

RESEARCH ARTICLE

Taxonomy and dated molecular phylogeny of *Allium oreophilum* sensu lato (*A.* subg. *Porphyroprason*) uncover a surprising number of cryptic taxa

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Abstract *Allium oreophilum*, hitherto the representative of the monotypic *A.* subg. *Porphyroprason* from the second evolutionary lineage of *Allium*, is studied in detail. Over about 150 years, *A. oreophilum* was regarded as a somewhat polymorphous species with two synonyms, all described in the 19th century. A detailed molecular analysis (ITS and three chloroplast DNA regions: *trnQ-rps16* and *trnL-trnF* intergenic spacers, *rps16* intron) of altogether 33 living samples and herbarium specimens showed, however, that the previously described species *A. oreophilum*, *A. ostrowskianum* and *A. platystemon* must be considered good species, and two additional taxa must be newly described. All these taxa are morphologically compared, and an identification key is provided. Three species were karyologically investigated, possessing $2n = 16$ chromosomes but showing different karyotypes. A dated phylogeny based on the ITS mutation rate revealed that *A.* subg. *Porphyroprason* and subg. *Vvedenskya* diversified into two sister groups around 21.52 million years ago, in the early Miocene. The possible biogeographic scenario of the origin of *A.* subg. *Porphyroprason*, subg. *Vvedenskya* and other subgenera is presented. A morphological comparison of specimens available from different cultures showed an astonishing variation of characters, and other unidentified taxa of this subgenus likely exist in nature.

Keywords *Allium aksuzhabagliense* sp. nov.; *Allium kujukense*; *Allium ostrowskianum*; *Allium platystemon* s.str.; *Allium platystemon* var. *longitepalum* var. nov.; phylogeny; biogeography

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Allium L., one of the largest petaloid genera in the monocots with more than 1100 currently accepted species (POWO, 2024), is a member of the family Amaryllidaceae, subfamily Allioideae (Chase & al., 2009). Subfamily Allioideae is divided into four tribes: Allieae – Northern Hemisphere; Tulbaghieae – South Africa; Gilliesieae and Leucocoryneae – Central and South America (Sassone & al., 2014; APG IV, 2016). Tribe Allieae comprises only the genus

Allium. Molecular phylogenies demonstrated a strong monophyly of this genus (Friesen & al., 2006; Nguyen & al., 2008; Li & al., 2010, 2012; Wheeler & al., 2013; Xie & al., 2019, 2020; Namgung & al., 2021; Friesen, 2022; Zhang & al., 2024), which is naturally distributed in the holarctic region from the dry subtropics to the boreal zone. Its major centre of diversity stretches from the Mediterranean basin to Central Asia and West China. About 100 *Allium* species occur in North America from Alaska to Mexico (Friesen, 2022). Within the genus *Allium*, 15 subgenera and more than 80 sections are recognized,

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belonging to three evolutionary lineages (Fritsch & Friesen, 2002, Friesen & al., 2006; Friesen, 2022).

Allium oreophilum C.A.Mey. is the only currently accepted species in the monophyletic *A. sect. Porphyroprason* Ekberg and belongs to the second evolutionary lineage (Fritsch & Friesen, 2002; Friesen, 2022). The distribution of this species covers the area from East Turkey (Ispiriz Dağ, Başkale), North-East Caucasus (Mt. Bazardüzü and Mt. Dyul'tytag, Russia, Dagestan and Chechnja; Mt. Tufandagh (type location), Azerbaijan; Mt. Kaputdschugh, Nakhichevan, Azerbaijan), and the mountains of Central Asia (Ekberg, 1969; Hanelt & al., 1989) with large gaps in between. From the beginning, the separate populations have received different names (*A. oreophilum* C.A.Mey. [Meyer, 1831: 37 – Caucasus]; *A. platystemon* Kar. & Kir. [Karelin & Kirilow, 1842: 514 – Dzhungar Alatau]; *A. ostrowskianum* Regel [Regel, 1881: 545 – Tian-Shan]). Later, Regel (1887: 356) downgraded *A. ostrowskianum* to a variety of *A. oreophilum*. Ledebour (1852), in *Flora Rossica*, already listed *A. platystemon* as a synonym of *A. oreophilum*. These taxa were affiliated to *A. sect. Molium* G.Don ex Koch by Regel (1875) and all subsequent botanists; only Ekberg (1969) singled out *A. oreophilum* in a separate section *A. sect. Porphyroprason* by recognizing special morphological and anatomical characteristics, but still within *A. subg. Molium* (Koch) Wendelbo (= *A. subg. Amerallium* Traub). The most important morphological feature that distinguishes *A. sect. Porphyroprason* from other *Allium* species is a bulb with two storage scales. Hanelt & al. (1989) studied morphological, anatomical, chorological, and especially serological data. They supported the proposal of Kamelin (1973) to include *A. sect. Porphyroprason* in *A. subg. Melanocrommyum* (Webb & Berthel.) Rouy, albeit in an isolated position because the other species in that subgenus have a bulb with one storage scale. After a detailed molecular study, *A. oreophilum* was placed in a separate subgenus, *A. subg. Porphyroprason* (Ekberg) R.M.Fritsch (Friesen & al., 2006: 386). *Allium* subg. *Porphyroprason*, together with *A. kujukense* Vved. (monotypic *A. subg. Vvedenskya* Kamelin) and the subgenera *A. subg. Caloscordum* (Herb.) R.M.Fritsch, *A. subg. Anguinum* G.Don ex Koch and *A. subg. Melanocrommyum*, constitutes the second evolutionary lineage in the genus *Allium* (Fritsch & Friesen, 2002; Friesen & al., 2006).

During exploratory fieldwork in the Susamyr Mountains (Kyrgyzstan) in the summer of 2021, Georgy Lazkov found a large population of the rare *A. oreophilum* var. *ostrowskianum* (Regel) Regel with white flowers and a red midvein. This form was first collected by the Russian botanist Fetisov in 1878 and later described as a new species *Allium ostrowskianum* Regel (Regel, 1881: 545). In the description, however, Regel gives the colour of the tepals as “rosea” and not white; later, he subsumed this taxon as var. *ostrowskianum* in *A. oreophilum*. It must be pointed out that with *Allium* species it is important to consider the colour of flowers in living plants, as the colours often fade or change otherwise during drying or in the herbarium (Stearn, 1946; Fritsch & Friesen, 2002), which is regularly the case with *A. oreophilum* s.l.

When Igor Levichev studied seven accessions of *Allium oreophilum* in the collection of IPK Gatersleben and one accession in the botanical garden of the University Osnabrück, he recognized at least five different morphotypes among them. Unfortunately, only two samples had a known geographic origin; the others had been obtained from botanical gardens without information about the original collection site; these morphological studies were not pursued further.

Chromosome numbers of *Allium oreophilum* ($2n = 16$) were published several times (see Index to Plant Chromosome numbers: www.tropicos.org). However, only a few records are from plants with known origins: Vakhtina (1964 – Tajikistan: Shakhristan Pass), Pogolian (1983 – Azerbaijan: Nakhichevan, southern slope of Mt. Kaputdschugh), Astanova (1990 – Tajikistan: Turkestan Range), Fritsch (2016 – Tajikistan: Turkestan Range, Kusawlisai), Genç & Firat (2016 – East Türkiye: Ispiriz Dağ, Başkale). Several differing karyotypes of *A. oreophilum* have been published in the past, starting with Badr & Elkington (1977: figs. 6, 7), who also reported chromosome banding patterns found only on the satellited chromosomes. The more detailed analyses of chromosome morphology in Hanelt & al. (1989) indicated an incongruence between chromosome shape and Giemsa banding patterns. Maragheh & al. (2019) presented another karyotype and applied CMA/DAPI and fluorescence banding patterns for the recognition of single chromosomes. All these analyses investigated plants from the flower bulb trade or botanical gardens. Fritsch (2016: 272, 274, 276) again reported a somewhat different karyotype found in plants from Tajikistan, Turkestan Range. Further deviating results were published by Genç & Firat (2016) from Turkey (mentioned above).

Preliminary molecular studies of the white-flowered samples and the accessions of *Allium oreophilum* from Gatersleben and Osnabrück showed significant differences in the sequences between the accessions. For this reason, the analysis was extended to include material from the entire distribution area of *A. oreophilum*. On the website plantarium.ru, Davkaev (2011) published photos of *A. oreophilum* from the Aksu-Zhabagly National Reserve (Kazakhstan) on limestone substrate that showed only one leaf. In the summer of 2023, we visited this location and collected specimens from these plants. It should be noted that *A. oreophilum* s.l. grows mainly on acidic substrates, such as granite and gneiss. Georgy Lazkov also found plants with only one leaf in Kyrgyzstan in the Chatkal Range, also on limestone substrate, in the summer of 2023.

In this work we applied morphological, karyological and molecular methods on the collected accessions from most parts of the entire distribution area to determine, whether *Allium oreophilum* s.l. is a single species or comprises several species.

■ MATERIALS AND METHODS

Distribution. — We compiled distribution maps from literature and online databases and analysed herbarium collections (AA, DAG, FR, KNYA, LE, LENUD, MW, OSBU).

Taxon sampling. — Plant material for DNA extraction was obtained from the *Allium* collections of the Botanical Garden of the University of Osnabrück, the Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, and from different herbaria (AA, DAG, FR, KNYA, LE, MW, OSBU). Newly sequenced accessions are marked with Am or Tax numbers in the trees, and their origin is shown in Appendix 1. Sequences from NCBI GenBank are labelled with GenBank accession numbers in the trees.

DNA extraction, amplification, and sequencing. — Total genomic DNA was isolated from herbarium specimens or living plants using the InnuPREP Plant DNA Kit (Analytik Jena, Jena, Germany) according to the manufacturer's instructions and used directly in PCR amplification. The complete nuclear ribosomal internal transcribed spacer (ITS) region (ITS1, 5.8S, ITS2) was amplified using the primers ITS-A (Blattner, 1999) and ITS-4 (White & al., 1990). PCR conditions and primers for the chloroplast regions *trnL-rpl32* and *trnQ-rps16* are described in Shaw & al. (2007), and for *rps16* intron in Oxelman & al. (1997). PCR products were sent to Microsynth SeqLab (Göttingen, Germany, www.microsynth.seqlab.de) for sequencing. The sequences from all the individuals were manually edited in Chromas Lite v.2.1 (Technelysium, Helensvale, Queensland, Australia) and aligned with ClustalX2 (Thompson & al., 1997), and the alignment was manually corrected using MEGA 7 (Kumar & al., 2016).

