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ORIGINAL ARTICLE

Morphological and molecular investigations of *Gagea* (Liliaceae) in southeastern Kazakhstan with special reference to putative altitudinal hybrid zones

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Abstract The most important center of speciation in the genus *Gagea* is thought to be in Central Asia. Here, we focus on species diversity in southeastern Kazakhstan (around Almaty, Ili-Alatau range of the Western Tian-Shan mountains). We studied an elevational transect, reaching from lowland steppes to the alpine zone (500–2750 m a. s. l.), and carried out detailed morphological and molecular investigations for populations of *Gagea* spp. Nine species were identified in different altitudinal zones; one of these (*Gagea almaatensis*) is described as new to science. We could detect two altitudinal contact zones between closely related species: *G. filiformis* and *G. granulosa* (sect. *Minimae*), and *G. almaatensis* and *G. kuraminica* (sect. *Gagea*). Morphological and molecular investigations (ITS data and cpDNA networks) indicate ongoing hybridization of co-occurring *G. filiformis* into *G. granulosa* and putative bidirectional hybridization events between *G. almaatensis* and *G. kuraminica.*

Keywords cpDNA · *Gagea* · Hybridization · ITS · Phylogeny · Taxonomy

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Introduction

The species-rich, complex genus *Gagea* Salisb. (Liliaceae; more than 320 species, see Levichev 2013) comprises small bulbiferous geophytes, which are mainly vegetatively propagated. Diversification in the genus is generally influenced by polyploidization and reticulated intra-sectional hybridization (e.g., Peruzzi 2008; Peterson et al. 2009, 2011; Peruzzi et al. 2011; Zarrei et al. 2012; Tison et al. 2013).

Within the last two decades, morphological characters of the genus *Gagea* were intensively studied based on wild and cultivated plants and available herbarium vouchers. As a result, several new species were described especially in the species-rich sections *Didymobulbos* s.l. (Tison et al. 2013; Kayıkçı et al. 2014; Tekşen and Erkul 2014) and *Gagea* (e.g., Levichev 1988, 1998, 2001; Henker 2005; Peruzzi et al. 2007; Peterson et al. 2011; Henker et al. 2012). The plants express species-specific growth patterns during ontogenesis (e.g., Levichev and Jezniakowsky 2008), which are already documented for a number of species (e.g., Levichev 2011, 2013). Vegetative reproduction (via bulbils) is combined with generative reproduction (via seeds), but the proportion of both reproductive modes varies widely among species. One extreme is the virtually

clonal *Gagea spathacea* (Hayne) Salisb., reproducing by bulbils only (Levichev et al. 2010; Pfeiffer et al. 2012). In contrast, some species such as *G. incrustata* Vved., *G. taurica* Steven or *G. alexeenkoana* Miscz. never form vegetative bulbils (Levichev 2005). If bulbils are present, their quantity, location, form and structure represent important features for species differentiation (e.g., Levichev 1999a; Peterson et al. 2011; Tison et al. 2013). In addition, patterns of bulbil formation are highly species-specific and much diversified within the genus and its sections (Schnittler et al. 2009, 2013; Beisenova et al. 2015). Based on the comparison of several *Gagea* species (Schnittler et al. 2013), two main patterns of bulbil formation were found: "type I bulbils" (a single or several bulbils are produced as soon as the replacement bulb has reached a certain diameter and then formed throughout the life of the plant as long as the bulb stays above this threshold) and "type II bulbils" (only temporarily produced in immature, sufficiently large non-flowering plants). In addition, both strategies may occur simultaneously for bulbils with different locations (for instance, type I basal bulbils accompanied by type II suprabasal bulbils).

According to current knowledge, southwestern Central Asia harbors about 70 % of all described *Gagea* species (Levichev 2013). The Western Tian-Shan and the Pamir Alai mountains are considered as two centers of speciation (Levichev 1999b; Levichev and Jezniakowsky 2008; discussed in Peterson et al. 2009). The Flora of Uzbekistan lists 68 species (Tojibaev et al. 2014; 82 species according to I.G. Levichev, unpubl. data), and the flora of China includes 17 species (Xinqi and Turland 2000). Numerous species have been described recently for the Chinese region of Inner Mongolia (three species: Zhao and Zhao 2003, 2004; Zhao and Yang 2006), Xinjiang, China (three species: Peterson et al. 2011) and Pakistan (17 species: Ali 2006; Levichev 2006; Levichev and Ali 2006; Ali and Levichev 2007). In the Flora of Kazakhstan (Baitenov 2001), 39 *Gagea* species are recorded. Of these, 12 taxa (31 %) are endemic to the country.

In southeastern Kazakhstan, we studied an elevational transect (500–2750 m a. s. l.) reaching from lowland steppes around Almaty until the alpine zone of the Ili-Alatau range (Zailiysky Alatau) in the Northern Tian-Shan mountain range. For speciation, altitudinal gradients are interesting due to gradients in numerous abiotic (e.g., temperature, hours of sunshine, ultraviolet radiation, moisture) and biotic factors (discussed, e.g., in Abbott and Brennan 2014). In the contact zones between different altitudinal vegetation zones, previously isolated lineages can come in contact and interspecific crossing can take place. However, only a few hybrid zones have been studied until now (discussed in Levichev 2013; Abbott and Brennan 2014). In general, interspecific crossings in the hybrid zones will result in complex patterns of genetic variation and the formation of new genotypes (see Levichev 2013; e.g., Harrison and Larson 2014; Marques et al. 2014). In some cases, these new genotypes, resulting from introgression, are able to colonize new habitats.

Depending on the weight given to morphological and/or molecular characters, different infrageneric classifications exist (Levichev in Peterson et al. 2008 vs. Zarrei et al. 2011: discussed in Peterson et al. 2011; Peruzzi 2012a). This study generally adopts (except for sect. *Didymobulbos* s.l.; including sect. *Fistulosae* according to Peruzzi et al. 2008a) the infra-generic classification of Levichev (see Peterson et al. 2008). However, the taxonomic status of *Gagea serotina* (L.) Ker-Gawl. is controversial (also between the authors of this study). This species is either included into the genus *Gagea* (Peruzzi et al. 2008b, 2011; Peruzzi 2012a; Zarrei et al. 2009, 2011), or excluded [*Lloydia serotina* (L.) Rchb.: e.g., Levichev 2002: 236, 2013; Levichev et al. 2010: 478; Peterson et al. 2008].

The aim of this study was (1) to investigate the species composition of *Gagea* within different altitudinal ranges in the Ili-Alatau range, (2) to identify altitudinal contact zones of closely related species, and (3) to find evidence for putative hybridization between closely related co-occurring species by using a combination of morphological and molecular methods. In addition to the analysis of the ITS region (ITS1 + 5.8S rRNA + ITS2) obtained by direct sequencing, we employed a network approach successfully used in taxonomically difficult species complexes (e.g., *Gagea*: Peterson et al. 2010, 2011; Tison et al. 2013; *Erythronium*: Bartha et al. 2015; *Allium*: Gurushidze et al. 2008, 2010; *Bellevalia*: Borzatti von Loewenstern et al. 2013; *Crocus*: Harpke et al. 2014, 2015; *Doronicum*: Peruzzi et al. 2012; Pachschwöll et al. 2015) to analyze the genealogical relationships between chloroplast haplotypes. ITS types and cpDNA haplotypes (*psb*A-*trn*H IGS + *trn*L-*trn*F IGS) were investigated and considered regarding the altitudinal distribution of the respective species. The applied markers already proved to be suitable to solve phylogenetic and taxonomic problems within the genus (Peruzzi et al. 2008a; Peterson et al. 2008, 2011; Zarrei et al. 2009; Tison et al. 2013; see also discussion for *psb*A-*trn*H haplotypes in Pang et al. 2012; Naciri and Linder 2015), but as well for the detection of parental species of hybridogenic taxa (Peterson et al. 2004, 2009, 2011; Tison et al. 2013). In addition, we describe a new species of sect. *Gagea*.

Materials and methods

Studied altitudinal vegetation zones

Within the study region, five major vegetation zones can be distinguished. Zone I is formed by lowland steppes around Almaty (500–800 m a. s. l.). Zone II is formed by the foothills (800–1100 m a. s. l.) of the Ili-Alatau range where species-rich deciduous forests alternate with tall grass steppes. This zone includes as well the city of Almaty. Zone III extends to species-rich deciduous forests on lower slopes (1100–2000 m a. s. l.) of the Ili-Alatau range, which intergrade with shrubby mountain steppes on south-exposed, steep and rocky slopes. Zone IV is constituted by the belt of spruce forests (*Picea schrenkiana* Fisch. & C.A.Mey, 2000–2400 m a. s. l.). Since recruitment of spruce is slow to absent on steep south-exposed slopes, especially with rock outcrops, the conifers may as well be replaced by shrubby mountain steppes in such places. Zone V includes alpine meadows above the timberline (ca. 2400 m a. s. l.). All these vegetation zones, but especially valley plains and shallow slopes, are moderately grazed by livestock. Zones III–V can be disturbed by avalanches occurring on steep slopes. Further information about the studied region, climate data, and maps are provided by Gurikov (1981), Bolch (2007), and Bolch et al. (2011).

Sampling of plant material

The field study was carried out in the second half of April 2013. All taxa of *Gagea* were preliminary determined in the field. Wherever possible, several populations for a species were sampled from different sites and from different altitudes and vegetation zones. Numbers of collected individuals depended on (1) the size of population, (2) the extent of observed morphological variability, (3) the altitudinal distribution of populations, and (4) taxonomic criteria. Morphological variable populations and such in areas with co-occurring species were intensely sampled. For molecular studies and reference material (see "Appendix"), several individuals per site were preserved as herbarium specimens. All individuals of a given site received the same number (Arabic numerals ending with-*AP2013*). At least ten individuals for each species were deposited in the herbaria HAL and LE. Vouchers for the new species were prepared in duplicate and deposited in HAL (holotype) and LE, HAL (isotypes). For morphological analyses, we sampled patches of plants of all stages (juvenile non-flowering individuals and flowering individuals) exhaustively, analyzing as well all young and non-flowering plants around the older ones, to obtain a sample representing all growth stages.

Morphological investigations

Morphological investigations were carried out on fresh plant material (for detailed voucher information, see "Appendix"). For *Gagea kuraminica* Levichev, a total of 263 plants were analyzed (*AP16-2013*: $n = 48$; *AP24-2013*: $n = 73$; *AP27-2013*: $n = 54$; *AP49-2013*: $n = 88$); for *G. filiformis* (Ledeb.) Kar. & Kir. measurements were taken from 300 plants (*AP20-2013*: $n = 182$; *AP26-2013*: $n = 118$); for *G. granulosa* Turcz. 247 plants (*AP1-2013*: $n = 218$; *AP4-2013*: $n = 29$) were studied. For *G. almaatensis* sp. nov. (*AP43-2013*: $n = 13$), sampling was limited by small population sizes. Quantitative morphological studies were carried out as described in Schnittler et al. (2009). For plants the following traits were analyzed: the diameter of replacement bulb (if deviating strongly from a spherical form, two perpendicular measurements were taken), the number of flowers, the number and size of bulbils, the length and width of the first (basal) leaf, and the width of the first inflorescence bract. On a separate set of plants being ahead in flowering due to lower elevation or more suitable exposure, seeds were counted separately for each capsule of a plant. These counts included 105 capsules of *G. filiformis* (*AP52-2013*), 109 of *G. granulosa* (*AP1-2013*) and 104 of *G. kuraminica* (*AP49-2013*).

Genomic DNA extraction, PCR amplification and sequencing

Molecular analyses included 83 individuals of *Gagea* (for detailed voucher information, see "Appendix") sampled within the five investigated altitudinal vegetation zones, representing nine taxa and 60 populations: *Gagea almaatensis* sp. nov.: $n = 4$ (three populations), *G. bulbifera* (Pall.) Salisb.: $n = 7$ (6 populations), *G. divaricata* Regel: $n = 2$ (one population), *G. filiformis*: $n = 28$ (18 populations), *G. granulosa*: $n = 13$ (9 populations), *G. liotardii* (Sternberg) Schult. & Schult.f. (=*G. fragifera* (Vill.) Ehr.Bayer & G.López; see also Levichev 2006: 942): $n = 5$ (5 populations), *G. kuraminica*: $n = 11$ (9 populations), *G. tenera* Pascher: $n = 1$ (one population), and *G.* cf. *turkestanica* Pascher: $n = 10$ (8 populations). In addition, two individuals (*AP24b-2013*; *AP40-2013*) morphologically intermediate between *G. almaatensis* and *G. kuraminica* were investigated. A small segment of air-dried leaf material (about 10 mg per voucher) was used for DNA isolation with the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany), following the manufacturer's protocol. PCR was performed with 50 ng genomic DNA in 20 µl reactions (Ready To Go™ PCR Beads, Amersham Bioscience) in a GeneAmp PCR System 9700 (Perkin Elmer). Primers for amplification of *trn*L-*trn*F intergenic spacer

(IGS) and *psb*A-*trn*H IGS were taken from Sang et al. (1997); primers (ITS 5 and ITS 4) for the ITS region (ITS1 + 5.8S rRNA + ITS2) were used according to White et al. (1990). Gel-purified PCR products (50–200 ng) were prepared as "u-mixes" via the StarSEQ® Sequencing Service (StarSeq, Mainz, Germany).

