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Molecular and morphological revision of the *Allium saxatile* group (Amaryllidaceae): geographical isolation as the driving force of underestimated speciation

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The taxonomic circumscription of *Allium saxatile s.l.* (Amaryllidaceae), widely distributed from Italy to China, has been controversial with the number of accepted species ranging from three to seven. The aims of this study include a morphological and molecular revision of the group, a thorough nomenclatural study of available names and the reconstruction of possible phylogenetic relationships in the *A. saxatile* group. We studied *c.* 2000 herbarium specimens and successfully sampled 86 accessions of the *A. saxatile* group and a few related species to reconstruct a molecular phylogenetic tree based on internal transcribed spacer (ITS) and two plastid DNA regions (*rpl32–trnL* and *trnL–trnF*). The monophyletic *A. saxatile* group consists of 15 geographical entities united in two geographically justified clades. Two yellow-flowered species, *A. obliquum* and *A. petraeum*, were clearly nested in the *A. saxatile* clade in the ITS and plastid DNA analyses. The oldest names in the group, i.e. *A. saxatile* and *A. globosum* from the Caucasus, represent genetically identical populations and should be synonymized. The taxonomic conspectus in this article includes 15 species and a nothospecies. We describe five new species (***A. austrodanubiense* sp. nov.**, ***A. schistosum* sp. nov.**, ***A. cretaceum* sp. nov.**, ***A. montanostepposum* sp. nov.**, ***A. kirilovii* sp. nov.**), a nothospecies (***A. × agarmyschicum* nothosp. nov.**) and raise a variety to species level (***A. rubriflorum* comb. nov.**).

INTRODUCTION

Allium L. is one of the largest genera of monocots. Currently, the number of species in the genus is estimated to be 920 (original counts based on Govaerts *et al*., 2005–2014). Meanwhile, according to the International Plant Names Index (IPNI), *c.* ten new *Allium* spp. are described annually. Many new species are presumed to be rare local endemics; some have been described as a direct result of field work on a limited number of collections with no genetic background provided.

No comprehensive monograph of the genus has been compiled since Regel (1875), and it is highly unlikely that a new monograph will appear in the near future. The phylogenetics of the genus based on internal transcribed spacer (ITS) sequences have been resolved at subgeneric and sectional levels (Friesen, Fritsch & Blattner, 2006), but we still know little about the taxonomic and genetic diversity within established sections.

In this article, we present a partial revision of section *Oreiprason* F.Herm. (subgenus *Polyprason* Radić) as described by Friesen *et al*. (2006). As a result of the lack of recent collections from the mountains of Central Asia, several species attributed to the

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section by Bajtenov & Kameneckaja (1990) have been excluded from the present study. Thus, the main target group is a pool of species closely related to *A. saxatile* M.Bieb., the type of section *Oreiprason*.

Allium saxatile in the broad sense has been reported from various countries, from Italy to China (Garbari, 1982; Xu & Kamelin, 2000; Govaerts *et al*., 2005–2014), although the geographical heterogeneity of this group has been repeatedly confirmed by the description of new taxa (Nyman, 1882; Gandoger, 1890; Adamović, 1908; Grossheim, 1928; Krylov, 1929; Vvedensky, 1935, 1971; Bedalov & Lovrić, 1978; etc.).

Allium saxatile and its allies are plants of medium size (usually 20–30 cm high) forming loose patches of several flowering stems. The cylindrical or oblong bulb-like base of the stem ('false bulb' or 'bulb') has brown or black coriaceous tunics and is usually attached to a short (sometimes almost invisible) rhizome. The stem leaves sheath the lowest quarter to third of the stem. The bivalved, persistent spathe is divided into unequal valves, the longer with a filiform beak, the shorter with a short beak. The compact, semiglobose to globose umbels bear white, purple or yellow flowers. The anthers and styles are clearly exserted.

In the protologue, Marschall von Bieberstein (1798) briefly described *A. saxatile* from Kurt-Bulak (Azerbaijan) without any detailed floral characteristics. Later, he transferred the name *A. saxatile* from east Caucasian to the Crimean plants ('*in lapidosis calcareis Tauriae frequens*') and amended the description reporting the tepal colour ('*varietas floribus purpurascentibus in subalpinis Caucasi orientalis reperitur*') (Marschall von Bieberstein, 1808).

Another widely used name, *A. globosum* M.Bieb. ex DC., first appeared in the '*Liliacées*' paintings by Redouté (1807). The authority of the name refers to A.P. de Candolle, because Redouté himself did not publish descriptions and made no herbarium (Stafleu & Cowan, 1983). This Caucasian purple-flowered plant was illustrated with a colour painting. This morphotype is known to occur in lower altitudes of the Caucasus region, in Russia and Georgia. Subsequently, Marschall von Bieberstein (1819) accepted three species: *A. globosum*; *A. saxatile* from the Crimea; and *A. caucasicum* M.Bieb. from the eastern Caucasus region ('*planta inter A. globosum et saxatile veluti media*').

This archaic concept was widely used all over Eurasia for almost two centuries. As a rule, purple-flowered collections were identified as *A. globosum*, whereas morphotypes with white or slightly rose flowers were usually named *A. saxatile,* irrespective of their origins. Vvedensky (1935) slightly modified the names, although not the concept. Following nomenclatural rules, he used the name *A. saxatile* according to Marschall von Bieberstein (1798) for the subalpine *A. caucasicum* and named the Crimean plants *A. marschallianum* Vved.

Seregin (2007b) reported an undescribed species from the Crimea closely related to *A. marschallianum* and sent a few samples of the Crimean and Caucasian plants to Friesen. Later, the new Crimean species was formally described as *A. tarkhankuticum* Seregin (2012), solely on a morphological basis. At that time, ITS sequences performed by Friesen disclosed that relations between the species of the *A. saxatile* group were complicated and required further extensive study involving plants from Europe, Siberia and Central Asia. This gave rise to the 'Globosum-project', which was launched as a collaborative initiative of Friesen and Seregin. Later, Anačkov joined the studies when the unexpectedly high speciation of the *A. saxatile* group in the Balkan Peninsula was revealed genetically.

Sennikov & Seregin (2015) compiled a concise review of early names used in the group. There are no modern estimates of how many species exist in the *A. saxatile* group. Govaerts *et al*. (2005–2014) accepted two widely distributed species (*A. saxatile* and *A. marschallianum*) and three local endemics (*A. psebaicum* Mikheev, *A. horvatii* Lovrić and *A. tarkhankuticum*). Also, at least three additional names were accepted in regional checklists: *A. globosum*; *A. savranicum* 'Besser'; and *A. saxatile* ssp. *tergestinum* (Gand.) Bedalov & Lovrić, *nom. inval*. (Omelczuk-Mjakushko, 1979; Friesen, 1988; Silletti, 2007; Seregin, 2007b; Kovtonyuk, Barkalov & Friesen, 2009).

There is a lack of molecular phylogenetic data in *A.* section *Oreiprason*. Van Raamsdonk *et al*. (2003) sequenced *trnL–trnF* of *A. saxatile*, *A. globosum* and *A. obliquum* L. (one accession per species), among another 33 accessions from former subgenus *Rhizirideum* (W.D.J.Koch) Wendelbo. These three species formed an unambiguous clade, confirming previous unexpected results by Van Raamsdonk, Vrielink-van Ginkel & Kik (2000) in a nuclear DNA phylogenetic analysis based on the same accessions.

Sequences of ITS for a few species from Central Asia (*A. kaschianum* Regel, *A. kurssanovii* Popov, *A. petraeum* Kar. & Kir., *A. setifolium* Schrenk and *A. talassicum* Regel) were included by Friesen *et al*. (2006) when they studied the intrageneric classification of *Allium*. As shown by Van Raamsdonk *et al*. 2000, 2003), the species of section *Oreiprason* formed a clade including the morphologically distinct *A. obliquum*. Thus, the monotypic section *Petroprason* F.Herm. was included in section *Oreiprason* (Friesen *et al*., 2006). Sequences of ITS for plants identified as *A. obliquum*, *A. petraeum* and *A. saxatile* and the *rps16* intron of *A. saxatile* from Xinjang, China were sampled by Li *et al*. (2010). Apart from a misidentified ITS sequence of *A. saxatile* auct. (AY427545; Ricroch *et al*., 2005), which, in fact, clearly refers to *A. schoenoprasum* L., other published molecular data on *A. saxatile* relatives are absent.

In the *A. saxatile* group, exclusively diploids were found with $2n = 16$ chromosomes (Levan, 1935; Vakhtina, 1965, 1985; Tscheschmedjiew, 1973; Gagnidze & Chkheidze, 1975; Magulaev, 1976; Zakirova & Vakhtina in Moore, 1977; Bedalov & Lovrić, 1978; Vakhtina & Kudrjashova, 1978, 1981; Van Loon & Kieft in Löve, 1980; Miceli & Garbari, 1980; Pogosian, 1983, 1997; Friesen, 1988; Kudrjashova, 1988; Agapova *et al*., 1990; Özhatay, Koçyiğit & Akalın Uruşak, 2012; Draghia *et al*., 2013). Obligate diploidy is a helpful tool for the correct interpretation of ITS and plastid (chloroplast) DNA sequences.

Our taxonomic treatment of the *A. saxatile* group includes results of molecular, morphological and nomenclatural studies, and biogeographical assumptions on the origin and migrations of the ancestors of the group. Three DNA regions (ITS and two plastid fragments) were isolated from 86 samples representing almost all geographical populations. In addition, five ITS sequences were downloaded from GenBank (http://www.ncbi.nlm.nih.gov/GenBank/).

MATERIAL AND METHODS

Herbarium data and distribution database

Over the last 15 years, we have checked all relevant collections of the *A. saxatile* group from the herbaria LE (*c*. 700 specimens), MW (*c*. 200), YALT (*c*. 140), KW (*c*. 140), MHA (*c*. 100), BUNS (*c*. 80) and GAT (*c*. 60). Fewer than 50 specimens were studied in many other herbaria [LECB, CWB (CWU), WIR, SIMF, GMU, DSU, CSAU, CSUH, B, OSBU, ALTB, NS, NSK, TK, BEO, BEOU, ZA, MKNH, BP, SO, SOM and SOA]. The curators of BM, G, TK and LY kindly sent us scans or photographs of selected specimens.

The distribution database includes a source citation (specimen or literature record) and coordinates (latitude and longitude). We used published records where they could be interpreted correctly, especially for *A. horvatii* (Bedalov & Lovrić, 1978; Miceli & Garbari, 1980; Nikolić, 2013) and *A. austrodanubiense* (Zahariadi, 1966). We searched the geographical coordinates using data from the Wikimapia on-line project (http://www.wikimapia.org) and a direct search in Google (http://www.google.com). Finally, *c*. 600 individual georeferenced localities were transferred to the maps (Figs 1–4) by Sergey V. Dudov using MapInfo software.

Taxon sampling

Since 2010, we have been sampling plant material for molecular analysis from all probable relatives of *A. saxatile*. The DNA was extracted from leaves and flowers of voucher herbarium specimens deposited in MW (30 successful samples), MHA (17), GAT (14), OSBU (7) and ALTB, SO, SOM, LE, BUNS and FR. Additional samples were extracted directly from the *Allium* collections in the Botanical Garden of the University of Osnabrueck and Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK, Gatersleben, Germany).

Ninety-one ITS and 71 plastid DNA sequences were included in the phylogenetic analysis. GenBank accession numbers and voucher information of the original sequences (HG794148–HG794233 for 86 ITS sequences; HG794008–HG794077 and HG794078–HG794147 for 70 *trnL–trnF* and *rpl32–trnL* sequences) are listed in Appendix 1. Total genomic

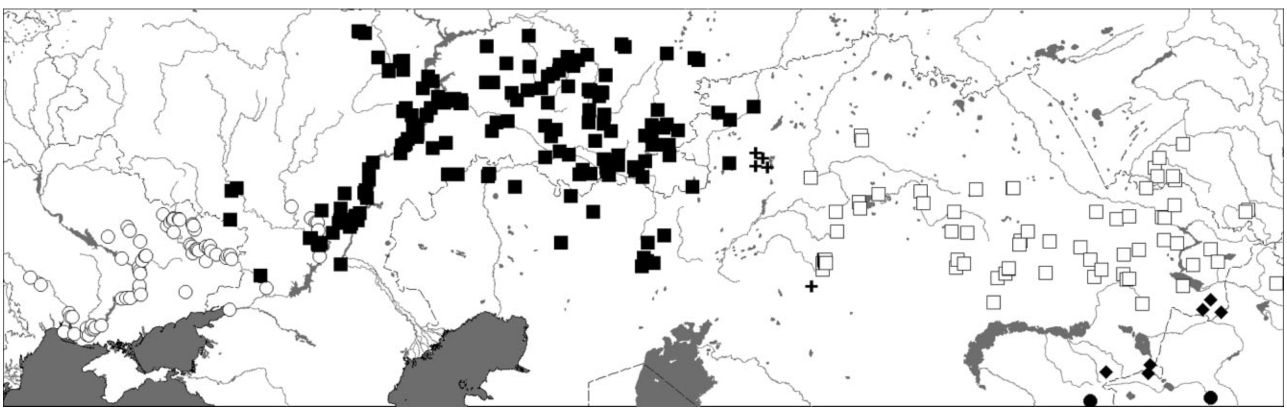

Figure 1. Distribution of *Allium savranicum* (○), ***A. cretaceum*** (·), ***A. montanostepposum*** (□), ***A. cretaceum*** × ***montanostepposum*** (+), *A. dshungaricum* (♦) and ***A. kirilovii*** (●).

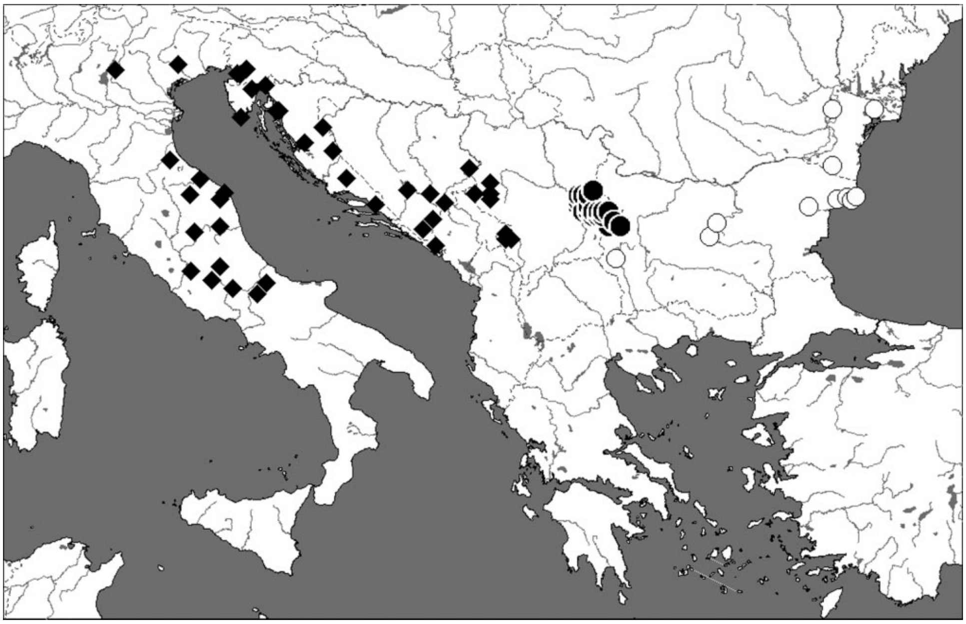

Figure 2. Distribution of *Allium horvatii* (◆), ***A. rubriflorum*** (●) and ***A. austrodanubiense*** (○).

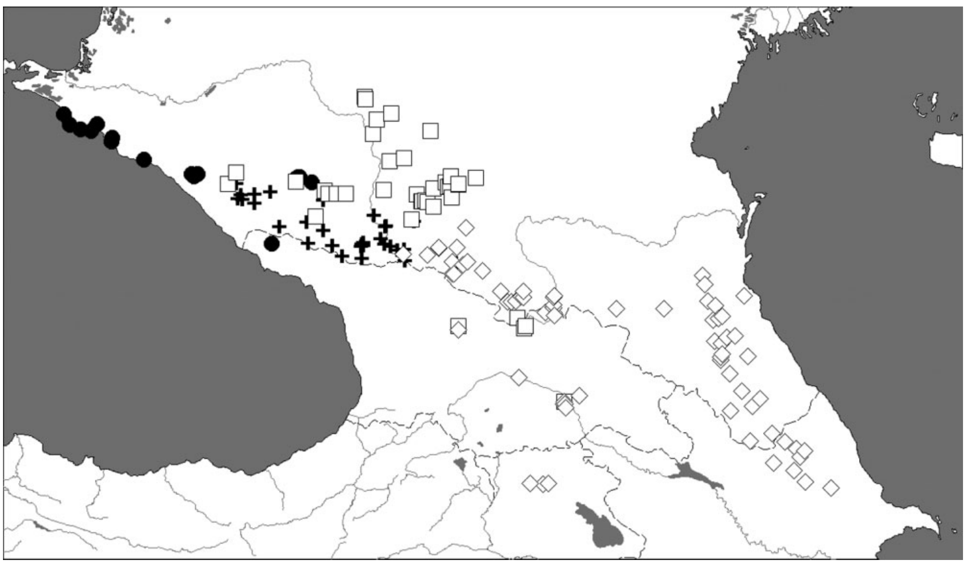

Figure 3. Distribution of *Allium psebaicum* (●), ***A. schistosum*** (+) and *A. saxatile* (◇)–*A. globosum* (□) complex.

DNA was sampled using the 'InnuPREPP Plant DNA Kit' (Analytic Jena AG) according to the instructions of the manufacturer, and was used directly in polymerase chain reaction (PCR) amplifications.

In addition, we downloaded five additional ITS sequences from GenBank: AJ411865 of *A. kirilovii* by Friesen *et al*. (2006, sub nom. *A. talassicum* auct.) from Tianshan Glaciological Station, Xinjiang, China; AM418363 of *A. petraeum* by Gurushidze *et al*. (2007) from Kurdai Pass, Kindyktash Massif, Kazakhstan; GQ181106 of *A. dshungaricum* Vved. by Li *et al*. (2010, sub nom. *A. petraeum* auct.) from Yumin, Xinjiang, China; GQ181108 of *A. montanostepposum* by Li *et al*. (2010, sub nom. *A. saxatile* auct.) from Ürümqi, Xinjiang, China; AM949624 of outgroup *A. austrosibiricum* N.Friesen by T. A. Sinitsyna & N. Friesen (unpubl. data) from the Mogen-Buren River, Tuva Republic, Russia. Plastid DNA *trnL–trnF*

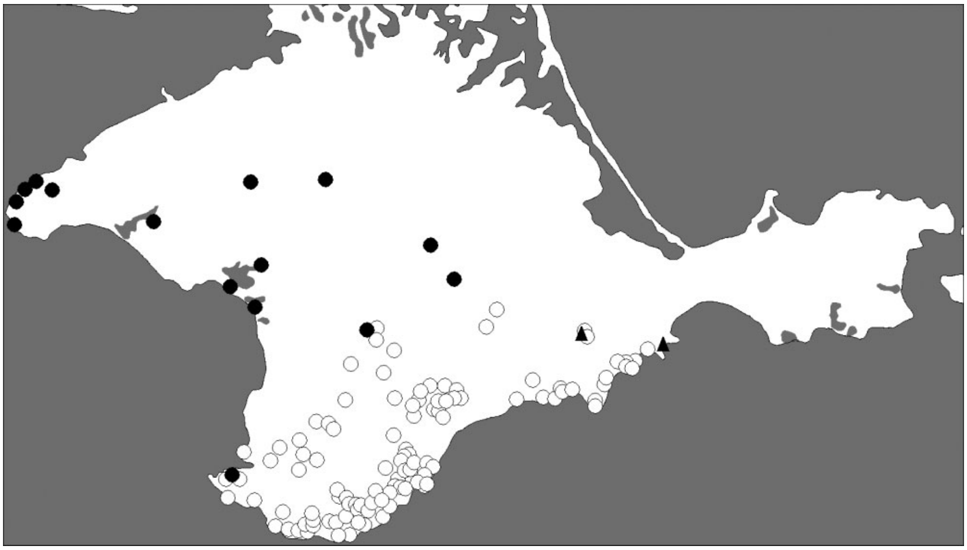

Figure 4. Distribution of *Allium tarkhankuticum* (●), *A. marschallianum* (○) and ***A. × agarmyschicum*** (▲).