Phylogenetic analyses. — *Allium microdictyon* Prokh., *A. victorialis* L. (*A.* subg. *Anguinum*), *A. inutile* Makino, *A. neriniflorum* (Herb.) Baker (*A.* subg. *Caloscordum*), and *A. kujukense* (*A.* subg. *Vvedenskya*) from the second evolutionary lineage (Fritsch & Friesen, 2002; Friesen & al., 2006) were chosen as outgroup. Both datasets (nrITS; combined cpDNA markers *trnL-rpl32*, *trnQ-rps16* and *rps16* intron) were analysed separately to identify the phylogenetic position in the second evolutionary lineage and to find the relationships within representatives of *A. oreophilum* s.l. from different areas through parsimony (PAUP) and Bayesian phylogenetic analysis (MrBayes). Fitch parsimony was determined with the heuristic-search option in PAUP v.4.0b10 (Swofford, 2002) with MULTREES, TBR branch swapping and 100 replicates of random addition sequence. Gaps were treated as missing data. The consistency index (CI) (Kluge & Farris, 1969) was calculated to estimate the amount of homoplasy in the character set. The most parsimonious trees returned by the analysis were summarised in a consensus tree using the strict consensus method. Bootstrap analyses using 1000 pseudoreplicates were performed to assess the bootstrap support (BS) of the clades (Felsenstein, 1985). Bayesian phylogenetic analyses were performed using MrBayes v.3.1.23 (Ronquist & Huelsenbeck, 2003). The sequence evolution model was chosen following the Akaike information criterion (AIC) obtained from jModelTest2 v.2.1.6 (Darriba & al., 2012). Two independent Markov chain Monte Carlo (MCMC) analyses with four chains were run for 10 million generations, sampling trees every 100 generations.

The first 25% of trees were discarded as burn-in. The remaining trees were combined into a single dataset, and a majority-rule consensus tree was obtained along with posterior probabilities (PP).

Divergence time estimation. — BEAST v.1.8 was used to estimate the divergence times in the second evolutionary lineage of the genus *Allium* (Drummond & Rambaut, 2007). The BEAUti v.1.8 interface was used to create input files for BEAST. For the estimation, a reduced subset of 19 accessions was selected from the nrITS sequences. We used the uncorrelated lognormal relaxed clock (ucln) with the substitution model selected by the AIC (GTR + I + Γ). The Yule process was chosen as the speciation process. The ucln.mean for the ITS data was set to a normal distribution, with a mean of 4.13×10^{-9} substitutions per site per year and a standard deviation of 1.0×10^{-9} according to the works of Kay & al. (2006). Other parameters were set to default. First, several short BEAST runs were performed to examine the performance of the MCMC. Additional runs with empty alignments were carried out to ensure that the priors alone did not determine the results. Finally, three independent BEAST runs were performed for every substitution rate setting with the MCMC chain length of 10^8 generations and a sampling frequency of every 10,000.

The ESS values were >200, with a 25% burn-in for all parameters, as confirmed by analysing the output files with Tracer v.1.6. The tree output files from BEAST were summarised with LogCombiner v.1.8 and annotated with the program TreeAnnotator v.1.8; the burn-in was set to 25% with the aid of Tracer. The “mean node heights” option was selected, and the posterior probability was set to 0.5. The trees were visualised using FigTree v.1.4.0 with mean ages and 95% highest posterior density (HPD).

Morphological analyses. — A total of 9 individuals of *Allium oreophilum* from 5 herbarium sheets were analysed, as well as 30 individuals of *A. platystemon* from 22 herbarium sheets, and 12 individuals of *A. ostrowskianum* from 5 herbarium sheets. The measurements on the plants were made using a ruler and a hand lens. Arithmetic means with standard deviations were calculated from the measurements.

Karyological analysis. — Bulbs were planted in pots, and growing roots were used for the karyotype analysis. Root tips were excised from the bulbs and kept overnight in distilled water on ice. They were then transferred to room temperature for 20 min, pre-treated for 3 h at room temperature in an aqueous solution of 0.1% colchicine, and were then fixed in a freshly prepared mixture of 96% ethanol and glacial acetic acid (3:1 v/v). Root tips were stained using hematoxylin according to the protocol reported by Smirnov (1968). Well-spread metaphase plates were digitally photographed, and finally, the chromosomes of the best plates were measured and arranged pairwise using the KaryoType software (<http://mnh.scu.edu.cn/soft/blog/karyotype/>, Altinordu & al., 2016). Because the idiograms automatically assembled by the software were not satisfactory, we manually ordered the chromosome pairs according to their length and shape. The idiograms were

designed using the bar graph function implemented in MS Excel. The terminology of Levan & al. (1964) was applied.

■ RESULTS

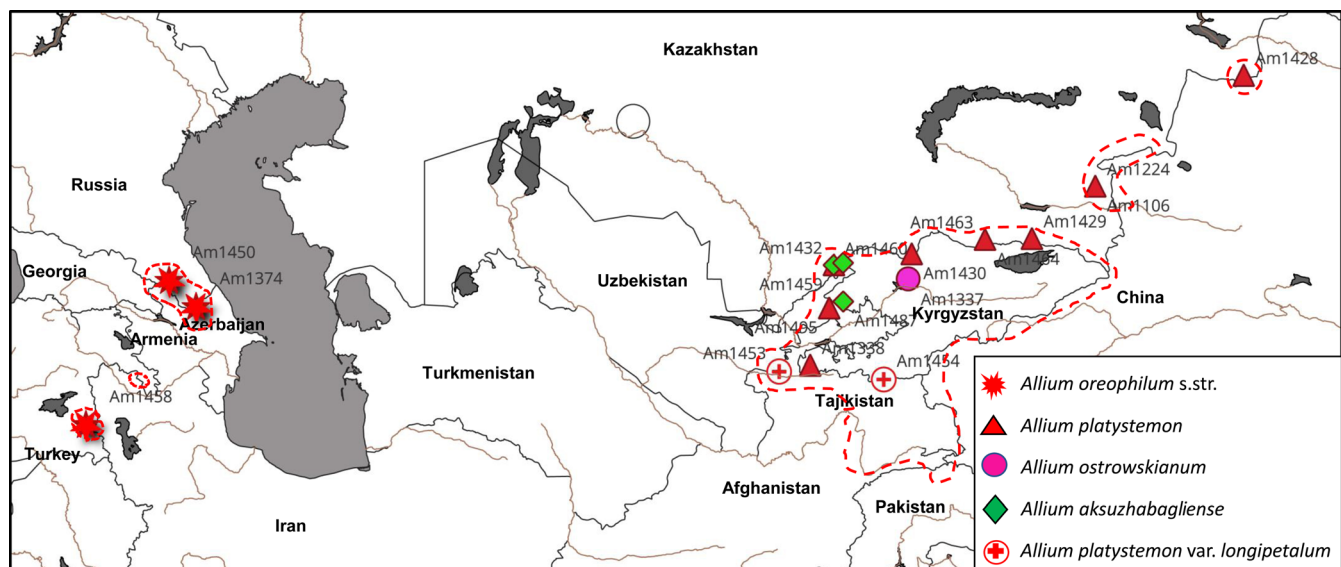
Distribution. — Compared to the distribution of *Allium oreophilum* s.l. reported by Ekberg (1969) and Hanelt & al. (1989), there have been no changes (see the dashed red lines in Fig. 1).

Molecular data. — In total, 140 new sequences (ITS, 37; *rpl32-trnL*, 35; *trnQ-rps16*, 35; *rps16*, 35) were generated from accessions of *Allium oreophilum* s.l. (124 sequences) and *A. kujukense* (16 sequences) and were deposited in GenBank (accession numbers are given in Appendix 1, and a number of used accessions from GenBank are given on the trees (Figs. 2, 3).

Nuclear ITS sequences data. — Among the 37 accessions of *Allium* species from *A. subg. Porphyroprason* and subg. *Vvedenskya*, the length of the ITS region ranged from 611 bp in *A. kujukense*, 612 bp in white-flowering *A. ostrowskianum* to 613 bp in the rest of *A. oreophilum* s.l. Aligning the individual sequences, including outgroup taxa, resulted in an alignment of 627 bp length (suppl. Appendix S1). Of these, 388 characters are constant, 15 variable characters are parsimony uninformative, and 224 are parsimony informative. Unweighted parsimony analysis resulted in 11,324 most parsimonious trees of 281 steps (CI = 0.98; RI [retention index] = 0.99). The substitution model HKY + Γ was chosen by the AIC in jModelTest2 for the Bayesian analysis. In the phylogenetic tree both *A. subg. Vvedenskya* and subg. *Porphyroprason* form sister clades with very strong support (Fig. 2). The clade of *A. subg. Porphyroprason* is clearly

divided into two strongly supported clades, with East Caucasian and East Turkish accessions of *A. oreophilum* s.str. as sister to the rest. The Central Asian accessions of *A. oreophilum* s.l. are divided into four subclades, but only one clade is strongly supported, comprising accessions of plants with one leaf growing on limestone substrate from the Aksu-Zhabagly National Reserve and the Chatkal mountain range (*A. aksuzhabagliense* sp. nov.). White-flowering accessions (*A. ostrowskianum*) form a clade with good support (0.96 PP and 88% BS). It is interesting that morphologically barely distinguishable accessions from Tajikistan (Am1453) and western Kyrgyzstan (Am1454), together with three accessions (Am1451, Am1452, Am1494) of unknown origin, also form a clade with no support. All remaining accessions of *A. oreophilum* s.l. from Tian-Shan, Dzhungar Alatau and Saur Mountains (*A. platystemon*) have identical ITS sequences (Fig. 2).

Plastid DNA sequence data. — The combined plastid data matrix of accessions of *Allium subg. Porphyroprason* and the outgroup from the second evolutionary lineage includes 3072 characters divided into three partitions: 1–772 *rpl32-trnL* intergenic spacer, 773–2231 *trnQ-rps16* intergenic spacer, 2232–3072 *rps16* intron, of which 2894 are constant, 3 variable characters are parsimony uninformative and 175 parsimony informative (suppl. Appendix S2). The heuristic search found 17 most parsimonious trees, which are 207 steps long (CI = 0.898, RI = 0.963). The individual analyses of the plastid regions show different resolutions, with the best being shown by the *rps16* intron and the *rpl32-trnL* spacer. Most groups almost always form their own clades; only the resolution of *A. platystemon* accessions is often missing. Some accessions are found in the “wrong” position (e.g., Am1495, Am1496, Am1451 in the *trnQ-rps16* tree,



suppl. Fig. S1B), which may indicate hybridization events. Only a combined alignment of all three plastid regions provides a good resolution. Such phenomena have been observed in the genus *Allium*, for example, in *A.* subg. *Amerallium* (Friesen & al., 2024). The best-fit model for the combined cpDNA data selected by the AIC in jModelTest2 (Darriba & al., 2012) was GTR + Γ . It should be mentioned at this point that the *trnQ-rps16* spacer is strikingly long in *A. oreophilum* s.l. (from 1390 bp in *A. oreophilum* s.str. to

1426 bp in *A. platystemon*), compared to other *Allium* species from the second evolutionary lineage, e.g., *A. kujukense*, with only 696 bp. We have repeated the amplification and sequencing of this region in *A. oreophilum* s.l. several times, with identical results. Many *Allium* species and all accessions of *A. kujukense* have a very long (ca. 700 bp) insertion in the middle of the *trnQ-rps16* region. Interestingly, in the NCBI gene bank, the *trnQ-rps16* fragment is only present with a length of up to about 900 bp. When blasted, the 1400 bp