Sequence and phylogenetic analyses

All newly obtained sequences (234) were submitted to the EMBL nucleotide database (for details and accession numbers, see "Appendix"). In addition, we included in the analysis sequences obtained during previous studies (Peterson et al. 2008, 2009, 2011). Sequence alignment was performed utilizing the Clustal-W multiple alignment procedure (Thompson et al. 1994) in Bioedit (version 7.0.9.0; Hall 1999), followed by manual adjustment. For each locus, the best-fitting model of DNA evolution was assessed with MRMODELTEST 2.3 (Nylander 2004). Nuclear data were subjected to phylogenetic analyses using Bayesian phylogenetic inference (BI) with MRBAYES 3.2 (Ronquist et al. 2012). *Tulipa cretica* Boiss. & Heldr. was used as outgroup (see Peterson et al. 2008, 2011). Generally, all ITS regions are putatively functional, checked according to Harpke and Peterson (2008a, b). For BI 2 times 4 chains were run for two million generations under the appropriate models of sequence evolution (nuclear data set: GTR + Gamma + I), sampling a tree every 1000 generations. Converging log-likelihoods, potential scale reduction factors for each parameter and inspection of tabulated model parameters in MRBAYES suggested that stationarity had been reached in all analyses. The first 25 % of trees of each run were discarded as burn-in. Two independent runs of BI analysis were performed to confirm that separate analyses converged on the same result. Each of these two analyses resulted in the same topology and similar posterior probabilities (pp) for nodal support.

By comparing the positions in which the ITS (ITS1 + 5.8S rRNA + ITS2) sequences of *Gagea filiformis* and *G. granulosa* differed, the putative hybrid ITS sequence was generated. For the detection of molecular intermediates of *Gagea granulosa* and *G. filiformis*, direct sequencing data of the ITS region were compared to this putative hybrid sequence.

To utilize the advantage of networks (e.g., Gurushidze et al. 2010) over tree-building methods for analyzing cpDNA sequence data in closely related species, we calculated haplotype networks for the species of sect. *Minimae* and sect. *Gagea* using TCS (Clement et al. 2000). The sequences of both chloroplast loci (*psb*A-*trn*H IGS + *trn*L-*trn*F IGS) were concatenated. To obtain a chloroplast haplotype genealogy, insertions/deletions (indels) in the alignment that likely originated from single mutational events were reduced to single alignment positions. Length variation at one mono-nucleotide repeat (T) in the *trn*L-*trn*F IGS was generally excluded from the analyses due of the uncertain homology of the respective sequence positions. This shortened alignment was subjected to statistical parsimony analysis in TCS where gaps are treated as a fifth character state.

The number of parsimony-informative sites (ITS region; *psb*A-*trn*H IGS + *trn*L-*trn*F IGS) was determined using DnaSP v5.10.01 software; excluding gap sites (Librado and Rozas 2009).

Results

Species diversity within altitudinal ranges

The lowland steppes (Fig. 1, zone I) around Almaty were inhabited by *Gagea bulbifera* (Pall.) Salisb. and *G. divaricata* Regel (520 m a. s. l.). Here, *G. bulbifera* was the only very abundant species on moderately grazed steppes with light, sandy soils and on remnants of rich steppe of mixed soil (520–864 m a. s. l.). Together with *G. bulbifera*, *G.* cf. *turkestanica* Pascher (Table 1) was found on isolated patches of remaining steppe around Almaty (790–1119 m a. s. l.; zone II); with uniform, relatively large populations on rich steppes on mixed soil (*AP54-2013*) and small, scattered populations on cultivated regions such as parks and gardens (e.g., *AP46-2013*: within the city center of Almaty; *AP50-2013*: Kok-Tobe Park). In addition, at a single location within the city limits (zone II) *G. tenera* Pascher (831 m a. s. l.) was found. Four species were regularly found in the Ili-Alatau range, occupying different altitudinal zones. These are *G. liotardii* (Sternberg) Schult. & Schult.f. [synonyms: *G. emarginata* Kar. & Kir., *G. fragifera* (Vill.) Ehr.Bayer & G.López; see Levichev 2006: 942; 1498–2733 m a. s. l.; zones III–V], *G. granulosa* Turcz. (839–1994 m a. s. l.; zones II–III), *G. filiformis* (Ledeb.) Kar. & Kir. (1089–2733 m a. s. l.; zones III–V), and *G. kuraminica* Levichev (1192–2380 m a. s. l.; zones III–IV). The alpine meadows (zone V) are characterized by *G. filiformis* as the by far most common species. In addition, *G. almaatensis* sp. nov. (see Taxonomic treatment), a new taxon of sect. *Gagea*, occurred in small populations. This species inhabits open alpine meadows and was occasionally observed in lower altitudes in avalanche gullies (1994–2557 m a. s. l.; zones IV–V). In addition, a single small population of *G. bulbifera* was recorded on rock outcrops in open, shrubby mountain steppe (2003 m a. s. l.; zone III) of the upper Medeu valley. Two of the nine investigated species (*G. bulbifera* of sect. *Bulbiferae* and *G. divaricata* of sect. *Platyspermum*) were the only

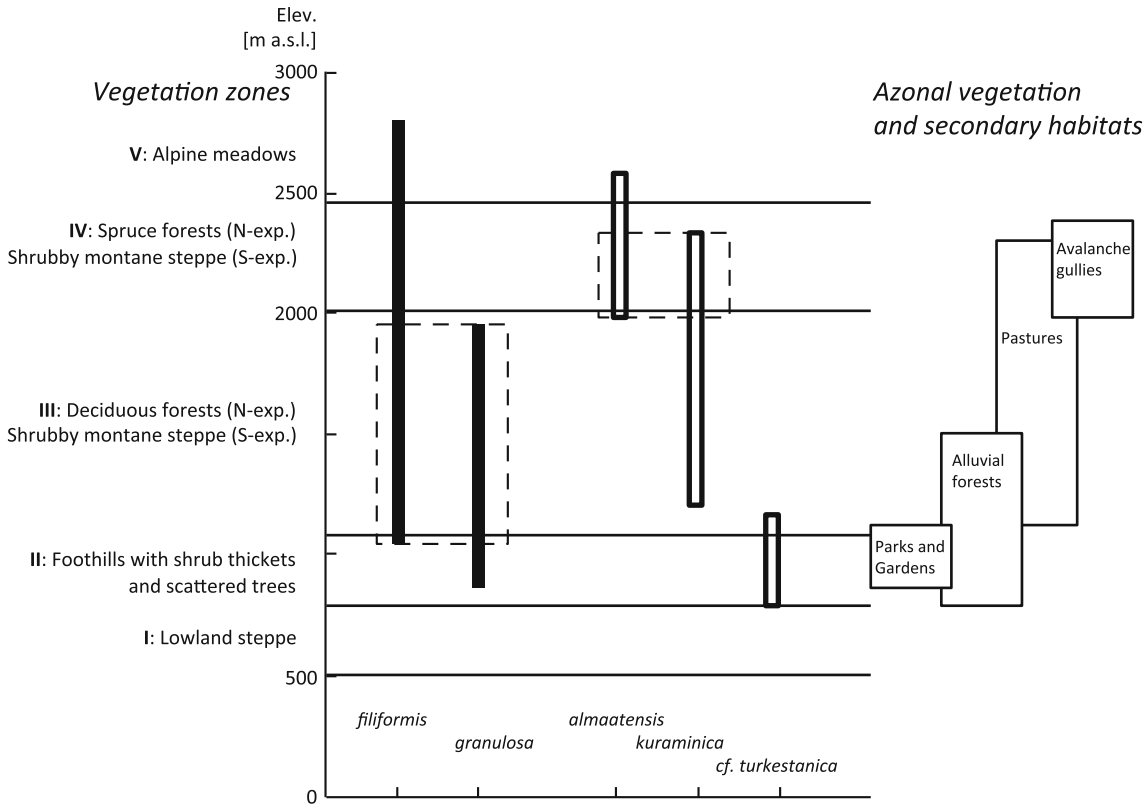

Fig. 1 Elevational range (*bars*) and vegetation zones inhabited by the investigated species of *Gagea* sect. *Minimae* and sect. *Gagea* in the Ili-Alatau range. *Horizontal lines* delimit roughly the *vertical* vegetation zones. Contact zones between hybridizing species are *marked with dotted boxes*

Table 1 Description of habitats, distribution, and altitudinal contact zones of closely related species of sect. *Gagea* and sect. *Minimae* in the Ili-Alatau range. Elevations where hybrids were detected by molecular data are written in italics

	Section	Habitats	Distribution altitudes (m a. s. l.)	Contact zone: *hybrids* (m a. s. l.)
G. filiformis	*Minimae*	Disturbed alluvial forests, open places in the spruce belt, intensely grazed pastures, alpine meadows	1089–2733	1089–1994: *839; 1192; 1301; 1721; 1941; 1994*
G. granulosa		Parks and gardens, disturbed alluvial forests, mountain steppe, intensely grazed pastures, rarely alpine meadows	839–1994	
G. almaatensis	*Gagea*	Alpine meadows, avalanche gullies	1994–2557	1994–2380: *1994; 2733*
G. kuraminica		Alpine meadows, shrubby mountain steppes, pastures, open shrubland, and disturbed alluvial forests	1192–2380	
G. cf. *turkestanica*		Remnants of rich steppes with mixed soil, lowland steppe, parks and gardens	790–1119	

representatives of their sections. Sect. *Didymobulbos* s.l. was represented by two species (*G. tenera* and *G. liotardii*), which occurred in different altitudinal zones without any contact. The other five species belong to section *Minimae* and *Gagea*, respectively, and occurred in different, yet overlapping, altitudinal zones (for contact zones, see Table 1; Fig. 1; for comparison of habitat preferences, see Table 1).

In *Gagea filiformis* and *G. granulosa* (sect. *Minimae*), neither juvenile nor flowering plants could be told apart without a close examination of the bulbils (for morphological characters, see Table 2). Both species possess persistently formed type I bulbils. However, plants of *G. filiformis* possess a cream to pale yellow tunica of the parent bulb and older individuals form a single lateral bulbil. In contrast, plants of *G. granulosa* show typically a purple-tinted outer tunica; older plants develop on average 4.3 (up to 13) bulbils arranged in a belt around the parent bulb. *Gagea granulosa* also has lower threshold for bulbil formation than *G. filiformis* (>50 % of young *G. granulosa* form bulbils if the bulb has reached 1 mm in diameter; in *G. filiformis,* the 50 % threshold is around 2 mm bulb diameter). Nevertheless, very young plants of both species lacking bulbils cannot be distinguished. Especially plants of *G. filiformis* (spanning a larger elevational belt than *G. granulosa*; Fig. 1; Table 1) were variable in size. Also *G. granulosa* populations were found to be variable except for two isolated populations within the city of Almaty (*AP1-2013*, 839 m a. s. l.; *AP4-2013*, 862 m a. s. l.), which were morphologically uniform. On several other sites, *G. filiformis* and *G. granulosa* were growing together (e.g., *AP7-2013*, *AP20-2013*, *AP23-2013*, *AP45-2013*, *AP58-2013*; found between 1192 m and 1994 m a. s. l.; see "Appendix").

The two species of sect. *Gagea*, *Gagea kuraminica* and *G. almaatensis*, are morphologically well differentiated (e.g., by features of bulbil, width of the basal leaf, and form of the inflorescence). Individuals of *G. kuraminica* with a candelabrum-like inflorescence are 8–16 cm tall; basal leaves are 3–4.5 mm wide. Flowering plants have obliquely drop-shaped bulbs with a thin and papery, light brownish gray tunic. Bulbils of type II (absent in flowering plants) develop on the tip of a very short stolon which does not exceed 0.5 mm in length. Dormant bulbils possess a smooth gray tunic with brown tints. Individuals of *G. almaatensis* (see also Taxonomic treatment) lack the candelabrum-like inflorescence and are 7.5–15 cm tall, basal leaves are 2–4 mm wide. Flowering plants have obliquely drop-shaped bulbs with a thin and coriaceous, pale brown tunic. Dormant vegetative bulbils of *G. almaatensis* are characterized by a dark brown tunic with a heavily pitted structure that resembles honey combs. The two species also prefer different elevations (*G. almaatensis*: 1994–2557 m a. s. l.; *G. kuraminica*: 1192–2380 m a. s. l.; Fig. 1; Table 1).

Some individuals of *G. kuraminica* were found to be morphologically intermediate between *G. kuraminica* and *G. almaatensis* (*AP24b-2013*: alpine meadow below an avalanche gully, vegetation zone III, 1994 m a. s. l.; *AP40-2013*: open alpine meadows, vegetation zone V, 2733 m a. s. l.). Within the investigated populations of *G. kuraminica*, we observed as well individuals with deviating morphology (*AP29-2013*: plants smaller than usual for all ontogenetic stages; bulbils olivaceous gray, tunic with an inconspicuous pitted structure, region zone II, 2437 m a. s. l., moist alpine meadow with many tall forbs).