(AM940991) and *rpl32–trnL* (HE603130) regions of *A. austrosibiricum* were sampled by T. A. Sinitsyna & N. Friesen (unpubl. data) from the same locality in the Tuva Republic.

DNA SEQUENCING

We sequenced ITS from nuclear ribosomal DNA (nrDNA) of all samples. For most samples, the nrDNA ITS region (ITS1, 5.8S and ITS2) was amplified using primers ITS-A and ITS-B (Blattner, 1999). ITS1 and ITS2 were amplified separately when DNA was taken from old herbarium specimens; in these cases, the primers ITS-E and ITS-C, together with ITS-A and ITS-B, were used. The PCR conditions were the same as in Friesen *et al*. (2006). As a result, almost all species of the *A. saxatile* group in the ITS analysis were represented by at least three accessions, except for *A. kirilovii* (a rare species sampled only from one locality) and *A. dshungaricum* (two accessions). In addition, the plastid *trnL–trnF* and *rpl32–trnL* regions were sequenced. We used primers described by Shaw *et al*. (2007) for *rpl32–trnL* and Taberlet *et al*. (1991) for *trnL–trnF*.

PCR products were sent to SeqLab (Göttingen, http://www.microsynth.ch). Forward and reverse sequences from each individual were manually edited in CHROMAS Lite 2.1 (Technesylum Pty Ltd) and combined in single consensus sequences. The sequences of all samples were aligned with CLUSTAL X (Thompson *et al*., 1997) with subsequent manual correction of alignments in MEGA 5 (Tamura *et al*., 2011). The simple indel coding method of Simmons & Ochoterena (2000) was used in aligned sequences.

To search for multiple ITS copies within the individuals of the presumed interlineage hybrid *A. × agarmyschicum*, we also cloned PCR amplicons using the TOPOTA Cloning kit (Invitrogen) according to the instructions of the manufacturer. The DNA of ten clones was isolated with a NucleoSpin plasmid kit (Macherey-Nagel, Düren, Germany) according to the instructions of the manufacturer, and prepared for sequencing. Sequencing was performed on an ABI 377XL automatic sequencer with universal M13 forward and reverse primers.

PHYLOGENETIC ANALYSIS

Allium austrosibiricum (*A.* section *Rhizirideum* G. Don ex W.D.J. Koch *s.s.*) was chosen as an outgroup based on the analysis by Friesen *et al*. (2006). Parsimony analysis was performed with PAUP* 4.0b10 (Swofford, 2002) using heuristic searches with tree bisection–reconnection (TBR) and 100 random addition sequence replicates. Bootstrap support (BS) (Felsenstein, 1985) was estimated with 1000 bootstrap replicates, each with 100 random addition sequence searches.

Bayesian analysis was implemented with MrBayes 3.1.23 (Ronquist & Huelsenbeck, 2003). Sequence evolution models were evaluated using the Akaike information criterion (AIC) with the aid of Modeltest 3.7 (Posada & Crandall, 1998). Two independent runs were initiated for 10 million generations using Markov chains, sampling every 100 trees.

One-quarter (25%) of the initial trees were discarded as burn-in and excluded from the analysis. The remaining trees were combined into a single dataset, and a majority-rule consensus tree was obtained. Bayesian posterior probabilities were calculated for this tree in MrBayes 3.1.23.

Nomenclature

We traced and studied the original protologues and type specimens of all relevant taxa. This nomenclatural study resulted in the description of six new species (including one hybrid), making a new combination based on a variety and designating two lectotypes and a neotype following the Melbourne Code (McNeill *et al.*, 2012). Two most critical nomenclatural cases were resolved earlier with the kind assistance of Alexander N. Sennikov and have already been published (Sennikov & Seregin, 2014, 2015).

A taxonomic conspectus includes 15 species arranged in two clades: 'Siberian' (six species) and 'Balkan–Caucasian' (nine species). One interlineage hybrid in the latter clade is described as a distinct nothospecies (*A.* × *agarmyschicum*), whereas *A. cretaceum* × *A. montanostepposum* hybrids were left without a formal name. Amended descriptions were compiled for new, poorly known or completely recircumscribed species (see Nomenclatural summary).

The descriptions, diagnoses of new species and a key were based on direct measurements of herbarium specimens. For flower details, we used on-site photographs available on-line and our own observations in the field or in gardens. We received permissions from 20 professional and amateur botanists from eight countries to publish their photographs from various localities (Figs 5–8) (see also Acknowledgements).

RESULTS

Sequences of nrITS and plastid DNA fragments (*trnL–trnF* and *rpl32–trnL*) were analysed separately. The summary of statistics for the phylogenetic framework is presented in Table 1 and the Bayesian phylograms are shown in Figures 9 and 10.

ITS sequence data

Direct sequencing of the ITS PCR products produced unambiguous sequences, except for the *A.* × *agarmyschicum* accessions. We cloned ITS PCR products of accession GL-114 of this hybrid. Eight of ten sequenced clones were identical to *A. marschallianum*, whereas two sequences were almost identical to *A. tarkhankuticum*. These additional copies were included in the analysis.

The alignments of the combined ITS region (ITS1 and ITS2 and the 5.8S gene) are shown in Supporting Information Appendix S1. The matrix generated consists of 651 characters, 139 of which are potentially parsimony-informative variable characters.

The substitution model TVM+G was chosen by AIC in Modeltest 3.7 for the Bayesian analysis. Unweighted parsimony analysis of the 91 sequences resulted in 2045 most parsimonious trees of 290 steps [consistency index (CI) = 0.8069; Fig. 9]. All accessions of poorly sampled Central Asian species (*A.* cf. *kastekii* Popov, *A. kokanicum* Regel and *A. tianschanicum* Rupr.) form sister clades to the *A. saxatile* group and have a minor influence on the tree topology. All taxa of the *A. saxatile* group, including yellow-flowered *A. obliquum* and *A. petraeum*, form a clade supported by a 100% bootstrap value (bootstrap probability, BP) and Bayesian posterior probability (PP) of 1.00. This clade is divided into the 'Siberian' and 'Balkan–Caucasian' (or 'European') sister clades.

The 'Siberian' clade consists of two groups. In both lineages, purple-flowered taxa are closely related to yellow-flowered species. For instance, three accessions of the yellow-flowered *A. petraeum* form a sister group to the slender rose-flowered *A. dshungaricum* from eastern Kazakhstan and closely related *A. kirilovii* from Tianshan. *Allium obliquum*, well-known among gardeners for showy, dense, yellow flower heads, forms a well-supported sister group to the purple-flowered '*A. globosum*' from the steppe regions of European Russia, Siberia, northern Kazakhstan and Xinjiang.

'*Allium globosum*' is divided into two distinct geographical groups: *A. cretaceum* (eastern Europe and north-western Kazakhstan) and *A. montanostepposum* (Xinjiang, central and north-eastern Kazakhstan and southern Siberia), separated by the border along the Turgay Valley. Two accessions have intermediate features in the ITS sequences, indicating a hybrid origin.

The 'Balkan–Caucasian' (or 'European') clade is also divided into two sister groups: Caucasian and south-east (SE) European. The Caucasian group, with 100% BP and 1.00 PP, has three lineages: *A. schistosum*; *A. psebaicum*; and *A. saxatile* + *A. globosum*. *Allium saxatile* and *A. globosum* accessions do not differ in ITS sequences.

Another clade, the SE European group, received only 74% BP and 0.70 PP support. It is composed of three lineages. There are two strongly monophyletic early branching lineages: (1) the Crimean endemic *A. marschallianum* (including hybrid accessions from Mt. Argamysh); and (2) *A. savranicum* from riverine sands of the Ukraine and south-western Russia. The third lineage comprises three Balkan taxa (*A. horvatii*, *A. austrodanubiense* and *A. rubriflorum*) and the western Crimean endemic *A. tarkhankuticum*.

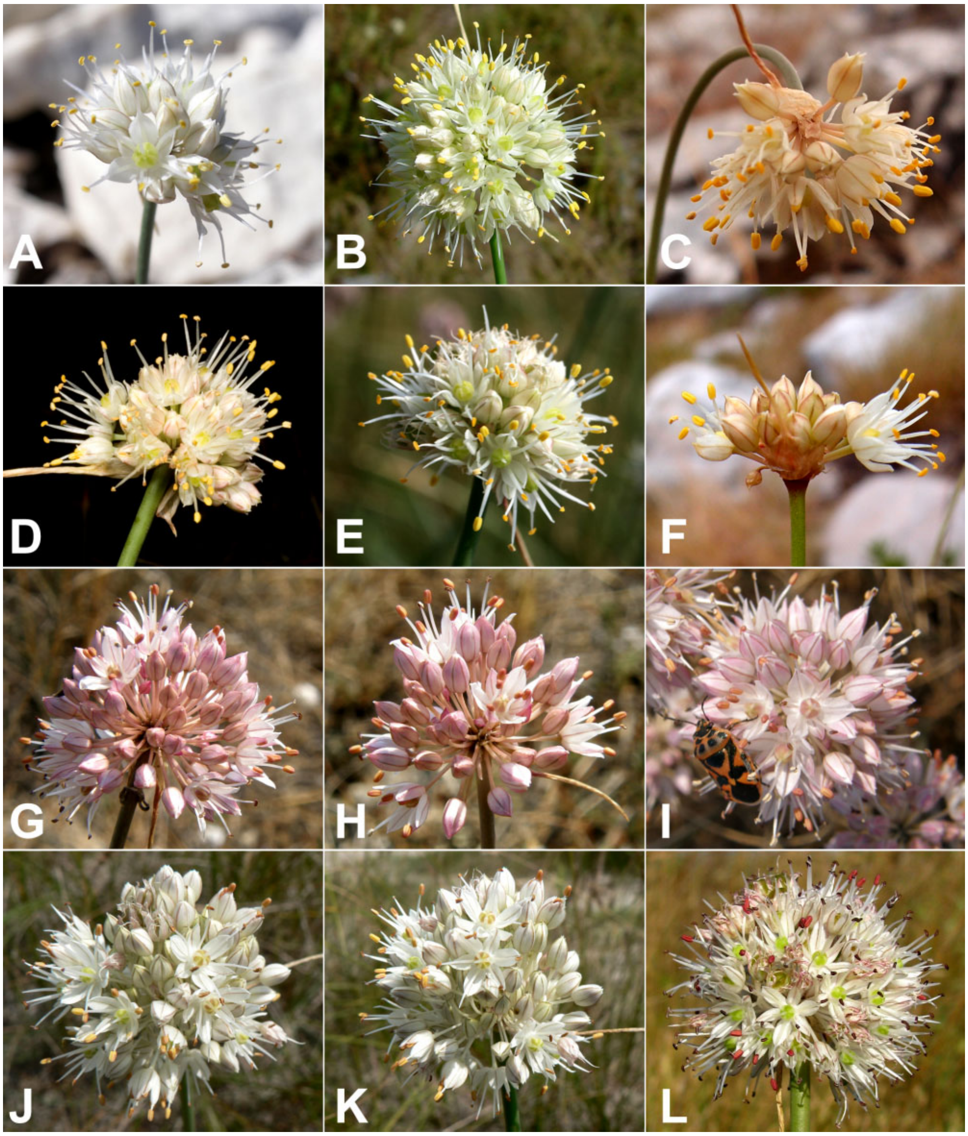

Figure 5. Umbels of Balkan species of the *Allium saxatile* group. A–F, *Allium horvatii*: A, CROATIA, Krk Island, Baška, close to *locus classicus*, 8.ix.2012 (by S. Bogdanović); B, CROATIA, Istria, Buzet – Brest, 15.ix.2009 (by J. Topić); C, F, CROATIA, Mt Poštak, 15.vii.2012 (by L. Borovecki-Voska); D, E, ITALY, Marche-Umbria, Mt Catria, 6.viii.2008 (by F. Barbadoro). G–I, ***Allium austrodanubiense***: BULGARIA, Varna Province, Banovo, 5.ix.2011 (by Ant. Petrova). J–L, *Allium savranicum*: J, K, RUSSIA: Rostov Oblast, the Don River delta, 10.viii.2005 (by O. Demina); L, UKRAINE: Zaporozhye, Khortitsa Island, 11.ix.2010 (by S. Odinets).

Plastid DNA sequence data

Normally, the *rpl32–trnL* spacer of all sequenced *Allium* spp. is *c*. 800 bp. However, all Caucasian and Crimean taxa (as well as *A. savranicum*) have a long, peculiar deletion of *c*. 400 bp that is extremely pronounced in the topology of the combined plastid DNA tree. All three Balkan taxa and those from the 'Siberian' ITS clade do not have this deletion.

The alignment of combined *trnL–trnF* and *rpl32–trnL* sequences from 71 accessions generated a matrix of 1236 characters divided into two partitions (*trnL–trnF* spacer, 1–350; *rpl32–trnL*, 352–1236), 122 of which are potentially parsimony-informative variable characters. The alignment of plastid DNA sequences is presented in Supporting Information Appendix S2.

Parsimony and Bayesian analysis yielded the same topology, but with lower BP than PP. For the Bayesian analysis, the substitution model TVM+I + G was chosen by AIC in Modeltest 3.7. Unweighted parsimony analysis of the 71 sequences resulted in five

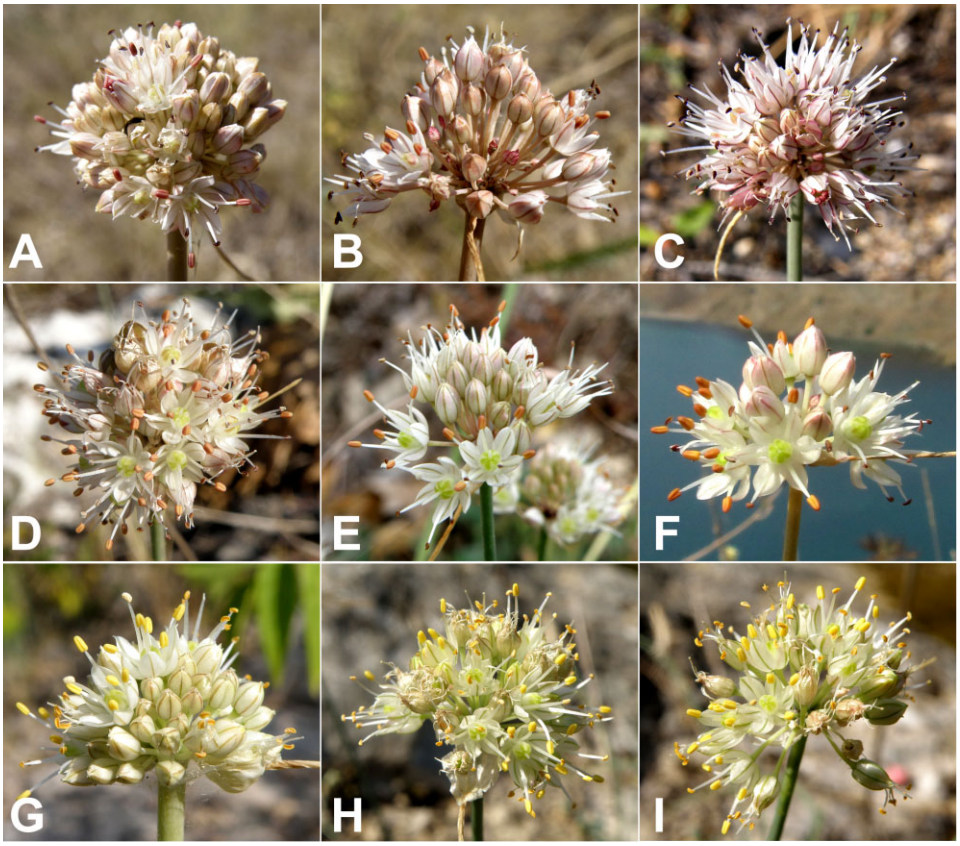

Figure 6. Umbels of the Crimean species of the *Allium saxatile* group (UKRAINE, Crimea). A–C, *Allium tarkhankuticum*: A, B, Lake Donuzlav, Novoozernoye, *locus classicus*, 15.viii.2008 (by A. Seregin); C, Yevpatoria – Pribrezhnoye, Lake Sasıq sand spit, 6.ix.2009 (by P. Yevseyenkov). D–F, ***Allium × agarmyschicum***: D, E, Mt. Bolshoy Agarmysh, *locus classicus*, 18.viii.2012 (by A. Seregin); F, Ordhonikidze, Mt Dzhan-Kutoran, 5.ix.2011 (by P. Yevseyenkov). G–I, *Allium marschallianum* (by A. Seregin): G, Balaklava, 17.viii.2008; H, I, Crimean Mts., Orlinoye, Maltash-Uzen, 25.viii.2008.

most parsimonious trees of 178 steps (CI = 0.8250; Fig. 10).

Three Bulgarian accessions of *A. austrodanubiense* (GL-107, GL-108, GL-109) form the sister group to all tested accessions from section *Oreiprason* including Central Asian species. Three accessions of *A. rubriflorum* form the sister group to the *A. saxatile* group including *A. obliquum* and *A. petraeum*. Four accessions of *A. horvatii* form the sister group to all Crimean and Caucasian taxa. All terminal plastid DNA lineages are identical with the terminal lineages from the ITS tree, except *A. schistosum* accessions, which are unresolved from other Caucasian *A. saxatile* + *A.globosum* accessions in plastid DNA analysis.

DISCUSSION

Phylogeographical assumptions

Our results show that the ITS tree explains well the possible phylogenetic relationships of the *A. saxatile* group, although plastid DNA fragments could help to interpret correctly the time and route of migrations.

We consider the Altai and adjacent mountain ranges of eastern Kazakhstan and north-western China as the centre of origin of the ancestral species (*A. 'pre-saxatile'*), because the sister clades of the monophyletic *A. saxatile* group are exclusively Central Asian (*A. talassicum*, *A. kokanicum*, etc.). Then, the 'Siberian' clade could be regarded as having retained ancestral morphological and genetic characters.