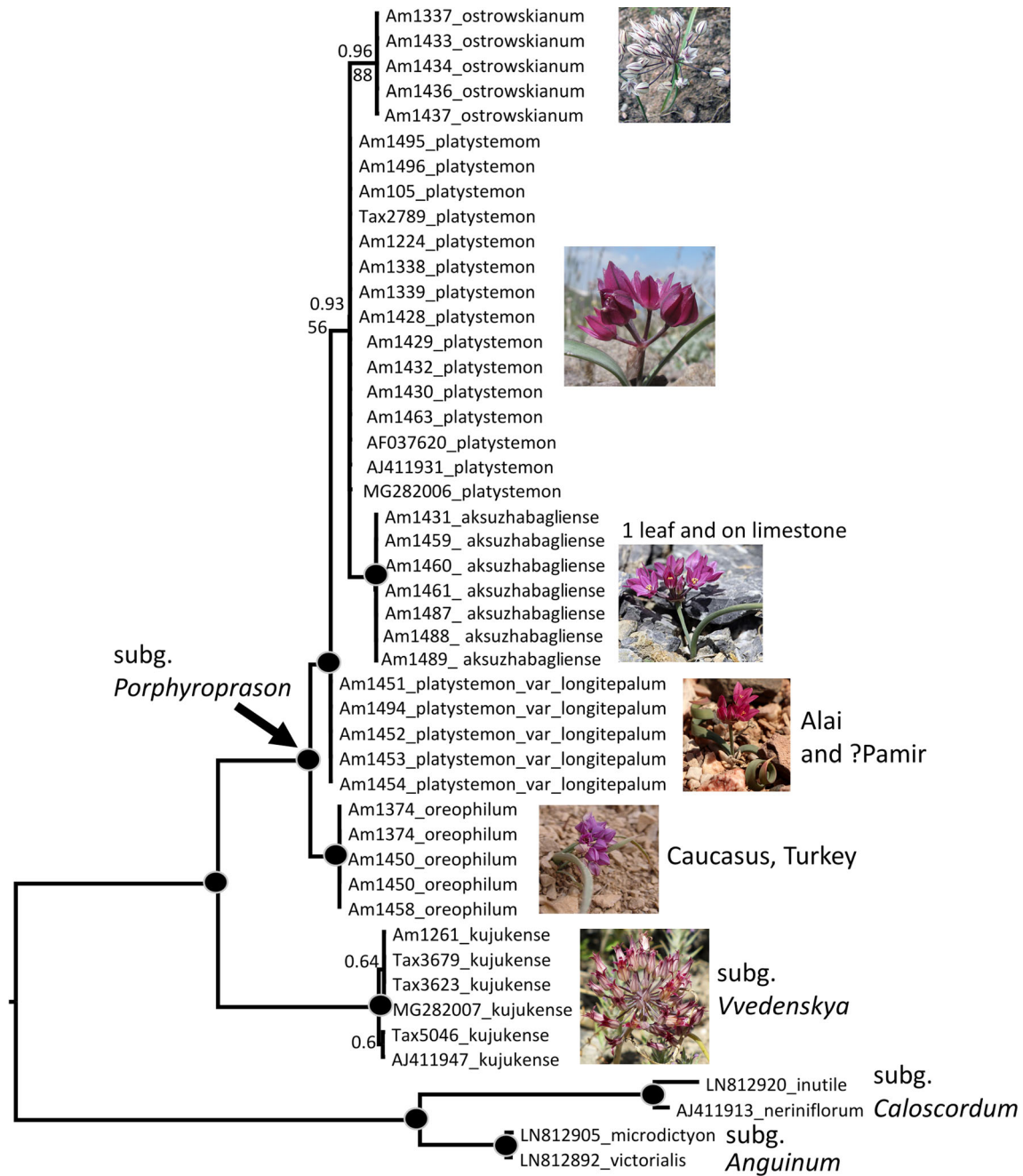


Fig. 2. Phylogenetic tree of the second evolutionary lineage (except *Allium* subg. *Melanocrommyum*) of the genus *Allium*, based on ITS sequences. Numbers at nodes represent Bayesian posterior probabilities (PP) and bootstrap support (BS, 1000 replicates). The joint presence of PP > 0.98 and BS > 95% is indicated with a black dot. For the origin of the Am and Tax sequences, see Appendix 1.

trnQ-rps16 region of *A. oreophilum* s.l. is compatible with a whole range of *Allium* species with a complete plastid genome, especially with *A. monanthum* Maxim. (MT348452), *A. ramosum* L. (MN159131), *A. siculum* Ucria (NC_057584), *A. tuberosum* Rottler ex Spreng. (MN158715, OQ701015, NC_044709), and others, which also show a very long *trnQ-rps16* region. Apparently, many sequences of the *trnQ-rps16* region in the NCBI gene bank are incomplete. In phylogenetic analyses, such insertions or deletions do not play a major role, as they are automatically ignored in the analysis unless they are specially formatted. In the combined plastid phylogenetic tree (Fig. 3), the groupings in the monophyletic clade of *A. subg. Porphyroprason* are the same as in the nrITS tree, but the topology is very different. The clade consisting of accessions of plants with one leaf distributed

on the limestone substrate from the Aksu Zhabagly National Reserve and Chatkal mountain range (*A. aksuzhabagliense* sp. nov.) is sister to the rest. Plants with white flowers (*A. ostrowskianum*) and East Caucasian and East Turkish accessions (*A. oreophilum* s.str.) form strongly supported clades. Also, in the plastid tree, the plants from Tajikistan (Am1453) and Alay Mountains (Am1454), together with two accessions (Am1451, Am1452) without known origin, are separated from all other plants in *A. oreophilum* s.l., with relatively good support (0.89 PP, 64 BS) (Fig. 3).

Divergence time estimation. — Divergence time estimation analyses of the second evolutionary lineage in the genus *Allium* (Fig. 4) generated a highly congruent topology compared to the Bayesian inference analysis (Fig. 2). According to the analysed taxon sets, *A. subg. Vvedenskya* and subg.

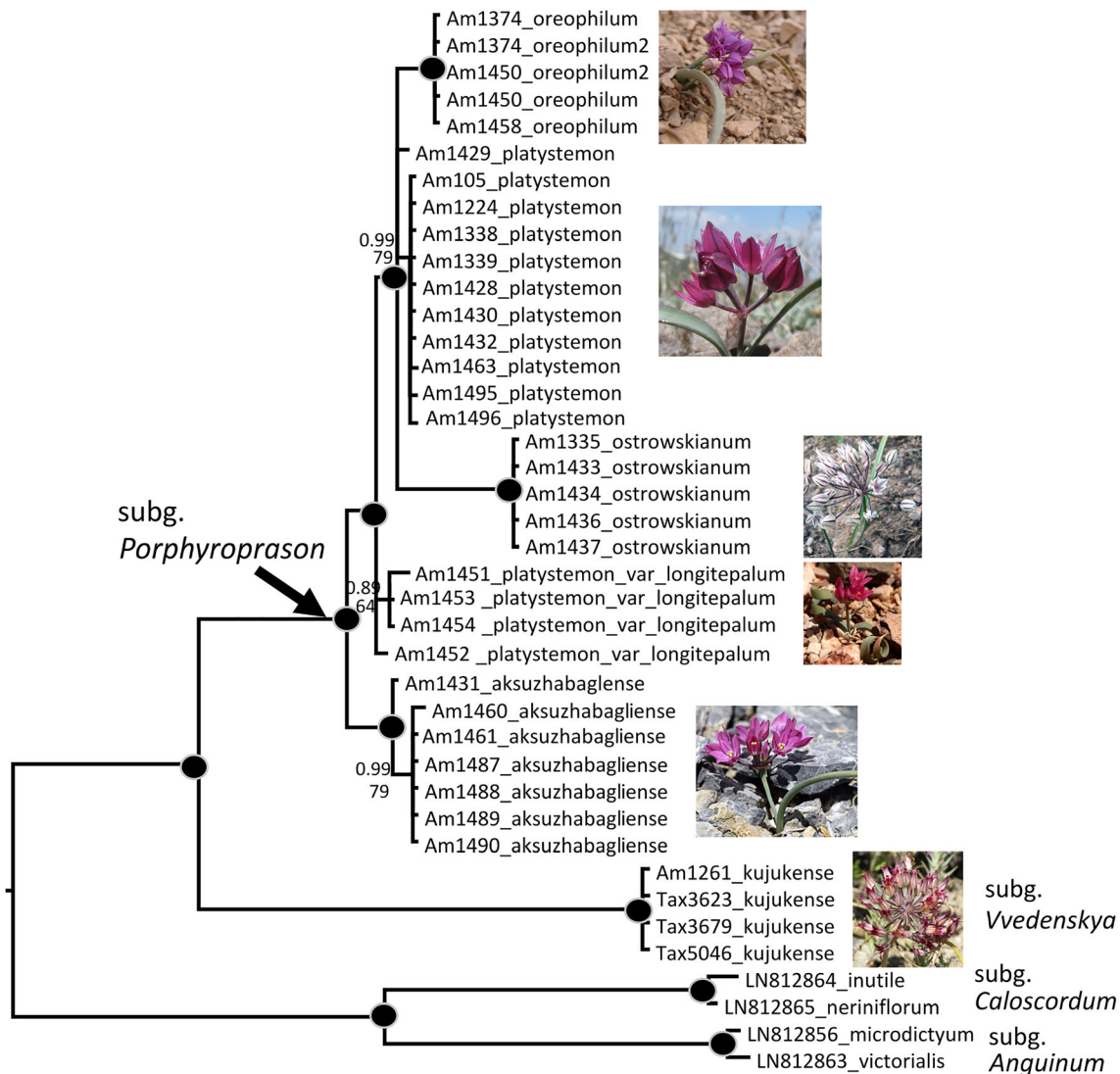


Fig. 3. Phylogenetic tree of the second evolutionary lineage (except *Allium* subg. *Melanocrommyum*) of the genus *Allium*, based on combined chloroplast fragments (*rpl32-trnL*^(UAG), *trnQ-rps16*, *rps16*). Numbers at nodes represent Bayesian posterior probabilities (PP) and bootstrap support (BS, 1000 replicates). The joint presence of PP > 0.98 and BS > 95% is indicated with a black dot. For the origin of the Am and Tax sequences, see Appendix 1.

Porphyroprason diversified into two sister groups around 21.52 million years ago (Mya), in the early Miocene. The split of *A. oreophilum* s.str. (East Caucasian and East Turkish plants) from the Central Asian taxa of *A. subg. Porphyroprason* is took place at 8.71 Mya, in the end of Miocene. The separation of the accessions Am1453 and Am1454 is estimated at 4.37 Mya. Differentiation of Central Asian calcareous plants (*A. aksuzhabagliense*) from plants growing on acidic rocks is calculated at 3.61 Mya, and the separation of white-flowered plants (*A. ostrowskianum*) from purple-flowered plants (*A. platystemon*) at 1.5 Mya.

Morphological comparison. — Except for very few qualitative characters, such as the colour of the tepals, the other characters are quantitative (Table 1). However, there are statistically significant differences between species in *Allium* subg. *Porphyroprason* (see Table 1 and Fig. 5). The bulbs of *A. oreophilum* are larger than those of all other species in the subgenus (e.g., 1.27 ± 0.49 cm wide versus 0.64 ± 0.45 cm wide in *A. ostrowskianum*). There are also significant differences in the length of the basal filament fusion between *A. oreophilum* s.str. and Central Asian taxa (3.2 ± 1.14 mm

versus 1.14 ± 0.24 mm in *A. ostrowskianum* and 1.6 ± 0.8 mm in *A. aksuzhabagliense*). Morphological features can also be seen in Fig. 5.