ITS phylogeny

In the ITS (ITS1 + 5.8S rRNA +ITS2) tree (Fig. 2 based on 55 ingroup taxa and *Tulipa cretica* as outgroup taxon; including 166 sequences; 290 variable and 217 parsimony-informative sites out of 580 total sites; alignment: Online Resource 1; for voucher information, see "Appendix") samples of *Gagea tenera*, *G. liotardii* and *G. bulbifera* were found to be monophyletic grouping together with accessions from other origins. All included taxa of *Gagea* sect. *Minimae* (Fig. 2: clade A; pp 1.00) form a strongly supported monophyletic clade splitting into two subclades: first, a polytomic subclade comprising all samples of *G. filiformis*, *G. granulosa*, *G. davlianidzeae* Levichev (Fig. 2: subclade A-1; pp 0.90) and *G. minima* and *G. nigra* L.Z.Shue, emend. Schnittler, the latter two forming a highly supported clade; second, a subclade comprising all samples of *G. confusa* A.Terracc.: (Fig. 2: subclade A-2; pp 1.00). In the strongly supported monophyletic clade of

Table 2 Summary of morphological data for bulbs, bulbils, flowers, and seed set (SEM) of *Gagea filiformis* and *G. granulosa* in the Ili-Alatau range

	Number of investigated plants	Diameter bulb (mm)	Plants with flowers[a]	Flowers per plant	Plants with bulbils[a]	Bulbils per plant	Means size of bulbils (mm)	Seeds per flowering plant (n = capsules)
G. filiformis	300	2.59 ± 1.22	91	3.03 ± 2.17	193	1.00 ± 0.00	1.25 ± 0.44	41.7 ± 26.7 (105)
G. granulosa	246	2.98 ± 1.24	46	2.47 ± 1.47	186	4.25 ± 3.03	1.58 ± 0.33	31.5 ± 18.7 (109)

All measurements are given with standard deviations

[a] Number of investigated individuals developing the respective structure (flowers and/or bulbils)

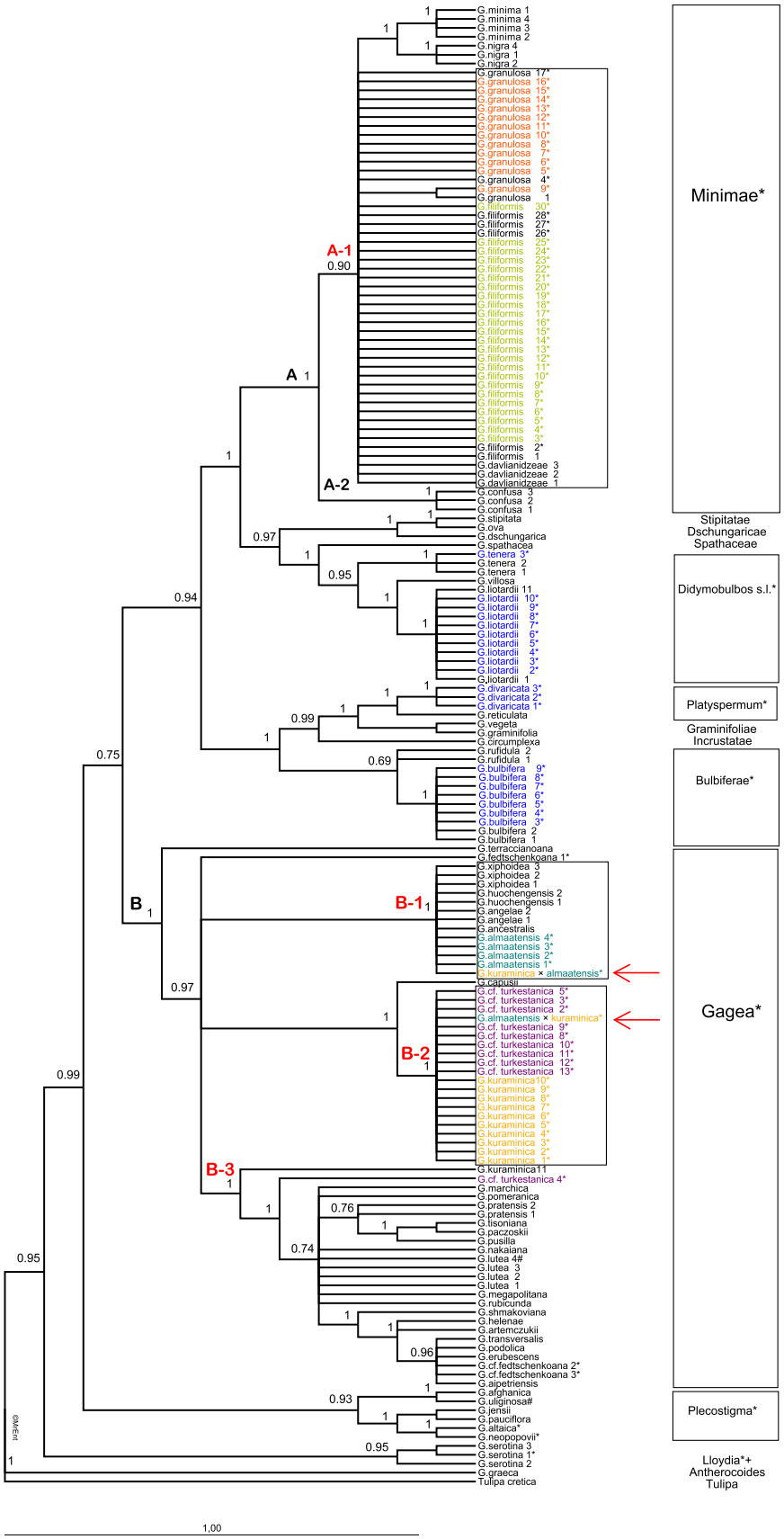

Fig. 2 General time-reversible (GTR + Γ) tree calculated via Bayesian analysis (8 million cycles) of the ITS region (ITS1 + 5.8S rRNA + ITS2) including 165 accessions from 55 species of *Gagea*. The posterior probabilities for the clades are given above the nodes. On the *right side*, the infrageneric classification of *Gagea* according to Levichev in Peterson et al. (2008) (except of sect. *Didymobulbos* s.l.) is indicated by *vertical bars*. Investigated individuals from the Ili-Alatau range are *color-coded*. *Boxes* show the positions of the genetically differentiated *G. almaatensis* and *G. kuraminica* (from the Ili-Alatau range), and the polytomy of *G. filiformis* and *G. granulosa*. Positions of morphological intermediates of *G. almaatensis* and *G. kuraminica* are marked by *red arrows*. (*Asterisks*) Accessions from Kazakhstan; (*Hash*) sequences taken from EMBL/NCBI; (*Plus*) for *Lloydia* see introduction; Peterson et al. (2011); Peruzzi (2012a, b); and Levichev (2013)

sect. *Gagea* (Fig. 2: clade B; pp 1.00) *G. terraccianoana* Pascher is separated from all other species. The latter form a polytomic subclade with *G. xiphoidea*, *G. huochengensis, G. angelae, G. almaatensis* and *G. kuraminica* × *G. almaatensis* clustering together (Fig. 2: subclade B-1; pp 1.00). A second subclade includes all samples of *G. kuraminica* from Kazakhstan, *G. almaatensis* × *G. kuraminica* and nine accessions of *G.* cf. *turkestanica* (Fig. 2: subclade B-2; pp 1.00). Finally, *G. kuraminica* 11 (holotype from Uzbekistan) and one accession of *G.* cf. *turkestanica* grouped together with all European species in subclade B-3 (Fig. 2; pp 1.00).

ITS data of *Gagea filiformis* and *G. granulosa*

Results from direct sequencing of the ITS region (ITS1 + 5.8S rRNA + ITS2) of *Gagea filiformis* (23 individuals of 13 populations) and *Gagea granulosa* (12 individuals of 8 populations) are given in Table 3 together with the altitudinal occurrence of the investigated plants in the Ili-Alatau range (for voucher information, see "Appendix").

The ITS sequence of the investigated individual of *Gagea granulosa* (*gra*) from a morphologically uniform population (*gra*5: *AP4-2013*, 862 m a. s. l.; below the contact zone: 1089–1994 m a. s. l.) showed no ambiguous sites and corresponded to a published sequence of *G. granulosa* from Kazakhstan (EMBL/NCBI Accession Number AM287278; Peterson et al. 2008). Sixteen out of 17 *G. filiformis* individuals (*fil*) sampled in the contact zone and all six individuals of *G. filiformis* (*fil*10 and *fil*11: *AP30-2013*, *fil*12 and *fil*13: *AP33-2013*, *fil*14: *AP34-2013*, *fil*17: *AP42-2013*; Table 3) in altitudes above the contact zone (2380–2733 m a. s. l.) shared the identical ITS sequence lacking any ambiguous site. For both species, the ITS region differs in the Ili-Alatau range at 16 positions (ITS1: seven point mutations; ITS2: eight point mutations plus one indel of 1 bp length; Table 3). Based on these differences between *G. filiformis* and *G. granulosa*, we generated the putative ITS hybrid sequence resembling the

Table 3 Parsimony-informative ITS sites and cpDNA haplotypes of *Gagea granulosa* (*gra*), *G. filiformis* (*fil*) and putative intermediates in the altitudinal contact zone (1089–1994 m a. s. l.) in the Ili-Alatau range

		ITS1						ITS2										
ITS position[a]		21	59	72	124	147	152	182	416	465	482	489	510	546	579	580	602	
G. filiformis		t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	
G. granulosa		C	T	C	G	C	C	C	C	T	G	T	T	A	A	A	T	
Hypothetic hybrid sequence		**Y**	**Y**	**Y**	**R**	**S**	**Y**	**Y**	**Y**	**Y**	**K**	**W**	**T**	**R**	**W**	**W**	**Y**	
Investigated individuals (collection site *AP-2013*)[b]	cpDNA haplotype																	Altitude (m a.s.l.)
fil 17 (*AP42*)	c4	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	2733
fil 10 & 11 (*AP30*)	c4	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	2437
fil 12 & 13 (*AP33*); *fil* 14 (*AP34*)	c4	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	2380
fil 24 (*AP25*)	c1	C	**Y**	C	G	C	C	**Y**	**Y**	**Y**	G	**W**	**T**	A	A	*r*	T	1994
gra 11 (*AP28*)	c1	**Y**	**Y**	C	G	C	C	**Y**	**Y**	**Y**	G	**W**	T	A	A	**W**	T	1994
gra 9 (*AP13*)	c1	t	c	C	G	C	**Y**	C	C	c	G	a	T	A	A	**W**	T	1721
fil 6 & 7 (*AP20*)	c3	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1941
fil 8 & 9 (*AP20*)	c4	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1941
gra 12 (*AP45*)	c1	**Y**	**Y**	**Y**	**R**	**S**	**Y**	**Y**	**Y**	**Y**	**K**	**W**	T	**R**	**W**	**W**	**Y**	1941
gra 13 (*AP45*)	c2	C	**Y**	C	G	C	C	**Y**	**Y**	**Y**	G	*y*	T	A	A	*r*	T	1941
gra 14 (*AP45*)	c1	**Y**	**Y**	**Y**	**R**	**S**	**Y**	**Y**	**Y**	**Y**	**K**	**W**	T	**R**	**W**	**W**	**Y**	1941
gra 10 (*AP21*)	c1	C	**Y**	C	G	C	C	**Y**	C	**Y**	G	**W**	T	A	A	*r*	T	1941
fil 23 (*AP60*)	c3	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1875
fil 5 (*AP14*)	c3	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1821
fil 4 (*AP14*)	c4	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1821
fil 15 &16 (*AP38*)	c4	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1498
fil 22 (*AP59*)	c5	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1301
fil 20 & 21 (*AP59*)	c6	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1301
gra 15 (*AP58*)	c1	**Y**	**Y**	**Y**	**R**	**S**	**Y**	**Y**	**Y**	**Y**	**K**	**W**	T	**R**	**W**	**W**	**Y**	1301
gra 16 (*AP58*)	c1	**Y**	**Y**	**Y**	**R**	**S**	**Y**	**Y**	**Y**	**Y**	**K**	**W**	T	**R**	**W**	t	**Y**	1301
fil 3 & 30 (*AP7*)	c4	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1192
gra 8 (*AP7*)	c1	C	**Y**	C	G	C	C	**Y**	C	T	**K**	**W**	T	A	A	t	T	1192
fil 18 (*AP51*)	c4	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1099
fil 19 (*AP52*)	c3	t	c	t	a	g	t	t	t	c	t	a	-	g	t	t	c	1089
gra 5 (*AP4*)	c1	C	T	C	G	C	C	C	C	T	G	T	T	A	A	A	T	862
gra 6 (*AP1*)	c1	**Y**	**Y**	**Y**	**R**	**S**	**Y**	**Y**	*w*	**Y**	**K**	*y*	T	**R**	**W**	**W**	**Y**	839
gra 7 (*AP1*)	c1	**Y**	**Y**	C	**R**	**S**	**Y**	**Y**	**Y**	**Y**	**K**	**W**	T	**R**	**W**	**W**	**Y**	839

Nucleotides in green and big letters corresponding to *G. granulosa*, and in blue and small letters corresponding to *G. filiformis*; letters in italics did not correspond to the latter two taxa. Direct sequenced ITS data (K = G and T; M = A and C; R = A and G; S = G and C; W = A and T; Y = C and T) in brown and bold resembling the parental sequence variation

[a] Position of informative sites are numbered according to EMBL/NCBI Accession Number LN874835 (*gra*5); [b] see "Appendix"