Such a clear separation of the ancestral 'Siberian' clade from the evolutionarily young 'European' clade in the *A. saxatile* group is similar to the situation in the *A. senescens* L. complex (*A.* section *Rhizirideum*) based on ITS sequences. The phylogenetic tree of this alliance by Friesen & Herrmann (1998), based on 166 random-amplified polymorphic DNA (RAPD) markers, showed that young and morphologically similar European taxa (*A. lusitanicum* Lam., *A. angulosum* L. and *A. incensiodorum* Radić) form a single clade. This

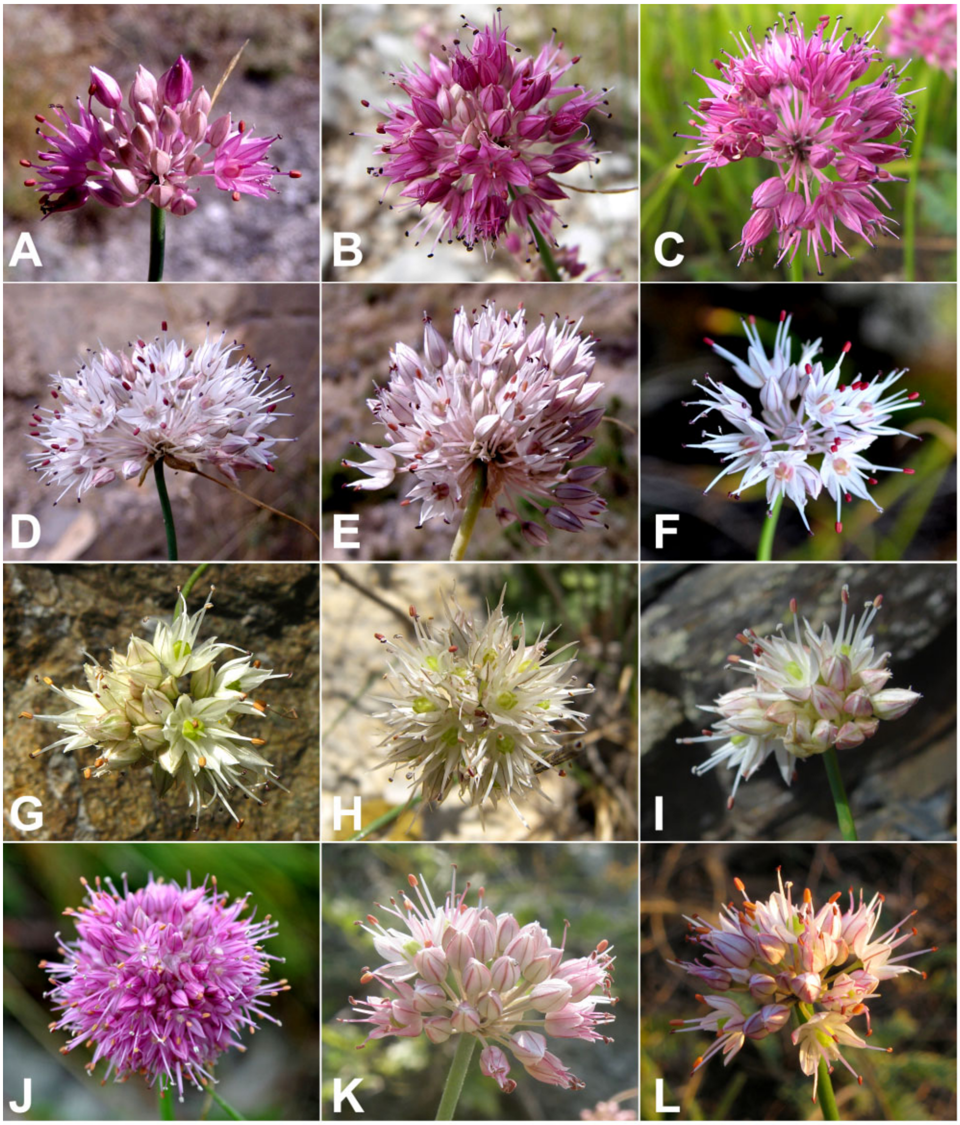

Figure 7. Umbels of species from the 'Caucasian' lineage of the *Allium saxatile* group. A–C, Purple-flowered morphotype of *Allium saxatile* (*A. globosum s.s.*) (RUSSIA, Stavropol Krai): A, Pyatigorsk, Mt. Goryachaya, 15.viii.2011 (by A. Ivanov); B, Pyatigorsk, Mt. Lysaya, 20.viii.2008 (by S. Banketov); C, Kislovodsk, Borgustansky Range, 5.viii.2008 (by S. Banketov). D–F, White-flowered morphotype of *Allium saxatile* (*A. saxatile s.s.*) (RUSSIA, North Ossetia) (by A. Ivanov): D, Mamison, 14.viii.2011; E, Unal, 12.viii.2011; F, the Ardon River basin, Chekhatsirtit Range, elev. 1800 m, 13.viii.2011. G–I, ***Allium schistosum*** (RUSSIA, Karachay-Cherkessia): G, Teberda State Reserve, 20.viii.2009 (by V. Onipchenko); H, Skalistyi Range, Dolina Narzanov valley, 11.viii.2007 (by S. Banketov); I, Arkhyz, Sofiyskoye Sedlo pass, elev. 2300 m, *locus classicus*, 6.viii.2008 (by A. Zernov). J–L, *Allium psebaicum* (RUSSIA): J, Karachay-Cherkessia, Urup District, Akhmat-Kaya Mts., elev. 930 m, not far from *locus classicus*, 4.viii.2011 (by A. Zernov); K, Krasnodar Krai, Black Sea Coast, Praskoveyevka, 24.viii.2013 (by A. Lyubchenko); L, Krasnodar Krai, Black Sea Coast, Sheskharis near Novorossiysk, 20.vii.2013 (by T. Vinokurova).

clade is sister to the more diverse Siberian lineage (*A. senescens*, *A. austrosibiricum*, *A. spirale* Willd. and *A. nutans* L.). Penetration and further speciation of the Siberian *A. 'pre-senescens'* may have the same age as the penetration of the Siberian/Central Asian *A. 'pre-saxatile'* to the Balkan Peninsula.

'SIBERIAN' CLADE

The final species composition of this clade was absolutely unpredictable for us because its two lineages include distinct species. One lineage consists of the yellow-flowered *A. petraeum* and two closely

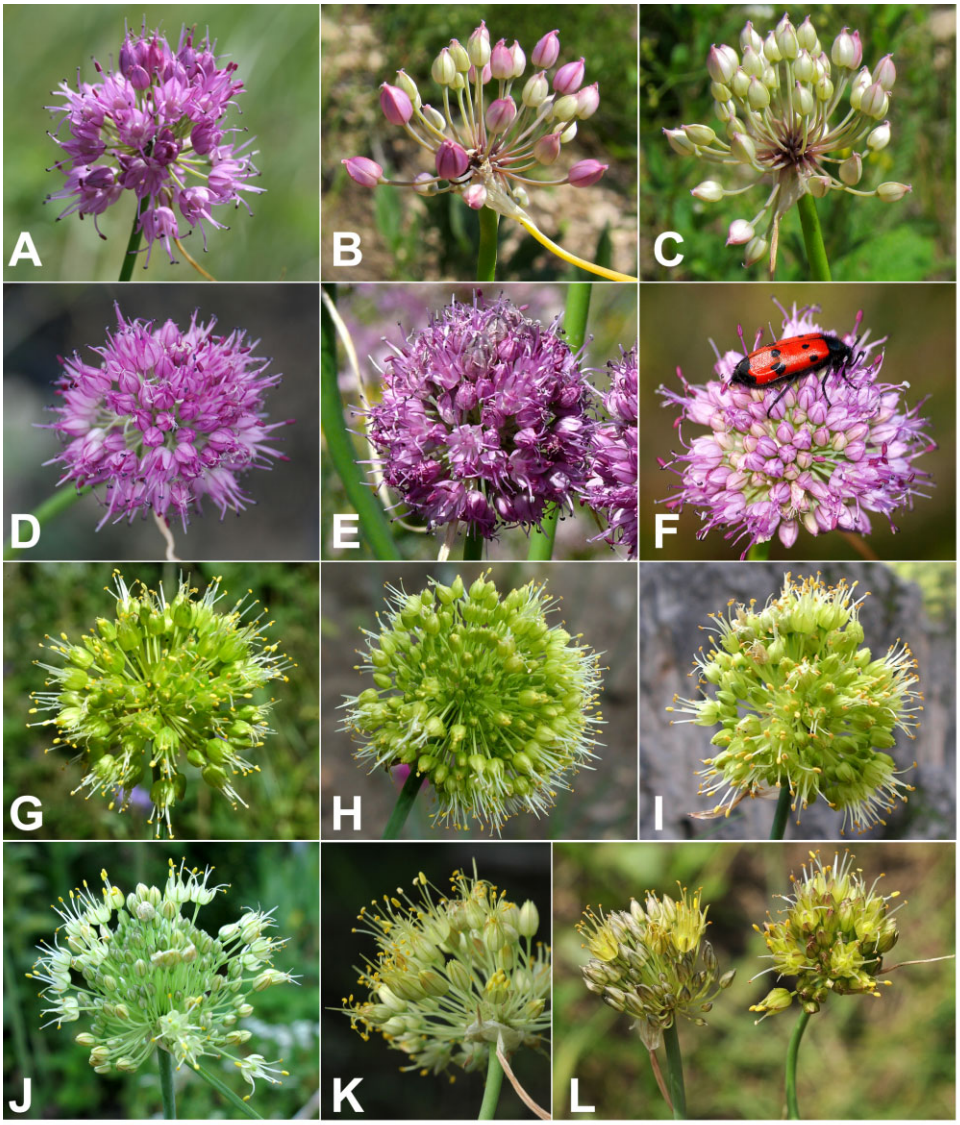

Figure 8. Umbels of species from the 'Siberian' clade of the *Allium saxatile* group. A–C, ***Allium cretaceum*** (RUSSIA, Tatarstan): A, Tatarskiye Shatrashany, 25.vii.2007 (by V. Prokhorov); B, C, Bavly, 12.vii.2011 (by E. Izmaylov). D–F, ***Allium montanostepposum***: D, RUSSIA, Altai Republic, Tyungur, viii.2008 (by N. Friesen); E, KAZAKHSTAN, East Kazakhstan Oblast, Ust-Kamenogorsk Reservoir, 15.viii.2009 (by E. Glazunova); F, KAZAKHSTAN, East Kazakhstan Oblast, Glubokovsky distr., Kozhokhovo, viii.2013 (by E. Glazunova). G–I, *Allium obliquum*: G, KYRGYZSTAN, Küngöy Ala-Too, Grigoryevskoye gorge, elev. 2400 m (by V. Epiktetov); H, GERMANY, Osnabrück University Botanical Garden, origin: RUSSIA, Altai Republic, Lake Teletskoye (by N. Friesen); I, ROMANIA, Cluj County, Trascau Mts., Cheile Turzii, v.2008 (by D. Turtureanu). J–L, *Allium petraeum*: J, RUSSIA, Moscow, garden, 15.vii.2012, origin: KAZAKHSTAN, Zhetyzhol Range (by Y. Pirogov); K, KAZAKHSTAN, Almaty, garden, 5.v.2009, origin: KAZAKHSTAN, Almaty Oblast, Aykharly Pass (by V. Epiktetov); L, KAZAKHSTAN, Almaty, garden, 14.vi.2013, origin: Eastern KAZAKHSTAN (by V. Epiktetov).

related species, rose-flowered *A. dshungaricum* and *A. kirilovii* with white, rose and yellowish flowers. The second lineage includes the robust yellow-flowered *A. obliquum* and two evidently young purple-flowered species, *A. montanostepposum* and *A. cretaceum*. At least three species from the 'Siberian' clade (*A. dshungaricum*, *A. montanostepposum* and *A. cretaceum*) were formerly merged in '*A. globosum*' (Vvedensky, 1935; Friesen, 1988).

Allium obliquum is a large plant with flat leaves up to 2(–3) cm wide and yellow flowers; for a long time, it was not considered to be a member of section

Table 1. Summary of phylogenetic analysis of the *Allium saxatile* group from Modeltest and maximum parsimony (MP) analysis of separate and combined datasets (AIC, Akaike information criterion; CI, consistency index; RI, retention index)

	ITS	*trnL–trnF*	*rpl32–trnL*	Combined *trnL–trnF* + *rpl32–trnL*
No. of included accessions	91	71	71	71
No. of included characters	651	350	886	1236
No. of constant characters	455	318	768	1093
No. of variable characters	196	33	120	143
No. of potentially parsimony-informative sites	139	30	101	122
No. of trees	2045	60	2	5
No. of steps (tree length)	290	39	144	178
CI	0.8069	0.8462	0.8611	0.8250
RI	0.9630	0.9676	0.9654	0.9568
Model selected by AIC	TVM+G	K81uf+G	HKY+G	TVM+I + G

Oreiprason (Hermann, 1939; Kamelin, 1973). It was widely distributed in Eurasia in previous times, but its current range consists of three fragments: (1) Romania and western Ukraine; (2) the southern Urals; and (3) south-western Siberia, Altai and the mountains of Central Asia (see maps by Alexeev, 1967; Friesen, 1988, 1995; Chukhina & Sinitsyna, 2005). There are a few collections from the 19th and early 20th centuries from other localities of European Russia: Penza, Novocherkassk, Surgut (Samara Oblast), Buzuluk and Buguruslan (MW, LE), where *A. obliquum* is now apparently extinct (Seregin, 2007b).

The other yellow-flowered species, *A. petraeum*, has terete leaves and is more similar to an 'average' habitus of the *A. saxatile* group. It is unexpectedly close to the slender rose-flowered *A. dshungaricum*.

Allium montanostepposum and *A. cretaceum* are closely related species, formerly merged into the Euro-Siberian '*A. globosum*'. Their separation is most probably connected with the last glacial maximum. The Turgai Strait linked the periglacial west-Siberian Lake and the Aral Sea depression and formed a natural barrier which cut the distribution range of the common ancestor. The western descendant, *A. cretaceum*, became adapted to the specific conditions of calcic outcrops, whereas the eastern descendant, *A. montanostepposum*, prefers petrophytic steppe communities.

Some populations in Central Kazakhstan with intermediate morphological characters between *A. cretaceum* and *A. montanostepposum* have been found in the Ulutau Mts. and a few adjacent localities (Fig. 1). Plants collected west of Ulutau undoubtedly belong to *A. cretaceum*, but more eastern plants refer to *A. montanostepposum*. The Ulutau plants of *A.* cf. *cretaceum* (GL-117) could be interpreted as introgressive hybrids. Meanwhile, a plant from the northern Tarbagatai foothills in eastern Kazakhstan (AM-556), which was identified morphologically as *A.* cf. *montanostepposum*, is also clearly introgressed by *A. cretaceum* genes.

Almost the same phylogeographical results have been published previously by Franzke *et al*. (2004) for *Clausia aprica* (Stephan) Korn.-Trotzky (Brassicaceae), another Eurasian steppe plant. Based on ITS and plastid DNA sequences, they revealed a similar range split. Yin *et al*. (2010) detected similar patterns in plastid DNA variation within native populations of *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae). In particular, a clade consisted of accessions from Karagandy (Central Kazakhstan) and north-western European Russia (N22442, N22479) in the neighbor-joining (NJ) tree and had a sister lineage of two samples from the Chinese Altai (PKU101, PKU102).

When interpreted from the positions of large-scale glacial oscillations, these similar range splits of species of Brassicaceae have different age estimates. For instance, Yin *et al*. (2010) concluded that the isolation of *Arabidopsis* populations in Altai refugia could have been forced by late Pleistocene glaciations (*c*. 11 000–110 000 years ago), whereas Franzke *et al*. (2004) presumed an early Quaternary range split for *Clausia aprica* (i.e. *c*. 1.0 Mya).

Asian species of section *Oreiprason* require further morphological and molecular revision. The species from the 'Siberian' clade (i.e. *A. obliquum*, *A. petraeum* and *A. montanostepposum*) are genetically more diverse than any other European or Caucasian species (Figs 9, 10). This might point to further speciation with perhaps dozens of hitherto undescribed narrow endemics in mountainous areas of Central Asia. Here, we describe *A. kirilovii* as a new distinct species from Tianshan, which is an isolated

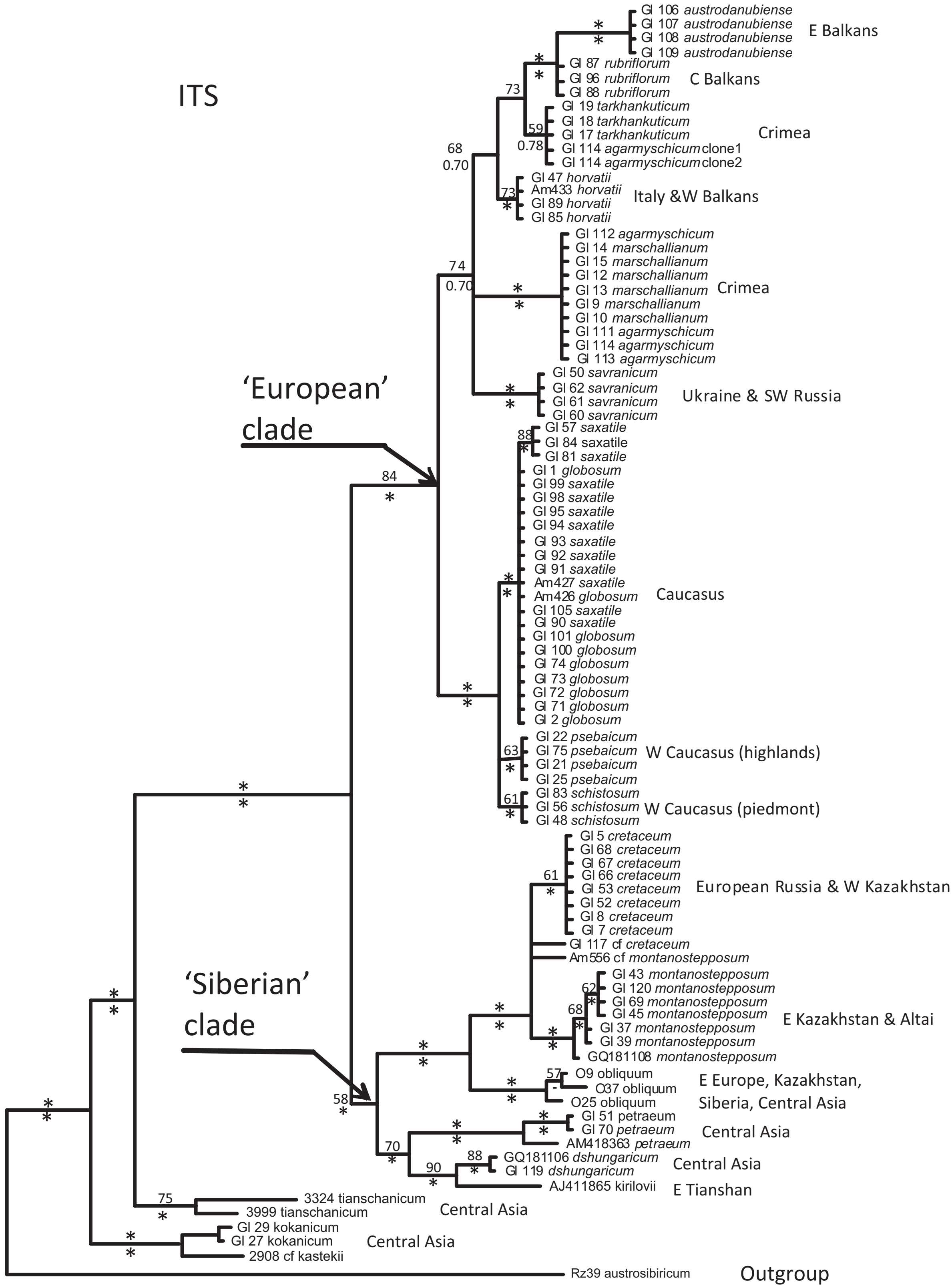

Figure 9. Internal transcribed spacer (ITS) Bayesian consensus tree of the *Allium saxatile* group. Numbers by nodes represent bootstrap support (100 replicates) and Bayesian probabilities. Bayesian probabilities > 0.95 and bootstrap support > 90% indicated with an asterisk (*).