Morphological features of some representatives of *Allium* subg. *Porphyroprason* and subg. *Vvedenskya* (*A. kujukense*). — In Fig. 6, different morphological characters are compiled showing differences in the taxa of the *Allium* sect. *Porphyroprason*, and in Fig. 7 the morphological characters of *A. kujukense* from sister subgenus *A. subg. Vvedenskya* are presented. One of the most important differences in the morphology of the bulb between these two subgenera (Figs. 6J,N, 7B) becomes visible. All taxa in *A. subg. Porphyroprason* have two storage scales in the bulb, while in *A. subg. Vvedenskya* (and in many other subgenera of the genus *Allium*), the bulb consists of only one storage scale.

Karyological data. — Unfortunately, we had no living plants of *Allium ostrowskianum*, so that the chromosomes of only three species were examined: *A. oreophilum* s.str. from Dagestan (Am1374), the origin of which is only 10 km away from Mt. Tufandagh, the *locus classicus*; *A. aksuzhabagliense* Am1460; and *A. platystemon* Am1495 (Fig. 8). All species

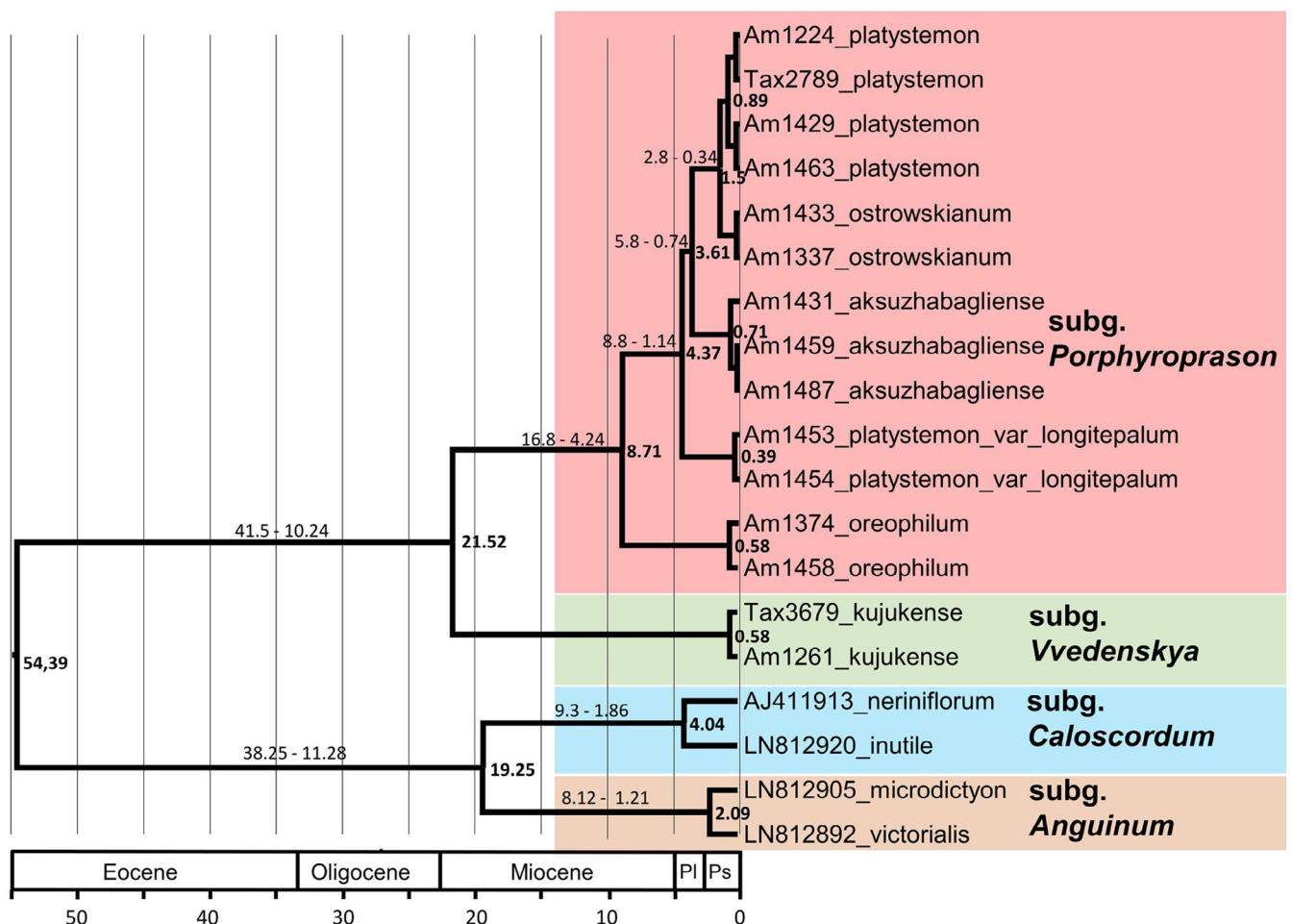


Fig. 4. Dated phylogeny based on nrITS sequences of the second evolutionary lineage (except *Allium* subg. *Melanocrommyum*) of the genus *Allium*. Bold numbers at nodes represent the absolute ages in a million years, ranges are confidence intervals (95% HPD). PI, Pliocene; Ps, Pleistocene.

examined have a similar karyotype with 14 metacentric chromosomes and 2 subtel- or submetacentric satellite chromosomes (CI = 24%–26%). It is striking that the satellite chromosomes in *A. oreophilum* s.str. are much larger than in the Central Asian species (see Fig. 8E and Table 2).

■ DISCUSSION

Molecular, morphological and cytological data have clearly shown that *Allium oreophilum* s.l. consists of several taxa, allowing the revival of names from synonymy and describing a new species. The name *A. oreophilum* s.str. belongs to the Caucasian and Turkish plants; the name *A. ostrowskianum* to the plants with white flowers from the Susamyr Range; and the name *A. platystemon* to the plants with purple flowers and two leaves that grow on acidic soil. Single-leafed plants growing on limestone substrate in the Aksu-Zhabagly National Reserve in Kazakhstan and the Chatkal Range in Kyrgyzstan are described below as *A. aksuzhabagliense*. In addition, among representatives of the genus cultivated in various botanical collections, specimens with noticeable morphological deviations from those already established were found. These deviations include different capacities for vegetative reproduction: either a

complete absence of reproduction, or present only in the juvenile period, late juvenile age or immature age, or throughout the entire ontogenesis. The absence or length of stolons also correlates with age. If present, the stolons are either short (1–2 cm) or long (9–12 cm) (Fig. 6F,J). In addition, among the sets of characteristics of the established morphotypes, the features of the cross-sections of the leaves are important: flat-concave with rounded ends without a central cavity (Fig. 6C,E) or with a slit-like cavity, having sharp ends along the edge and a keel on the dorsal surface; or trapezoidal with a large cavity (Fig. 6D). Unifacial, typically cylindrical leaves characterise plants of all groups in the early stages of the juvenile period. Finally, the number of leaves (1–2), which differs species-specifically at different stages of ontogenesis, is of doubtless importance. As noted earlier, *A. subg. Porphyroprason* has a two-scaled storage bulb (Fig. 6I,N).

A discrepancy in the topologies of the nuclear and plastid trees of the different taxa in *A. oreophilum* s.l. points to a possible ancient hybridogenic event between these taxa.

Although the molecular data indicate the plants from the Alay Mountains and Turkestan Range (accession Am1453 and Am1454) are only distantly related to *Allium platystemon*, we did not find enough morphological characters to distinguish these plants from it. There are only small differences

Table 1. Main morphometric diagnostic characters of taxa in *Allium* subg. *Porphyroprason*.

Characters	<i>Allium aksuzhabagliense</i>	<i>Allium oreophilum</i>	<i>Allium ostrowskianum</i>	<i>Allium platystemon</i>	<i>Allium platystemon</i> var. <i>longitepalum</i>
Length OF (mm)	2.1 ± 0.16	2.47 ± 1.44	3.5 ± 0.28	3.36 ± 1.12	3.33 ± 0.28
Length IF (mm)	1.96 ± 0.63	2.96 ± 0.99	4 ± 0.28	3.7 ± 1.2	3.83 ± 0.28
Width OF (mm)	1 ± 0	2.4 ± 0.5	1 ± 0.28	1.4 ± 0.8	1.1 ± 0.28
Width IF (mm)	1.16 ± 0.4	1.93 ± 0.26	3.07 ± 0.67	2.7 ± 0.89	3.33 ± 0.57
Length of basal fusion of IF (mm)	1.6 ± 0.8	3.2 ± 1.14	1.14 ± 0.24	1.49 ± 0.43	1.5 ± 0
Pistil length (mm)	1 ± 0	1.22 ± 0.13	2.14 ± 0.37	1.3 ± 0.47	1.16 ± 0.76
Width IT (mm)	1.66 ± 0.51	3.8 ± 0.85	3.5 ± 0.5	3.25 ± 1.02	3 ± 0
Width OT (mm)	2.3 ± 1.03	4.96 ± 0.71	4.21 ± 0.9	4.11 ± 1.23	4 ± 0
Length IT (mm)	6.5 ± 3.3	8.7 ± 0.97	8.4 ± 1.27	8.2 ± 1.6	9.8 ± 0.28
Length OT (mm)	7.8 ± 1.83	8.6 ± 1.2	7.7 ± 0.9	7.35 ± 1.74	8.8 ± 0.28
Peduncle length (cm)	1.65 ± 0.4	1.33 ± 0.32	1.4 ± 0.31	1.52 ± 0.57	1.3 ± 0.4
Stem height (cm)	11.16 ± 0.4	14.8 ± 3.05	15.4 ± 5.85	11.2 ± 6.75	12 ± 3.6
Number of leaves	1 (or 2) (1.16 ± 0.4)	2	2	2 (or 3) (1.95 ± 0.21)	2 (or 3) (1.98 ± 0.2)
Width of leaves (mm)	2.65 ± 0.6	5.25 ± 1.5	3.28 ± 1.11	3.04 ± 1.48	4.3 ± 0.57
Length of leaves (cm)	11.7 ± 6.39	20.1 ± 5.3	13.4 ± 9.6	10.79 ± 8.5	18 ± 3.6
Supraterranean length of leaf sheaths (cm)	3.5 ± 3.1	9.5 ± 1.8	3.14 ± 3	5.4 ± 3.5	5.6 ± 2.25
Width of bulb (cm)	0.76 ± 0.38	1.27 ± 0.49	0.64 ± 0.45	0.75 ± 0.34	0.8 ± 0.69
Length of bulb (cm)	1.33 ± 0.75	1.48 ± 0.59	0.88 ± 0.62	1.04 ± 0.38	1.0 ± 0.86

IF, inner filaments; IT, inner tepals; OF, outer filaments; OT, outer tepals.