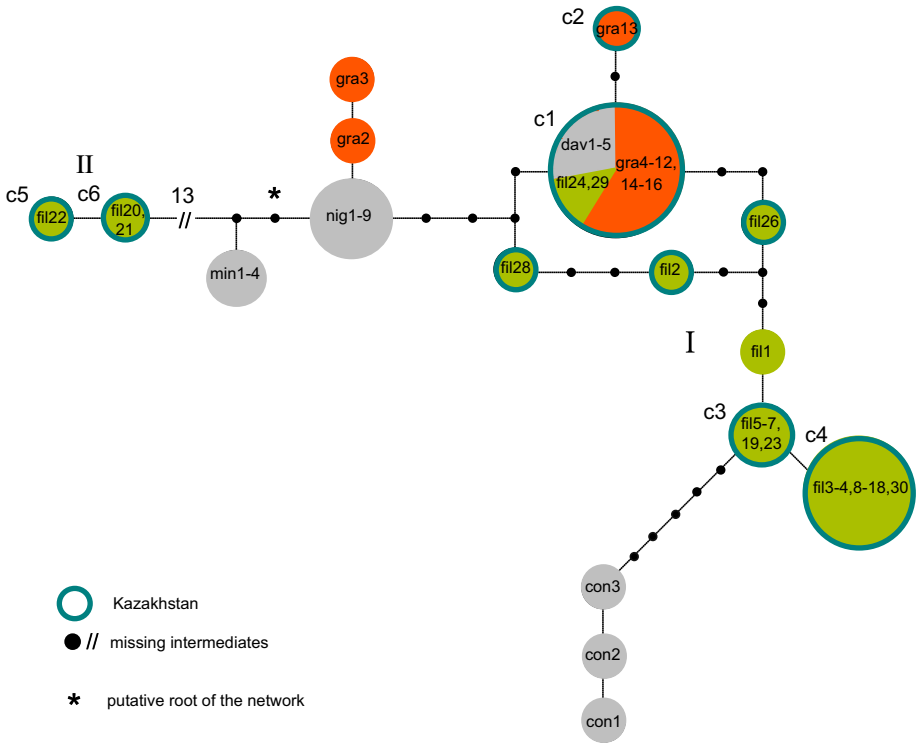

Fig. 3 Network for cpDNA haplotypes (*psb*A-*trn*H IGS + *trn*L-*trn*F IGS) including 64 sequences from six species of *Gagea* sect. *Minimae*: *Gagea confusa* (con), *G. davlianidzeae* (dav), *G. filiformis* (fil), *G. granulosa* (gra), *G. minima* (min), and *G. nigra* (nig); for further details, see "Appendix". A total of 49 haplotypes were recognized; 32 of them occur as missing intermediates. The *size of circles* denotes the number of accessions sharing the same haplotype. Haplotypes of *G. granulosa* (c1, c2) and *G. filiformis* (c1, c3–c6) recognized in the Ili-Alatau range are indicated

parental sequence variation (see Table 3). The ITS sequence of three *G. granulosa* individuals (*gra*12 and *gra*14: *AP45-2013*, *gra*15: *AP58-2013*; Table 3) collected in the contact zone corresponded to the putative hybrid sequence. The ITS sequence of six further investigated individuals of *G. granulosa* from the contact zone also corresponded to this sequence in most of their position and corresponded to *G. filiformis* and *G. granulosa*, respectively, at the other positions (see Table 3). In addition, at same locations (*AP45-2013*, *AP58-2013*; Table 3) *G. granulosa* individuals with slightly different ITS sequences were found. Finally, two individuals of a morphologically uniform population of *G. granulosa* growing below the contact zone (*gra*6 and *gra*7: *AP1-2013*, 839 m a. s. l.) corresponded to the putative hybrid sequence at most but not all positions.

cpDNA haplotype network of sect. *Minimae*

For all accessions of sect. *Minimae*, including six species (including 64 sequences; 16 variable and parsimony-informative sites out of 418 total sites; alignment: Online Resource 2; for voucher information, see "Appendix"), TCS inferred a network with a connection limit of 19 steps and 49 haplotypes, 32 of these are recognized as missing intermediates (Fig. 3). Closest to the putative root of the network was the haplotype of *Gagea nigra* (separated by one step; Fig. 3). All samples of *G. davlianidzeae*, *G. nigra* and *G. minima* were found each with a single haplotype. The different haplotypes of *G. filiformis* ($n = 9$) and *G. granulosa* ($n = 4$) were found at distinct positions within the network separated by up to 30 (*G. filiformis*) and up to 9 steps (*G. granulosa*), respectively (Fig. 3). Also in the Ili-Alatau range, different haplotypes were observed for the two species of sect. *Minimae* (*G. filiformis*: $n = 5$, haplotypes c1, c3–c6; *G. granulosa*: $n = 2$, haplotypes c1 and c2; see Fig. 3). Eleven out of 12 *G. granulosa* individuals sampled in the elevational transect in the Ili-Alatau range (839–1994 m a. s. l.) had the haplotype c1 (Fig. 3; Table 3). Only for one *G. granulosa* individual (*gra*13: *AP45-2013*, 1941 m a. s. l.; Fig. 3) haplotype c2 was found. In contrast, in *G. filiformis* from the Ili-Alatau range transect, five cpDNA haplotypes were found with different altitudinal distributions (c1: 1994 m a. s. l.; c3: 1089–1941 m a. s. l., c4: 1099–2733 m a. s. l., c5 and c6: 1301 m a. s. l.; Fig. 3; Table 3).

cpDNA haplotype network of sect. *Gagea*

For the accessions of sect. *Gagea* including 27 species (including 69 sequences; 40 variable and 35 parsimony-informative sites out of 410 total sites; alignment: Online Resource 3; for voucher information, see "Appendix"), TCS inferred a network with a connection limit of 20 steps and 111 haplotypes, with 83 of these as missing intermediates (Fig. 4). Closest to the putative root of the network (*Gagea* cf. *fedtschenkoana* Pascher: fed2, fed3) was the haplotype of *G. aipetriensis* Levichev (separated by four

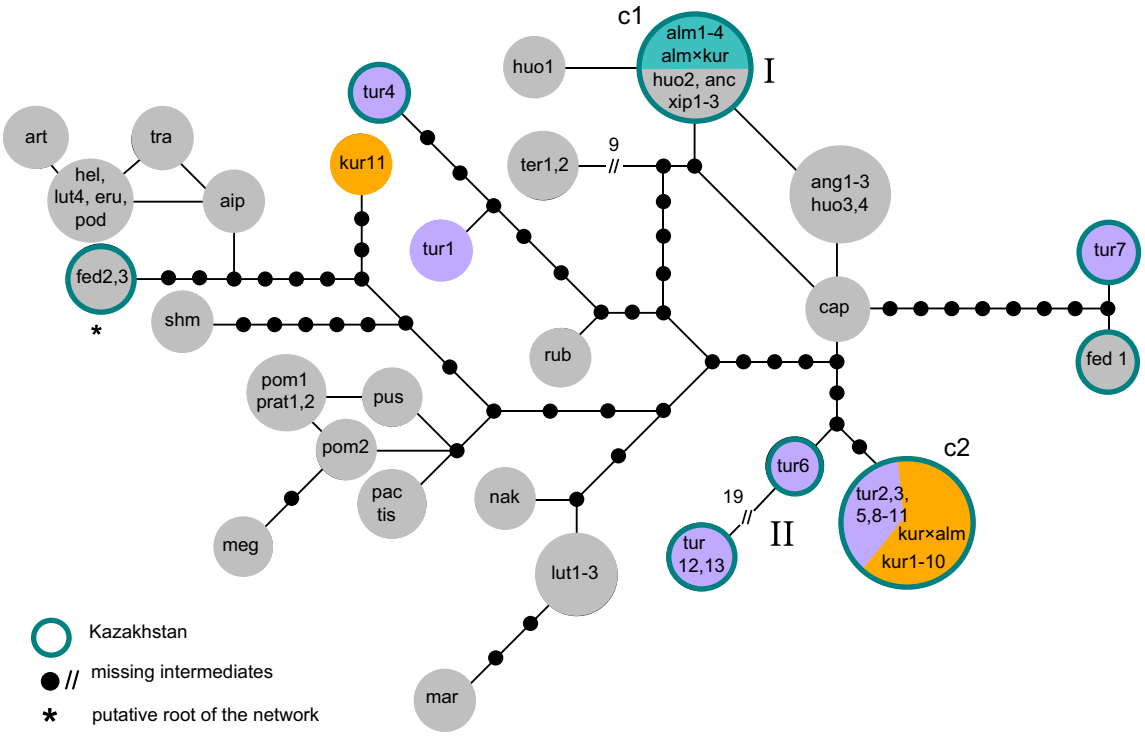

Fig. 4 Network for cpDNA haplotypes (*psb*A-*trn*H IGS + *trn*L-*trn*F IGS) including 69 sequences from 27 species of *Gagea* sect. *Gagea*: *Gagea aipetriensis* (aip), *G. almaatensis* (alm), *G. ancestralis* (anc), *G. angelae* (ang), *G. artemczukii* (art), *G. capusii* (cap), *G. erubescens* (eru), *G. fedtschenkoana* (fed), *G. helenae* (hel), *G. huochengensis* (huo), *G. kuraminica* (kur), *G. lutea* (lut), *G. marchica* (mar), *G. megapolitana* (meg), *G. nakaiana* (nak), *G. paczoskii* (pac), *G. podolica* (pod), *G. pomeranica* (pom), *G. pratensis* (pra), *G. pusilla* (pus), *G. rubicunda* (rub), *G. shmakoviana* (shm), *G. terraccianoana* (ter), *G. tisoniana* (tis), *G. transversalis* (tra), *G. turkestanica* (tur), *G. xiphoidea* (xip); for further voucher information, see "Appendix." A total of 111 haplotypes were found; 83 of them are missing intermediates. The *size of circles* denotes the number of accessions sharing the same haplotype. Haplotypes of *G. almaatensis* (c1), *G. kuraminica* (c2), and of morphologically intermediate individuals of *G. almaatensis* × *G. kuraminica* (c1), and *G. kuraminica* × *G. almaatensis* (c2) are indicated

steps only). *Gagea almaatensis* had a single haplotype (Fig. 4), which was observed as well for an individual morphologically intermediate between *G. almaatensis* and *G. kuraminica* (alm × kur: *AP24b-2013*), *G. ancestralis*, *G. xiphoidea*, and one accession from *G. huochengensis*. Also the haplotype of all investigated *G. kuraminica* samples from the Ili-Alatau range (Fig. 4) was identical (separated by 18 steps from the holotype from Usbekistan) but found as well for seven accessions of *G.* cf. *turkestanica* and a morphological intermediate between *G. kuraminica* and *G. almaatensis* (kur × alm: *AP40-2013*). For *G.* cf. *turkestanica* from Kazakhstan, we found five haplotypes separated by 3−36 steps (Fig. 4).

Discussion

Gagea species in the Ili-Alatau

Six of nine species found by us have already been recorded for Kazakhstan (Pavlov 1958; Baitenov 1969, 1985, 2001; for synonyms, see Levichev and Jezniakowsky 2008; and WCSP 2015): *Gagea bulbifera* (sect. *Bulbiferae*), *G. divaricata* (sect. *Platyspermum*), *G. granulosa* and *G. filiformis* (sect. *Minimae*), *G. liotardii* and *G. tenera* (sect. *Didymobulbos* s.l. according to Peruzzi et al. 2008a; see also Peruzzi et al. 2011; and Tison et al. 2013). *Gagea liotardii* (sect. *Fistulosae*, according to Levichev in Peterson et al. 2008), whose name is controversial (*G. liotardii* vs. *G. fragifera*; see Levichev 2006 and discussion and references in Peterson et al. 2011), was found in the Ili-Alatau not only in the alpine zone but also at lower altitudes (*AP39-2013*: disturbed alluvial forest, 1498 m a. s. l.), whereas the species occurred only between 2150 and 2350 m a. s. l. in the Chinese Tian-Shan (Peterson et al. 2011). According to our knowledge (see also Pavlov 1958; Baitenov 1958, 1969) *G. granulosa* constitutes a new record for the Ili-Alatau (Zailiysky Alatau).

Furthermore, we found three morphologically distinguishable species belonging to sect. *Gagea*. One of these species has morphological characters which allow to differentiate it from closely related species and is therefore

described as *G. almaatensis* sp. nov. Based on morphological characters (see also Beisenova et al. 2014), individuals of several populations could be circumscribed as *G. kuraminica* although they were genetically clearly differentiated by both ITS and cpDNA data from the holotype (from Uzbekistan; Levichev 1988). In addition, we found plants resembling *G. turkestanica* Pascher. This taxon is considered as conspecific with *G. capusii* A.Terracc. in WCSP (2015) and in the Flora of Kazakhstan (Pavlov 1958), but Levichev recognizes it as an independent species (Levichev and Jezniakowsky 2008). Our material, here named *G.* cf. *turkestanica*, differs from *G. capusii* and *G. turkestanica* by candelabrum-like pedicels and a lower number of flowers. In contrast to *G. almaatensis* and *G. kuraminica*, the populations of *G.* cf. *turkestanica* have mostly individuals with a single flower (populations *AP50-2013*, *AP54-2013*, *AP56-2013*); some individuals possess a yellow tunic of the parent bulbs and darker, finely granulated bulbils (*AP54-2013*). According to the molecular results *G.* cf. *turkestanica* was found to be polymorphic in cpDNA sequences. Most investigated individuals were related to but clearly different from *G. capusii* (cpDNA and ITS data). Almost all investigated vouchers from Kazakhstan differ from material from Kyrgyzstan determined as *G. turkestanica* (cpDNA; ITS data not available). Several samples of *G.* cf. *turkestanica* are identical with *G. kuraminica* from Kazakhstan, in both ITS and cpDNA sequences. Therefore, the taxonomic status of our plants determined as *G.* cf. *turkestanica* remains unclear. The material may belong to a species complex including some closely related lowland species, or could represent a hybrid swarm between *G. turkestanica* and related species. The phylogenetic tree obtained in this study confirms earlier results: first, the monophyly of the sections *Bulbiferae* and *Minimae* [according to the classification of Levichev presented in Peterson et al. (2008), Peruzzi (2012a)], and second, the molecular differentiation of *G. nigra* from *G. filiformis* and all other representatives of sect. *Minimae* (Peterson et al. 2011).