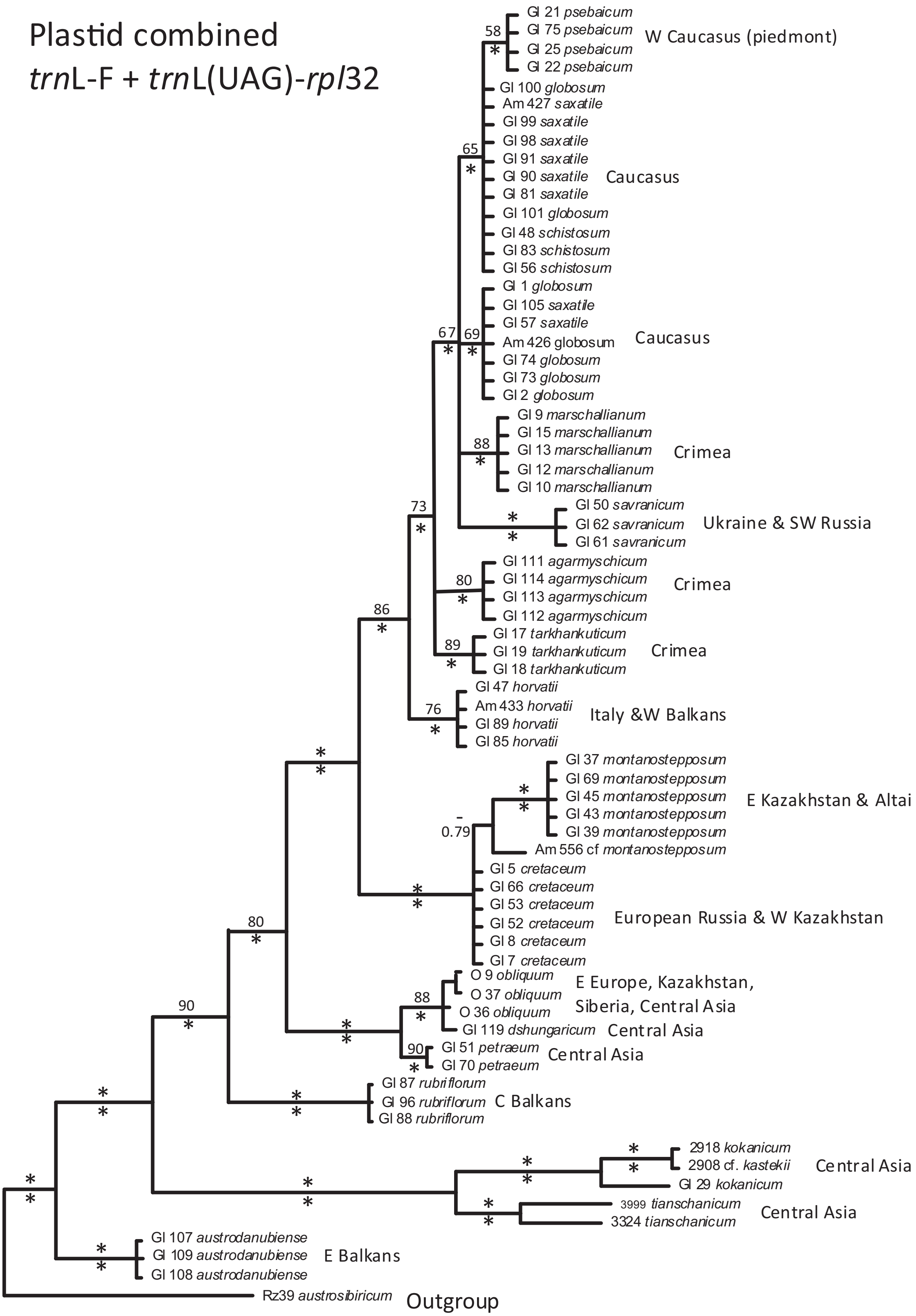

Figure 10. Plastid DNA Bayesian consensus tree of the *Allium saxatile* group from *trnL–trnF* and *rpl32–trnL* (UAG) sequences. Numbers by nodes represent bootstrap support (100 replicates) and Bayesian probabilities. Bayesian probabilities > 0.95 and bootstrap support > 90% indicated with an asterisk (*).

sister offspring of *A. dshungaricum*. Special attention should be paid to entangled *A. talassicum*. Fritsch & Friesen (2009) pointed out that, for a long time, *A. talassicum* was misinterpreted wrongly, following Vvedensky's concept (1935), and therefore a large alliance of diverse Central Asian species from section *Oreiprason* as yet remains un-named.

Outstanding examples of accurate molecular and morphological revisions of the extremely diverse Central Asian group are to be found in the articles of Gurushidze, Fritsch & Blattner (2008, 2010), in which species-level phylogenetic relationships of *A.* subgenus *Melanocrommyum* based on ITS and *trnL–trnF* sequences have been resolved for 100 species (including 20 recently described species). Probably, this is still the only large Central Asian group thoroughly researched with molecular phylogenetics.

Underestimated speciation within the Central Asian Mountains was revealed by RAPD data for Mongolian *Galitzkya* V.V.Botschantz. (Brassicaceae) by Wesche, Hensen & Undrakh (2006). For instance, *G. potaninii* (Maxim.) V.V.Botschantz. consists of at least two independent entities, whereas the more genetically uniform *G. macrocarpa* (Ikonn.-Gal.) V.V.Botschantz. has a clear spatial pattern in the distribution of local haplotypes. Another signal of hidden Central Asian taxonomic diversity can be found in the wild relatives of crop cereals. Jakob & Blattner (2006) reported extremely diverse plastid DNA in one of the Central Asian species of *Hordeum* L. (Poaceae). The TCS network of 88 global *Hordeum* plastid haplotypes suggests that *H. brevisubulatum* (Trin.) Link alone comprises nine revealed and at least 15 missing haplotypes!

'Balkan–Caucasian' (or 'European') clade

A long combined plastid DNA length is common for species of the 'Siberian' clade and two Balkan taxa, *A. rubriflorum* and *A. austrodanubiense* (*A. horvatii* has a shorter plastid DNA). This could be interpreted by a single ancient long-distance dispersal event: the Siberian/Central Asian *A. 'pre-saxatile'* with a 'long' plastid DNA once invaded the Balkan Peninsula. In this context, *A. rubriflorum* and *A. austrodanubiense* should be regarded as taxa which are still close to the ancestral *A. 'pre-saxatile'*.

There are five lineages in the 'Balkan–Caucasian' clade of the ITS tree: (1) the early diverging 'Caucasian' lineage; (2) the core 'Balkan' lineage (*A. austrodanubiense*, *A. rubriflorum* and *A. tarkhankuticum*) forming a sister clade to (3) *A. horvatii*; (4) *A. marschallianum*; and (5) *A. savranicum*. All of these species might have a common Balkan ancestor, although the topology of this tree does not necessarily reflect the relations of these lineages. The 'Caucasian' lineage is monophyletic and currently consists of three closely related and phylogenetically young species (see separate paragraph below).

Allium marschallianum (Crimean Mountains) and *A. savranicum* (steppe zone of the Ukraine and European Russia) are highly specialized and genetically uniform species. The latter is exclusively psammophytic (somewhat exceptional for the section) and widely distributed on alluvial sands of the major rivers from the Yuzhnyy Bug up to the Don (Fig. 1).

We consider allopatric geographical isolation to play a leading role in the radiation in the *A. saxatile* group. Thus, the complex system of the mountain ranges of the Balkan Peninsula harbours secluded areas for new species. Adriatic *A. horvatii* is apparently the closest relative of the core 'Balkan' lineage, which includes two species in the Balkan Peninsula (*A. rubriflorum* and *A. austrodanubiense*), and the Crimean endemic *A. tarkhankuticum*. *Allium horvatii* became one of the most successful species; it moved up to the Apennine Peninsula and now shows a circum-Adriatic distribution. It is locally common in some localities in the Dinaric Alps along the eastern Adriatic coast. *Allium rubriflorum*, an endemic species of south-eastern Serbia and western Bulgaria, and *A. austrodanubiense* apparently persisted in the region in which the ancestral *A. 'pre-saxatile'* with a long plastid DNA occurred. Adapted to rocky places, the highly specialized *A. austrodanubiense* invaded the plains of Dobrogea and the Bulgarian Black Sea coast from the Stara Planina Mountains.

The Balkan species (*A. horvatii*, *A. austrodanubiense* and *A. rubriflorum*) grow at a wide range of elevations. *Allium horvatii* can be found from sea-level up to 2000 m; *A. rubriflorum* prefers limestone cliffs in the lower belt, but reaches 500 m a.s.l. in Belava (Serbia); and *A. austrodanubiense* occupies the Black Sea coast and highlands of Mt Konjavsko and Mt Koru-Dere in Stara Planina (Bulgaria). We did not find genetic variation in ITS or the plastid DNA regions within these species; thus, there is no elevational speciation in the Balkan Peninsula in the *A. saxatile* group. A similar picture of prevalence of geographical speciation over elevationally paraphyletic isolation was detected by Frajman & Oxelman (2007) for the Balkan species of *Heliosperma* Rchb. (Caryophyllaceae) based on ITS and the *rps16* intron. The same is largely true for the diverse *Veronica chamaedrys* L. *s.l.* (Plantaginaceae; Bardy *et al.*, 2010) for which morphometric and genetic data [amplified fragment length polymorphism (AFLP), plastid DNA sequences] from the Balkan Peninsula showed little congruence with the formerly adopted taxonomy. As a result, two allopatric subspecies were recognized by Bardy *et al*. (2010), instead of six partly sympatric taxa. Kučera *et al*. (2008, 2010) recognized seven local western Balkan endemics in the *Cardamine maritima* Port. ex DC. group (Brassicaceae), strongly supported by ITS, plastid DNA and AFLP. They form three geographically justified ITS lineages along the Adriatic coast, irrespective of elevation. Similar results of underestimated local speciation have been reported by Lakušić *et al*. (2013) for the *Campanula pyramidalis* L. (Campanulaceae) complex in the western Balkans.

The Balkan species and subspecies of *Veronica* L. subgenus *Stenocarpon* (Boriss.) M.M.Mart.Ort., Albach & M.A.Fisch. (Plantaginaceae) show large congruence in the results obtained from the chalcone synthase intron, ITS, the plastid *rpoB–trnC* spacer and the *trnL–trnL–trnF* region. This phylogenetic analysis was also supported by AFLP fragments (Albach *et al*., 2009). In *Soldanella* L. (Primulaceae), an exclusively high-mountain genus, the whole Balkan lineage (*S. chrysosticta* A.Kress, *S. rhodopaea* F.K.Meyer and *S. pindicola* Hausskn.) displays no ITS variation at all, but was readily separated in an analysis of 731 polymorphic AFLP fragments (Zhang, Comes & Kadereit, 2001). These species probably do not merit taxonomic recognition.

Thus, the Balkan Peninsula harbours places for the diversification of local endemics. These species usually form monophyletic lineages with variable ITS and plastid DNA fragments composed of a few closely related and genetically homogeneous species. These patterns were revealed independently in *Heliosperma*, *Veronica*, *Cardamine*, *Campanula* and the *A. saxatile* group.

Two colonization events in the Crimea

The Crimea is an area which was colonized by two related species, *A. tarkhankuticum* from the core 'Balkan' lineage and the early diverging *A. marschallianum* from the large 'SE European' clade. These species have different ecological preferences and ranges. Younger *A. tarkhankuticum* is confined to the western side of the Crimean peninsula and grows in petrophytic steppes dominated by *Festuca* L. or *Stipa* L., whereas *A. marschallianum* is a plant of rock crevices widely distributed in the Crimean Mountains (Fig. 4). Undoubtedly, *A. tarkhankuticum* arrived to the Crimea considerably later than did *A. marschallianum*.

Describing *A. tarkhankuticum* as a new species, Seregin (2012) paid attention to plants from Mt Bolshoy Agarmysh (north-eastern edge of the Crimean Mountains). Two morphotypes, i.e. *A. marschallianum* and a rose-flowered *Allium*, not identical to *A. tarkhankuticum*, were collected in this locality. Seregin (2012) presumed the second morphotype to be an undescribed narrow endemic species.

In August 2012, Seregin collected extensive material on Mt Bolshoy Agarmysh and made photographs *in situ*. In the ITS tree, initial samples of *A.* × *agarmyschicum* combined with *A. marschallianum*, whereas both clones merged with *A. tarkhankuticum*. This is clear evidence of a hybrid origin of Agarmysh plants. Moreover, plastid DNA sequences unambiguously pointed to *A. tarkhankuticum* as the maternal species.

Once established on Mt Bolshoy Agarmysh, a population of *A. tarkhankuticum* was strongly influenced by the pollen rain of abundant *A. marschallianum*. As a result of the permanent presence of diaspores of pure *A. marschallianum*, both morphotypes are recognizable, i.e. *A. marschallianum* with yellow young anthers and hybrids with tawny anthers (typically, *A. tarkhankuticum* in western Crimea has brown, brick red or almost violet anthers). Thus, we describe here *A.* × *agarmyschicum* as a new interclade hybrid. A similar plant with tawny anthers was photographed near Feodosia by P. Yevseyenkov (Fig. 6). This locality is situated 25 km away from Bolshoy Agarmysh, within the range of *A. marschallianum*. Intermediate plants should be looked for in other localities of the Crimean foothills where both parents occur.

Currently, only a few scattered phylogeographical studies have involved Crimean plants, and they draw a complicated picture of relations of the Crimean flora. For instance, Gussarova *et al*. (2008) revealed that both ITS and plastid DNA fragments of the Crimean endemic *Euphrasia taurica* Ganesch. ex Popl. (Orobanchaceae) display a close relationship to the Caucasian *E. petiolaris* Wettst. Both species are geologically young and genetically similar. Peterson *et al*. (2009) studied the molecular phylogenetics of selected species of *Gagea* Salisb. (Liliaceae *s.s.*) based on ITS sequences. In the type section, the Crimean diploid lineage includes at least one Caucasian species, *G. helenae* Grossh. Kadereit *et al*. (2007) detected that the external transcribed spacer (ETS) region of an undescribed Crimean taxon of *Salicornia* L. (from the diploid *S. 'crassa'* group, Amaranthaceae) is similar to plants from inland Turkey, but overall the distribution of this lineage remains obscure, because of a lack of collections.

Demesure, Comps & Petit (1996) studied and recorded two exclusively Crimean plastid DNA haplotypes of *Fagus sylvatica* L. *s.l.* (Fagaceae) which are completely absent in Europe (Caucasian beeches known to occur in the Crimea were not sampled for this article). King & Ferris (1998) revealed that the only tested Crimean plastid DNA haplotype of *Alnus glutinosa* (L.) Gaertn. (Betulaceae) is present in

Georgia and widely distributed in north-eastern Turkey.

In a large-scale study, Trewick *et al*. (2002) sequenced one sample of the polyploid fern *Asplenium ceterach* L. (Aspleniaceae) from the Crimea, and this haplotype was referred to the tetraploid race which is widely distributed from Spain to Pakistan, but completely absent in the Balkan Peninsula. Diametric patterns of plastid DNA haplotype distribution were revealed by Dvořáková, Fér & Marhold (2010) for *Hordelymus europaeus* (L.) Jessen ex Harz (Poaceae), a perennial grass. The Crimean haplotype of this species is extremely specialized with no obvious relations in Europe, Turkey or the Caucasus (but somewhat similar to a haplotype represented by a single accession from Italy). A plastid DNA haplotype from the Crimean populations of another forest grass *Brachypodium sylvaticum* (Huds.) P.Beauv. belongs to the widely distributed European haplotype and not to a rarer haplotype known from the Caucasus and the Carpathians (Rosenthal, Ramakrishnan & Cruzan, 2008).

We have not found any genetically proven examples of Balkan relations to any Crimean species. Haplotypes widely distributed across Europe are present in the Crimean populations of *Asplenium ceterach* and *Brachypodium sylvaticum*. Obvious Caucasian influences were traced in *Euphrasia*, *Gagea* and *Alnus glutinosa*. Anatolian relations were detected for a single neglected early branching group of *Salicornia*, whereas, in *Hordelymus europaeus*, an endemic Crimean haplotype was discovered. Our data show that the closest genetically confirmed relative of the Crimean *Allium decipiens* Fisch. ssp. *quercetorum* Seregin occupies the forest-steppe region of eastern Europe (Seregin, 2007a; N. Friesen, unpubl. data).

Wulff (1926, 1927) insisted that the Balkan relations of the Crimean flora were over-estimated at the beginning of the 20th century. He regarded the 'Balkan route' (*via balcanica*) through a hypothetical land bridge as having only a minor influence on the modern Crimean flora. Moreover, following the recent checklists by Yena (2001, 2012), we could assume that, apart from *A. tarkhankuticum* and *A. marschallianum*, there are virtually no Crimean endemics of obvious Balkan origin. New phylogeographical studies of Crimean plants may reveal that the Balkan relations of the Crimean flora should be reassessed.

'Caucasian' lineage

We publish here the first data on the molecular phylogenetics of a lineage of vascular plants which are endemic to the Caucasus. Although dozens of endemic groups display an extreme radiation here (e.g. some sections of *Campanula*, *Symphyandra* A.DC., *Heracleum* L., *Galanthus* L., *Sorbus* L., etc.), phylogeographical studies are virtually absent for this region.

The Caucasus is an important centre of recent radiation in the *A. saxatile* group. The entangled picture of morphological and genetic patterns within the *A. saxatile–A. globosum* complex confirms ongoing modern speciation. Three doubtless young entities were found in the Caucasus: *A. schistosum* in the highlands of the western Caucasus; *A. psebaicum* in the foothills of the western Caucasus; and *A. saxatile s.l.* occupying the rest of the Caucasus.

Unexpectedly, we have to unite *A. saxatile* and *A. globosum* into a single species, although white-flowered (*A. saxatile s.s.*) and purple-flowered ('*A. globosum*') plants differ in clear distributional and ecological patterns. Purple-flowered plants are restricted to two regions of the Caucasus: (1) Pyatigorsk–Kislovodsk area of Stavropol Krai and adjacent localities in Karachay–Cherkessia and Kabardino–Balkaria; and (2) a few localities in central Georgia and South Ossetia (Fig. 3). The purple-flowered race occupies foothills and the lower mountain belt and usually prefers steppe communities rather than rocks. White-flowered plants are distributed more widely in the Caucasus and Transcaucasia, but occupy higher mountain belts (up to 2500 m a.s.l.). They prefer the rocky terrain of Armenia, Azerbaijan, Georgia, Dagestan and Chechnya (Fig. 3).

Apart from *A. schistosum* and *A. psebaicum*, plants from the Caucasus and Transcaucasia have almost identical ITS sequences. This means that *A. saxatile* and *A. globosum* are morphologically distinct, but this could not be recognized genetically. Nonetheless, inside the *A. saxatile–A. globosum* complex, there is a well-supported small paraphyletic group of *A. saxatile s.s.* from the northern slope of the Caucasus (Tsey, Kazbegi and Mashuk).

In plastid DNA, *rpl32–trnL* fragments have two variable positions, but they split the *A. saxatile–A. globosum* complex in an unexpected manner. Russian *A. globosum*, one Georgian *A. globosum* and some *A. saxatile* from the northern slope of the Caucasus form one group ('steppe group'), whereas all other *A. saxatile* and *A. globosum* from Georgia are members of the second group ('rock group'). The second group also includes *A. schistosum* and paraphyletic *A. psebaicum* accessions.

Thus, neither *A. globosum* nor *A. saxatile* could be interpreted as monophyletic entities. It should be mentioned that we failed to find clear morphological differences between Russian and Georgian plants (the latter are usually more robust and sometimes have dark yellow young anthers). We are observing a modern speciation process in the *A. saxatile–A. globosum* complex, but no taxonomic races could be recognized so far inside this group.

The revision of *Allium* by Kudrjashova (2006), part of the most recent Caucasian checklist, united *A. saxatile s.s.* and *A. globosum s.s.* for the first time since Marschall von Bieberstein (1819). Although these species were united as *A.* aggr. *saxatile*, with a consequential recognition of *A. saxatile*, *A. globosum* and *A. psebaicum*, this concept matches our molecular results.