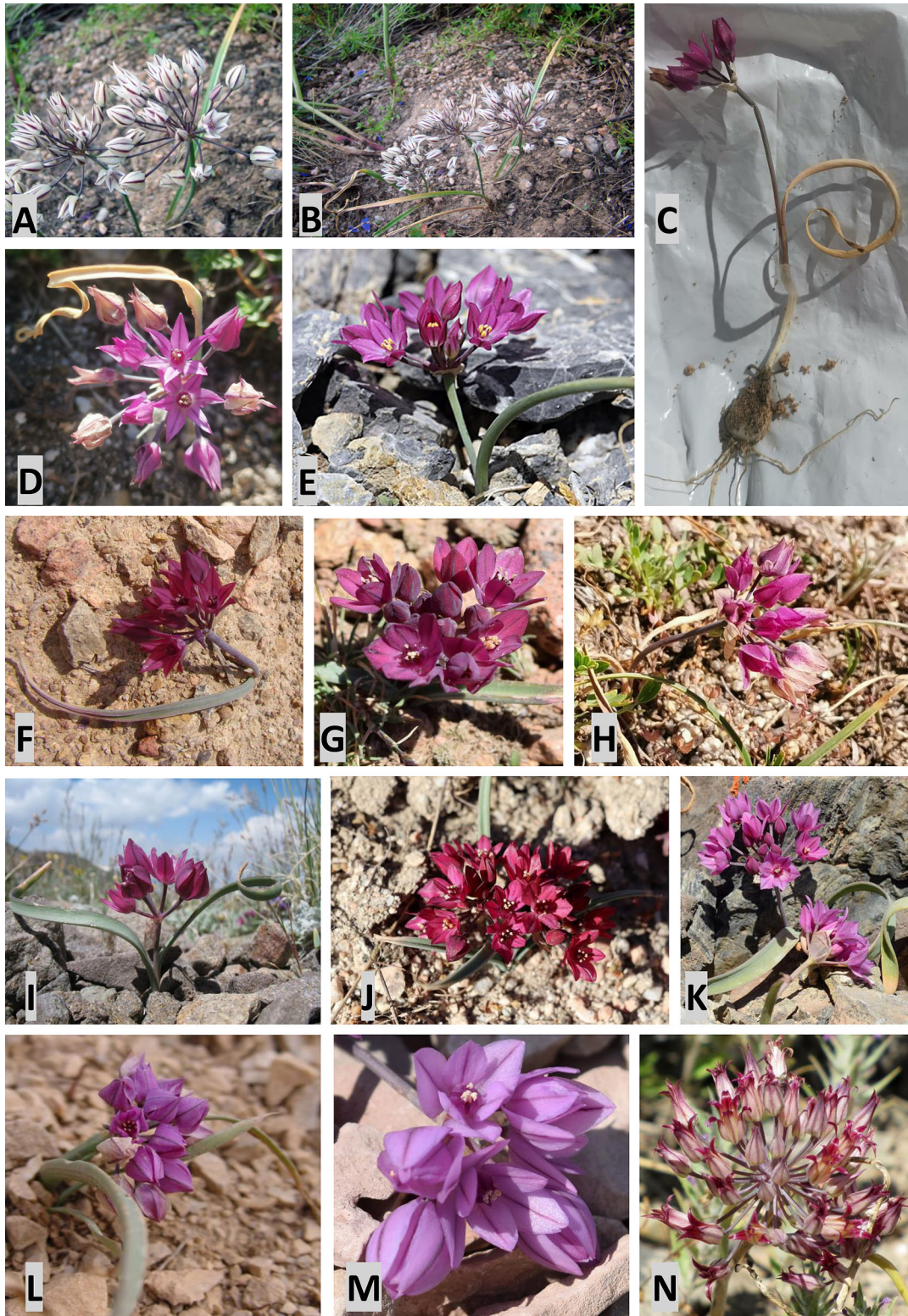


Fig. 5. A & B, *Allium ostrowskianum*, Kyrgyzstan, Susamyr Range (Lazkov, 2022). C–F, *Allium aksuzhabagliense*: C & D, Kazakhstan, Talas Alatau, Aksu-Zhabagly, Kalaoi (photos N. Friesen); E, Kazakhstan, Talas Alatau, Aksu-Zhabagly, Koksay (Davkaev, 2011); F, Kyrgyzstan, Chatkal Range, Chal-Kayndy (Lazkov, 2022). G–K, *Allium platystemon*: G, Uzbekistan, Kuramin Range, Angren Plato (Tillaev, 2020); H, Kazakhstan, Dzhungar Alatau, Toksanbai (photo N. Friesen); I, Kazakhstan, Talas Alatau, Aksu-Zhabagly, Kaskabulak (Kolbintsev, 2017); J, Uzbekistan, Chatkal Range, lake Arashan (Beshko, 2023); K, *Allium platystemon* var. *longitepalum*: Kyrgyzstan, Alai Range, Taldyk (Gorbunov, 2022). L & M, *Allium oreophilum* s.str.: L, Turkey, Mt. Ispiriz (photo E. Kuddisi); M, Russia, Dagestan, Mt. Bazardüzü (photo R. Murtazaliev). N, *Allium kujukense* (Grebenjuk, 2016).

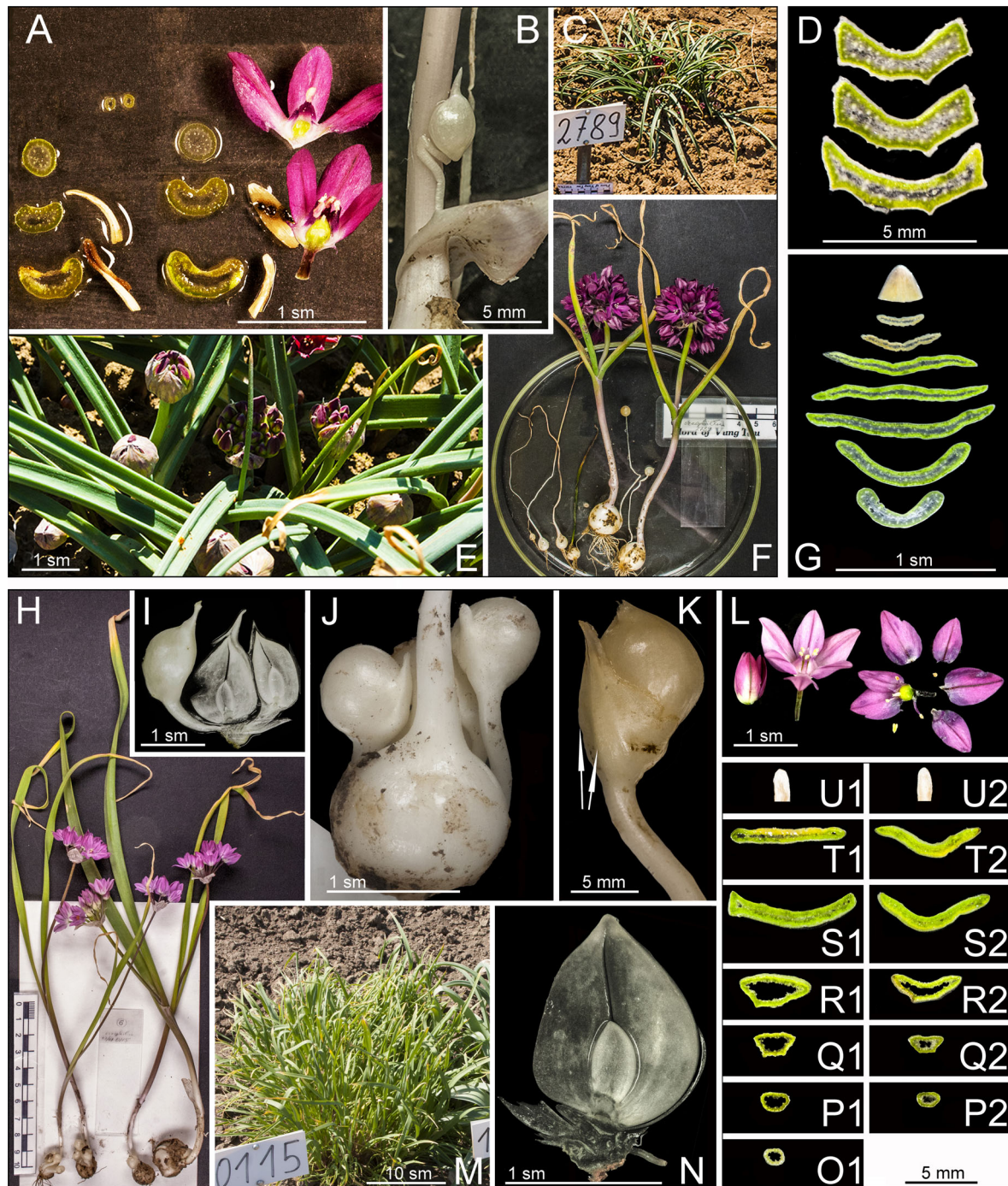


Fig. 6. Morphological diversity of *Allium* subg. *Porphyroprason*. **A–C, E & F**, *A. platystemon* s.l. (Tax2789), 2 fistulous, semicircular-grooved basal leaves, short peduncle and a group of very long stolons at the generative age. **A**, Cross-sections of leaves of young (vertical row on the left) and old (vertical row on the right) plants: in the lower horizontal row, sections of the first basal leaves and their apex (next to each other); the horizontal row above, sections of the second basal leaves and their apex (next to each other); above, sections of peduncles; at the top in the centre, 2 sections of the only leaf of a juvenile plant; on the right, vertically cut flower, stamen filaments are dark purple, anthers are yellow. **B**, Each stolon is in the leaf axil, therefore the inner stolon is clamped by the closed base of the leaf. **C, E & F**, Appearance in culture and in the laboratory. **D**, *A. platystemon* s.l. (Am0105), successive cross-sections upwards from the middle of the leaf blade, in young generative age there are 2 basal leaves, in old plants there is 1, in all with superficial stiffening ribs, a long peduncle almost equal to the length of the leaves. **G–U2**, *A. platystemon* var. *longitepalum* (Am1451, Am1453). **G** (Tax1453), Successive cross-sections of the first leaf blade (from base to top) of an old plant. **H–U2** (Am1451, Am1453), Bifoliate (sometimes with 3 leaves, see Fig. 10) slender plants with reproduction throughout ontogenesis by short, upwardly curved stolons (**I, J**) with a 2-keeled adossial prophyllum (**K**, arrows), with light purple tepals and stamen filaments (**L**), two storage scales of bulbs (**I, N**). **O1–U2**, Cross-sections of the first (left) and second (right) basal leaves: first year of life (**O1**), second year (**P1, P2**), juvenile (**Q1, Q2**), immature (**R1, R2**), young generative (**S1, S2**), old age (**T1, T2**), leaf tips (**U1, U2**). — All photographs by I. Levichev.

in leaf shape and in the colour and length of the tepals. According to molecular data, accessions Am1451 (cultivated in IPK Gatersleben as Tax0115), Am1452 (as Tax0705), and Am1494, all without known geographic origin, are also part of this group. This presumably means that the karyotype published by Hanelt & al. (1989) belongs to this cryptic taxon. Currently, we consider it a variety of *A. platystemon* s.l. that needs further investigation, including plants from the Pamir Mountains and Afghanistan that presumably belong to this taxon. Most likely, these five taxa accepted by us do not represent the full diversity of *A.* subg. *Porphyroprason*. *Allium oreophilum* is a popular ornamental species that has been available for a long time from many bulb plant suppliers. If one looks at all the photos of *A. oreophilum* available on the Internet, there are very different morphological types (e.g.,

<https://www.plantarium.ru/page/view/item/2099.html>). Some do not fit at all with the five taxa characterised above. Some variations may have arisen spontaneously in culture or have not yet been rediscovered in nature. It was also impossible to determine the exact origin of the plants offered for sale; there were probably several plant sources.