However, the phylogenetic tree based on ITS sequences was characterized by polytomies within sect. *Gagea* which includes the apparently new taxon. Highly similar ITS and/or cpDNA regions between morphologically distinguishable taxa are frequently observed within sect. *Gagea* (China, Xinjiang province: *Gagea angelae* Levichev & Schnittler, *G. huochengensis* Levichev, Peterson et al. 2011; Europe: *G. pomeranica* Ruthe, *G. megapolitana* Henker, *G. marchica* Henker, Kiesew., U.Raabe & Rätzel; Henker et al. 2012; Peterson et al. 2004, 2009; this study) but as well in other sections of the genus (sect. *Platyspermum*: Zarrei et al. 2012; sect. *Didymobulbos* s.l.: Tison et al. 2013). In general, low variability in molecular markers indicates recent speciation (e.g., *Eryngium*: Calviño et al. 2008; *Pimpinella*: Wang et al. 2014) which is often connected with rapid radiations that coincided with the colonization of new territories. Also, Fernández-Mazuecos and Vargas (2015) found only low taxonomic signals in plastid DNA sequences of *Linaria* sect. *Versicolores* but a pronounced geographic structure and assumed rapid diversification of plastid DNA lineages. Our cpDNA network of the taxa from sect. *Gagea* seems to be geographically structured, too. For instance, European and eastern Asian species occur usually at the tips (see also Peterson et al. 2009). However, additional sampling is needed, including further taxa and geographical areas to allow for meaningful analyses. Furthermore, the resolution of phylogenetic relationships in *Gagea* could be improved by the application of additional molecular markers, e.g., additional cpDNA regions or low-copy genes. Increasing the number of cpDNA markers has been successfully used to obtain a higher resolution (Harpke et al. 2014) and better branch support although this is not guaranteed (discussed, e.g., in Calviño et al. 2010; Naciri and Linder 2015). Chloroplast capture/hybridization and incomplete sorting of ancestral lineages could confound phylogenetic inference (Gurushidze et al. 2010), and often, it is difficult to distinguish between incomplete lineage sorting and hybridization. However, nuclear single-copy markers can contribute to the detection of hybridization events. In *Gagea*, data from partial sequences of the nuclear single-copy conserved ortholog set (COS) gene pCOS*At*103 (Peterson et al. 2011) revealed intra-sectional gene flow between closely related species in the sections *Minimae* and *Gagea*. This was in agreement with ITS and cpDNA data demonstrating these incongruences to be caused by hybridization. However, while such nuclear single-copy markers are suitable to detect recent or ancient hybridization (e.g., Erol et al. 2015), their suitability to define species borders of morphologically well differentiated species is limited. For instance, in allopolyploids frequently multiple copies can be found (Peterson et al. 2011; Harpke et al. 2015). Zarrei et al. (2012) found that haplotype lineages of the low-copy nuclear gene malate synthase from 12 taxa and 609 sequences in the *Gagea reticulata* species complex were not fully congruent with current species circumscription and morphology. The latter authors expect that additional data will not reveal a simple phylogenetic pattern in the actively evolving genus *Gagea*. This is in agreement with our experience from many years of morphological and molecular studies. AFLP (amplified fragment length polymorphism) or microsatellites may help to disentangle relationships among closely related taxa in the genus. This approach was successfully used in hybridizing and polyploid complexes (*Doronicum*, Asteraceae: Pachschwöll et al. 2015) as well as in young and or relatively rapidly evolving groups (*Leptinella*, Asteraceae:

Himmelreich et al. 2014). Oberprieler et al. (2014) argue that the joint investigation of sequence and fingerprint data with biogeographical and ecological data is an effective way to disentangle reticulate relationships in polyploid species complexes. Although AFLPs are capable to resolve relationships among closely related species or within species, the marker is dominant and fragments are anonymous. This disadvantage can be avoided, when restriction-site-associated DNA sequencing (RADseq; e.g., Miller et al. 2007) or genotyping by sequencing (GBS; Elshire et al. 2011) is applied, as these methods generate mostly biallelic single nucleotide polymorphism (SNP) information in addition to dominant characters (0/1; if fragments are absent within certain individuals). These methods were already successfully applied in detecting hybridization events (e.g., Eaton and Ree 2013).

Hybridization among *Gagea* species in altitudinal contact zones

Hybridization has been shown to be an important evolutionary mechanism in plants (e.g., Abbott et al. 2013; Gómez et al. 2015) and an important driver of speciation processes in the species-rich genus *Gagea* (e.g., Peruzzi 2008; Peterson et al. 2009; Tison et al. 2013). Hybrid zones have the potential to generate evolutionary novelties through introgression (discussed, e.g., in Abbott and Brennan 2014; Gómez et al. 2015). For *Gagea*, hybridization can be expected in areas where closely related species come into contact. In the Ili-Alatau, in habitats with co-occurring, closely related species, morphologically and/or genetically intermediate individuals were observed. This study reveals intra-sectional hybridization in two species complexes, *G. filiformis*/*Gagea granulosa* (sect. *Minimae*) and *G. almaatensis*/*G. kuraminica* (sect. *Gagea*) in the Ili-Alatau range.

Morphological and molecular data indicate an ongoing introgression (for "introgressive hybridization," see discussion in Harrison and Larson 2014) of *Gagea filiformis* into *G. granulosa*. In the broad contact zone (observed from 1089 to 1994 m a. s. l.) of these species, all investigated *G. granulosa* individuals had the same cpDNA haplotype (maternal part: *G. granulosa*) but intermediate ITS sequences resembling the parental sequence variation in *G. filiformis* and *G. granulosa* in different ways. The assumption of ongoing hybridization is supported by the observed co-occurrence of both species in almost all investigated sites in the altitudinal contact zone in the Ili-Alatau. In contrast, almost all investigated individuals of *G. filiformis* within and above the contact zone were found to have identical ITS sequences lacking any intermediate or ambiguous sites. Explanations could be that (i) hybridization is mostly unidirectional with *G. granulosa* as the maternal parent or (ii) it is presumably easier to differentiate *G. filiformis* (developing always one bulbil) from putative hybrids than *G. granulosa*, since hybridogenous plants are likely to develop more than one bulbil.

In the absence of reproductive isolation, species boundaries might easily be disrupted (discussed for Orchidaceae in Marques et al. 2014). This was also found in the *Gagea lutea*/*G. pratensis* species complex (sect. *Gagea*) where both parental species normally occurring in different habitats (in the same elevation) came in contact (Peterson et al. 2004, 2009; Zonneveld et al. 2015). Pfeiffer et al. (2013) showed that the taxa of the latter hybrid complex are not reproductively isolated and can interbreed, forming a hybrid swarm (see also discussion in Wörz et al. 2012). Several species of the taxonomically difficult sect. *Minimae* (eight species, Levichev in Peterson et al. 2008) frequently co-occurred (e.g.; *G. filiformis*, *G. davlianidzeae,* and *G. lowariensis* Pascher: Ali and Levichev 2007; I.G. Levichev personal observation; *G. nigra* and *G. davlianidzeae* in the Chinese Tian-Shan: Peterson et al. 2011; *G. filiformis* and *G. granulosa* in the Ili-Alatau: this study). In contrast to the situation found in the Chinese Tian-Shan (Peterson et al. 2011) where gene flow between *G. nigra* (990–2250 m a. s. l.) and *G. davlianidzeae* (1928–2250 m a. s. l.) was only rarely indicated in the small altitudinal contact zone (1928–2250 m a. s. l.) by molecular data (incongruent ITS and cpDNA data; data of pCOS*At*103), in this study abundant gene flow between *G. filiformis* and *G. granulosa* was found. This is underlined by the observation that both *G. filiformis* and *G. granulosa* showed a comparably high seed set (Table 2). In contrast, seed set was observed in the Chinese Tian-Shan for *G. nigra* only but not for the morphologically uniform *G. davlianidzeae*. ITS and cpDNA data indicate a differentiation of *G. nigra* from all other representatives of its section which can be explained by stronger reproduction barriers leading to the endemic species *G. nigra*, which is closely related to *G. filiformis* but differs in both morphology and molecular traits. Several species of the sect. *Minimae* were found with different ploidy levels (discussed in Peterson et al. 2011; Peruzzi 2012b: 37 % of the investigated vouchers were polyploids) indicating intra-sectional hybridization. Although cpDNA lineages can display a clear geographic structure and are not necessarily in agreement with patterns of nuclear DNA data and/or taxonomic concepts (e.g., Fernández-Mazuecos and Vargas 2015), we expect haplotype pattern within sect. *Minimae* to be created mainly by hybridization. The network positions of the cpDNA haplotypes of *G. filiformis* from Kazakhstan separated by many steps are not in agreement with the geographical distribution of the respective accessions.

In contrast to the situation in the Chinese Tian-Shan, where gene flow between *Gagea angelae* (1980−2250 m a. s. l.) and *G. huochengensis* (1550−2250 m a. s. l.) was

only evident in data of pCOS*At*103 (Peterson et al. 2011), in this study hybridization between morphologically and molecularly well-differentiated *G. kuraminica* and *G. almaatensis* was indicated by incongruent ITS and cpDNA data found in morphologically intermediate individuals. In the latter, we did not found any intermediate or ambiguous position in ITS sequences. This indicates ancient hybridization events followed by concerted ITS evolution (discussed, e.g., in Koch et al. 2003). *Gagea kuraminica* showed regular seed set in the Ili-Alatau (34.7 ± 2.0 seeds per plant; $n = 100$). Unfortunately, for *G. almaatensis* no data on seed set are available (due to later flowering time and small population sizes). In the small contact zone between 2000 and 2400 m a. s. l. both species seem to prefer different habitats: *G. almaatensis* grows in avalanche gullies, while *G. kuraminica* grows in pastures. In addition, we expect hybridization events between *G. kuraminica*, inhabiting elevations from 1200 to 2400 m a. s. l., and the lowland populations of *G.* cf. *turkestanica* (800–1100 m a. s. l.), which may involve further, yet undiscovered lowland species. In the present study dealing with 27 of 56 species known for sect. *Gagea* (Peterson et al. 2008), 111 haplotypes were recognized with a high proportion (74.5 %) of missing intermediates. Even if the number of missing intermediates should decrease if further species are included, the distances in the cpDNA haplotype network are rather large. This indicates that the chloroplast genomes within the section had enough time to differentiate, probably benefiting from geographical isolation (e.g., between Europe and Asia). However, the presence of distinct haplotypes within one species or even population is better explained by assuming recent hybridization between previously differentiated species rather than incomplete lineage sorting.

Recent hybridization events are often expected to be caused by human activities, which facilitate contact between potentially hybridizing but geographically isolated species. About 25 % of the species endemic for the Spanish Sierra Nevada currently form hybrids, mostly with widespread lowland congeners (Gómez et al. 2015). A similar scenario was also discussed for the *Gagea liotardii/Gagea villosa* species complex of sect. *Didymobulbos* s.l. (Peruzzi et al. 2011). Both putative hybrids of the two species (*Gagea microfistulosa* Levichev and *G. polidorii* J.-M.Tison) grow at elevations lower than found for *G. liotardii* (alpine) but higher than *G. villosa* (lowlands and foothills). In the vicinity of the city of Almaty, still the largest urban center of Kazakhstan, we can as well expect hybridization caused by human impacts. The region has a long history of transhumance: livestock grazing on lowland steppes in winter and moves up to alpine meadows in summer. The pastures replacing forest vegetation were invaded by species from open grasslands of lowland steppes and alpine meadows, like *Gagea* species, where they came in contact and hybridized. In mountain ranges, dispersal of seeds, vegetative bulbils, and bulbs of *Gagea* is probably influenced by flooding, wind, avalanches, or animals (Levichev 2013). In a park within the city, we found a morphological uniform hybrid population of *G. filiformis* and *G. granulosa* below the altitudinal range of *G. filiformis*, and possibly this population was introduced from higher elevations by soil transport or plant stock. *G. filiformis* and *G. granulosa* abundantly grow together and hybridized over the whole broad contact zone (observed from 1089 to 1994 m a. s. l.). In contrast, we recorded putative hybrids of *G. kuraminica* and *G. almaatensis* also above the altitudinal distribution of both parental species (2733 m a. s. l.). Dispersal of seeds or bulbils by birds may provide an explanation (Levichev et al. 2010).

Conclusions

In different ranges of the Tian-Shan (for the eastern Chinese Tian-Shan, see Peterson et al. 2011) characterized by different assemblages of closely related *Gagea* species, hybridization in altitudinal contact zones seems to be evident. Our observations on species and their altitudinal distribution indicate that speciation in *Gagea* sect. *Minimae* could be driven mainly by hybridization, but in sect. *Gagea* by both hybridization and geographical isolation (see also Peterson et al. 2009, 2011). For the mesophilic species of sect. *Gagea*, we expect a high rate of diversification, speciation, and endemism especially in the mountains of the Tian-Shan range surrounded by steppes or irrigated farmland. The sharp differences in meso-climate between N- and S-exposed slopes, but as well the strong altitudinal precipitation gradient should favor ongoing local speciation processes. As a consequence of our geographically restricted studies and according to our cpDNA network, we expect that more, yet undiscovered species of sect. *Gagea* exist in the Tian-Shan mountains, representing a center of species diversity for *Gagea.*

Taxonomic treatment

Gagea almaatensis Levichev, A.Peterson & J.Peterson, **sp. nov**.—TYPE: Kazakhstan, Ili-Alatau range, Almaty, ca. 22 km S Almaty, Lake Bol. Almatinskoje, 2557 m a. s. l., 43°03′09″N, 76°59′23″E, 23 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP43-2013* (holotype: HAL119703, isotypes: HAL119702, LE01010036) (Figs. 5, 6).