Evolution of characters: flower colour

Flower colour in the *A. saxatile* group is diverse (Figs 5–8). We assume purple flowers to be the primary character, because purple-flowered plants appear in all lineages and are common in the related groups (*A. kokanicum*, *A. hymenorrhizum* Ledeb., *A.* section *Rhizirideum*, etc.). Species with purple tepals, e.g. *A. cretaceum*, *A. montanostepposum* and *A. saxatile*, usually have intense purplish or rose filaments and ovaries. The Balkan *A. rubriflorum*, regarded here as a species retaining ancestral plastid DNA, is usually purple-flowered, whereas other Balkan species are white-flowered (sometimes with purplish buds). In both the 'Caucasian' and core 'Balkan' lineages, there are species with two colour forms, namely *A. saxatile* and *A. rubriflorum*. Flower colour is not a taxonomically important character in these species, but it might be an evidence of ongoing speciation.

Species with white flowers are present in all lineages, but, in every case, they were clearly derived from the common ancestors with corresponding purple-flowered species. For instance, *A. kirilovii* is a specialized entity in the *A. dshungaricum* lineage, whereas young *A. schistosum* from the 'Caucasian' lineage is closely related to both *A. psebaicum* and *A. saxatile*. White-flowered species have white filaments and either green or purple ovaries. Veins on tepals might be purple or purplish even in one population. The independent origin of white-flowered paraphyletic species from widely distributed purple-flowered complexes in *Allium* section *Allium* was pointed out previously by Seregin (2004) for *A. scythicum* Zoz (derived from *A. regelianum* A.Becker) and *A. albiflorum* Omelczuk (from *A. rotundum* L. *s.l.*).

Yellow-flowered species (*A. petraeum*, *A. obliquum*) are members of the 'Siberian' clade. They are nested in lineages with purple- (or rose-) flowered species, and so evidently yellow flowers appeared here independently at least twice.

The scenario of recurrent evolutionary changes in flower colour within a lineage of closely related *Allium* spp. is somewhat exceptional. For instance, Friesen & Herrmann (1998) studied the *A. senescens* complex and discovered that a small group of sampled species with yellow and white flowers (*A. stellerianum* Willd. and *A. albidum* Fisch. ex M.Bieb. = *A. denudatum* F.Delaroche) forms a sister clade to a large lineage which includes merely a dozen purple-flowered species. In this case, elimination of purple flowers in the *A. stellarianum–A. denudatum* group is a synapomorphic character state.

CONCLUSIONS

We failed to separate *A. saxatile* M. Bieb. and *A. globosum* M. Bieb. ex DC. genetically. We have made great headway since the recognition of two species by Marschall von Bieberstein (1808) to the 13 species in this study (excluding two yellow-flowered species). Ironically, *A. saxatile*, a name used for merely all white-flowered plants of the group, and *A. globosum*, a name used for purple-flowered plants, seem to be conspecific. Indeed, this is a provisional solution. Some ITS variation and the map (Fig. 3) suggest that this complex could be split by employing data from other DNA regions, but the traditional morphological recognition of white-flowered *A. saxatile s.s.* and purple-flowered *A. globosum s.s.* in the Caucasus is unjustified.

There are still some other questions left unresolved in the *A. saxatile* group. For instance, *A. savranicum* is not morphologically uniform (Fig. 5). Geographical patterns in the distribution of violet and tawny anthers through populations of *A. savranicum* confirm further speciation in the species. The same is true for *A. psebaicum*, which includes, in current documentation, plants of various anther colours (Fig. 7).

Although *Allium* is one of the largest monophyletic genera of monocots, its diversity is definitely underestimated. We revealed that there is a lack of valid names for morphologically and genetically distinct diploid entities, at least in the *A. saxatile* group. The remaining species of section *Oreiprason* from Tianshan and adjacent areas are also pending precise phylogenetic analysis. Consequent revision of other *Allium* lineages based on genetic background and accurate study of live collections will help us to reveal the real diversity of the genus.

In order to understand the modern speciation of *Allium* and to examine the real taxonomic value of numerous existing names, the *Allium* community should focus its research on complete sectional and subgeneric revisions based on deep morphological, anatomical, karyological and molecular studies.

NOMENCLATURAL SUMMARY

A KEY FOR THE *ALLIUM SAXATILE* GROUP (HYBRIDS EXCLUDED)

1. Young anthers yellow 2
   Young anthers brown, brick red or violet 9
2. Filaments purplish; tepals uniformly rose; young stems spirally arching............ *A. psebaicum*
   Filaments white or yellowish; tepals white, yellowish or greenish, sometimes tinged rose in the upper part, with obscure or conspicuous veins, which might be green or purple; young stems erect............3
3. Robust plant 70–100(–130) cm high with flat leaves 7–20 mm wide; flowers yellow............*A. obliquum*
   Slender plants with caniculate or semicylindrical leaves 0.5–2.0(–3.0) mm wide; flowers white, tinged rose or green, sometimes yellow 4
4. Tepals yellow, with conspicuous green veins; filaments > 2.0 times longer than tepals............ *A. petraeum*
   Tepals white or purple, with obscure or conspicuous veins which might be green or purple; filaments usually 1.5(–2.0) times longer than tepals 5
5. Fully dehisced (empty) anthers yellow 6
   Fully dehisced (empty) anthers light brown to violet............8
6. Filaments not widened at base; tepals white or purple .... *A. rubriflorum*
   Odd filaments (those attached to inner tepals) widened at base; tepals whitish or yellowish (might be tinged rose or become rose after anthesis)............7
7. Tepals turn rose after anthesis .... *A. marschallianum*
   Tepals ± whitish or tinged green after anthesis, but might be tinged rose prior to or at anthesis ..... *A. horvatii*
8. Young anthers always yellow; filaments < 1.5 times longer than tepals; perianth cup-shaped; plants of stony habitats or steppes ....*A. austrodanubiense*
   (NB: yellow young anthers were reported for *A. saxatile s.s.* from Georgia by Pistrick, Akhalkatsi & Nakhutsrishvili, (2008), but has odd filaments widened at base)
   Young anthers usually light brown, rarely yellow; filaments twice as long as tepals; perianth stellate–campanulate; more robust plants of open sands .... *A. savranicum*
9. Filaments rose to purple............10
   Filaments white............13
10. Tepals lanceolate; odd filaments (those attached to inner tepals) slightly widened at base............ *A. saxatile* (including *A. globosum*)
    Tepals oblong; filaments uniformly not widened at base 11
11. Tepals light rose (with a purplish vein), acute .... *A. dshungaricum*
    Tepals purple, not distinctly acute............12
12. Pedicels 12–18 mm long at anthesis; inflorescence hemispherical at anthesis, loose (i.e. pedicels are readily visible and flowers do not touch each other)............ *A. cretaceum*
    Pedicels 7–9(–10) mm long at anthesis; inflorescence almost spherical at anthesis, dense (i.e. pedicels are hidden behind numerous flowers which touch each other)............ *A. montanostepposum*
13. All tepals distinctly attenuate .... *A. kirilovii*
    Tepals (especially outer) acute, but not attenuate............14
14. Ovary green (sometimes tinged purple) at anthesis............ 15
    Ovary purplish at anthesis 16
15. Young anthers light brown; pedicels two to three times longer than tepals; tepals white, sometimes rose in upper part............ *A. savranicum*
    Young anthers brick red (fully dehisced anthers could be yellow); pedicels almost equal to tepals; tepals white. .... *A. schistosum*
16. Tepals oblong; filaments 1.5 times longer than tepals; all filaments not widened at base......*A. tarkhankuticum*
    Tepals lanceolate; filaments twice as long as tepals; odd filaments (those attached to inner tepals) slightly widened at base .... *A. saxatile*

Taxonomic conspectus

See also Table 2 for a brief nomenclatural outline of accepted species names in major revisions and floras.

'Siberian' clade (species 1–6)

1. **Allium cretaceum** *N.Friesen & Seregin* ***sp. nov.*** *(Fig. 8)*

Type: RUSSIA: Volgograd Oblast, chalk outcrops near Stanitsa Kletskaya on the Don River, 12.viii.1964, *Yu.E. Alexeyev s.n.* (MW! – holotype, LE! - isotype).

A. confine Gand., Fl. Eur. 22: 83. 1890, nom. inval. [Art. 34.1].

A. wolgense Gand., Fl. Eur. 22: 83. 1890, nom. inval. [Art. 34.1].

A. globosum auct. p. p.

Description: Stems usually solitary or coupled, rarely three to five, attached to a short rhizome (sometimes forming loose patches), 20–50 cm high (NB: 10–20 cm high in extremely dry conditions of pure exposed chalk), 1.0–2.5 mm in diameter, terete. 'Bulb' 1–2 cm in diameter, (5–)7–10 cm long, almost cylindrical; outermost tunics brown to umber, coriaceous; inner tunics golden brown, shining. Leaves three to five (seven), filiform (or up to 2 mm wide in moist conditions), caniculate, sheathing the lower (1/2) 1/3 to 1/7 of the stem. Top leaves green at the beginning of anthesis, completely dry at the end of anthesis. Spathe bivalved, persistent; valves unequal, the longer (10–)20–35(–42) mm long with a long filiform beak, the shorter 4–7 mm long with a minute beak. Umbel lax, almost semiglobose at anthesis, (17–)22–30(–35) mm in diameter at anthesis, larger in fruiting. Number of flowers varies from 15–25 in xeric conditions to 100+ in moist conditions. Pedicels subequal at anthesis; flowers 1.5–3.0 times shorter than pedicels. Perianth cup-shaped; tepals slightly unequal, 4.0–4.5(–5.0) mm long, 1.5–2.0 mm wide, rose to purplish with a dark purple vein. Stamens long exserted; filaments filiform, purplish, not widened at base, 1.5 to almost 2.0 times longer than tepals. Anthers 0.9–1.0 mm long, brown to dark purple; fully dehisced anthers 0.8 mm, dark violet. Ovary purplish. Seeds black, angled, 3 mm long.

Diagnosis: From the closely related *A. montanostepposum*, it differs by longer pedicels (12–18 mm long at anthesis). As a result, the inflorescence of *A. cretaceum* looks loose (pedicels are easily visible and flowers do not touch each other) and hemispherical at anthesis. In addition, *A. cretaceum* almost exclusively prefers calcic substrates. From the Caucasian purple-flowered *A. saxatile* (including *A. globosum*), it differs with oblong tepals (vs. lanceolate), uniform filaments not widened at base [vs. odd filaments (those attached to inner tepals) slightly widened at base] and perianth shape (cup-shaped vs. stellate–campanulate).

Distribution: Russia, Kazakhstan (Fig. 1).

Paratypes (one per country subdivision): – RUSSIA: Bashkortostan: 45 km to E from Sterlitamak, the Sikara River, 15.viii.1960, *I.A. Gubanov & Yu.K. Dundin 5* (MW! LE! ex MOSM). – Volgograd Oblast: Kondrashi, the Ilovlya River, 23.viii.1999, *A. Sukhorukov s.n.* (MW!). – Voronezh Oblast: Kamenka, Polubyanskaya Balka, 15.vii.2002, *A.V. Berezhnoy s.n.* (LE! ex VOR). – Republic of Mordovia: 2 km to N from Selishchi, 1.viii.1988, *T.V. Tsaplenkova s.n.* (MW!, GMU!). – Nizhny Novgorod Oblast: Urazovka, 21.vii.1925, *P. Smirnow s.n.* (MW! × 2, LE!, GMU!). – Orenburg Oblast: 9 km to NW from Chesnokovka, Belye Gory Reserve, 29.vii.2002, *O.A. Legonkikh s.n.* (MW!). – Rostov Oblast: Stanitsa Ust-Belokalitvenskaya, the Kalitva River, 5.viii.1917, *N. Vlastova & N. Ivanova s.n.* (MW!). – Samara Oblast: Zhiguli State Reserve, Mount Zheludyak, 21.vii.1983, *S. Saksonov 618* (MW!, LE!). – Saratov Oblast: Nizhnyaya Bannovka, 5.viii.1963, *I.A. Gubanov s.n.* (MW! ex MOSM). – Tatarstan: 2 km to N from Tatarskiye Shatrashany, 2.vii.2003, *T.B. Silayeva et al. s.n.* (MW!). – Ulyanovsk Oblast: 8 km to SW from Praskovyino, the Arzhovat River, 19.vi.1991, *S. Majorov et al. s.n.* (MW!). – Chelyabinsk Oblast: Simsky Zavod [Sim], Sokolyata Range, 8.vii.1927, *S. Lipschitz 180* (MW!). – KAZAKHSTAN: West Kazakhstan Oblast: Uralsk, Belye Gorki, 4.vi.1903, *D. Yanishevsky s.n.* (LE!). – Aktobe Oblast: to NE from Uil, Akshatau Uplands, 15.vi.1965, *G.I. Tscherkassova s.n.* (MW! × 2; LE! × 2). – Kostanay Oblast: Naurzumsky State Reserve, between Naurzum-Karagay and Sypsyn-Agach, 19.vii.1935, *A. Demidova s.n.* (MW!).

Habitats: Herbaceous communities (usually steppe) on chalk, limestone or gypsum outcrops, rarely in saline habitats or sand.

Flowering period: July–September.

Chromosome number: $2n = 16$: – RUSSIA: Bashkortostan, Sterlitamak (Vakhtina & Kudrjashova, 1981 sub nom. *A. globosum* auct.).

Etymology: Species name refers to the most favourable (although not exclusive) habitat of the plant.

2. **Allium montanostepposum** *N.Friesen & Seregin* ***sp. nov.*** *(Fig. 8)*

Type: RUSSIA: Altai Republic, Western Altai, Ust-Koksa district, *c.* 65 km to E from Ust-Koksa, along the Katun River, 50°08′58″N, 86°27′49″E, elev. *c.*

Table 2. A review of the name applications in the *Allium saxatile* group

Species	*Locus classicus*	Govaerts *et al.* (2005–2014)	Vvedensky (1935)	Stearn (1980)	Omelczuk-Mjakushko (1979)	Kudrjashova (2006)	Seregin (2012)
A. cretaceum N.Friesen & Seregin	European Russia	*A. saxatile* auct.	*A. globosum* auct.	*A. saxatile* auct.	*A. globosum* auct.	–	*A. globosum* auct.
A. montanostepposum N.Friesen & Seregin	Russian Altai	*A. saxatile* auct.	*A. globosum* auct.	–	–	–	–
A. dshungaricum Vved.	E Kazakhstan	*A. saxatile* auct.	*A. globosum* auct.	–	–	–	–
A. kirilovii N.Friesen & Seregin	SE Kazakhstan	*A. saxatile* auct.	–	–	–	–	–
A. obliquum L.	Russian Altai	***A. obliquum***	***A. obliquum***	***A. obliquum***	***A. obliquum***	–	–
A. petraeum Kar. & Kir.	E Kazakhstan	***A. petraeum***	***A. petraeum***	–	–	–	–
A. austrodanubiense N.Friesen & Seregin	E Romania	*A. marschallianum* auct. & *A. saxatile* auct.	–	*A. saxatile* auct.	–	–	–
A. rubriflorum (Adamović) Anačkov, N.Friesen & Seregin	E Serbia	*A. marschallianum* auct. & *A. saxatile* auct.	–	*A. saxatile* auct.	–	–	–
A. tarkhankuticum Seregin	Ukraine, W Crimea	***A. tarkhankuticum***	*A. globosum* auct.	*A. saxatile* auct.	*A. saxatile* auct.	–	***A. tarkhankuticum***
A. × agarmyschicum N.Friesen & Seregin	Ukraine, E Crimea	*A. saxatile* auct.	*A. globosum* auct.	*A. saxatile* auct.	*A. saxatile* auct.	–	'Probably an undescribed narrow endemic species'
A. savranicum Besser	W Ukraine	*A. marschallianum* auct. & *A. saxatile* auct.	*A. saxatile* auct.	*A. saxatile* auct.	***A. savranicum***	–	***A. savranicum***
A. horvatii Lovrić	Croatia, Krk	***A. horvatii***, *A. marschallianum* auct. & *A. saxatile* auct.	–	***A. horvatii*** & *A. saxatile* auct.	–	–	–
A. marschallianum Vved.	Ukraine, Crimean Mts	*A. saxatile* auct.	***A. marschallianum***	*A. saxatile* auct.	*A. saxatile* auct.	–	***A. marschallianum***
A. psebaicum Mikheev	Russia, W Caucasus	***A. psebaicum***	*A. globosum* auct.	–	–	***A. psebaicum*** (ex *A.* aggr. *saxatile*)	***A. psebaicum***
A. schistosum N.Friesen & Seregin	Russia, W Caucasus	*A. saxatile* auct.	*A. saxatile* auct.	–	–	*A. saxatile* auct. (ex *A.* aggr. *saxatile*)	*A. saxatile* auct.
A. saxatile M.Bieb. (including *A. globosum* M.Bieb. ex DC.)	Azerbaijan	***A. saxatile***	***A. saxatile*** & *A. globosum*	–	–	***A. saxatile*** & *A. globosum* (ex *A.* aggr. *saxatile*)	***A. saxatile*** & *A. globosum*

–, not covered in the publication; **bold** type, accepted names.

830–1330 m, rocks in steppe, 13.vii.2008, *Neuffer, Hurka & Friesen s.n.* (OSBU 18724! – holotype & isotype, MW! – isotype, ALTB! – isotype).
A. globosum auct. p. p.

Diagnosis: Clearly related and similar to *A. cretaceum*, but usually more robust. A new species *A. montanostepposum* differs with shorter pedicels [usually 7–9(–10) mm long at anthesis]. As a result, the inflorescence of *A. montanostepposum* looks dense (pedicels are hidden behind numerous flowers which touch each other) and almost spherical. *Allium montanostepposum* is apparently absent on limestone or chalk.

Distribution: Russia, Kazakhstan, China (Fig. 1).

Paratypes (one per country subdivision): – RUSSIA: Altai Republic: the Katun River between the Dety-Kochek and the Turgunda Rivers, 13.vii.2008, *A.I. Shmakov et al. 1339* (OSBU 22278! ex ALTB). – Altaisky Krai: Beloglazovo–Shipunovo (Shatayevo), 4.vii.1913, *V. Reverdatto s.n.* (LE!). – KAZAKHSTAN: East Kazakhstan Oblast: Shemonaikha District, Rulikha–Rassypnoye, 12.vii.2011, *A.A. Kechaykin s.n.* (OSBU! 22277 × 2). – Pavlodar Oblast: Bayan-Aulsky District, Lake Boskul, 23.vii.1955, *N.N. Tzvelev et al. 1319* (LE!). – Akmola Oblast: to N from Lake Tengiz, 22.viii.1954, *E. Leontyeva 705* (LE!). – CHINA: Xinjiang: SW of Altai City, 4.viii.2005, *Chen et al. s.n.* (ALTB!, PE); to NE from Kektogai [= Fuyun], Mt Shi Zong Shan, 7.viii.2005, *Chen et al. s.n.* (ALTB!, PE).

Habitats: Steppe communities on stony slopes and rarely on saline ground.

Flowering period: July–August.

Chromosome number: $2n = 16$: – KAZAKHSTAN: Ust-Kamenogorsk (Vakhtina & Kudrjashova, 1981 sub nom. *A. globosum* auct.). – RUSSIA: Altaisky Krai, Lokot; Gilevo; Karpovka (Friesen, 1988 sub nom. *A. globosum* auct.). – Altai Republic, the Kucherla River (Friesen, 1988 sub nom. *A. globosum* auct.).

Etymology: Species name refers both to the habitats and distribution of the plant. Its distribution is restricted to the steppe communities throughout the mountain ranges of Kazakhstan Melkosopochnik, Russian Altai and northern Xinjiang.

Notes: Ogura *et al.* (2007) unexpectedly reported $2n = 14$ for *A. globosum* auct. from Tianshan, Xinjiang, China, but the correct identity of the voucher is in doubt. ITS of *A. saxatile* auct. GQ181108 sequenced from Ürümqi, Xinjiang, China, by Li *et al.* (2010) clearly belongs to *A. montanostepposum*, but we did not check any specimens from this locality.