If we compare our karyotypes with those reported by other authors, we find an astonishing diversity. However, the idiogram of Genç & Firat (2016: fig. 2f) is similar to our Fig. 8E and should represent *Allium oreophilum* s.str. Concerning the origin of the studied plants, there are remarkable differences in the details; for example, our smallest chromosome VII is missing from Genç & Firat's idiogram. The karyograms of Hanelt & al. (1989: Abb. 8) and Fritsch (2016: 276), however, present chromosomes more

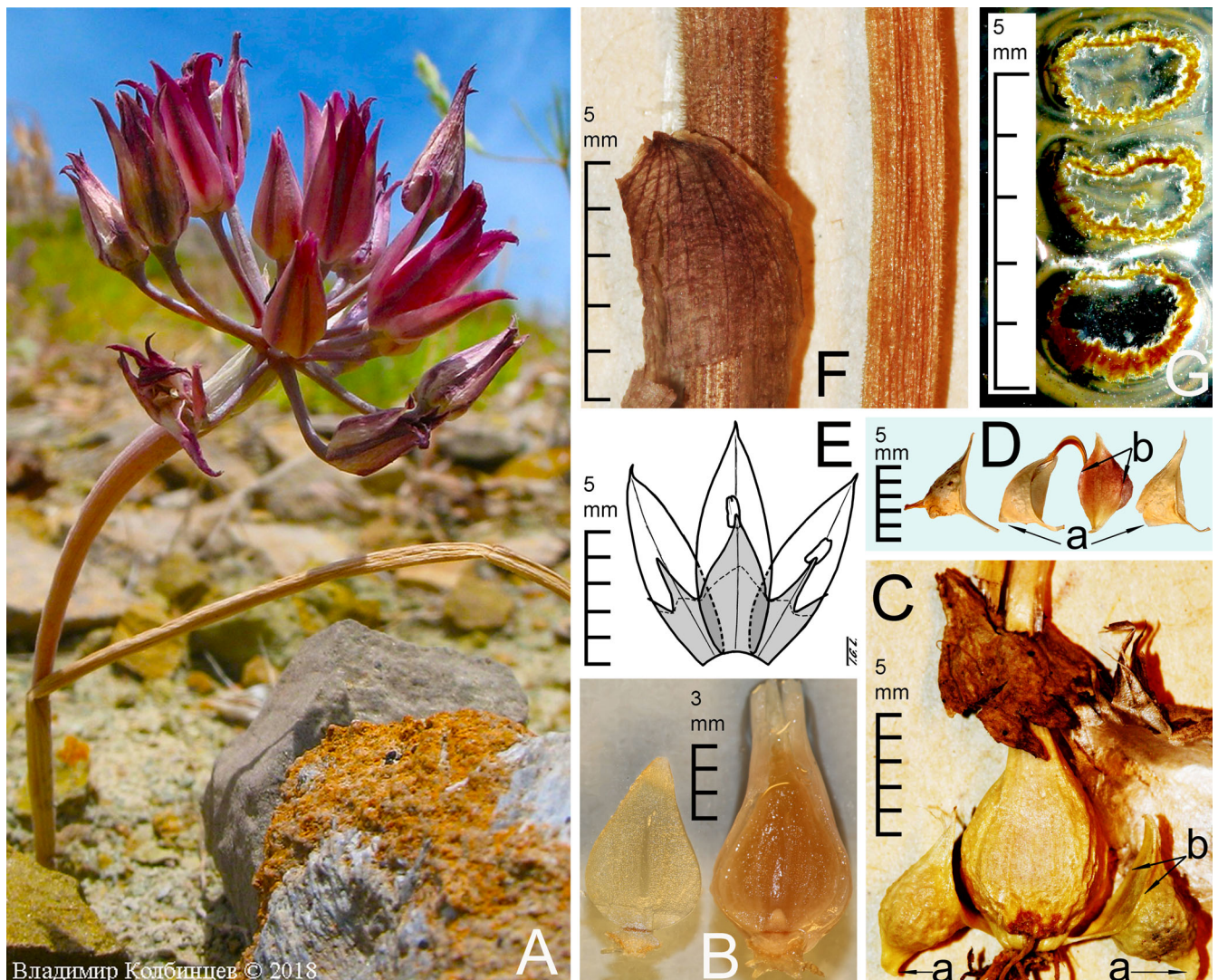


Fig. 7. *Allium kujukense*. **A**, General view, southern Kazakhstan, Syr-Darya Karatau Range, Berkara; **B**, Longitudinal section of the bulb (single storage scale); **C**, Replacement bulb of the future shoot with two vegetative bulbils of the current year (dead shells shifted upward); **D**, Vegetative bulbils with a beak-shaped outgrowth on the outer side (a), the adjoining surface is 2-keeled (b); **E**, Tepals (inner in the centre), filaments and anthers; **F**, Apex of sheath scale (glabrous), scape and leaf very short, densely bristly; **G**, Cross sections of the leaf blade at different levels above ground. — A by V. Kolbinzsev; B–G by I. Levichev.

similar to *A. platystemon* (our Fig. 8D) but with relatively larger SAT-chromosomes. Maragheh & al. (2019: fig. 1) did not show satellite chromosomes. Apparently, satellites were not important for their investigations. In the results and discussion in Fritsch & Astanova (1998) of idiograms for more than 20 species of *A. subg. Melanocrommyum*, a broader variation of chromosome morphology was determined (“random oscillation around a mean karyotype”), which could probably also be present in species of *A. subg. Porphyroprason*. Perhaps the current study can initiate a future search for additional locations for all species of *A. subg. Porphyroprason*, and richer material can be collected for a more detailed morphological, karyological and molecular investigation of those taxa.

Possible biogeographic-historical scenario of the origin of *Allium* subg. *Porphyroprason*, subg. *Vvedenskya*, and others. — Very different datings for the genus *Allium* have been published so far, from 11 Mya to 87 Mya (Janssen & Bremer, 2004; Li & al., 2016; Hauenschild & al., 2017; Costa & al., 2020; Xie & al., 2020; Namgung & al., 2021; Yang & al., 2023; Friesen & al., 2024), which can be attributed to different methods of calculation. As there are no fossil records of *Allium*, many analyses (Li & al., 2016; Hauenschild & al., 2017; Xie & al., 2020; Namgung & al., 2021; Yang & al., 2023) are based on data using a secondary calibration point estimated for other monocotyledons (Chen & al., 2013). Chen & al. (2013) used 100 Mya as a calibration point for the origin of palms, for example, but today palms are regarded to be at least 150 million years (Myr) old, or even much older (Li & al., 2019). Any further analysis with

“wrong” calibrations point produces further deviating results. We believe that applying nrITS substitution rates for herbaceous annual/perennial angiosperms is the most appropriate method to address this challenge (Kay & al., 2006). Of the published datings, we believe that only Costa & al. (2020) with 52.2 Myr (58.1–44.4 Myr: 95% HPD) and Friesen & al. (2024) with 45.79 Myr (62.3–32.4 Myr: 95% HPD) provided a close estimate of the actual age of the genus *Allium*. Due to the vicariance after the Gondwana breakup, the intercontinental disjunction hypothesis is also discussed in the Alliioideae tribes (Costa & al., 2020; Friesen, 2022; Friesen & al., 2024).

According to the analysis of the distribution of most subgenera of the genus *Allium*, the Turano-Iranian region seems to be the centre of the emergence of most subgenera in the genus (Friesen, 2022). Yusupov & al. (2022) indirectly confirmed this after analysing seed coat surfaces.

According to our data, the area of origin of many subgenera from the second and third evolutionary lineages of the genus *Allium* was located in the Irano-Turanian region, presumably in the zone of “closure” of the historical Neo-Tethys ocean by fragments of the Arabian platform. The docking and subduction of such fragments under the southern edge of the Eurasian continent led to the formation of the Tian-Shan, Pamir-Alay, Elburz, Caucasus and other alpine mountain systems. The north-eastern edge of the Iranian platform, in the subduction zone under Eurasia, formed a depression under the current Caspian Sea and marked the valley of the Amu-Darya River, and the corresponding part of this edge of the

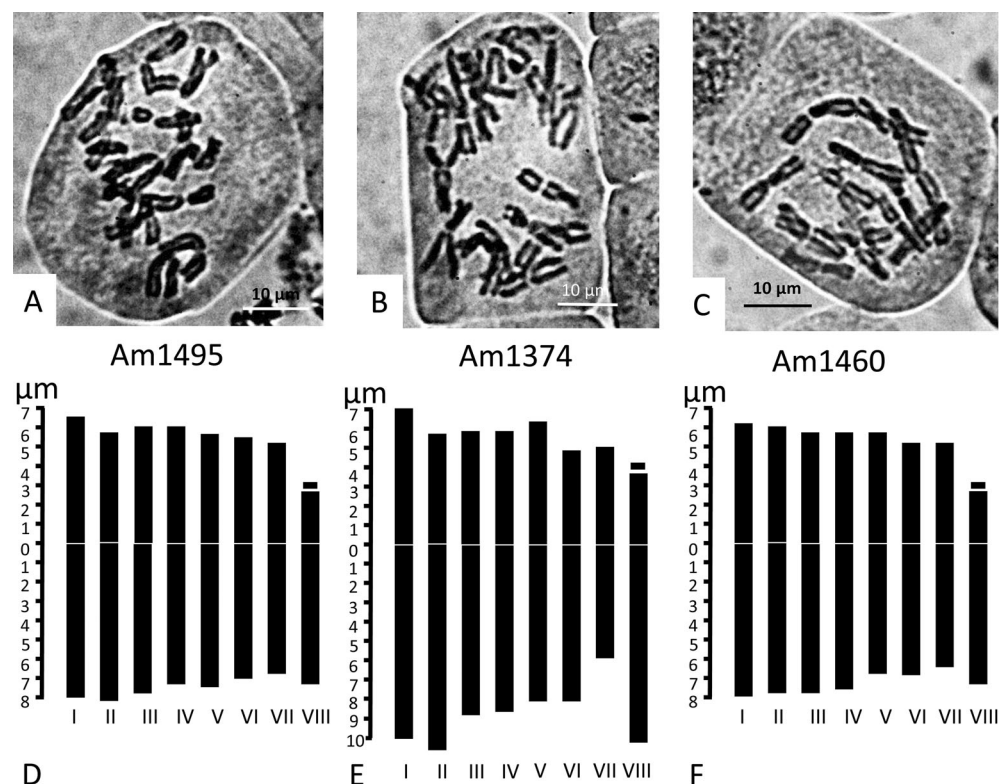


Fig. 8. Metaphase plates (A–C) and idiograms (D–F) of *Allium oreophilum* s.l.: A & D, *A. platystemon*; B & E, *A. oreophilum* s.str.; C & F, *A. aksuzhabagliense*.

Arabian fragment raised the Kugitang Mts. and pressed on the previous Arabian fragment (Afghanistan), which piled up the western part of the Pamir-Alay ridge system. Thus, the Neo-Tethys was previously gradually “closed” by the platforms that piled up the Altai, Tian-Shan, Sayan mountain ranges, etc., and caused depressions such as Balkhash, Issyk-Kul, and Fergana (Monin & Zonenshain, 1987; Khain, 2001; Popov & al., 2009; Hurka & al., 2019).

It turned out that this series of events initiated the emergence of the bulbous genera *Allium* and *Gagea* L. (part of *G.* sect. *Bulbifera* Levichev), and, among others, perhaps of the genera *Tulipa* L. and *Eremurus* M.Bieb. Therefore, the centres of origin of these genera were located in the region of the middle reaches of the Amu-Darya River (Levichev, 1999). Thus, their origin is associated with the “fusion” of representatives of the Eurasian “Ginkgo flora” and

Table 2. Morphometric parameters of karyotypes: Am1495: *A. platystemon* (12 metaphase plates), Am1374: *A. oreophilum* (5 metaphase plates), Am1460: *A. aksuzhabagliense* (11 metaphase plates).