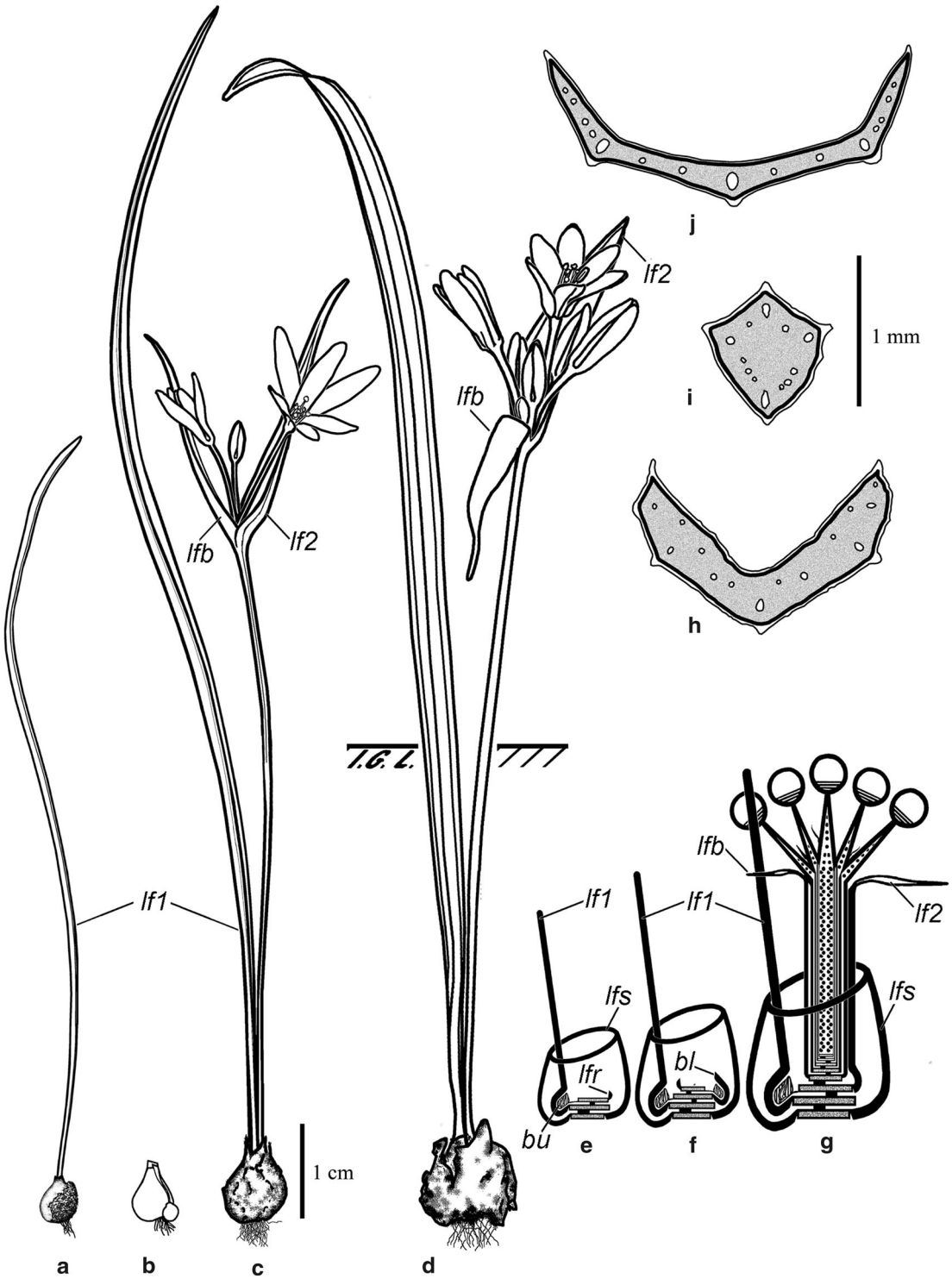

Fig. 5 Morphology of *Gagea almaatensis* sp. nov. **a** Vegetative plant, 2 years old, with a single assimilating leaf. **b** Bulb, tunics removed, of a non-flowering plant showing a lateral bulbil. **c** Flowering plant with a well-developed assimilating basal leaf. **d** Strong flowering plant with a bulb surrounded by several tunics. **e–g** Schematic drawings visualizing subsequent stages of plant ontogenesis. **h** Cross section of the basal assimilating leaf showing arrangement of vascular bundles. **i** Cross section of the peduncle with the concaulescent second basal leaf. **j** Cross section of the upper, free section of the second basal leaf. Morphological structures are *lf1*—first basal leaf (always developed as an assimilating leaf), *bu*—replacement bulb, *lfr* rudimentary second basal leaf (non-flowering plants), *lf2*—developed assimilating second basal leaf (flowering plants), concaulescent with the peduncle and appearing as lowermost bract of the inflorescence, *bl*—bulbil developed in the axil of the rudimentary second basal leaf (non-flowering plants), *lfb*—the true lowermost bract of the inflorescence, *lfs*—storage scale leaf of the one-leaved bulb (later shrinking and remaining as a tunic)

Fig. 6 Color plate of *Gagea almaatensis* sp. nov. **a**, **d** flowering plants, **b** inflorescence, **c** cross section of the basal leaf and the peduncle, **e** cross section of the bulb of a flowering adult plant without bulbils, **f** dormant bulbils

Description: Plants occurring solitary or in small groups, 7.5–15 cm tall; glabrous except for pedicels and margins of inflorescence bracts. Bulbs obliquely drop-shaped, 7–10 mm in diameter in flowering plants, tunic pale brown, thin, and coriaceous. Juvenile plants develop a single vegetative bulbil per year. Dormant vegetative bulbils are characterized by a dark brown tunic with a heavy pitted structure resembling honey combs. Generative plants do not develop bulbils. Peduncles are 5.5–10.5 cm tall (3–5.5 cm above soil), in cross-sectional quadrangular, and 0.3–0.8 mm in diameter. Basal leaf single, linear, exceeding the inflorescence one-fourth to one-fifth, 2–4(5) mm wide, cross-sectional angular, its lower side with three indistinct keels. Inflorescence bracts 2–4, nearly opposite to each other, the lowermost floral leaf (the second basal leaf) concaulescent with the peduncle, slightly exceeding the inflorescence, (12)38–52 mm long and 1.5–3 mm wide, narrowly lanceolate, erect, sometimes the upper end slightly reclining. All inflorescence leaves possess white ciliate hairs on their margins. Inflorescence fasciculate, with (1)3–7 flowers, short branched, pedicels of different length, in length equal to the perigon of the flower or slightly exceeding it, erect, not candelabrum-like. Perigon leaves narrowly lanceolate, ends rounded, those of the external whorl hooded, 0.7–1.5 cm long and 1.5–2.5 mm wide, inside yellow, outside greenish; leaves of the outer whorl slightly larger than those of the inner whorl, the latter with yellow margins at the outer side. Ovary oblong, sessile. Anthers yellow.

Diagnosis: Gagea almaatensis differs from *G. brevistolonifera* Levichev, *G. ancestralis* Levichev, and *G. xiphoidea* Levichev by a single sessile bulbil; from *G. praemixta* Vved. and *G. angelae* Levichev & Schnittler by the absence of stolons; from *G. longiscapa* Grossh. by the bulbil focused downwards (not pressed up); from *G. huochengensis* Levichev by the heavily pitted tunic of the dormant bulbil, a basal leaf slightly exceeding the inflorescence and straight pedicels; therefore, the inflorescence lacks the candelabrum-like appearance.

Habitats: Alpine meadows and avalanche gullies between 2000 and 2500 m a. s. l.

Distribution area: Kazakhstan, Ili-Alatau range.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix

Voucher information and GenBank accession numbers of the sequences used in this study. Taxon: place, date, collector, collection number: voucher number: EMBL/NCBI accession numbers: *trn*L–*trn*F IGS, *psb*A–*trn*H IGS, ITS1 + 5.8S rRNA + ITS2 (#sequences taken from EMBL/NCBI;—denotes lacking sequences). Information of collection dates, collectors, and collection numbers are only given for the material sampled in the Ili-Alatau range during the field excursion in 2013.

Gagea afghanica A.Terracc.: Iran, Province Khorasan: 52/04DNALevichevLE: HAL101785: –, –, AM087953. ***G. aipetriensis*** Levichev: Ukraine, Crimea: 15/04DNALevichevLE, HAL01801: AJ970178, AM049259, AM087955. ***G. almaatensis*** Levichev, A.Peterson & J.Peterson **sp. nov.**: (1) Kazakhstan, Ili-Alatau range, Almaty, 22 km S Almaty, Lake Bol. Almatinskoje, 2557 m a. s. l., 43°03′09″N, 76°59′23″E, 23 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler, AP43a-2013*: HAL119703, LE01010036: LN874781, LN874710, LN874873. (2) Kazakhstan, Ili-Alatau range, Almaty, 22 km S Almaty, Lake Bol. Almatinskoje, 2557 m a. s. l., 43°03′09″N, 76°59′23″E, 23 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP43b-2013*: HAL119702: LN874782, LN874711, LN874874. (3) Kazakhstan, Ili-Alatau range, Almaty, 1.2 km NNW Shymbulak ski ressort, 1994 m a. s. l., 43°08′24″N, 77°04′25″E, 21 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP44a-2013*: HAL119714: LN874783, LN874712, LN874875. (4) Kazakhstan, Ili-Alatau range, Almaty, 1.9 km S Shymbulak ski ressort, 2437 m a. s. l., 43°06′44″N, 77°04′26″E, 23 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP32-2013*: HAL119695: LN874784, LN874713, LN874876. ***G. almaatensis* × *kuraminica***: Kazakhstan: Ili-Alatau range: Almaty, 1.2 km NNW Shymbulak ski ressort, 1994 m a. s. l., 43°08′24″N, 77°04′25″E, 21 Apr 2013, A. and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP24b-2013*: HAL119688: LN874785, LN874714, LN874877. ***G. altaica*** Schischk. & Sumnev.: Kazakhstan, 51/04DNALevichevLE, HAL101786: –, –, AM162670. ***G. ancestralis*** Levichev: Russia, Republic Altai: 144/10DNALevichevLE: FR690249, FR690844, FR691052. ***G. angelae*** Levichev & Schnittler: (1) China, Xinjiang, Tian-Shan: LE00002135: FR690259, FR691028, FR690104. (2) China, Xinjiang, Tian-Shan: HAL108473: FR690266, FR691035, FR690111. (3) China, Xinjiang, Tian-Shan: HAL108477: FR690262, FR691031, –. ***G. artemczukii*** Krasnova: Ukraine, Crimea: 19/04DNALevichevLE, HAL101481: AM180470, AM409339, AM409331. ***G. bulbifera*** (Pall.) Salisb.: (1) China, Xinjiang, Urumqi: HAL107953: –, –, FR689753. (2) Russia, District Astrakhan: 2/04DNALevichevLE, HAL101840: –, –, AM162669. (3) Kazakhstan, Almaty, 14 km S Kapchagay, 521 m a. s. l., 43°44′24″N, 77°01′16″E, 19 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP11-2013*: HAL118024: –, –, LN874788. (4) Kazakhstan, Almaty, 14 km S Kapchagay, 521 m a. s. l., 43°44′18″N, 77°00′43″E, 19 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP12-2013*: HAL118026: –, –, LN874789. (5) Kazakhstan, Ili-Alatau range, Almaty, 2.1 km NE Medeu statium, 2003 m a. s. l., 43°10′12″N, 77°04′42″E, 20 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP18-2013*: HAL118081: –, –, LN874790. (6) Kazakhstan, Ili-Alatau range, Almaty, 2.1 km NE Medeu statium, 2003 m a. s. l., 43°10′12″N, 77°04′42″E, 20 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler AP19a-2013*: HAL119676, LE01010034: –, –, LN874791. (7) Kazakhstan, Ili-Alatau range, Almaty, 2.1 km NE Medeu statium, 2003 m a. s. l., 43°10′12″N, 77°04′42″E, 20 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP19b-2013*: HAL119675: –, –, LN874792. (8) Kazakhstan, Ili-Alatau range, Almaty, 28 km W Almaty, small hills S Turar, 790 m a. s. l., 43°14′58″N, 76°32′13″E, 26 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler, AP55-2013*: HAL118028, LE01010035: –, –, LN874793. (9) Kazakhstan, Ili-Alatau range, Almaty, 29 km W Almaty, near settlement Uschkonyr, 864 m a. s. l., 43°13′15″N, 76°33′10″E, 26 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP57-2013*: HAL118030: –, –, LN874794. ***G. capusii*** A.Terracc.: Uzbekistan: 24/04DNALevichevLE, HAL101839: AJ969123, AM085143, AM422455. ***G. circumplexa*** Vved.: Uzbekistan: 30/04DNALevichevLE, HAL101795: –, –, AM265529. ***G. confusa*** A.Terracc.: (1) Iran, Teheran: 13/04DNALevichevLE, HAL101803: AJ890369, AJ973173, AM087949. (2) #Iran: Zarrei&Zarrei35266(TUH)(Kew 23137): EU912267, EU939238, EU912040. (3) #Iran: TUH-EBOT.EXP.35712(TUH)(Kew 23169): EU912268, EU939239, EU912041. ***G. davlianidzeae*** Levichev: (1) China, Xinjiang, Tian-Shan: HAL107948: FR690236, FR690831, FR689755. (2) China, Xinjiang, Tian-Shan: HAL107943: FR690240, FR690835, FR689759. (3) China, Xinjiang, Tian-Shan: HAL107941: FR690241, FR690836, FR689760. (4) China, Xinjiang, Tian-Shan: HAL107946: FR690237, FR690832, –. (5) China, Xinjiang, Tian-Shan: HAL107939: FR690242,