1 × 2. **Allium cretaceum** *N.Friesen & Seregin* × **A. montanostepposum** *N.Friesen & Seregin*
Specimens studied: KAZAKHSTAN: Karaganda Oblast: Granite massif of Ulutau, SE slope, 14.vii.1955, *V. Grubov & N. Lyubarsky s.n.* (LE); Melkosopochnik, 18 km to SW from Karsakpay Station, 13.vi.1968, *Karamysheva 27* (LE).

Notes: The 'Ulutau hybrids' from Central Kazakhstan (Fig. 1) have intermediate morphological characters. Similar specimens from Karsakpay were named in the molecular analysis as *A.* cf. *cretaceum*, whereas plants from eastern Kazakhastan (northern foothills of Tarbagatai Range) were tagged as *A.* cf. *montanostepposum*. Evidently, both accessions refer to the hybrid complex *A. cretaceum* × *A. montanostepposum*. We did not establish a new nothospecies in this case, because the hybrids are not morphologically consistent and could only be correctly identified on a molecular basis.

3. Allium dshungaricum *Vved., Consp. Fl. As. Med. 2: 66. 1971*
Replaced name: A. globosum forma *dilute-roseum* Krylov, Fl. Zapadnoi Sibiri 3: 632. 1929.
*Lectotype (designated here):*KAZAKHSTAN: [former] Semipalatinsk Governorate, [former] Zaysansky Uyezd, vicinity of the Zaysan City, the Dzhemeni River gorge, stony slopes, 4.vii.1928, *P. Krylov & L. Sergiyevskaya s.n.* (TK!). We studied photographs of three syntypes cited in the protologue and deposited in Krylov's herbarium (TK). The designated lectotype is a set of seven dwarf plants from rocky habitats.
A. globosum auct. p. p.
A. saxatile auct. p. p.

Distribution: Kazakhstan, China (Fig. 1).

Habitats: Stony slopes of lower and middle mountain belts (Vvedensky, 1971).

Flowering period: June–July (Bajtenov & Kameneckaja, 1990).

Chromosome number: $2n = 16$: – KAZAKHSTAN: Sarybel in Dzhungarian Alatau (Vakhtina & Kudrjashova, 1981 sub nom. *A. talassicum* auct.).

Notes: Krylov (1929) recognized two distinct forms in *A. globosum*: the new forma *dilute-roseum* Krylov from the Tarbagatai Mts and Lake Zaisan and 'typical' forma *globosum* from Altai (i.e. *A. montanostepposum*). Krylov characterized his new forma as having 'tepals pale rose with a darker midvein' (vs. tepals rose-purple but greenish in the lower part with darker midvein in *A. montanostepposum*). Egorova (1977) supposed that *A. dshungaricum* is a *nomen invalidum* because Vvedensky did not cite the nomenclatural type, but in fact *A. dshungaricum* was published as a *nomen novum* for *A. globosum* forma *dilute-roseum* and based on the same type (A. N. Sennikov, pers. comm.).

Allium dshungaricum is usually treated in floras as *A. globosum* auct. (Vvedensky, 1935; Pavlov & Poljakov, 1958; Egorova, 1977) or *A. saxatile* auct. (Xu & Kamelin, 2000; Govaerts *et al*., 2005–2014). ITS of *A. petraeum* auct. GQ181106 sequenced from Xinjiang, China by Li *et al*. (2010) belongs to *A. dshungaricum*, but we did not check any specimens from this locality.

4. **Allium kirilovii** *N.Friesen & Seregin* ***sp. nov.***
Type: KAZAKHSTAN, Semirechye [Zhetysu], Kegensky District, vicinity of Sardzhas, on rocks in Tyute Gorge, 20.vii.1932, *S. Lipschitz 289a* (MW 22846x! – holotype), *S. Lipschitz 289* (MW 228460! – isotype), [*S. Lipschitz*] *289* (MW 228470! – isotype), *S. Lipschitz 2[89]* (LE! ex MW 228231 – isotype). – Holotype has collector's note 'flowers yellow', whereas specimen in LE annotated as 'flowers rose'. No difference present on dry material.

Description: Stems two to six, sometimes in loose patches of 15–20 stems, 20–37 cm high, 1–2 mm in diameter, terete. 'Bulb' 1.0–2.0(–2.5) cm in diameter, 3–7 cm long, almost cylindrical to fusiform; outermost tunics brown, coriaceous; inner tunics golden brown, shining. Leaves (2–)3–6, filiform, 1.0–1.2(–1.5) mm wide, caniculate, ciliate on margins, sheathing the lower (1/5–)1/4(–1/3) of the stem. Top leaves green at anthesis. Spathe bivalved, persistent; valves unequal, the longer 12–41 mm long with a long filiform beak, the shorter 3–7 mm long with a minute beak. Umbel compact, almost globose at anthesis, 20–27 mm in diameter. Number of flowers (15–)20–40(–70). Pedicels subequal at anthesis, (3–)4–6(–8) mm long; flowers equal to or shorter than pedicels. Perianth cup-shaped; tepals slightly unequal, (4.0–)4.1–4.4(–4.5) mm long, 1.5–2.0 mm wide, white with a purple (or greenish?) vein, distinctly attenuate on top, rose in buds. Stamens exserted; filaments filiform, whitish, not widened at base, 1.3 to 2.0 times longer than tepals. Anthers 0.9 mm long, light brown to dark brown; fully dehisced anthers considerably shorter and darker. Ovary purplish.

Diagnosis: This new species is the only one in the 'Siberian' clade with white flowers. From the closely related *A. dshungaricum* it differs with shorter pedicels, whitish filaments and tepals (not rose or purplish) and distinctly attenuate tepals.

Distribution: Kazakhstan, China.

Paratype: GERMANY: cultivated in Gatersleben, TAX 3376, 11.vii.2005, *anonymous* (Origin: CHINA, Xinjiang, Ürümqi valley around Tianshan Glaciological Station, *Juniperus* dwarf-scrub, 1992, *S. Miehe 8922*) (GAT 20124!). – Pictures of living plants could be accessed at http://apex.ipk-gatersleben.de/apex/f?p=265:1:14749158353070 under TAX 3376 (Taxonomic *Allium* Reference Collection of IPK, Gatersleben).

Habitats: On rocks and stony ground (for instance, amongst *Juniperus*).

Flowering period: June–August.

Etymology: Species is named after Ivan Petrovich Kirilov (Kiriloff, Kirilow) (1821–1842), an outstanding Russian explorer of the Dzhungarian flora.

Notes: ITS of this species AJ411865 (TAX 3376) was sequenced by Friesen *et al*. (2006) and reported under the name *A. talassicum* auct. An additional ITS accession was sequenced recently from the holotype to confirm identification (sample GL-166, not included in the analysis).

5. Allium obliquum *L., Sp. Pl.: 296. 1753 (Fig. 8)*
Lectotype: Herb. Linn. № 419.7 (LINN!). Designated by Friesen (1995).

Distribution: Romania, Ukraine, Russia, Kazakhstan, Kyrgyzstan, China, Mongolia (see maps by Alexeev, 1967; Friesen, 1988, 1995; Chukhina & Sinitsyna, 2005).

Habitats: Meadows, steppes, mountain slope forests, floodplains of mountain streams, shelves on rocky outcrops.

Flowering period: June–August.

Chromosome number: $2n = 16$: – RUSSIA: Novosibirsk, Akademgorodok (Friesen, 1988). – Altai Republic, Lake Teletskoye (Friesen, 1988). – Kemerovo Oblast, Novokuznetsky District (Friesen, 1988). – CHINA: Xinjiang, Tianshan (Ogura *et al*., 2007). – UNKNOWN ORIGIN (Levan, 1935; Komissarov & Tarasova, 1979).

6. Allium petraeum *Kar. & Kir., Bull. Soc. Imp. Naturalistes Moscou 15: 511. 1842 (Fig. 8)*
Lectotype: KAZAKHSTAN: In lapidosis montium Alatau ad fl. Lepsa, 1841, *Karelin & Kiriloff 2029* (LE! – lectotype, MW! – isolectotype, NY! – isolectotype, K! – isolectotype (000464500 & 000464501), etc.). Designated by Gubanov, Bagdasarova & Balandina (1998). Duplicates of collections by Karelin & Kirilow (1842) are widely distributed in world herbaria. Vvedensky (1935) indicated that 'type is in Leningrad'. This was interpreted by Gubanov *et al*. (1998) as a lectotype designation by Vvedensky, but, in fact, Gubanov, Bagdasarova and Balandina are the true authors of lectotypification in this case (Sennikov, pers. comm.).

Distribution: Kazakhstan, Kyrgyzstan, China.

Habitats: Stony slopes and rocks.

Flowering period: (May) June–July.

Chromosome number: 2*n* = 16: – KAZAKHSTAN: Tianshan, Alma-Ata (Vakhtina, 1965); Terskey Alatoo, Narynkol (Vakhtina & Kudrjashova, 1977).

'Balkan–Caucasian' ('European') clade (species 7–15)

7. **Allium austrodanubiense** *N.Friesen & Seregin* ***sp. nov****. (Fig. 5).*
Type: ROMANIA: Dobrogea, Distr. Tulcea, in graminosis petrosisve collis, Movila Hîrtop, prope pag. Mahmudia, solo calc., elev. 88 m, 27.vii.1949, *Nyárády s.n.* (GAT 7548! – holotype, CL 15439 – isotype).
A. saxatile auct. p. p.

Description: [Largely follows Zahariadi (1966) for the Romanian plants corrected against holotype and the photographs of the Bulgarian plants from SOM and SO.] Stems grouped in two or three or more, attached to a short rhizome, (10–)15–35 cm high (up to 50–80 cm as an exception), 1.5–2.5 mm in diameter, terete, glaucous. 'Bulb' 0.5–1.6 cm in diameter, 1.5–5.0 cm long (rarely longer), ovoid oblong to oblong lanceolate, with tapered tip; outermost tunics brown to reddish brown, membrano-coriaceous, older ones inconspicuously fibrous. Leaves three to five, filiform to linear, 1.0–1.5(–2.0) mm wide, caniculate, sheathing up to 1/3 of the stem. Leaves shorter than stem at anthesis; top leaves usually green at anthesis. Spathe bivalved, persistent; valves very unequal, the longer with a filiform beak, usually slightly exceeding the inflorescence (sometimes up to two to three times longer than the inflorescence). Umbel hemispherical at anthesis, 15–30 mm in diameter, almost globose in fruits. Pedicels subequal at anthesis, 5–10 mm long, up to 15 mm long in fruits; flowers 1.5–2.0(–3.5) times shorter than pedicels. Perianth cup-shaped; tepals unequal, inner 4.0–4.5(–5.0) mm long, 1.8–2.0 mm wide, subobtuse, outer 3.0–3.5(–4.0) mm long, 1.5–1.8 mm wide, acute, light purple or lilac in buds, whitish or pink at anthesis, with a purple vein (Bulgarian plants clearly purplish after anthesis). Stamens long exserted; filaments filiform, white, not widened at base, 1.5–2.0 times longer than tepals. Anthers 0.8–1.1 mm long, yellow, yellow–brown or orange; fully dehisced anthers 0.8 mm long, dark violet, almost black or red. Ovary purplish. Seeds black, angled, 2.8–3.2 mm long.

Diagnosis: From the closely related *A. savranicum*, it differs with yellow young anthers (vs. usually light brown), shorter filaments which are < 1.5 times longer than tepals (vs. filaments two-fold longer than tepals) and cup-shaped perianth (vs. stellate–campanulate). In addition, *A. austrodanubiense* grows in steppe communities or stony habitats (not sands). From the Caucasian *A. saxatile*, it differs with yellow young anthers (vs. brick red or violet), cup-chaped perianth (vs. stellate–campanulate) and longer pedicels.

Distribution: Bulgaria, Romania (Fig. 2).

Paratypes (one per locality): – BULGARIA: Varna Province: Vetrino, 30.viii.2002, *Ant. Petrova s.n.* (SOM!). – Dobrich Province: Kaliakra Reserve, 13.ix.1999, *Ant. Petrova s.n.* (SOM!); Balchik, Ovcharski Lager, 27.ix.1980, *D. Delipavlov s.n.* (SOA!); Kavarna, 24.viii.1993, *M. Filipov s.n.* (SO 96937!). – Gabrovo Province: Zdravkovets, 22.vi.2008, *Ant. Petrova s.n.* (SOM!). – Kyustendil Province: Konjavsko Mt., Smudertsi, 1.viii.1992, *Ch. Gusev s.n.* (SO 96081!). – Stara Zagora Province: Stara Planina, Koru-Dere, 28.ix.1971, *Cheshmedzhiev s.n.* (SOA!). – See also a list of localities in ROMANIA by Zahariadi (1966).

Habitats: Rocky slopes, cracks in rocks, especially on limestone.

Flowering period: (July) August–September (October).

Chromosome number: 2*n* = 16: – BULGARIA: Koru-Dere; Burgas Province, Sadovo (Tscheschmedjiew, 1973 sub nom. *A. saxatile* auct.). – ROMANIA: Turcoaia; Cheia (Draghia *et al*., 2013 sub nom. *A. saxatile* auct.).

Etymology: Species name refers to the distributional range of the species stretched along the southern bank of the Danube River.

Notes: Özhatay *et al*. (2012) recently reported *A. saxatile* auct. from Turkey in Europe (also with a chromosome number of 2*n* = 16). This record is supported with high-quality photographs showing white-flowered plants of apparently unknown identity.

8. **Allium rubriflorum** *(Adamović) Anačkov, N.Friesen & Seregin,* ***comb. nov.***

Basionym: A. saxatile var. *rubriflorum* Adamović, Rad Jugosl. Akad. Znan. Umjetn. 175, Mat.-Prirod. Razr. 44: 200. 1908.

Neotype (designated here): SERBIA: Southeast Serbia, 43°12′20.5″N, 22°29′28.1″E, Belava, vicinities of Staničenje village, 17.viii.2006, *G. Anačkov s.n.* (BUNS!). – The largest part of collections by Adamović is currently deposited in B and W. Also, some specimens were distributed to BP, IBF, K, LAU, M, F, G, GB, LY, MANCH and WU (Stafleu & Cowan, 1976). In addition, some Adamović specimens were traced in ZA, BEO and BEOU. Adamović lived and worked in Vienna for a long time, and we assumed that his material would be found in Vienna herbaria (WU and W). Unfortunately, we did not trace any relevant specimens there. Neither we, nor the curators of BP, BEO and BEOU, have detected any collections of *A. saxatile* var. *rubriflorum* either. Adamović (1908) indicated 'Belava and Sedlar' in SE Serbia as *locus classicus*. A single specimen from BP herbarium from the vicinity of Bela Palanka, dated 1885 and labelled as *A. saxatile* MB., does not match the protologue and therefore could not be the type. The designated neotype was collected in Belava and clearly belongs to the rose-flowered form.

A. saxatile auct. p. p.

Description: Stems attached to a short rhizome, 36–52 cm high, 1.5–2.5 mm in diameter, terete. 'Bulb' 0.6–1.5 cm in diameter, 4.5–5.0 cm long, almost cylindrical; outermost tunics brown, coriaceous; inner tunics golden brown, somewhat shining. Leaves 3–6 (–7), filiform, caniculate, sheathing the lower 1/7 of the stem. Top leaves almost dry at the end of anthesis. Spathe bivalved, persistent; valves unequal, the longer (25–)30–50(–65) mm long with a long filiform beak, the shorter 6–10 mm long with a short beak. Umbel almost globose at anthesis, 20–30 mm in diameter at anthesis, larger in fruiting. Pedicels subequal at anthesis 4.5–10 mm long; flowers (15–)45–55(–90), 1–1.5 times shorter than pedicels. Perianth narrowly campanulate (later widely open); tepals unequal, inner (4.0–)4.5(–5.0) mm long, 1.8–2.0 mm wide, almost subobtuse, outer (3.0–)4.0(–4.2) mm long, *c*. 1.6 mm wide, markedly acute; two distinct forms present, i.e. (1) with yellowish tepals and green veins; and (2) with rose tepals and purple veins. Stamens long exserted; filaments filiform, white, not widened at base, up to 1.5 times longer than tepals (3.8–6.2 mm long). Anthers 0.7–1.1 mm long, yellow; fully dehisced anthers 0.8 mm, dark yellow to light brown. Ovary greenish to yellow greenish. Seeds black, angled, *c*. 3 mm long.

Distribution: Serbia, Bulgaria (Fig. 2).

Habitats: Open limestone outcrops, xeric shrubs, cracked rocks on a barren substrate.

Flowering period: July–August.

Chromosome number: 2*n* = 16: – BULGARIA: Dragomanski Chepan (Tscheschmedjiew, 1973 sub nom. *A. saxatile* auct.).

Notes: Adamović (1908) mentioned that, on Belava (Sedlar, the second mentioned locality, is situated within Belava hill), his new variety with light rose flowers grows together with 'yellow-flowered' plants which he attributed to *A. saxatile* var. *saxatile*. According to our data, there is only one molecular entity in SE Serbia, for which we are using the valid name published by Adamović.

In Serbia, there are several known localities of the species in the south-eastern part. Most sites are located along the Nišava River – starting from Sićevačka gorge and almost to Dimitrovgrad (BUNS!, BEO! and Herbarium moesiacum!). In Bulgaria, *A. rubriflorum* is present in a single locality on Dragomanski Chepan near Dragoman (GAT!, MKNH!, SOA!, SOM!, SO!). Another specimen from western Bulgaria (Konjavsko Mt., *Gusev SO 96081*) is clearly nested within the *A. austrodanubiense* clade according to ITS sequences. Some specimens from Stara Planina (SOM!, SO!) should be reviewed once again.

9. Allium tarkhankuticum *Seregin, Phytotaxa 42: 11. 2012 (Fig. 6)*

Type: UKRAINE: Crimea, Saki District, 45°22′50″N, 33°06′30″E, S shore of Lake Donuzlav, W outskirts of Novoozernoye, petrophytic steppe (*Artemisia taurica*, *Festuca valesiaca*, *Agropyron cristatum*, etc.), elev. 10 m, 19.viii.2008, *Seregina s.n.* (MW! – holotype & isotype, LE! – isotype).

A. globosum auct. p. p.

Distribution: Crimea (Fig. 4).

Habitats: Petrophytic steppes on limestone dominated by *Stipa capillata*, *Festuca valesiaca*, *Agropyron cristatum*, *Artemisia* spp. It was also recorded twice in low fixed dunes of the Lake Sasıq sand spit.

Flowering period: August–September.

10. Allium marschallianum *Vved.* [‘marschalianum’]*, Fl. URSS 4: 184. 1935 (Fig. 6)*
Lectotype (designated here): Same as for *A. saxatile* M. Bieb. 1819, non M. Bieb. 1798.

A. saxatile M. Bieb., Fl. Taur.-Cauc. 3: 260. 1819, non M. Bieb. 1798.
Lectotype (designated here): ‘*Allium stellerianum* (*A. saxatile* M.). Ex Tauria. Herb. M. a Bieberst.’ (LE! – left plant only). – Vvedensky (1935) did not describe a new species, but made a reference on three descriptions, i.e. *A. saxatile* M. Bieb. 1808, *A. saxatile* M. Bieb. 1819 and *A. steveni* var. γ Ledeb. using *A. marschallianum* as *nomen novum*. – Above-mentioned specimen was labelled as ‘Typus’ by Tscholokashvili in the 1960s and as ‘LectoTypus *Allium marschallianum* Vved.’ by N. Fedoronchuk & L. Krytzka in 2001. Both choices were left unpublished.