AM1495							
Pair no.	TAL (μm)	RL (%)	LA (μm)	SA (μm)	SAT	CI (%)	Type
1	14.5	13.97	8.0	6.5		44.8	m
2	14.0	13.49	8.1	5.9		42.1	m
3	13.8	13.29	7.8	6.0		43.5	m
4	13.1	12.62	7.1	6.0		45.8	m
5	12.9	12.42	7.3	5.6		43.4	m
6	12.5	12.04	7.1	5.4		43.2	m
7	11.9	11.46	6.8	5.1		42.9	m
8	10.1 + 1	10.68	7.3	2.8	1	25.5	sm
TKL = 207.6, KCI = 40.3%							
Am1374							
Pair no.	TAL (μm)	RL (%)	LA (μm)	SA (μm)	SAT	CI (%)	TYPE
1	16.3	14.31	10.0	5.6		41.2	m
2	14.6	12.81	10.7	5.7		34.5	m
3	14.4	12.64	8.9	5.7		39.0	m
4	14.4	12.64	8.7	6.3		39.6	m
5	14.1	12.37	5.9	3.7		45.9	m
6	12.9	11.32	8.1	4.8		43.7	m
7	10.9	9.57	8.1	5.0		37.2	m
8	16.3	14.31	10.4	5.6	2	26.2	sm
TKL = 227.8, KCI = 38.3%							
AM1460							
Pair no.	TAL (μm)	RL (%)	LA (μm)	SA (μm)	SAT	CI (%)	TYPE
1	14.1	14.02	7.9	6.2		43.9	m
2	13.6	13.50	7.6	6.0		44.1	m
3	13.3	13.22	7.6	5.7		42.8	m
4	13.2	13.12	7.5	5.7		43.2	m
5	12.4	12.42	6.7	5.7		45.9	m
6	11.9	11.82	6.8	5.1		42.9	m
7	11.5	11.43	6.4	5.1		44.3	m
8	10 + 0.6	10.53	7.3	2.7	0.6	27.0	sm
TKL = 201.2, KCI = 40.3%							

TAL, total absolute length; RL, relative length; LA, long arm; SA, short arm; SAT, satellite; CI, centromeric index; TYPE, chromosome nomenclature according to Levan & al. (1964); TKL, total karyotype diploid length; KCI, karyotype centromeric index.

the Afro-Arabian “Welwitschia flora” (Popov, 1983). They belong to “one historical age” in the interval of 50–20 Mya. Our dating of the second evolutionary lineage fits very well with this time period (Fig. 5). The genera *Kharkevichia* Levichev, *Amana* Honda, *Tulipa*, and some subgenera of *Allium* also occurred during this period and at different places in the Asian continent. Like the emergence of some subgenera of *Allium*, the genera *Lloydia* Salisb. ex Rchb., *Plecostigma* Turcz., and *Huolirion* F.T.Wang & T.Tang should be associated with the uplift of Tibet and the Himalayas as a result of the earlier docking of the Indian platform, which brought *Iphigenia* Kunth, *Trichopetalum* Lindl., the ancestor of *Allium*, and who knows what other genera, from the Southern Hemisphere (Antarctica, Australia, South Africa and Madagascar).

In general, the formation of the bulbous genera of Eurasia seems to be associated with adaptation to a frost season. These taxa did not move southwards (although they had 40–20 million years to do so) into the frost-free regions of the subtropics. In this respect they differ from the morphologically more primitive bulbous and truly tropical genera such as *Crinum* L. and others. Members of the latter genus grow in the equatorial region of Africa and in the tropical part of South-East Asia, even under water. In Central America and Madagascar, they have become obligate aquatic plants with all their organs in the water layer. The formation of new frost-resistant bulbous plants in Eurasia took place gradually over perhaps even more than a hundred million years, which cannot be traced in any way from fossil remains. There is not only evidence from morphology and neoteny, but molecular dating methods can also redraw such events. As new continental fragments of Africa and Arabia merged (after the Indian subcontinent reached the Asian Continent, see fig. 9 in Friesen & al., 2024), new taxa of the “Welwitschia flora” introduced new genomic features. The most important selection factor remained the frost season, and various protection methods were developed and improved: the ephemeral type of annual life cycle of a plant, biennial, and unique morphology of bulbs remaining underground. Therefore, not flowers, but underground organs – bulbs and their vegetative reproduction – very actively diverged and formed a series of new taxa of different ranks (from subgenera to species and races). According to Peterson & al. (2019: fig. 3), *Gagea* sect. *Bulbifera* arose about 40 million years ago in flat areas, apparently after the junction of India and clearly outside India, and then dispersed throughout the steppe zone. But *Allium* (p.p., concerning ancestors occupying higher altitudes), *Huolirion*, *Lloydia*, and *Plecostigma* originated already on the microthermal platform of Tibet and the mountains around (Levichev, 2013). Such frost-resistant bulbous plants had the opportunity to migrate to the tundra. They moved to Chukotka and along the periodically emerging Bering bridges (Kozhevnikov & Zheleznov-Chukotsky, 2014) to Alaska and along the mountain ranges down to Mexico (*A. subg. Ameralium* and *A. tricoccum* Aiton, *A. subg. Anguinum*, *Lloydia*, etc.). But *A. subg. Porphyroprason*, subg. *Vvedenskya*, subg. *Melanocrommyum* and others evolved at low altitudes. They

moved very late into higher altitudes when other mountains of the Alpine orogeny began to rise (hitherto in *A. subg. Melanocrommyum* not at all successfully).

■ NOMENCLATURE

Allium subg. *Porphyroprason* (Ekberg) R.M.Fritsch in Aliso 22: 386. 2006 ≡ *Allium* sect. *Porphyroprason* Ekberg in Bot. Not. 122: 65. 1969 ≡ *Allium* [sect. *Molium*] ser. *Oreophila* Tzag. in Bot. Mater. Gerb. Inst. Bot. Akad. Nauk. Kazakhsk. S.S.R. 10: 14. 1977, p.p. – Type: *A. oreophilum* C.A.Mey.

Allium aksuzhabagliense N.Friesen & Lazkov, **sp. nov.** – Holotype: Kazakhstan, Turkestan region, Tyulcubas District, Talas Alatau, Aksu-Zhabagly National Park, Kalaoi gorge at the pass. Limestone outcrops, 2600 m, 42.363468°N, 70.487798°E, 17 Jul 2023, N. Friesen, S. Dzumanov & al. s.n. (AA barcode 0003319!, left plant).

The new species is illustrated in Fig. 5C–F, the holotype in Fig. 9.

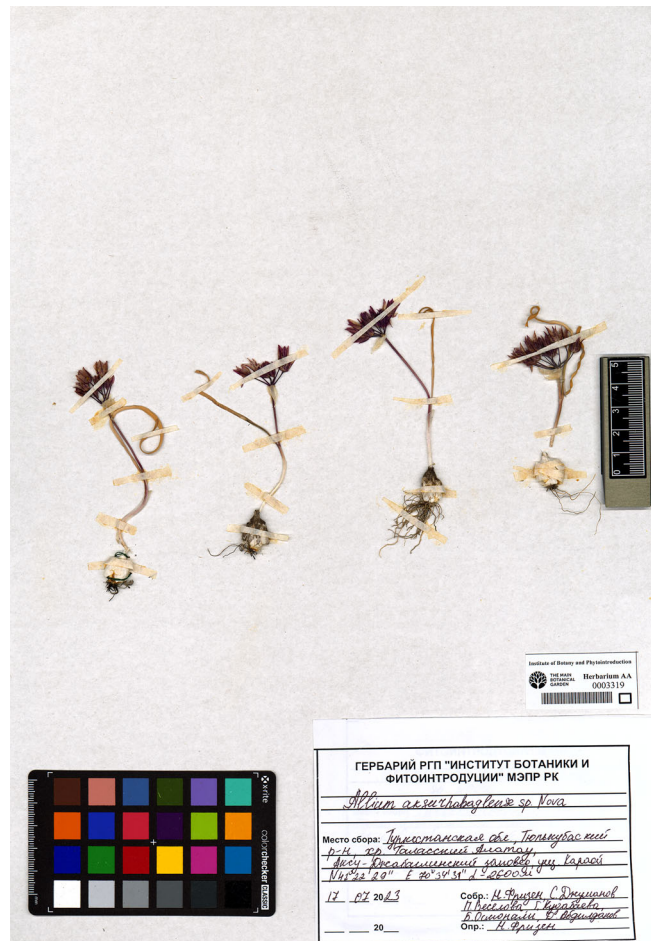


Fig. 9. Holotype of *Allium aksuzhabagliense* (left plant).

Diagnosis. – It differs from the related *Allium oreophilum* and *A. platystemon* by having only one leaf instead of two, and it grows on calcareous rock instead of granite or gneiss.

Description. – Bulbs subglobose, 7–8(10) mm in diameter; outer tunics thin, whitish to brownish grey, soon decaying. Peduncle (often S-like) flexuous, terete, smooth; 5–15 cm long, 2–3 mm in diam.; green, brown suffused at least near the base. Leaves 1, laminae narrowly linear to lanceolate, steep to flat arcuately ascending with recurved upper part, thick, fleshy, shallowly canaliculate; upper side smooth or somewhat grooved, lower side with a few flat ribs; margin smooth or slightly toothed, shortly tapering into the not cucullate apex; 10–13(18) cm long, 2.6–3.6 mm broad; green, basal red-brown suffused with glaucous bloom, at least in the sprouting stage flushed violet. Sheathy squama vaginalis is short, hyaline, and long-lasting. Vernation planar. Inflorescence broadly fastigiate to semi-globose; $\pm$ loose, (5)8–10 (15)-flowered; 3–4.5 cm in diam. Pedicels moderately thick, straight to somewhat ascending; 1.1–1.5 cm long; green, brown or purplish suffused. Anthesis in June to July. Flowers are broadly campanulate and triangular. Tepals ovate to elliptic, free at the base, tip sub-obtuse, dorsally slightly concave, obliquely upright positioned; after anthesis strawlike stiff and $\pm$ incurved; outer tepals 6.8–8.5 mm long, 2.3–3.3 mm broad, sometimes with three veins, inner tepals in the mean c. 1.6 mm shorter and 1–1.4 mm narrower, always with one median vein; deep pink or deep brownish purple, fading towards the base, vein(s) greenish to brown, narrow. Filaments $1/3$ – $1/2$ as long as the tepals, fleshy; connate at the base, inner filaments broadly ovate to triangular with a short, narrow tip, outer filaments twice narrower and somewhat shorter; colour basal like adjacent tepals but upper part much darker coloured. Anthers ovoid; c. 1 mm long; yellow. Pollen yellow. Ovary sessile, depressed globose, triangular or nearly hexangular with 3 rather broad and 3 very narrow furrows, 2–3.5 mm long, 2–4 mm in diameter; surface papillose. Style sub-conical, slightly angled, c. 1 mm long; green to purplish. Stigma shortly tripartite; white. Capsule enclosed by stiff, dry tepals, 5–6 mm long and 6–7 mm in diameter, depressed to globose or depressed, triangular, with very finely coarse surface.