FR690837, –. ***G. divaricata*** Regel: (1) Kazakhstan, Almaty, 14 km S Kapchagay, 520 m a. s. l., 43°44′28″N, 76°01′20″E, 19 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler, AP9a-2013*: HAL118078, LE01010032: –, –, LN874795. (2) Kazakhstan: Almaty, 14 km S Kapchagay, 520 m a. s. l., 43°44′28″N, 76°01′20″E, 19 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler, AP9b-2013*: HAL118079: –, –, LN874796. (3) Kazakhstan, Kapchagay: 146/10DNALevichevLE: –, –, LN874797. ***G. dschungarica*** Regel: Kyrgyzstan: 14/04DNALevichevLE, HAL101802: –, –, AM087952. ***G. erubescens*** (Besser) Besser: Ukraine: 25/04DNALevichevLE, G-103LE, HAL103861: AM180469, AM238516, AM493953. ***G. fedtschenkoana*** Pascher: (1) Kazakhstan, Astana, mown lawns with steppe remnants near the administration building of the Gumilev University, Republican Ave, 360 m a. s. l., 51°10′52″N, 71°25′23″E: HAL117627: LN874767, LN874696, LN874849. ***G.* cf. *fedtschenkoana***: (2) Kazakhstan, Tenis-Korgalshinskii nature reserve ca. 115 km WSW Astana, environs of the station 50°28′38″N, 250 m a. s. l., 69°32′44″E: HAL117626, LE01010043: LN874768, LN874697, LN874850. (3) Kazakhstan, Tenis-Korgalshinskii nature reserve ca. 115 km WSW Astana, steppe 2 km N of the station, 260 m a. s. l., 50°29′45″N, 69°32′48″E: HAL117628, LE01010044: LN874769, LN874698, LN874851. ***G. filiformis*** (Ledeb.) Kar. & Kir.: (1) Western Tian-Shan: 72/09DNALevichevLE: FR690250, FR690845, FR689768. (2) Kazakhstan: 12/04DNALevichevLE, HAL101804: AM084904, AM161459, AM180457. (3) Kazakhstan, Ili-Alatau foothills, Almaty, 5 km SE Almaty, Medeu valley, 1192 m a. s. l., 43°11′15″N, 77°00′07″E, 18 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP7b-2013*: HAL118049: LN874716, LN874645, LN874809. (4) Kazakhstan: Ili-Alatau range: Almaty, 1.1 km NE Medeu statium, 1821 m a. s. l., 43°09′60″N, 77°04′28″, 20 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP14a-2013*: HAL118050: LN874717, LN874646, LN874810. (5) Kazakhstan, Ili-Alatau range, Almaty, 1.1 km NE Medeu statium, 1821 m a. s. l., 43°09′60″N, 77°04′28″, 20 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler, AP14b-2013*: HAL118051: LN874718, LN874647, LN874811. (6) Kazakhstan, Ili-Alatau range, Almaty, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°08′30″N, 77°03′51″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP20a-2013*: HAL118057, LE01010046: LN874719, LN874648, LN874812. (7) Kazakhstan, Ili-Alatau range, Almaty, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°08′30″N, 77°03′51″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler AP20b-2013*: HAL118055: LN874720, LN874649, LN874813. (8) Kazakhstan, Ili-Alatau range, Almaty, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°08′30″N, 77°03′51″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP20c-2013*: HAL118054: LN874721, LN874650, LN874814. (9) Kazakhstan, Ili-Alatau range, Almaty, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°08′30″N, 77°03′51″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP20d-2013*: HAL118053: LN874722, LN874651, LN874815. (10) Kazakhstan, Ili-Alatau range, Almaty, 1.9 km S Shymbulak ski ressort, 2437 m a. s. l., 43°06′44″N, 77°04′06″, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler AP30a-2013*: HAL119715: LN874723, LN874652, LN874816. (11) Kazakhstan, Ili-Alatau range, Almaty, 1.9 km S Shymbulak ski ressort, 2437 m a. s. l., 43°06′44″N, 77°04′06″, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP30b-2013*: HAL118062: LN874724, LN874653, LN874817. (12) Kazakhstan, Ili-Alatau range, Almaty, 1.5 km SSW Shymbulak ski ressort, 2380 m a. s. l., 43°06′59″N, 77°04′26″E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP33a-2013*: HAL118065: LN874725, LN874654, LN874818. (13) Kazakhstan, Ili-Alatau range: Almaty, 1.5 km SSW Shymbulak ski ressort, 2380 m a. s. l., 43°06′59″N, 77°04′26″E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP33b-2013*: HAL118064: LN874726, LN874655, LN874819. (14) Kazakhstan, Ili-Alatau range, Almaty, 1.5 km SSW Shymbulak ski ressort, 2380 m a. s. l., 43°06′59″N, 77°04′26″E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP34-2013*: HAL118063: LN874727, LN874656, LN874820. (15) Kazakhstan, Ili-Alatau range, Almaty, 1.5 km NW Medeu stadium, 1498 m a. s. l., 43°10′09″N, 77°02′25E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP38a-2013*: HAL118067: LN874728, LN874657, LN874821. (16) Kazakhstan, Ili-Alatau range, Almaty, 1.5 km NW Medeu stadium, 1498 m a. s. l., 43°10′09″N, 77°02′25″E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP38b-2013*: HAL118068: LN874729, LN874658, LN874822. (17) Kazakhstan, Ili-Alatau range, Almaty, 22 km S Almaty, Lake Bol. Almatinskoje, 2733 m a. s. l., 43°03′22″N, 76°58′05″E, 23 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP42-2013*: HAL118069: LN874730, LN874659, LN874823. (18) Kazakhstan, Ili-Alatau foothills, Almaty, 4 km SE Almaty, around TV tower, 1099 m a. s. l., 43°13′36″N, 76°58′26″E, 25 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP51-2013*: HAL118070: LN874731, LN874660, LN874824. (19) Kazakhstan, Ili-Alatau foothills, Almaty, 4 km SE Almaty, around TV tower, 1089 m a. s. l., 43°13′50″N, 76°58′29″E, 25 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP52-2013*: HAL118073: LN874732, LN874661, LN874825. (20) Kazakhstan: Ili-Alatau foothills: Almaty, 3 km NW Medeu stadium, 1301 m a. s. l., 43°10′48″N, 77°00′43″E, 27 Apr 2013, *A.* and *J.Peterson*,

S.Beisenova, *M.Schnittler*, *AP59a-2013*: HAL118074: LN874733, LN874662, LN874826. (21) Kazakhstan: Ili-Alatau foothills, Almaty, 3 km NW Medeu stadium, 1301 m a. s. l., 43°10′48″N, 77°00′43″E, 27 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP59b-2013*: HAL118075: LN874734, LN874663, LN874827. (22) Kazakhstan: Ili-Alatau foothills: Almaty, 3 km NW Medeu stadium, 1301 m a. s. l., 43°10′48″N, 77°00′43″E, 27 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP59c-2013*: HAL118076: LN874735, LN874664, LN874828. (23) Kazakhstan: Ili-Alatau range: Almaty, 1 km SSE Medeu stadium, 1875 m a. s. l., 43°09′06″N, 77°04′01″, 29 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP60-2013*: HAL118077: LN874736 LN874665, LN874829. (24) Kazakhstan, Ili-Alatau range, Almaty, 1.2 km NNW Shymbulak ski ressort, 1994 m a. s. l., 43°08′24″N, 77°04′25″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP25-2013*: HAL118059: LN874737, LN874666, LN874830. (25) Kazakhstan, Mountains over Almaty, at Observatory: DNAIPK12KZ-123: –, –, LN874831. (26) Kazakhstan: Sharyn Canyon: HAL115984: LN874738, LN874667, LN874832. (27) Kazakhstan, Mramornij (Marble) pass, W end of Altai: DNA IPK12KZ-102: –, –, LN874833. (28) Kazakhstan, near Kegen Pass, HAL116095: LN874739, LN874668, LN874834. (29) Kazakhstan, Ili-Alatau range, Almaty, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°8′30″N, 77°03′51″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP23-2013*: HAL118058: LN874740, LN874669, –. (30) Kazakhstan, Ili-Alatau foothills: Almaty, 5 km SE Almaty, Medeu valley, 1192 m a. s. l. 43°11′15″N, 77°00′07″, 18 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP7c-2013*: HAL118039: LN874753, LN874682, LN874847. ***G. graeca*** (L.) Irmisch.: Greece, Crete: HAL105185: –, –, AM939649. ***G. graminifolia*** Vved.: Kyrgyzstan, 114/09DNALevichevLE: –, –, FR689769. ***G. granulosa*** Turcz.: (1) –: 11a/04DNALevichevLE, HAL101805: –, –, AM265533. (2) Russia, Sibiria: 141/09DNALevichevLE: FR690253, FR690848, –. (3) Ukraine, Poltava: 100/09DNALevichevLE: FR690252, FR690847, –. (4) Kazakhstan, Tian-Shan: 11b/04DNALevichevLE, HAL101836: AM180463, AM238517, AM287278. (5) Kazakhstan, Ili-Alatau foothills, Almaty, 862 m a. s. l., 43°13′34″N, 76°54′49″E, 18 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP4-2013*: HAL118037: LN874741, LN874670, LN874835. (6) Kazakhstan, Ili-Alatau foothills, Almaty, 839 m a. s. l., 43°14′57″N, 76°56′42″E, 17 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP1a-2013*: HAL118035, LE01010049: LN874742, LN874671, LN874836. (7) Kazakhstan, Ili-Alatau foothills, Almaty, 839 m a. s. l., 43°14′57″N, 76°56′42″E, 17 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP1b-2013*: HAL118033: LN874743, LN874672, LN874837. (8) Kazakhstan, Ili-Alatau foothills, Almaty, 5 km SE Almaty, Medeu valley, 1192 m a. s. l., 43°11′15″N, 77°00′07″E, 18 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP7a-2013*: HAL118038: LN874744, LN874673, LN874838. (9) Kazakhstan, Ili-Alatau range, Almaty, 300 m NW Medeu statium, 1721 m a. s. l., 43°09′37″N, 77°03′33″E, 20 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP13-2013*: HAL118040: LN874745, LN874674, LN874839. (10) Kazakhstan, Ili-Alatau range, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°08′30″N, 77°03′51″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP21-2013*: HAL118042: LN874746, LN874675, LN874840. (11) Kazakhstan, Ili-Alatau range, Almaty, 1.2 km NNW Shymbulak ski ressort, 1994 m a. s. l., 43°08′24″N, 77°04′25″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP28-2013*: HAL118043: LN874747, LN874676, LN874841. (12) Kazakhstan, Ili-Alatau range, Almaty, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°08′30″N, 77°03′51″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP45a-2013*: HAL118046: LN874748, LN874677, LN874842. (13) Kazakhstan, Ili-Alatau range, Almaty, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°08′30″N, 77°03′51″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP45b-2013*: HAL118045: LN874749, LN874678, LN874843. (14) Kazakhstan, Ili-Alatau range, Almaty, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°08′30″N, 77°03′51″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP45c-2013*: HAL118044: LN874750, LN874679, LN874844. (15) Kazakhstan, Ili-Alatau foothills, Almaty, 3 km NW Medeu stadium, 1301 m a. s. l., 43°10′48″N, 77°00′43″E, 27 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP58a-2013*: HAL118048: LN874751, LN874680, LN874845. (16) Kazakhstan, Ili-Alatau foothills, Almaty, 3 km NW Medeu stadium, 1301 m a. s. l., 43°10′48″N, 77°00′43″E, 27 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP58b-2013*: HAL118047: LN874752, LN874681, LN874846. (17) Kazakhstan, near Panteleimonovka vil.,: DNA12KZ-117: –, –, LN874848. ***G. helenae*** Grossh: Russia, Dagestan: 22/04DNALevichevLE, HAL101798: AJ969120, AM161461, AM265531. ***G. huochengensis*** Levichev: (1) China, Xinjiang, Tian-Shan: HAL108466: FR690269, FR691038, FR690114. (2) Kazakhstan: 132/09DNALevichevLE, HAL107949: FR690274, FR691042, FR690118. (3) China, Xinjiang, Tian-Shan: HAL108468: FR690272, FR691041, –. (4) China, Xinjiang, Tian-Shan: HAL108467: FR690271, FR691040, –. ***G. jensii*** Levichev & Schnittler: China, Xinjiang: HAL108482: FR690256, FR691025, FR690101. ***G. kuraminica*** Levichev (1) Kazakhstan, Ili-Alatau foothills, Almaty, 5 km SE Almaty, Medeu valley,