A. saxatile auct. non M. Bieb. 1798: M. Bieb., Fl. Taur.-Cauc. 1: 264. 1808.

A. saxatile auct. p. p.

Distribution: Crimea (Fig. 4).

Habitats: Rocks and other stony habitats in steppe communities, xeric *Juniperus* and *Quercus* forests.

Flowering period: July–September.

Chromosome number: 2*n* = 16: – UKRAINE: Crimea, Ai-Petri; Karadag (Vakhtina & Kudrjashova, 1978).

Notes: In this revision, we regard *A. marschallianum* as an endemic species of the Crimean Mountains, i.e. in the original circumscription by Vvedensky (1935).

9 × 10. **Allium × agarmyschicum** *N.Friesen & Seregin* ***nothosp. nov.***
(Fig. 6) = ♀A. tarkhankuticum × ♂A. marschallianum
Type: UKRAINE: Crimea, 45°01′40″N, 35°01′55″E, vicinity of Staryy Krym, ascent to Mount Bolshoy Agarmysh from west along the ridge, petrophytic glades, elev. 640 m, 18.viii.2012, *Seregin T-1750* (MW! – holotype, B! – isotype, GAT! – isotype).

Diagnosis: Similar to *A. tarkhankuticum*, female parental species. Differs chiefly with lighter colour of anthers – dark yellow, tawny, or light brown within the same population (not brick red, brownish or purplish).

Distribution: Crimea.

Paratypes: – UKRAINE: Crimea: 45°01′40″N, 35°02′20″E, vicinity of Staryy Krym, ascent to Mount Bolshoy Agarmysh from west along the ridge, shelves on rocks with herbs on the edge of xeric oak forest, elev. 700 m, 18.viii.2012, *Seregin T-1763* (MW!, OSBU!); 45°01′45″N, 35°02′30″E, vicinity of Staryy Krym, summit of Mount Bolshoy Agarmysh, limestone outcrops covered by small debris, elev. 710 m, 18.viii.2012, *Seregin T-1764* (MW!).

Habitats: Petrophytic steppe communities on calcareous rocks on top and south slope of Mount Bolshoy Agarmysh.

Flowering period: August–September.

Etymology: Species name refers to the *locus classicus* of the nothospecies.

11. Allium savranicum *(Nyman) Oxner, Fl. URSR 1: 301. 1935 (Fig. 5)*
A. globosum var. *savranicum* Nyman, Consp. Fl. Eur.: 741. 1882.
Lectotype: UKRAINE: in arenosis Sawrań, s.d., *[Besser] s.n.* (KW 001001817!). Designated by Krytzka *et al*. (2000).

A. saxatile auct. p. p.

Description: Stems attached to a short rhizome, (23–) 30–40(–52) cm high, *c.* 2 mm in diameter. ‘Bulb’ up to 1.5 cm in diameter, 3–6 cm long, cylindrical to almost fusiform; outer tunics light brown, coriaceous, with parallel obscure fibres; remains of old outer tunics grey to almost black. Leaves 3–5(–6), shorter than scape, filiform, caniculate, sheathing the lower 1/3 (to 1/2) of the stem, dry at anthesis. Spathe bivalved, persistent; valves unequal, the longer 25–40(–70) mm long and distinctly longer than the umbel, the shorter ± equals pedicels. Umbel globose, 2.0–2.5 cm in diameter (up to 3.5 cm after anthesis), many-flowered; pedicels subequal at anthesis, flowers 1.5–2.5 times shorter than pedicels (up to 4.0 times after anthesis). Perianth stellate–campanulate; tepals subequal, 4.0(–4.5) mm long, tinged rose in buds, almost whitish later with a purplish vein; inner ones *c.* 1.0 mm wide; outer ones *c.* 1.5 mm wide. Stamens long-exserted; filaments filiform, white (rarely rose on tip), not widened at base, up to 2.0 times longer than tepals. Anthers 1.0(–1.2) mm long, light brown, brick red, or rarely almost dark violet; fully dehisced anthers 0.7 mm, dark brown to violet. Ovary greenish. Seeds black, angled, 3 mm long.

Distribution: Ukraine, Russia (Fig. 1).

Habitats: Various xeric communities on ancient alluvial sands of the major rivers – psammophytic steppes, pine forests margins, pioneer communities on shifting dunes.

Flowering period: July–September (October).

Notes: The details of the entangled nomenclatural history of *A. savranicum* 'Besser' were highlighted recently by Sennikov & Seregin (2014).

12. Allium horvatii *Lovrić, Oesterr. Bot. Z. 119(4–5): 569. 1972 ['1971'] (Fig. 5)*
Type: CROATIA: rupes montis Nedotiš (Q278) in promontorio Njilovac, E extremum insulae Krk, 44°58′N, 14°48′E, elev. 50 m, exp. E inclin. 70°, $CaCO_3$, 9.viii.1967, *A. Lovrić Bš-43/67* (ZA–holotype).
A. tergestinum Gand., Fl. Eur. 22: 83. 1890, nom. inval. [Art. 34.1].
A. saxatile ssp. *tergestinum* (Gand.) Bedalov & Lovrić, Comun. Soc. Stud. Veget. Alp. Orient. Dinar. 14: 122. 1978, nom. inval. [Art. 33.4].
A. saxatile auct. p. p.

Description: Stems attached to a short rhizome, (5–)10–35(–47) cm high, 0.9–1.5(–2) mm in diameter. 'Bulb' 0.4–0.8(–1) cm in diameter, 4.5–5.0 cm long, narrowly ovoid, clustered by 30–50 in compact patches; bulb tunics obscurely longwise stripped, outer tunics dark brown to black, inner tunics dark red–brown to grey–purple. Leaves 2–4(–7) to 6–15(–19) cm long, 0.5–1.8(–2) mm in diameter, filiform, sheathing the lower 1/6 of the stem, green at the end of anthesis. Spathe bivalved, persistent; valves unequal, the longer (10–)12–15(–18) mm long (sometimes distinctly longer). Umbel almost semiglobose at anthesis, 15–20 mm in diameter at anthesis, larger in fruiting. Pedicels 2–5 mm long at anthesis; flowers (2–)5–25(–29), slightly shorter than pedicels. Perianth campanulate to wide open; tepals (3.5–)4(4.5) mm long, 1–1.5 mm wide, yellowish-white with green veins, sometimes light pink with greenish veins. Stamens long exserted; filaments filiform, white, longer than tepals (3.5–5.2 mm long). Anthers 0.6–1.1 mm long, yellow; fully dehisced anthers 0.6 mm, dark yellow. Ovary greenish. Seeds black, angled, *c.* 3 mm long.

Distribution: Italy, Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, SW Serbia (Fig. 2).

Habitats: Rocks, screes, limestone cliffs; elev. 3–2000 m (Miceli & Garbari, 1980).

Flowering period: (June) July–September.

Chromosome number: 2*n* = 16: – ITALY: Umbria, Val Nerina (Miceli & Garbari, 1980 sub nom. *A. saxatile* auct.). – CROATIA: Krk Island (Bedalov & Lovrić, 1978). – MONTENEGRO: Mojkovac (Van Loon & Kieft in Löve, 1980 sub nom. *A. saxatile* auct.).

Notes: Allium horvatii was described as a local endemic of exposed saline maritime rocks (elev. 3–350 m a.s.l.) of Krk Island, Croatia. Lovrić (1971) compared his new species with a description of *A. saxatile* by Vvedensky (1935) based on plants from Ukraine and the Caucasus currently attributed to *A. savranicum*, *A. schistosum* and *A. saxatile*. Later, Bedalov & Lovrić (1978) recognized five taxa in the Dinaric Alps: *A. horvatii* (with three forms), *A. saxatile* ssp. *saxatile* and *A. saxatile* ssp. *tergestinum*. Although, morphologically, the Adriatic entity is not uniform with regard to the colour of the tepals (Fig. 5), number of flowers, length of spathe valves and general habit, we failed to find any consistent characters to separate *A. horvatii* from *A. saxatile* ssp. *tergestinum*, which is known to occur all around the Adriatic coast. No genetic variation was detected within the Adriatic entity from central Italy to Montenegro. Thereby, we recognize the westernmost entity of the *A. saxatile* group as a single species, and *A. horvatii* is its oldest valid name.

13. Allium psebaicum *Mikheev, Novosti Sist. Vyssh. Rast. 36: 96. 2004 (Fig. 7)*
Type: RUSSIA: Caucasus Borealis, Prov. Krasnodar, haud procul ab urb. Psebaji, 10.viii.1991, *A. Mikheev s.n.* (LE! – holotype).
A. globosum auct. p. p.

Description: Stems in small patches or solitary, attached to a short rhizome, 21–50 cm high, terete, distinctly glaucous. 'Bulb' 1.2–2.5 cm in diameter, 3–9 cm long, cylindrical to almost fusiform; outermost tunics brown, almost coriaceous; inner tunics golden brown, shining. Leaves 3–4, filiform, caniculate, sheathing the lower 1/10–1/4 of the stem. Leaves usually dry at anthesis. Spathe bivalved, persistent; valves unequal, the longer (12–)15–30(–60) mm long including a long filiform beak, much longer than the widened part of the valve, the shorter 3–7 mm long, without a beak. Umbel hemispherical at the beginning of anthesis, later globose, (19–)23–30(–32) mm in diameter. Number of flowers (20–)40–60(–?). Pedicels subequal at anthesis, *c.* 5–7 mm long; flowers ± equalling pedicels (pedicels elongating in fruits). Perianth stellate–campanulate. Tepals slightly unequal, inner 4.0–4.2(–4.5) mm long and 1.8–2.2 mm wide, outer (3.2–)3.6–4.0 mm long and 1.8–2.2 mm wide, rose, with a purplish vein. Stamens long exserted; filaments filiform, rose, odd ones (those attached to inner tepals) widened at base, with purple vein and whitish margins, *c.* 1.5 times longer than tepals. Anthers 0.7–0.8 mm long, violet to umber; fully dehisced anthers 0.35–0.40 mm long. Ovary purplish. Seeds black, angled.

Distribution: Russia, Abkhazia (Fig. 3).

Habitats: Cracks and shelves of rocky outcrops (gypsum, carbonate argillite and limestone), either exposed or in open xeric forests.

Flowering period: (July) August–September.

Notes: This species was described as a local endemic of the Psebay area (most probably from the gypsum outcrops of the Gerpegem Range). Psebay is the easternmost locality of the range of the western Caucasian taxon with rose filaments. Unfortunately, we did not study DNA samples from the *locus classicus* to check the identity of Psebay plants. Thereby, we are using this name for the whole western Caucasian entity which has no other name. This new broad species circumscription markedly differs from Mikheev's (2004) point of view, and so a new amended description was compiled. The only collection outside Russia originates from Abkhazia: Bzybsky Ridge, the Gegi River bank near waterfall, elev. 500 m, 27.vii.1930, *S.I. Petyayev s.n.* (LE). Although anthers are absent, it probably refers to *A. psebaicum*.

14. **Allium schistosum** *N.Friesen & Seregin* ***sp. nov.*** *(Fig. 7)*

Type: RUSSIA: Karachay-Cherkessia, Zelenchuksky District, Arkhyz branch of the Teberda State Reserve, the Kizgych River gorge, right bank of the river, 24 km above cordon, Sofiyskoe Sedlo pass, elev. 2570 m, shale scree, 6.viii.2008, *Zernov & Onipchenko 7011* (MW! – holotype).

A. saxatile auct. p. p.

A. ruprechtii auct. p. p.

Description: Stems usually solitary or coupled, attached to a short rhizome (sometimes forming very loose patches), (15–)18–30(–32) cm high, (0.5–)0.9–1.5(–1.9) mm in diameter, terete. 'Bulb' 0.5–1.2 cm in diameter, (2.5–)3.0–6.0(–8.0) cm long, narrow-cylindrical to fusiform; outermost tunics brown to dark brown, coriaceous, older ones inconspicuously fibrous; inner tunics golden brown, somewhat shining. Leaves (3–)4–5(–7), filiform, 0.3–1.5(–1.8) mm wide depending on habitat, caniculate, sheathing the lower (1/7–)1/6–1/4(–1/3) of the stem. Leaves often equalling stem at anthesis; top leaves usually green at anthesis. Spathe bivalved, persistent; valves unequal, the longer (8–)12–23(–29) mm long including a filiform beak (if present) shorter or equalling widened part of the valve, the shorter (3–)4–7(–12) mm long, without a beak. Umbel hemispherical at anthesis, (16–)20–25(–30) mm in diameter, almost globose in fruits. Number of flowers 10–40. Pedicels subequal at anthesis, 4–7(–8) mm long, up to 10 mm long in fruits; flowers 1.0–1.5 times shorter than pedicels. Perianth stellate–campanulate. Tepals slightly unequal, 1.8–2.3 mm wide, inner (4.0–) 4.5–5.6(–6.0) mm long, outer (3.7–)4.1–4.8 (–5.0) mm long, whitish, sometimes tinged rose, almost white in fruits, slightly rose along vein and on tip, with a greenish or purplish vein. Stamens long exserted; filaments filiform, white, odd ones slightly widened at base, *c.* 1.5–1.6 times longer than tepals. Anthers 0.9–1.3 mm long, tawny (rarely almost yellow) to violet or brick red; fully dehisced anthers 0.6–0.7 mm long, violet. Ovary greenish. Seeds black, angled, up to 3.3 mm long.

Diagnosis: From eastern Caucasian *A. saxatile s.s.*, it differs by its greenish ovary (vs. purple), tawny (rarely almost yellow) to violet or brick red anthers (vs. exclusively violet) and compact umbels which are generally whitish or tinged rose (vs. purplish). Tepals of *A. schistosum* usually rigid after anthesis.

Distribution: Russia, Abkhazia (Fig. 3).

Paratypes (one per country subdivision): – RUSSIA: Krasnodar Krai: Western Caucasus, Mount Aishkha III, 17.vii.1937, *V. Olyunin s.n.* (MW!). – Adygea: Caucasus State Reserve, E slope of Mount Oshten, Armyansky Pass, 20.vii.2004, *A.S. Zernov 3798* (MW!). – Karachay-Cherkessia: Karachay District, the Daut River gorge, 20.viii.2009, *V.G. Onipchenko s.n.* (MW!). – Kabardino-Balkaria: the Cherek Bezengiysky River basin, Karasu, 18.vii.1982, *Yu. Menitsky s.n.* (LE! × 2). – [No details, probably from ABKHAZIA]: Abgzha locality, 1700 m, 16.viii.1930, *Zakharova 612b* (LE!).

Habitats: Screes and rocky outcrops; from forest to alpine belt (elev. 1400–2800 m above sea level).

Flowering period: (June) July–August.

Chromosome number: 2*n* = 16: – RUSSIA: Karachay-Cherkessia, Teberda (Magulaev, 1976 sub nom. *A. saxatile* auct.); Dombay (Vakhtina, 1985 sub nom. *A. ruprechtii* auct.). – Kabardino-Balkaria, Terskol (Kudrjashova, 1988 sub nom. *A. saxatile* auct.).

Etymology: Species name refers to the habitats of the plant (i.e. screes).

Notes: This western Caucasian alpine entity was encountered for the Caucasus as a distinct species under the name *A. ruprechtii* auct. (Grossheim, 1928; Vakhtina, 1985; Kolakovsky, 1986; etc.). Kudrjashova (1988) correctly transferred *A. ruprechtii* to the synonymy of *A. saxatile* M.Bieb., because Boissier (1884) described his species from the central Caucasus, where the western Caucasian alpine entity is absent (cf. Sennikov & Seregin, 2015).

Typical *A. schistosum* grows in subalpine and alpine zones of the western Caucasus in Abkhazia, Krasnodar Krai, Adygeya Republic and a large part of Karachay-Cherkessia. Some plants from the Mount Elbrus area (Ullukam in south-eastern Karachay-Cherkessia, and the south-western corner of the Kabardino-Balkarian Republic) could not be identified for sure because of a lack of field notes on tepal colour and the absence of photographs from this area. We cautiously assume this sector of the Great Caucasus to be a zone in which both *A. schistosum* and *A. saxatile* grow together (Fig. 3) without large-scale genetic introgression. In the absence of relevant field data, we prefer not to overlap the ranges of the western Caucasian *A. schistosum* and *A. saxatile*.

Allium schistosum is undoubtedly present in Abkhazia on the southern slope of the Great Caucasus, but we tested no precise collections from this territory. Kolakovsky (1986) reported for Abkhazia only one species from the *A. saxatile* group (i.e. *A. ruprechtii* auct.) as a fairly rare plant of forest and alpine belts (elevation up to 2500 m). Although *A. psebaicum* was also collected in Abkhazia, the morphological description by Kolakovsky (1986) clearly refers to *A. schistosum*.

15. Allium saxatile *M.Bieb., Tabl. Prov. Mer Casp.: 114. 1798, nom. cons. prop., non Pall. 1776, nec M.Bieb. 1808, nec M.Bieb. 1819 (Fig. 7)*

Proposed conserved type (Sennikov & Seregin, 2015*):* AZERBAIJAN: İsmayıllı District, vicinity of Lahıc, above the forest belt, elev. 1800–2000 m a.s.l., 3.ix.1982, *E. Nikolaev 234* (LE!).

A. globosum M.Bieb. ex DC. in Redouté, Liliac. (Redouté) 3: table 179. 1807.

Neotype: RUSSIA (or GEORGIA?): ex Caucaso rutheno, s.d., *Bieb[erstein] s.n.* (LE!). Designated by Kudrjashova (2006, as 'lectotype').

A. globosum M.Bieb., Fl. Taur.-Caucas. 1: 262. 1808. nom. illeg. [Art. 53.1], non M. Bieb. ex DC. 1807.

A. caucasium Poir. in Lamarck, Encycl. Suppl. 1(1): 273. 1810, nom. illeg. [Art. 53.3], non *A. caucaseum* Ker Gawl. 1808.

Lectotype: Same as for *A. globosum* M.Bieb. ex DC. Designated by Sennikov & Seregin (2015).

A. caucaseum Ker Gawl. in Sims, Curtis's Bot. Mag. 28: pl. 1143. 1808, nom. illeg. [Art. 52.1].

Type: Same as for *A. globosum* M.Bieb. ex DC.? (no types traced in BM).

A. caucasicum M.Bieb., Fl. Taur.-Caucas. 3: 258. 1819, nom. illeg. [Art. 53.3], non *A. caucasium* Poir. 1810.

Lectotype: [icon] *A. paniculatum* in Sims, Curtis's Bot. Mag. 25: pl. 973. 1806. Designated by Sennikov & Seregin (2015).

A. gmelinianum Grossh., Fl. Kavk. 1: 209. 1928.

Lectotype: RUSSIA: Stavropolsky Krai, Nevinnomyssk, 24.vi.1890, *V. Lipsky s.n.* (LE!). Designated by Sennikov & Seregin (2015).

A. ruprechtii Boiss., Fl. Orient. 5: 264. 1882 ['1884'].

Type: RUSSIA: Northern Ossetia, ad moles glaciales Zei, *F. Ruprecht s.n.* (G-Boiss! – holotype).

