Bot S Siberia Mongolia 18:343–346 (**In Russian**). https://doi.org/10.14258/pbssm.2019068

Osmonali BB, Akhtaeva NZ, Vesselova PV, Kudabayeva GM, Kurbatova NV (2020) The anatomical structure peculiarities of various species of the genus *Salsola* L. Probl Bot S Siberia Mongolia 19:146–154 (**In Russian**). https://doi.org/10.14258/pbssm.2020093

Popov MG (1936) Anabasis pauciflora Popov. In: Schischkin, VK (ed) Flora of the URSS VI. Academiae Scientiarum URSS, Mosqua, Leningrad, pp 299 (**in Russian**)

Pratov U (1972) Chenopodiaceae. In: Bondarenko ON, Nabiev MM (eds) Plant identifier of plants of central Asia, III. FAN Publishing House, Tashkent, pp 20–98 (**in Russian**)

Pyankov VI, Voznesenskaya EV, Kondratschuk AV, Black CC (1997) A comparative anatomical and biochemical analysis in *Salsola* (Chenopodiaceae) species with and without a kranz type leaf anatomy: a possible reversion of c4 to c3 photosynthesis. Amer J Bot 84:597–606. https://doi.org/10.2307/2445895

Pyankov VI, Artyusheva EG, Edwards GE, Black CC, Soltis PS (2001) Phylogenetic analysis of tribe Salsoleae (Chenopodiaceae) based on ribosomal ITS sequences: implications for the evolution of photosynthesis types. Amer J Bot 88:1189–1198. https://doi.org/10.2307/3558329

Ronquist R, Huelsenbeck JP (2003) Mr Bayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Rudov A, Mashkour M, Djamali M, Akhani H (2020) A review of C4 plants in Southwest Asia: an ecological, geographical and taxonomical analysis of a region with high diversity of c4 eudicots. Frontiers Pl Sci 11:546518. https://doi.org/10.3389/fpls.2020.546518

Safronova IN (2010) Botanical and geographical zoning of Turan deserts as a basis for rational nature use. Arid Ecosyst 16:47–53 (**In Russian**)

Schüssler C, Freitag H, Koteyeva N, Schmidt D, Edwards G, Voznesenskaya E, Kadereit G (2016) Molecular phylogeny and forms of

photosynthesis in tribe Salsoleae (Chenopodiaceae). J Exp Bot 68:207–223. https://doi.org/10.1093/jxb/erw432
Shaw J, Lickey EB, Schilling EE, Small RL (2007) Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. Amer J Bot 94:275–288
Sukhorukov AP, Nilova MV, Krinitsina AA, Zaika MA, Erst AS, Shepherd KA (2018) Molecular phylogenetic data and seed coat anatomy resolve the generic position of some critical Chenopodioideae (Chenopodiaceae–Amaranthaceae) with reduced perianth segments. PhytoKeys 109:103–128. https://doi.org/10.3897/phytokeys.109.28956
Sukhorukov P, Kushunina MA, Lomonosova MN (2022) A new Kalidium species (Amaranthaceae s. l.) from northern Central Asia. Turczaninowia 25:24–33
Sukhorukov AP (2014) The carpology of the Chenopodiaceae with reference to the phylogeny, systematics and diagnostics of its representatives. Grif and Co, Tula
Sumbembayev AA, Abugalieva SI, Danilova AN, Matveyeva EV, Szlachetko DL (2021) Flower morphometry of members of the genus *Dactylorhiza* Necker ex Nevski (Orchidaceae) from the Altai Mountains of Kazakhstan. Biodiversitas 22:3545–3555. https://doi.org/10.13057/biodiv/d220855
Sumbembayev AA, Nowak S, Burzacka-Hinz A, Kosiróg-Ceynowa A, Szlachetko DL (2023a) New and noteworthy taxa of the genus *Dactylorhiza* Necker ex Nevski (Orchidaceae Juss.) in Kazakhstan flora and Its response to global warming. Diversity 15:369. https://doi.org/10.3390/d15030369
Sumbembayev AA, Lagus OA, Nowak S (2023b) Seed morphometry of *Rheum* L. (Polygonaceae) species from Kazakhstan and its implications in taxonomy and species identification. Biodiversitas 9:4677–4692
Swofford DL (2002) PAUP*: Phylogenetic analysis using parsimony (* and other methods), version 4. Sinauer Associates, Sunderland
Terletskaya NV, Turzhanova AS, Khapilina ON, Zhumagul MZ, Meduntseva ND, Kudrina NO, Korbozova NK, Kubentayev SA, Kalendar R (2023) Genetic diversity in natural populations of *Rhodiola* species of different adaptation strategies. Genes 14:794. https://doi.org/10.3390/genes14040794
Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The clustal X window interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucl Acids Res 25:4876–4882. https://doi.org/10.1093/nar/25.24.4876
Voznesenskaya EV, Koteyeva NK, Akhani H, Roalson EH, Edwards GE (2013) Structural and physiological analyses in Salsoleae (Chenopodiaceae) indicate multiple transitions among C3, intermediate, and C4 photosynthesis. J Exp Bot 4:3583–3604
Wang M, Zhang L, Tong Sh, Jiang D, Fu Zh (2022) Chromosome-level genome assembly of a xerophytic plant, *Haloxylon ammodendron*. DNA Res 29:dsac006. https://doi.org/10.1093/dnares/dsac006
White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Shinsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press, San Diego, pp 315–322
Zhaglovskaya A, Aidosova S, Akhtayeva N, Mamurova A, Yesimova D (2015) Anatomical and morphological stem features of two *Haloxylon* species (Chenopodiaceae Vent.) of drought stress Kazakhstan. Biosci Biotech Res Asia 12:1965–1974
Zhu GL, Mosyakin SL, Clemants SE (2004) *Haloxylon* Bunge (Chenopodiaceae). In: Flora of China Editorial Committee (eds) Flora of China 5. Science Press Missouri Botanic Garden Press, Beijing & St. Louis, pp 395–396