1192 m a. s. l., 43°11′15″N, 77°00′07″E, 18 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP6-2013*: HAL119683, LE01010038: LN874770, LN874699, LN874852. (2) Kazakhstan, Ili-Alatau range, Almaty, 1.5 km NE Medeu statium, 1920 m a. s. l., 43°10′02″N, 77°04′36″E, 20 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP16-2013*: HAL119685, LE01010050: LN874771, LN874700, LN874853. (3) Kazakhstan, Ili-Alatau range, Almaty, 1.5 km NW Medeu stadium, 1498 m a. s. l., 43°10′09″N, 77°02′25″E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP49-2013*: HAL119704, LE01010042: LN874772, LN874701, LN874854. (4) Kazakhstan, Ili-Alatau range, Almaty, 1.2 km NNW Shymbulak ski ressort, 1994 m a. s. l., 43°08′24″N, 77°04′25″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP24a-2013*: HAL119687: LN874773, LN874702, LN874855. (5) Kazakhstan, Ili-Alatau range, Almaty, 1.2 km NNW Shymbulak ski ressort, 1994 m a. s. l., 43°08′24″N, 77°04′25″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP24c-2013*: HAL119689: LN874774, LN874703, LN874856. (6) Kazakhstan, Ili-Alatau range, Almaty, 1.5 km SSW Shymbulak ski ressort, 2380 m a. s. l., 43°06′59″N, 77°04′26″E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP36c-2013*: HAL119697: LN874775, LN874704, LN874857. (7) Kazakhstan, Ili-Alatau range, Almaty, 1.2 km NNW Shymbulak ski ressort, 1994 m a. s. l., 43°08′24″N, 77°04′25″E, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP44b-2013*: HAL119713: LN874776, LN874705, LN874858. (8) Kazakhstan, Ili-Alatau range, Almaty, 1.5 km SSW Shymbulak ski ressort, 2380 m a. s. l., 43°06′59″N, 77°04′26″E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP37-2013*: HAL119700, LE01010038: LN874777, LN874706, LN874859. (9) Kazakhstan, Ili-Alatau range, Almaty, 1.9 km S Shymbulak ski ressort, 2437 m a. s. l., 43°06′44″N, 77°04′26″E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP29a-2013*: HAL119693, LE01010040: LN874778, LN874707, LN874860. (10) Kazakhstan, Ili-Alatau range, Almaty, 1.9 km S Shymbulak ski ressort, 2437 m a. s. l., 43°06′44″N, 77°04′26″, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP29b-2013*: HAL119692: LN874779 LN874708, LN874861. (11) Uzbekistan, Tian-Shan, Kurama range, 2500 m a. s. l.,: 151/14DNALevichevLE (holotype): LN874780, LN874709, LN874862. ***G. kuraminica* × *almaatensis*** Kazakhstan, Ili-Alatau range, Almaty, 22 km S Almaty, Lake Bol. Almatinskoje, 2733 m a. s. l., 43°03′22″N, 76°58′05″E, 23 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP40-2013*: HAL119701: LN874786, LN874715, LN874878. ***G. liotardii*** (Sternberg) Schult. et Schult.f. (= *G. fragifera* (Vill.) Ehr.Bayer & G.López): (1) China, Xinjiang, Tian-Shan: HAL107898: –, –, FN868162. (2) Ukraine, Crimea: 29a/04DNALevichevLE, HAL101797: –, –, AM265532. (3) Italy: CLU12693: –, –, AM422468. (4) Kazakhstan: 29b/04DNALevichev LE, HAL101796: –, –, AM180455. (5) Kazakhstan, Tenis-Korgalshinsky Nature Reserve, Astana: HAL117634: –, –, LN874799. (6) Kazakhstan, Ili-Alatau range, Almaty, 1.7 km NW Shymbulak ski ressort, 1941 m a. s. l., 43°08′30″N, 77°03′51″, 21 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP22-2013*: HAL118013, LE01010041: –, –, LN874800. (7) Kazakhstan, Ili-Alatau range, Almaty, 1.9 km S Shymbulak ski ressort, 2437 m a. s. l., 43°06′44″N, 77°04′26″, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP31-2013*: HAL118015: –, –, LN874801. (8) Kazakhstan, Ili-Alatau range, 1.5 km NW Medeu stadium, road to Medeu, 1498 m a. s. l., 43°10′09″N, 77°02′25″E, 22 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP39-2013*: HAL118018: –, –, LN874802. (9) Kazakhstan, Ili-Alatau range, Lake Bol. Almatinskoje, 2733 m a. s. l., 43°03′22″N, 76°58′05″E, 23 Apr 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP41-2013*: HAL118032: –, –, LN874803. (10) Kazakhstan, Mountains over Almaty: DNA IPKKZ124: –, –, LN874804. (11) Morocco: Marrakech: HAL116006: –, –, LN874805. ***G. lutea*** Ker Gawl.: (1) Germany, Saxony-Anhalt: –: AJ419165, AJ416368, AJ427544. (2) Russia, Caucasus: 16/04DNALevichevLE, HAL101800: AM110255, AM161456, AM265530. (3) Italy, Calabria CLU12696: AM265606, AM409354, AM287282. (4) #Iran: Zarrei35285(TUH)(Kew 23148): EU912281, EU939250, EU912052. ***G. marchica*** Henker, Kiesew., U.Raabe & Rätzel: Germany, Alt-Zeschdorf: HAL118006: LN874754, LN874683, LN874808. ***G. megapolitana*** Henker: Germany: HAL101644: AM084902, AM161455, AM931553. ***G. minima*** (L.) Ker Gawl.: (1) Italy, Calabria, Pollino Massif: CLU12698: AM283109, AM282996, AM287273. (2) Ukraine, Carpathians: 9/04DNALevichevLE, HAL101808: AM238539, AM238524, AM087948. (3) Russia, Republic Tatarstan, Nizhnyaya Kama: 10/04DNALevichevLE, HAL101806: AM180471, AM238519, AM180459. (4) Germany, Saxony-Anhalt: –: AJ419164, AJ416374, AJ427546. ***G. nakaiana*** Kitag.: Russia, Khabarovsk Territory: 17/04DNALevichev, 55LE, HAL101799: AM110256, AM161457, AM180454. ***G. neopopovii*** Golosk.: Eastern Kazakhstan, Za-Iliskii Altai: 120/09DNALevichevLE: –, –, FR689770. ***G. nigra*** L.Z.Shue, emend. Schnittler: (1) China, Xinjiang, Urumqi: HAL108464: FR690123, FR691010, FR690081. (2) China, Xinjiang, Urumqi: HAL108452: FR690135, FR691022, FR690095. (3) China, Xinjiang, Urumqi (N9714, Sichuan Univ., Chengdu): 134/10DNALevichevLE: FR690137, FR691024, –. (4) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake: HAL108459: FR690125, FR691012,

FR690083. (5) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake: HAL108460: FR690128, FR691015, –. (6) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake: HAL108456: FR690129, FR691016, –. (7) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake: HAL108183: FR690131, FR691018, –. (8) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake: HAL108457: FR690132, FR691019, –. (9) China, Xinjiang, Tian-Shan, Bogda-Shan: HAL108184: FR690134, FR691021, –. ***G. ova*** Stapf: China, Xinjiang, Urumqi: HAL107951: –, –, FR689762. ***G. paczoskii*** (Zapal.) Grossh.: Italy: HAL104323: AM903072, AM903061, AM903051. ***G. pauciflora*** Turcz. ex Ledeb.: Mongolia, Ulan Bator: HAL070423: –, –, AM409330. ***G. podolica*** Schult. & Schult.f.: Ukraine: 21/04DNALevichevLE, HAL101832: AM084903, AM238525, AM409334. ***G. pomeranica*** Ruthe: (1) Germany, Saxony-Anhalt HAL095842: AJ419167, AJ416375, AJ427543. (2) Germany, Mecklenburg-Western Pomeranica: HAL095846: LN874787, AJ429194, –. ***G. pratensis*** (Pers.) Dumort.: (1) Germany, Saxony-Anhalt: HAL095847: AJ419162, AJ416372, AJ427542. (2) Italy: CLU12703, AM265607, AM903059, AM903047. ***G. pusilla*** (F.W.Schmidt) Sweet: cultivated: 18/04DNALevichevLE, HAL101831: AM180464, AM161458, AM422453. ***G. reticulata*** (Pall.) Schult. et Schult.f.: Israel, Central Negev: Z34650: –, –, AM087954. ***G. rubicunda*** Meinsh. emend. Levichev: Estonia: 26/04DNALevichevLE, HAL103855: AM238541, AM409338, AM493954. ***G. rufidula*** Levichev: (1) China, Xinjiang, Tian-Shan: HAL107929: –, –, FR689764. (2) Kyrgyzstan: 149/09DNALevichevLE: –, –, FR689767. ***G. serotina*** (L.) Ker Gawl. (=*Lloydia serotina* (L.) Reichenb.): (1) Kazakhstan: 45a/04DNALevichevLE, HAL101789: –, –, AM087956. (2) Russia, Karachaevo-Cherkessian Rep.: HAL117624: –, –, LN874806. (3) USA, Alaska, Alaska range: HAL117490: –, –, LN874807. ***G. shmakoviana*** Levichev: Russia, Altai: 23/04DNALevichevLE, HAL101830: AM265520, AM287265, AM422454. ***G. spathacea*** (Hayne) Salisb.: Germany, Saxony-Anhalt: HAL095844: –, –, AJ427541. ***G. stipitata*** Merckl. ex Bunge: Iran, Province Khorasan: 49/04DNALevichevLE, HAL101828: –, –, AM409336. ***G. tenera*** Pascher: (1) Kyrgyzstan: HAL101843: –, –, AM422460. (2) Iran: Zarrei & Golzarian 35256(TUH)(-Kew 23152): –, –, EU912074. (3) Kazakhstan, Ili-Alatau foothills, Almaty, 831 m a. s. l., 43°15′0″N, 76°56′41″E, 18 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP3-2013*: HAL118080, LE01010033: –, –, LN874798. ***G. terraccianoana*** Pascher: (1) Russia: 55/04DNALevichevLE, HAL103853: AM287280, AM287268, AM493955. (2) Mongolia: Bogd-Ul Mountains: HAL070426: AJ890367, AJ973169, –. ***G. tisoniana*** Peruzzi, Bartolucci, Frignani & Minutillo: Italy: CLU14920: AM409358, AM409349, AM422466. ***G. transversalis*** Steven: Ukraine, Crimea: 56/04DNALevichevLE, 365LE, HAL101783: AJ890370, AJ973167, AM162671. ***G. turkestanica*** Pascher: (1) Kyrgyzstan: 20/04DNALevichevLE, HAL103850: AM238534, AM287267, –. ***G.* cf. *turkestanica*** (2) Kazakhstan, Ili-Alatau range, Almaty, 28 km W Almaty, small hills S Turar, 790 m a. s. l., 43°14′58″N, 76°32′13″E, 26 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP54a-2013*: HAL119707, LE01010039: LN874755, LN874684, LN874863. (3) Kazakhstan: Ili-Alatau range: Almaty, 28 km W Almaty, small hills S Turar, 43°14′58″N, 76°32′13″E, 790 m a. s. l., 26 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP54b-2013*: HAL119710: LN874756, LN874685, LN874864. (4) Kazakhstan, Ili-Alatau foothills, Almaty, Panfilov park, 831 m a. s. l., 43°15′00″N, 76°56′41″E, 24 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP46-2013*: HAL118082: LN874757, LN874686, LN874865. (5) Kazakhstan, Almaty: 130/09DNALevichevLE: LN874758, LN874687, LN874866. (6) Kazakhstan, Jezkazgan: 131/09DNALevichevLE: LN874759, LN874688, –. (7) Kazakhstan, Almaty, 950 m a. s. l.: 119/09DNALevichevLE: LN874760, LN874689, –. (8) Kazakhstan, Ili-Alatau foothills: Almaty, 831 m a. s. l., 43°15′00″N, 76°56′41″E, 18 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP2a-2013*: HAL119678: LN874761, LN874690, LN874867. (9) Kazakhstan, Ili-Alatau foothills, Almaty, 831 m a. s. l., 43°15′00″N, 76°56′41″E, 18 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP2a-2013*: HAL119679: LN874762, LN874691, LN874868. (10) Kazakhstan, Ili-Alatau foothills, Almaty, 862 m a. s. l., 43°13′34″N, 76°54′49″E, 18 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP2a-2013*: HAL119680: LN874763, LN874692, LN874869. (11) Kazakhstan, Ili-Alatau foothills, Almaty, 4 km SE Almaty, park around the TV tower, 1119 m a. s. l., 43°13′49″N, 76°58′38″E, 25 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP53-2013*: HAL119708: LN874764, LN874693, LN874870. (12) Kazakhstan, Ili-Alatau foothills, Almaty, 4 km SE Almaty, around TV tower, 1099 m a. s. l., 43°13′36″N, 76°58′26″E, 25 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP50-2013*: HAL119705: LN874765, LN874694, LN874871. (13) Kazakhstan, Ili-Alatau range, Almaty, 29 km W Almaty, near settlement Uschkonyr, 864 m a. s. l., 43°13′15″N, 76°33′10″E, 26 April 2013, *A.* and *J.Peterson*, *S.Beisenova*, *M.Schnittler*, *AP56-2013*: HAL119711: LN874766, LN874695, LN874872. ***G. uliginosa*** Siehe & Pascher: #Iran: Zarrei et al. TUH-EBOT.EXP.35304,(TUH)(Kew 23153): –, –, EU912089. ***G. vegeta*** Vved.: Uzbekistan: 32/04DNALevichev, 339aLE, HAL103691: –, –, AM287275. *G. villosa* (Bieb.) Sweet: Germany, Saxony-Anhalt: –: –, AJ427545. ***G. xiphoidea*** Levichev: (1)

Russia, Republic Altai: 71/09DNALevichevLE: FR690138, FR691044, FR690097. (2) Russia, Republic Altai, district Kosch-Agaczensis: 102/09DNALevichevLE: FR690139, FR691045, FR690098. ***G.* cf. *xiphoidea*** (3) China, Xinjiang, Tian-Shan: HAL108479: FR690140, FR691046, FR690099. ***Tulipa cretica*** Boiss. & Heldr.: Greece, Crete: HAL099934: **–**, **–**, AM180461.

Information on Electronic Supplementary Material

Online Resource 1 ITS alignment used for BI and resulting tree.
Online Resource 2 cpDNA alignment used for TCS of sect. *Minimae*.
Online Resource 3 cpDNA alignment used for TCS of sect. *Gagea*.

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