Description: Stems usually solitary or coupled, attached to a short rhizome, (11–)15–30(–60) cm high, 1.0–2.2 mm in diameter, terete. 'Bulb' (0.5–)0.7–1.0(–1.4) cm in diameter, (2–)3–7(–10) cm long, narrow-cylindrical to narrow fusiform, rarely elongated into a long neck covering lower leaf sheaths; outermost tunics greyish brown to brown, papyaceo-coriaceous, older ones somewhat fibrous; inner tunics golden brown, somewhat shining. Leaves three to five (to eight), filiform, 0.3–0.8(–1.2) mm wide depending on habitat, caniculate, sheathing the lower (1/10–)1/7–1/4(–1/3) of the stem. Leaves usually twice as short as stems at anthesis; top leaves green or dry at anthesis. Spathe bivalved, persistent; valves unequal, the longer (7–)10–30(–50) mm long including a long filiform beak (a beak might be absent in some smaller individuals within populations of beaked plants), usually much longer than widened part of the valve, the shorter 3–6 mm long, without a break. Umbel hemispherical at the beginning of anthesis, later globose, (17–)20–26(–31) mm in diameter. Number of flowers (10–)15–50. Pedicels subequal at anthesis, (4–)5–8(–10) mm long; flowers 1.0–1.5 times shorter than pedicels. Perianth stellate–campanulate. Tepals unequal, inner (3.9–)4.5–5.8(–6.0) mm long and (1.2–)1.5–1.8(–2.4) mm wide, outer (4.0–)4.2–4.8 mm long and (0.5–)1.1–1.6(–1.8) mm wide. Two distinct forms present: (1) with whitish to rose tepals (sometimes almost purple on top) and purplish veins ('*A. saxatile*'); and (2) rose to dark purple tepals and darker veins ('*A. globosum*'). Stamens long exserted; filaments filiform, white or purple, odd ones (those attached to inner tepals) slightly widened at base, *c.* 1.25–1.50 times longer than tepals. Anthers 0.65–0.90 mm long, dark brown to violet; fully dehisced anthers 0.5–0.7 mm long. Ovary rose to purplish or greenish with purplish segments. Seeds black, angled.

Distribution: Russia, Georgia (including South Ossetia), Azerbaijan, Armenia (Fig. 3).

Habitats: Steppes, petrophytic communities, alpine meadows, screes, crevices.

Flowering period: (June) July–September.

Chromosome number: $2n = 16$: – RUSSIA: Kislovodsk (Zakirova & Vakhtina in Moore, 1977); Dagestan, the Okhotlit-Lau River headwaters (Magulaev, 1976); Pyatigorsk, Mount Mashuk (Kudrjashova, 1988 sub nom. *A. globosum*). – GEORGIA: Lechkhumi, the Ladtskhanura River gorge (Gagnidze & Chkheidze, 1975 sub nom. *A. globosum*). – ARMENIA: Kapudzhikh Mount (Pogosian, 1983); Idzhevan District, Mount Aggaya (Pogosian in Agapova *et al*., 1990); Bazum Range, Pambak (Pogosian, 1997); Zangezur Range, Mount Zandzaler (Pogosian, 1997 – probably misidentification, because *A. saxatile* is definitely absent in Zangezur according to Oganesian & Agababyan, 2001). – UNKNOWN ORIGIN: Caucasus (Vakhtina, 1965 sub nom. *A. globosum*). – Counts by Magulaev (1976) from the Upper Baksan River (sub nom. *A. saxatile*) and from Teberda (sub nom. *A. globosum*) could refer to another species.

Notes: The details of the nomenclatural story of *A. saxatile*, additional rarely used synonyms and the formal proposal to conserve the name *A. saxatile* M.Bieb., with a conserved type, against *A. saxatile* Pall. 1776 (superfluous and illegitimate early homonym) can be found in Sennikov & Seregin (2015).

Pistrick *et al*. (2008) reported yellow anthers for some *A. saxatile* collections from Georgia (GAT 6319!, 6320!, 6321!). In northern Caucasus, fully dehisced brown and dark yellow anthers are typical for *A. schistosum*, whereas *A. saxatile* has violet anthers.

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APPENDIX 1

New accessions of *Allium* from which 86 ITS sequences and 70 plastid DNA (*trnL–trnF* and *rpl32–trnL*) sequences were obtained, with corresponding voucher information and GenBank reference numbers. The information for each taxon is listed as follows: **Country**, **Isolate name** (ITS, *trnL–trnF*, *rpl32–trnL*) – locality – herbarium (voucher information) and/or botanical garden accession number. En-dash indicates the region was not sampled.

Allium × *agarmyschicum*: **Ukraine, Gl-111** (HG794215, HG794062, HG794132) – Crimea, Mt Bolshoy Agarmysch – MW (*Seregin 1764*, 18.viii.2012); **Gl-112** (HG794216, HG794063, HG794133) – *ibidem* – MW (*Seregin 1763*, 18.viii.2012); **Gl-113** (HG794217, HG794064, HG794134) – *ibidem* – MW (*Seregin 1763*, 18.viii.2012); **Gl-114** (HG794218, HG794065, HG794135) – *ibidem* – MW (*Seregin 1750*, *holotypus*, 18.viii.2012); **Gl-114-clone1** (HG794219, –, –) – *ibidem* – MW (*Seregin 1750*, *holotypus*, 18.viii.2012); **Gl-114-clone2** (HG794220, –, –) – *ibidem* – MW (*Seregin 1750*, *holotypus*, 18.viii.2012).

A. austrodanubiense: **Bulgaria, Gl-106** (HG794211, –, –) – Gabrovo distr., Zdravkovets – SOM 164218 (*Ant. Petrova*, 22.vi.2008); **Gl-107** (HG794212, HG794059, HG794129) – Black Sea Coast, Kaliakra Reserve – SOM 159122 (*Ant. Petrova*, 13.ix.1999); **Gl-108** (HG794213, HG794060, HG794130) – Black Sea Coast, Kovarna – SO 96937 (*Filipov*, 24.viii.1993); **Gl-109** (HG794214, HG794061, HG794131) – Konjavsko Mt, Smudertsi – SO 96081 (*Gusev*, 1.viii.1992).

A. cretaceum: **Kazakhstan, Gl-52** (HG794175, HG794033, HG794103) – Aktyubinsk Oblast, to NE from Uil, Akshatau – MW (*Tscherkassova*, 15.vi.1965); **Gl-67** (HG794183, –, –) – Mugodzhary, Alga – MHA (*Gogina & Volkovskaya*, ix.1984); **Gl-68** (HG794184, –, –) – Kustanay Oblast, Naurzumsky reserve – MHA (*Shreter*, 10.viii.1940); **Russia, Gl-5** (HG794150, HG794010, HG794080) – Volgograd Oblast, Ilovlinsky distr., Kondrashi – MW (*Sukhorukov*, 23.viii.1999); **Gl-7** (HG794151, HG794011, HG794081) – Ulyanovsk Oblast, Karsunsky distr., 3 km to S from Kotyakovo – MW (*Silayeva et al*., 23.vii.2003); **Gl-8** (HG794152, HG794012, HG794082) – Samara Oblast, Samaraskaya Luka national park, Mt Verblyud – MW (*Zherebyatyeva*, 6.ix.2002); **Gl-53** (HG794176, HG794034, HG794104) – Bashkortostan, Chuyunchi-Chupanovo plateau – MW (*Tavasiyev*, 24.vi.1972); **Gl-66** (HG794182, HG794039, HG794109) – Bashkortostan, Belebey – MHA (*Mazurenko*, 29.vi.1965).

A. cf. *cretaceum*: **Kazakhstan, Gl-117** (HG794221, –, –) – Melkosopochnik, 18 km to SW from Karsakpay Station – LE (*Karamysheva 27*, 13.vi.1968).

A. dshungaricum: **Kazakhstan, Gl-119** (HG794222, HG794066, HG794136) – 100 km to SE from Ayaguz station, Mt Okpekty – LE (*Karamysheva et al*. *5307*, 18.vii.1966).

A. globosum s.s.: **Georgia, Am-426** (HG794224, HG794067, HG794137) – Racha-Lechkhumi, Lajanuri valley – OSBU (*Lobin & Gröger*, 30.viii.2012); **Gl-100** (HG794208, HG794056, HG794126) – road to Tkibuli, Nakerala Pass – GAT 7551 (*Fritsch et al*., 21.vii.2006) & Accession TAX 6595 in Gatersleben; **Gl-101** (HG794209, HG794057, HG794127) – Lower Racha, Ambrolauri, Mukhli – GAT 7553 (*Pistrik & Akhalkatsi*, 14.vii.2002) & Accession TAX 6045 in Gatersleben; **Russia, Gl-1** (HG794148, HG794008, HG794078) – Karachay-Cherkessia, Zelenchuksky distr., Kobu-Bashi – MW (*Zernov & Anurov 6471*, 8.viii.2007); **GL-2** (HG794149, HG794009, HG794079) – Stavropol Krai, B. Nebesnaya – MW (*Valtsova et al.*, 8.viii.1968); **GL-71** (HG794187, –, –) – Karachay-Cherkessia, Urup River, Ilyich – MHA (*Gogina*, 7.ix.1976); **GL-72** (HG794188, –, –) – Karachay-Cherkessia, Khabezsky distr., Mt Dzhangura, elev. 1400 m a.s.l. – MHA (*Gogina*, 4.ix.1980); **GL-73** (HG794189, HG794042, HG794112) – Stavropol Krai, Pyatigorsk, Mt Mashuk – MHA (*Dayeva 311*, 27.viii.1966); **GL-74** (HG794190, HG794043, HG794113) – Stavropol Krai, Kislovodsk – MHA (*Dayeva*, 31.viii.1966).

A. horvatii: **Italy, AM-433** (HG794226, HG794069, HG794139) – Lazio, Monte Autore, elev. 1850 m a.s.l. – FR (*Simbruini*, 30.viii.1969); **GL-47** (HG794171, HG794029, HG794099) – Trieste Prov., San Dorligo della Valle, Val Rosandra – Accession 09-08-0026-10 in Osnabrück Univ. BG; **Montenegro, GL-89** (HG794198, HG794050, HG794120) – Orjen Mt. – BUNS (*Ančkov & Zlatković*, 27.viii.2006); **Slovenia, GL-85** (HG794195, HG794047, HG794117) – Primorsko, Senožeče – MHA (*Meyer 0250/3*, 24.viii.1964).

A. cf. *kastekii*: **Kazakhstan, TAX2908** (HG794231, HG794074, HG794144) – Küngöy Ala-Too, the Bolshaya Almaatinka River gorge – GAT 16618 (*Fritsch & Pistrick* 1999) & Accession TAX 2908 in Gatersleben.

A. kokanicum: **Kyrgyzstan, GL-27** (HG794165, HG794075, HG794145) – Pamir-Alay, Trans-Alay Range – OSBU 15781 (*Neuffer et al.*, 1.viii.2004); **GL-29** (HG794166, HG794024, HG794094) – Tianshan, Kyrgyz Ala-Too, Ala-Archa National Park near Bishkek – OSBU 15360 (*Neuffer et al.*, 8.viii.2004).

A. marschallianum: **Ukraine, GL-9** (HG794153, HG794013, HG794083) – Crimea, Chatyrdag, lower plateau, Mramornaya Cave – MW (*Yena*, 30.viii.2003); **GL-10** (HG794154, HG794014, HG794084) – Crimea, Sevastopol – MW (*Seregin T-233*, 6.ix.2002); **GL-12** (HG794155, HG794015, HG794085) – Crimea, S suburb of Sevastopol, Cape Fiolent – MW (*Seregin & Privalova T-445*, 11.ix.2003); **GL-13** (HG794156, HG794016, HG794086) – Crimea, Balaklava, Chembolo citadel – MW (*Seregin T-1161*, 17.viii.2008); **GL-14** (HG794157, –, –) – Crimea, Demerdzhi, yayla – MW (*Sokoloff*, 19.vii.1996); **GL-15** (HG794158, HG794017, HG794087) – Crimea, Karadag – MW (*Kamenskikh 8284*, 28.ix.2005).

A. montanostepposum: **Kazakhstan, GL-69** (HG794185, HG794040, HG794110) – Semipalatinsk Oblast, Kokpekty – MHA (*Dayeva 132*, 27.vii.1967); **GL-120** (HG794223, –, –) – Chingiz-Tau, 17 km to SE from Birchik – LE (*Vasilevich et al. 544*, 4.vii.1966); **Russia, GL-37** (HG794167, HG794025, HG794095) – Altai Republic, Ust-Koksinsky distr., 65 km to E from Ust-Koksa – OSBU 18724 (*Neuffer et al.*, 13.vii.2008); **GL-39** (HG794168, HG794026, HG794096) – Altai Republic, Ust-Koksinsky distr., 11 km to S from Tyungur – Accession 08-31-0009-20 in Osnabrück Univ. BG; **GL-43** (HG794169, HG794027, HG794097) – Altai Krai, Antoshikha – Accession 10-20-0015-20 in Osnabrück Univ. BG; **GL-45** (HG794170, HG794028, HG794098) – Altai Krai, Krasnoshchekinsky distr., Akimovka, Sopka Mursinka – Accession 10–20-0021-20 in Osnabrück Univ. BG.

A. cf. *montanostepposum*: **Kazakhstan, AM-556** (HG794227, HG794070, HG794140) – Tarbagatai Range, N slope, the Taldor River near Mündung – ALTB (*Kechaykin*, 25.vii.2011).

A. obliquum: **Russia, O-9** (HG794228, HG794071, HG794141) – Altai Republic, Teletskoye Ozero, Estube – GAT 17604 (*Friesen 7*, 22.vii.1991); **O-25** (HG794229, HG794072, HG794142) – Altai Krai, Soloneshnikovsky distr., the Shereta River headwaters – ALTB (*Shmakov et al.*, 25.vi.1997); **O-37** (HG794230, HG794073, HG794143) – Bashkortostan, Kraka Range – Accession 04-48-0022-70 in Osnabrück Univ. BG.

A. petraeum: **Kazakhstan, GL-51** (HG794174, HG794032, HG794102) – W foothills of Dzungarian Alatau, 5 km to N from Altyn-Emel pass – MW (*Kljuykov 41*, 16.viii.1979); **GL-70** (HG794186, HG794041, HG794111) – Taldy-Kurgan Oblast, Dzungarian Alatau, Toksanbay – MHA (*Kuklina & Konovalova*, 16.viii.1985).

A. psebaicum: **Russia, GL-21** (HG794162, HG794021, HG794091) – Krasnodar Krai, Tuapsinsky distr., Krivenkovskoye – MW (*Zernov & Firsanov*, 10.vii.1995); **GL-22** (HG794163, HG794022, HG794092) – Krasnodar Krai, Tuapsinsky distr., Arkhipo-Osipovka – MW (*Zernov & Firsanov*, 1.viii.1995); **GL-25** (HG794164, HG794023, HG794093) – Krasnodar Krai, between Lake Abrau and Lake Limanchik – MW (*Zernov*, 21.ix.1996); **GL-75** (HG794191, HG794044, HG794114) – Krasnodar Krai, Kabardinka – MHA (*Dayeva 7*, 30.v.1966).

A. rubriflorum: **Hungary** (cultivated), **GL-96** (HG794205, HG794053, HG794123) – ex Hort. Bot. Univ. Budapest – GAT 7525 (*anonymous*, 12.vii.1984) & Accession TAX 631 in Gatersleben; **Serbia, GL-87** (HG794196, HG794048, HG794118) – East Serbia, Niš, Sićevo Gorge – BUNS (*Ančkov*, 17.viii.2006); **GL-88** (HG794197, HG794049, HG794119) – East Serbia, Babušnica, Koritnička Gorge – BUNS (*Ančkov et al.*, 23.viii.2004).

A. savranicum: **Russia, GL-50** (HG794173, HG794031, HG794101) – Rostov Oblast, the Chir River, Khutor Demin – MW (*Pimenov 18*, 21.viii.2006); **GL-60** (HG794179, –, –) – Volgograd Oblast, Frolovsky distr., Vyezdinsky – MHA (*Sagalayev & Matveyev*, 25.viii.1994); **GL-61** (HG794180, HG794037, HG794107) – Volgograd Oblast, Frolovsky distr., between Padok and Pilnya – MHA (*Shantser &*

Polonskaya, 25.vii.1993); **Gl-62** (HG794181, HG794038, HG794108) – Volgograd Oblast, the Buzuluk River – MHA (*Sagalayev 14724*, 24.viii.1987).

A. saxatile s.s.: **Georgia, Am-427** (HG794225, HG794068, HG794138) – Imeretia, between Tskaltubo and Tsageri – OSBU (*Lobin & Gröger*, 30.viii.2012); **Gl-81** (HG794192, HG794045, HG794115) – Kazbegi distr., Daryalskoye Gorge – MHA (*Gogina 2139*, 15.viii.1966); **Gl-90** (HG794199, HG794051, HG794121) – Lechkumi, Tskhenistskali Gorge – GAT 7508 (*Pistrik*, 23.viii.2005) & Accession TAX 6222 in Gatersleben; **Gl-91** (HG794200, HG794052, HG794122) – Shotasmta – GAT 7510 (*Pistrik & Akhalkatsi*, 22.vii.2002) & Accession TAX 6059 in Gatersleben; **Gl-92** (HG794201, –, –) – Manglisi – GAT 7505 (*Pistrik*, 20.ix.2005); **Gl-93** (HG794202, –, –) – Gombori Mts, Ujarma – GAT 7504 (*Fritsch et al.*, 13.vii.2006); **Gl-94** (HG794203, –, –) – 15 km S Gori, Didi-Ateni – GAT 7502 (*Fritsch et al.*, 17.vii.2006); **Gl-95** (HG794204, –, –) – the Tsenitskali valley below Zubi – GAT 7498 (*Fritsch et al.*, 18.vii.2006); **Gl-98** (HG794206, HG794054, HG794124) – Dariali Gorge, 8 km to N from Kazbegi – GAT 7515 (*Pistrik & Akhalkatsi*, 20.vii.2002) & Accession TAX 6047 in Gatersleben; **Gl-99** (HG794207, HG794055, HG794125) – to SW from Kazbegi, Pansheti – GAT 7513 (*Pistrik & Akhalkatsi*, 20.vii.2002) & Accession TAX 6054 in Gatersleben; **Gl-105** (HG794210, HG794058, HG794128) – Mtiuleti, Kazbegi – OSBU (*Lobin*, 27.vi.2005); **Russia, Gl-57** (HG794178, HG794036, HG794106) – North Ossetia, Tseyskoye Gorge, Nizhny Tsey – MW (*Amirkhanov*, 17.viii.1975); **Gl-84** (HG794194, –, –) – Stavropolsky Krai, Pyatigorsk, Mt Mashuk – MHA (*Dayeva 310*, 27.viii .1966).

A. schistosum: **Russia, Gl-48** (HG794172, HG794030, HG794100) – Karachay-Cherkessia, Arkhyz – MW (*Zernov & Onipchenko 7011*, *holotypus*, 6.viii.2008); **Gl-56** (HG794177, HG794035, HG794105) – Karachay-Cherkessia, the Daut River Gorge – MW (*Onipchenko*, 20.viii.2009); **Gl-83** (HG794193, HG794046, HG794116) – Karachay-Cherkessia, Uchkulan – MHA (*Gogina 203*, 29.vii.1968).

A. tarkhankuticum: **Ukraine, Gl-17** (HG794159, HG794018, HG794088) – Crimea, 3 km to WNW from Olenevka – MW (*Seregin & Seregina T-1110*, *paratypus*, 14.viii.2008); **Gl-18** (HG794160, HG794019, HG794089) – Crimea, Lake Donuzlav, Novoozernoye – MW (*Seregina*, *holotypus*, 19.viii.2008); **Gl-19** (HG794161, HG794020, HG794090) – Crimea, 4.5 km to NW from Olenevka – MW (*Seregin & Seregina T-1124*, *paratypus*, 14.viii.2008).

A. tianschanicum: **Kyrgyzstan, Tax3324** (HG794232, HG794076, HG794146) – Gulcha, the Kurshab River – GAT (*Fritsch* 1992) & Accession TAX 3324 in Gatersleben; **Tax3999** (HG794233, HG794077, HG794147) – Talas Ala-Too, Talas City – GAT (*Fritsch* 1994) & Accession TAX 3999 in Gatersleben.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. The alignments of the combined internal transcribed spacer (ITS) sequences (including ITS1 and ITS2 and the 5.8S gene).

Appendix S2. The alignment of the combined *trnL–trnF* and *rpl32–trnL* (UAG) sequences.