Etymology. – The epithet refers to the Aksu-Zhabagly National Reserve.

Distribution. – At present only known from the alpine zone of the Talas Alatau in the Aksu Zhabagly National Reserve (Kazakhstan) and from the Kyrgyz part of the Chatkal Mountains. It could also be present in neighbouring areas where limestone occurs in the alpine zone.

Allium oreophilum C.A.Mey., Verz. Pfl. Casp. Meer.: 37. 1831 – Holotype: Azerbaijan, “Tufandagh”, 31 Jul 1830, Meyer 271 (LE barcode LE 01191214!; isotype: LE barcode 01191212!).

Distribution. – East Caucasus, East Anatolia.

Etymology. – The epithet refers to the alpine distribution of this species (from Greek; “loving mountains”).

Allium ostrowskianum Regel in Trudy Imp. S.-Peterburgsk. Bot. Sada 7(2): 545. 1881 $\equiv$ *Allium oreophilum* var. *ostrowskianum* (Regel) Regel in Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 356. 1887 – Lectotype (designated by Fritsch in Taxon 39: 506. 1990): Ex horto bot. Petropolitano 81. 5 e *Turkestanica occidentalis* Fetisow misit (LE barcode LE 01182330!).

Distribution. – Locally distributed on the Susamyr Range in Kyrgyzstan.

Etymology. – The epithet refers to the former Imperial Russian minister M.N. v. Ostrowski.

Allium platystemon Kar. & Kir. var. *platystemon* in Bull. Soc. Imp. Naturalistes Moscou 15(3): 514. 1842 – Lectotype (designated by Gubanov & Bagdasarova in Pavlov & al., Gerbarij Moskovskogo Universiteta: 54. 1978): Kazakhstan. “In subalpinis petrosis Alatau ad fl. Sarchan”, 1841, Karelin & Kirilow s.n. (MW barcode MW0591691!).

Distribution. – Kazakhstan (Saur, Tarbagatai, Dzhungar Alatau, Tian-Shan); Uzbekistan, Kyrgyzstan, Tajikistan;



Fig. 10. Holotype of *Allium platystemon* var. *longitepalum*.

Northeast Afghanistan, Northeast Pakistan (Wendelbo, 1971: 67).

Etymology. – The epithet refers presumably to the wide, flat filaments of the stamens.

Allium platystemon var. *longitepalum* N.Friesen & R.M. Fritsch, **var. nov.** – Holotype: Cultivated in Gatersleben TAX 2565! (grown from bulbs collected in Tajikistan: Turkestan Mountains, Shakhristan Pass north of Aini, Gneiss slope, 3350 m), collected 1993 (GAT barcode 2543568! [No. 17790], the large plant on the right).

The holotype is illustrated in Fig. 10.

Diagnosis. – Larger plants with larger tepals (9.8 ± 0.28 mm) than the typical variety (8.2 ± 1.6 mm) and differing by pinkish-red (not purple) flowers.

Description. – Compared to *Allium platystemon* s.str., commonly large plants with two and sometimes three leaves (18 ± 3.6 cm long in *A. platystemon* var. *longitepalum* and 10.79 ± 8.5 cm in var. *platystemon*), scapes up to 15 cm long, and many-flowered inflorescences with pinkish-red tepals whitish at the base and with inside purplish and outside greenish median vein. The filaments are purplish, fading towards the base.

Distribution. – Known to occur in the Pamir-Alay region and possibly in Afghanistan and Pakistan. The dominating morphotypes in botanical gardens are most often distributed via the flower bulb trade, but the geographic source of this cultivated material is unknown.

Etymology. – The name refers to the large flowers.

Key for the determination of species of *Allium* subg. *Porphyroprason*

1. Flowers broadly campanulate, tepals lilac, rose, red or purple 2
1. Flowers campanulate, tepals white with red midvein.....*A. ostrowskianum*
2. Leaves always two (occasionally three).....3
2. Mostly one leaf (occasionally two)*A. aksuzhabagliense*
3. Mature bulbs over 11 mm wide, tepals lilac*A. oreophilum*
3. Mature bulbs less than 9 mm wide, tepals red or purple... 4
4. Outer tepals purple and shorter than 8.5 mm. Daughter bulbs with short stolons.....*A. platystemon*
4. Outer tepals red and longer than 9 mm. Daughter bulbs with long stolons*A. platystemon* var. *longitepalum*

■ AUTHOR CONTRIBUTIONS

NF: Conceptualization, formal analysis, data curation, writing the original draft. GL: initiation, data curation; ML: dating analysis; NT, DA and OT: data curation, morphological analysis of herbarium sheets. RM and KE: contributed tissue samples for sequencing. SD and VE: helped to collect plants. GTS and PV: financing and data curation. RMF and IL: data curation, writing discussion, reviewing and editing. All co-authors contributed to interpreting the results and writing the final version of the manuscript.

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Appendix 1. Voucher information for specimens newly sequenced (accession numbers for sequences downloaded from GenBank can be found in the phylogenetic trees).

Information is given here as follows: Species (names following the new nomenclature): Accession, Origin, Coordinates, Voucher, ITS, *trnQ-rps16*, *rps16*, *rpl32-trnL*, “–” indicates a missing sequence.

Allium aksuzhabagliense N.Friesen & Lazkov: Am1431, Kazakhstan, 42.419472, 70.825481, *Karmysheva s.n.* (AA): PP910265, PP908836, PP908870, PP908904; Am1459, Kazakhstan, 42.363468, 70.487792, *Friesen N., Dzumanov, S. s.n.* (OSB-2023-0573-1): PP910266, –, –, Am1460, Kazakhstan, 42.363468, 70.487798, *Friesen N., Dzumanov, S. s.n.* (AA 0003319): PP910267, PP908837, PP908871, PP908905; Am1461, Kazakhstan, 42.363467, 70.487700, *Friesen N., Dzumanov, S. s.n.* (OSB-2023-0573-2): PP910268, PP908838, PP908872, PP908906; Am1487, Kyrgyzstan, 41.40924, 70.83198, *Lazkov G. s.n.* (FRU): PP910269, PP908839, PP908873, PP908907; Am1488, Kyrgyzstan, 41.40920, 70.83193, *Lazkov G. s.n.* (FRU): PP910270, PP908840, PP908874, PP908908; Am1489, Kyrgyzstan, 41.40923, 70.831980, *Lazkov G. s.n.* (FRU): PP910271, PP908841, PP908875, PP908909; Am1490, Kyrgyzstan, 41.40924, 70.83198, *Lazkov G. s.n.* (FRU): PP910272, PP908842, PP908876, PP908910. *A. kujukense* Vved.: Am1261, Kazakhstan, 43.26682, 68.43349, *Kuprijanov A. Kaz07255* (KUJ): PP910278, PP908848, PP908882, PP908916; Tax3623, Kazakhstan, 43.39, 68.38, *Fritsch R. s.n.* (GAT 0016649): PP910279, PP908849, PP908883, PP908917; Tax3679, Kazakhstan, 43.35, 68.47, *Fritsch R. s.n.* (GAT 0016681): PP910280, PP908850, PP908884, PP908918; Tax5046, Kazakhstan, 42.54, 71.06, *Fritsch R. s.n.* (GAT 0016685): PP910281, PP908851, PP908885, PP908919. *Allium oreophilum* C.A.Mey.: Am1374, Russia, 41.255556, 47.870983, *R. Murtazaliev s.n.* (OSB-2022-0925): PP910245, PP908818, PP908852, PP908886; Am1450, Russia, 41.944668, 46.912706, *R. Murtazaliev s.n.* (DAG): PP910246, PP908819, PP908853, PP908887; Am1458, Turkey, 38.073687, 43.96201, *K. Ertugrul, O. Tugay s.n.* (KNYA 7951): PP910247, PP908820, PP908854, PP908888. *A. ostrowskianum* Regel: Am1337, Kyrgyzstan, 42.00375, 73.1341, *Lazkov G. s.n.* (FRU): PP910273, PP908843, PP908877, PP908911; Am1433, Kyrgyzstan, 42.00370, 73.1347, *Lazkov G. s.n.* (FRU): PP910274, PP908844, PP908878, PP908912; Am1434, Kyrgyzstan, 42.00378, 73.1349, *Lazkov G. s.n.* (FRU): PP910275, PP908845, PP908879, PP908913; Am1436, Kyrgyzstan, 42.00370, 73.1351, *Lazkov G. s.n.* (FRU): PP910276, PP908846, PP908880, PP908914; Am1437, Kyrgyzstan, 42.00377, 73.1340, *Lazkov G. s.n.* (FRU): PP910277, PP908847, PP908881, PP908915. *A. platystemon* Kar. & Kir.: Am0105, Kyrgyzstan, 41.223056, 73.692222, *N. Friesen s.n.* (OSBU 15482): PP910248, PP908821, PP908855, PP908889; Am1339, Kazakhstan, 44.373889, 79.769444, *N. Friesen s.n.* (OSBU 27844): PP910249, PP908822, PP908856, PP908890; Am1224, Kazakhstan, 44.373889, 79.769444, *Friesen s.n.* (OSB-2019-0735): PP910250, PP908823, PP908857, PP908891; Am1338, Kyrgyzstan, 39.714966, 69.660202, *Ganybarva M.R. s.n.* (FRU): PP910251, PP908824, PP908858, PP908892; Am1428, Kazakhstan, 42.21899, 85.03237, *Bykov s.n.* (AA), PP910252, PP908825, PP908859, PP908893; Am1429, Kazakhstan, 43.0505711, 77.522195, *Danilov M. s.n.* (AA): PP910253, PP908826, PP908860, PP908894; Am1430, Kazakhstan, 43.027101, 75.859168, *N.I. Rubzova, E. Stepanova s.n.* (AA): PP910254, PP908827, PP908861, PP908895; Am1432, Kazakhstan, 42.371289, 70.502478, *Karmysheva s.n.* (AA): PP910255, PP908828, PP908862, PP908896; Tax2789, Uzbekistan, 42.2333, 70.12224, *Fritsch R. s.n.* (GAT 2789): PP910256, PP908829, –, –, Am1463, Kazakhstan, 43.027105, 75.859161, *Friesen N., Epiktetov V. s.n.* (OSB-2023-0587): PP910257, PP908829, PP908863, PP908897; Am1495, Uzbekistan, 41.241481, 70.334545, *German D. s.n.* (OSB-2023-0603): PP910258, PP908830, PP908864, PP908898; Am1496, Uzbekistan, 41.241484, 70.334559, *German D. s.n.* (OSB-2023-0604): PP910259, PP908831, PP908865, PP908899. *A. platystemon* var. *longitepalum* N.Friesen & R.M.Fritsch: Am1451, Germany, 51.8263, 11.2782, *Fritsch R. s.n.* (GAT 17755): PP910260, PP908832, PP908866, PP908900; Am1452, Germany, 51.8263, 11.2782, *Fritsch R. s.n.* (GAT 17778): PP910261, PP908833, PP908867, PP908901; Am1453, Tajikistan, 39.542098, 68.559204, *Fritsch R. s.n.* (GAT 17790): PP910262, PP908834, PP908868, PP908902; Am1454, Kyrgyzstan, 39.330384, 72.268237, *Fritsch R. s.n.* (GAT 17789): PP910263, PP908835, PP908869, PP908903; Am1494, Germany, 51.818, 11.292, privat garden R.M. Fritsch: PP910264, –, –, –.